

THE BUTTERFLIES OF CALIFORNIA

John F. Emmel, Thomas C. Emmel, and Sterling O. Mattoon

DOI:10.5281/zenodo.17313658

Table of Contents

Preface	
Chapter 1. Early Lepidopterists in California	1
Chapter 2. The Geological Landscape of California	62
Chapter 3. The Relation of the California Climate to the Butterfly Fauna	66
Chapter 4. Plant Communities of California	69
Chapter 5. Patterns of Geography and Species Diversity in the State of California	124
Chapter 6. The California Islands and Their Butterfly Faunas	135
Chapter 7. Effects of Human Activities on Lepidopteran Populations in California	139
Chapter 8. Species Accounts of the Butterflies and Skippers of California	150
Map of localities	752
Literature cited	753

PREFACE

After the publication of **The Butterflies of Southern California** (T. C. Emmel and J. F. Emmel, 1973), a number of colleagues urged us to prepare a new book of similar depth covering all of the state of California. The fortunate availability of Sterling O. Mattoon as a co-author meant that the northern California fauna could be covered with the help of an expert resident lepidopterist whose legendary field work in that part of the state would add much to the proposed work.

Accordingly, the three of us joined forces in 1974 and signed a contract with Stanford University Press, ambitiously estimating that the new book would be published by 1979. Little did we realize the immensity of the task before us in 1974.

We began with a thorough survey form that was mailed to all western members of the Lepidopterists' Society, requesting information on unusual distributional records, dates, etc., for the California fauna as listed on a preliminary draft of the checklist of all recorded butterfly species for the state. That list rapidly expanded to include dozens of additional species, as we began to receive these checklists back from willing collaborators. The help continued to pour in from hundreds of lepidopterists as we pursued the preparation of this book over the ensuing 18 years. Additionally, the lengthy gestation time for this book allowed John F. Emmel in particular to eventually rear and photograph the life history stages of all of the species and virtually all of the subspecies of butterflies and skippers in the state of California. Mapping of distributional records was facilitated by visits to all major private and public collections in the state, as well as specially targeted field trips each year by the three authors and willing colleagues to unknown or relatively unknown parts of California. In the course of that effort, several new species and more than 100 new subspecies of butterflies were described in formal publications, particularly in the work entitled **Systematics of Western North American Butterflies** (1992).

Thus the present book represents an unusually thorough coverage of an incredibly diverse fauna in a huge state comprising some of the most varied geographical and ecological environments in the northern hemisphere. We know there are errors of commission and omission in a work of this size, but we hope that the reader will be encouraged to add to the knowledge represented in this volume and will communicate new data and discoveries to us so that they may be incorporated in future printings of this book. We also hope the appearance of this book will generate a great many independent publications on life histories, foodplant records, and all the basic ecology, behavior, genetics, and evolutionary biosystematic work that a basic knowledge of the California fauna should stimulate and encourage.

John F. Emmel
Thomas C. Emmel
Sterling O. Mattoon

Chapter 1

EARLY LEPIDOPTERISTS IN CALIFORNIA

Butterflies have probably fascinated mankind as long as both have existed on the earth. Even today, primitive tribes in areas as far apart as the South American Amazon and the interior highlands of New Guinea know intimately the natural world around them and include butterflies as objects to admire, revere, or even dread, depending on the particular folklore surrounding them.

As agricultural practices started and centers of civilization grew, mankind could not fail to note the depredations of certain species on cultivated crops, or the mass emergencies of migrants like the Painted Lady, or the sheer beauty and fragility of the adult butterfly. Thus with the invention of writing, early chronicles speak of such observations in Greek and Roman times, and eventually in medieval Europe. But it was not until the Age of Exploration, as European adventurers sailed the oceans of the world and explored the newly opened continents, that the study of natural history started on an organized, indeed enthusiastically pursued, basis. Collections began to be amassed by institutions and individuals alike, both from home territories and abroad, during the seventeenth and eighteenth century, and Linnaeus himself laid the groundwork for formal biological classification, including personally naming butterflies even from the Americas, in his great *Systemae Naturae* work of 1758. Virtually every new exploring expedition sent back unique and wonderful species of plants and animals to Europe to be named.

President Thomas Jefferson started the same tradition in America on 20 June 1803 by charging Meriwether Lewis and William Clark to go forth and explore his great new Louisiana Purchase and bring back all manner of information on the region's natural history. A year later, they set out from St. Louis up the Missouri River. Pushing westward from the headwaters of the Missouri to the Pacific Ocean itself, the Lewis and Clark Expedition was but the first of many government and private expeditions to follow throughout the West during the nineteenth century. Among them were lepidopterists traveling with Russian explorers, Army expeditions, gold miners, survey parties, and finally even museums and private collector sponsors. They set the stage for the wealth of lepidopterist interest in California's butterfly fauna during the twentieth century.

In this first chapter, then, we trace the history of Lepidoptera collecting and butterfly study in California. Not all individuals can be mentioned, of course, but the story covers the highlights -- both chief contributors and interesting oddities -- and gives the reader an appreciation for the sweep of history and the remarkable continuity and depth that Lepidoptera work has enjoyed for the past two centuries in California. The story is still being written today by thousands of naturalists and scientists interested in the butterflies of this great state, and it is hoped that the readers of this book will see themselves as an integral part of the effort to understand a little more about our natural world -- especially that world of the California butterfly fauna.

Looking back over the long stretch of years involved in the development of California butterfly study, we may identify six more-or-less distinct periods of activity.

1791-1848:	The Russians & Earliest Explorers during the Spanish-Colonial Period in California.
1849-1859:	The Gold Rush Era, Mexican Boundary Survey, and Pacific Railroad Survey.
1860: 1870:	The State Geological Survey Decade.
1870-1890:	The Federal Surveys of the West: Period following the Opening of the Transcontinental Railroad.
1890-1940:	The Golden Era of California Lepidoptera Discovery.
1940-Present:	The Modern Age of Lepidoptera Study: Recent Lepidopterists in California.

In the pages that follow, we shall follow the above outline, discussing the general activities and the principal figures involved during each period.

I. THE SPANISH-COLONIAL PERIOD (1791-1848)

Several early voyages of exploration brought the first naturalists to collect butterflies in California. These were Russians, surprisingly enough, who were surveying the Pacific Coast of North America from Alaska south to central California and collecting natural history specimens, mostly botanical but some entomological (Grinnell, 1914). Among these latter treasures were some of California's most notable butterflies.

Early Russian Explorers

The first naturalist to collect butterflies and other insects in California were Russian scientists and explorers. Grigory I. von Longsdorff, a Russian botanist and zoologist, shipped plant and animal specimens back to the Russian Academy of Sciences in 1806, but unfortunately these collections were lost and never described. In October, 1816, the Russian navigator, Captain Otto von Kotzebue brought the naturalist Adelbert von Chamisso and the entomologist Johann Friedrich Eschscholtz to San Francisco aboard the brig *Rurik*. When they landed on Yerba Buena Island, they found the Chalcedon Checkerspot, *Euphydryas chalcedona*, as verified later by H. H. Behr who saw the specimen in the Berlin Museum. On the same voyage, they visited San Jose and Monterey, and Eschscholtz collected insects in the Fort Ross area on his second trip with Kotzedue in 1823 to 1826 (Wells, 1987). The beautiful California Poppy, *Eschscholtzia californica*, was named by Chamisso for his collecting companion Eschscholtz. It is an historical oddity that our State Flower, the California Poppy, and the State Butterfly, the California Dogface (*Zerene eurydice*, originally *Z. wosnesenskii*), were named very early for the Russians.

Johann Friedrich Eschscholtz (1793-1831)

Though living only 38 years, Eschscholtz was the outstanding entomologist during the Russian occupation of California. He was born in Russia on November 1, 1793 and died at his birthplace on May 7, 1831. Trained in the medical profession, he acted as physician and naturalist on the ship *Rurik* which sailed around the world under the command of Otto von Kotzebue during the years 1815-1818. His close friend, a German poet and naturalist, Adelbert von Chamisso, received most of Eschscholtz's captures except for the insects. This ship arrived in San Francisco Bay on October 1, 1816, and remained until November 1. He confined his collecting on this trip to the Presidio at San Francisco, the mission and the area in between, and did not visit the Russian colony at Fort Ross in 1816. Little was taken in the way of insects but he did supposedly take two very common California species of butterflies, the Monarch, *Danaus plexippus*, and the Chalcedon Checkerspot, *Euphydryas chalcedona*. According to Fordyce Grinnell, Herman H. Behr saw the actual specimens taken by Eschscholtz in the collections of the Berlin Museum (Grinnell, 1914). It is not difficult to believe that Eschscholtz caught Monarchs in the fall of 1816, but it is less certain how he obtained the normally spring-flying *E. chalcedona* on the coast. Perhaps the single type specimen was from an unknown collector in the Russian colony. (However, R. L. Langston (*in litt.*) has found small numbers of fresh *E. chalcedona* flying in October in 1985 and 1991 in the San Bruno Mountains next to San Francisco Bay, so a sharp entomologist such as Eschscholtz could have picked up an unusually attractive butterfly like *chalcedona* if a similar fall brood was flying in 1816.) Essig (1972) believes that these butterfly specimens must have been placed in the Berlin Museum by Chamisso, whose plant collection is there. Incidentally, it was on the 1816 trip that the California Poppy was collected, which Chamisso afterwards named *Eschscholtzia californica* because of his friendship with Eschscholtz. Following their visit to California, they went to Hawaii in November 1816. He collected on the island of Oahu the beautiful endemic nymphalid which he subsequently named *Vanessa tameamea*.

Eschscholtz made a second voyage with Kotzebue in the ship *Predpriaetie* (*Enterprise*) during the years 1823 to 1826. Eschscholtz was chief naturalist and amassed a very large and important collection, including specimens from a California visit from September 27 to November 25, 1824, at San Francisco Bay. However, collections were made throughout the area, to Santa Clara, San Rafael, Fort Ross, Bodega Bay, and the lower portions of the Sacramento River, possibly to the present site of Rio Vista. Although he collected many new species of Coleoptera, Eschscholtz had less luck with the Lepidoptera, since their delayed systematic study commenced at the time (starting in 1850 or 1851) that Boisduval was already rapidly describing the new California butterflies collected by Lorquin.

Ilya Vosnesensky

Ilya Gavrilovich Vosnesensky followed the first Russian butterfly collectors by 24 years, when he arrived on a special trip to the Russian-American colonies at Fort Ross in Sonoma County on July 20, 1840, and remained until September 3, 1849 (Essig, 1972; Wells, 1987). Only 23 years old in 1839, he was selected to go to the Russian colonies in North America, and his efforts were so productive and successful that he extended his planned three-year journey to ten years. His Fort Ross sojourn was especially productive in insects, plants, and even mammals. Fort Ross had been established in California in 1812 with about 30 Russians and 150 Aleuts from Alaska, when Ivan A. Kuskof built a fortified village and called it "Ross" (a word from the same root as "Russia"), as

headquarters for their farms (to provide food for the Russian-Alaskan colony) and for trading with the Spanish and the Indians. This site was some 13 miles north of the presently named Russian River, and 18 miles north of Bodega Bay.

Vosnesensky was quite a successful collector and assembled a large collection of insects from the San Francisco Bay region, extending from Fort Ross and the Russian River to Bodega Bay and New Helvetia (Sutter's Fort). He was the first to collect the California Dogface butterfly, *Zerene eurydice* Boisduval, which was named by the Russian entomologist, Edouard Menetries, as *Zerene vosnesenskii* Ménétriés in 1855. However, shortly before his name was published, the French entomologist J. H. A. Boisduval published the description of the same butterfly (collected by Lorquin), giving the name *C. eurydice* priority.

Vosnesensky is perhaps best known in California history for having been the first person other than native Indians to climb and name Mount St. Helena (4,343 feet high) on June 12, 1841. This is the most conspicuous mountain in the vicinity of the Fort Ross site. On the summit, he and his Russian companion placed a small inscribed copper plate announcing the event. This plate was removed in 1853 and was subsequently destroyed in the San Francisco fire of April 1906. On the 100th anniversary of the founding of Fort Ross in June 1912, the plaque was restored and placed again on the summit. It is probable that a number of our California butterflies would have been named from Vosnesensky's collecting in North America, had Ménétriés not been forestalled by Boisduval (1852 and following papers) publishing the exciting finds made by his collector and friend, Pierre Lorquin, in California just ten years after Vosnesensky's visit there.

II. THE GOLD RUSH ERA (1849-1859)

Pierre Joseph Michael Lorquin

The most famous of our early California collectors, Lorquin was born in Valenciennes, France, on July 2, 1797, and died in Paris, France on February 8, 1873. While Essig (1972) summarizes many of the details of Lorquin's life with accuracy, the itinerary outlined by him has been corrected and given in greater detail in Emmel, Emmel, and Mattoon (1993a), from which the following account is taken. During his 75 years of life, Lorquin explored and collected in a number of areas around the world. As a student at the University of Douay, he became a graduate with honors and became a notary clerk, rising rapidly and taking a position in Algiers in 1848, where he collected a great deal of interesting lepidopterological material. On hearing of the discovery of gold in California in 1850, he left Algiers and headed for the new El Dorado, not just for gold but for the lepidopterological *terra incognita*. Upon arrival in California, he found an unexplored field for Lepidoptera and set to work to supply his intimate friend, the great French lepidopterist J. A. Boisduval (family physician for the Lorquins back in France), with specimens. His family followed in 1852 and he remained in the state until 1859.

Boisduval (1868) has a fascinating preface to his paper which we quote part of below to give the flavor of what Lorquin faced in the 1849 gold rush:

"A naturalist known to all for his zeal and love of science, M. Lorquin, was seduced as the others have been by the shining mirage and embarked for California to remake a fortune of which he had been so unjustly stripped. He left in 1849, his heart full of hope, believing that in this Eldorado one had only to bend over, so to speak, and pick up the gold nuggets.

As soon as he landed, and without pausing a moment to rest, he hastened to the Placers and worked like a common laborer, with as much courage as energy, from time to time finding a few particles of the precious metal; but the result of this hard work were not even enough to pay his expenses in a land where everything had a fabulous price: 30 francs for a dozen of eggs, and the rest in proportion!

Not knowing what to do, he braced himself against adversity, left the Placers, returned to San Francisco and, putting aside all pride, he did what many others were doing: he practiced many occupations well outside his usual ones, and this permitted him to live and amass a little money. From this moment dates the honorable reputation he has acquired today, by force of economy, for work and perseverance.

Having acquired a little free time, and having his family with him (they had come out to join him), he felt awakening in himself a love of natural science and above all of entomology. To indulge in these interests, he did not hesitate to endure rude privations and much hard work. He first explored all the environs of San Francisco, then the shores of the Sacramento and the Plume [Feather], made voyages into the chain of the Sierra Nevada and ventured even to the forests of the interior, braving the bear's tooth and the rattlesnake's fang.

These dangerous excursions, made in different seasons over two years, furnished him with fine collections of insects of which he sent us, eighteen years ago, two extremely outstanding shipments. A large part of the Lepidoptera being unknown and entirely new, we published their descriptions in the Annals of the Entomological Society of France in the form of a small local fauna. Since that time, M. Lorquin's zeal has not slackened. On the contrary, having more leisure time he undertook voyages to unexplored regions: He went to visit the mountains of the north; penetrated far to the East; and later went into the homeland of the Apaches, as far as Los Angeles in Sonora. The results of these collecting trips in these diverse parts of California confirmed fully to what we would expect of such a man as M. Lorquin. This indefatigable entomologist sent us three successive shipments of specimens collected in these different localities, each one including many new species, whose number exceeds that of the species we made known in the small fauna just mentioned.

We believed that with these new materials, we would render a service to lepidopterists by giving them now a second part, no less interesting than the first. To make this little work more useful and as complete as possible we have, in the interest of those who do not have our earlier work, reproduced all the diagnostic phrases of the species described in the Annals of the Entomological Society; we also give, in the form of an appendix at the end, a list of the Noctuids and Geometrids discovered by M. Lorquin and communicated by us to the specialist, M. Guèné, for his *Species Général*. One will have thus all the Lepidoptera found to date in California.

Now that M. Lorquin has returned to France we shall receive nothing more from this country; after him the spring will be dried up for a long time. One cannot count on gold seekers to collect insects."

Boisduval goes on to describe Lorquin's trip to the Philippines in 1857, via Hong Kong and Saigon and his subsequent return to China where he made a fine collection of Lepidoptera. He then returned to California briefly, but was unable to resist the urge to visit China and the Celebes again, he returned for nearly a year of exploration and collecting. Unfortunately, he followed Alfred Russell Wallace by several years, and Wallace had already collected most of the extraordinary species of this South Asian area and had them described in England.

One mention of the presence of Pierre Lorquin at a regular meeting on April 1, 1867, of the California Academy of Natural Sciences at San Francisco is made in the *Mining and Scientific Press* newspaper, published in San Francisco on April 6, 1867. The Minutes of that Academy meeting state that "Mr. Lorquin presented a case of butterflies from the Philippines, Molucca, and Arrow Islands and Brazil."

Lorquin had become a close friend of Herman H. Behr after meeting him in 1852 at the California Academy of Sciences. His specimens were split among Boisduval (who received the great bulk of them), H. H. Behr, A. Guenée, A. R. Grote, and C. T. Robinson. Some specimens also went to the Felders in Vienna. Boisduval always sent a specimen of each species when he described it from France back to Lorquin, and these co-types were turned over by Lorquin to Behr and preserved in the Museum of the California Academy of Sciences until the 1906 earthquake and fire. Interestingly, Lorquin never learned English well enough to converse fluently in it (Grinnell, 1904). Before Lorquin arrived in California, very few butterflies had been collected there. Of the large number of species of California Lepidoptera described by Boisduval (1852, 1859), all except five or six (those being supplied by E. Doubleday) were collected by Lorquin. Boisduval lists 95 species of Lepidoptera that Lorquin took in California, which included 83 butterflies. Some 53 butterflies were described as new species. One of them, Lorquin's Admiral, *Limenitis lorquini* (Boisduval), commemorates the name of this early collector. Especially appropriate is that this beautiful species occurs throughout much of the state. It is interesting to note that Lorquin did not overlook collecting many of the really abundant and widespread species of the 1850's. These included both new species and species already named by other workers such as Linnaeus, Hubner, and Lucas. The Lorquin Natural History Club, founded in 1913 and expired in 1919, and the Lorquin Entomological Society, founded in 1917 and thriving to the present date, preserve the name of this outstanding early California lepidopterist.

Jean Alphonse Boisduval (1799-1879)

One of the most famous French entomologists and a great systematicist in Lepidoptera, Boisduval was born in Normandy, France, on June 17, 1799, and died there on December 30, 1879. He produced some 50 publications, mostly dealing with Lepidoptera. In California lepidopterology, he is most famous for describing and publishing the new Lepidoptera species taken by P. J. M. Lorquin in California, though he also described a number of other important insects native to North America and various Homoptera and many Coleoptera. Boisduval's great

collection of Lepidoptera was sold to Charles Oberthur at Rennes, France. Some of the collection was purchased by William Barnes of Michigan, and the Sphingidae eventually reached the Carnegie Museum at Pittsburgh. Some types reached the British Museum and the Smithsonian Institution, the latter coming through the Barnes collection (see Emmel, Emmel, and Mattoon, 1993a, for more details). Boisduval's name, as abbreviated *Bdv.*, follows the names of many of our California butterfly species as a result of his indefatigable systematic work on the material collected in California by Lorquin (Essig, 1972).

III. THE STATE GEOLOGICAL SURVEY DECADE (1860-1870)

James Mason Hutchings (1824-1902)

Like Lorquin, Hutchings came to California in 1849 after news of the gold discovery reached him in New Orleans. As a young man of 25, he worked in the mines for a few years before turning to writing and publishing. From 1856 to 1861, he published *Hutchings' California Magazine*, which is widely acknowledged to have been one of the best illustrated magazines of its day. In 1855, he led the first tourist party into Yosemite Valley. His illustrated account of this trip appeared in the *California Magazine* and was widely reprinted, stimulating much early interest in Yosemite Valley. In 1861, Hutchings sold his magazine and bought the "Upper Hotel" in Yosemite, which he renamed "Hutchings' House" and operated it as a guesthouse until his death in 1902.

One of Hutchings' first employees in Yosemite was JOHN MUIR who worked for him as a carpenter, but they soon parted company as a result of philosophical differences involving the development versus preservation of Yosemite. During the years that Hutchings lived in Yosemite, he explored a number of areas in the Sierras and published guidebooks on California natural history, although not on butterflies. Nevertheless, he is known to have supplied specimens of *Parnassius phoebis behrii* W. H. Edwards to Henry Edwards (F. M. Brown, 1975), credited with the taking of the type specimen of *P. behrii* near the summit of Mount Lyell, and possibly as being the collector of the type specimen of *Parnassius clodius baldur* W. H. Edwards.

Masters (1980b) confirms that Hutchings undoubtedly collected Lepidoptera for Henry Edwards and possibly for others, but presents evidence that he did not collect the type specimen of *Parnassius behrii* (Masters, 1980a). It seems instead that the types of *P. behrii* were collected by the members of the California State Geological Survey, who supplied Behr with most of his "high Sierra" material during the summers of 1863 or 1864. The first persons to climb Mount Lyell were W. H. Brewer and C. F. Hoffman of the Survey, who both discovered the mountain and named it. They first climbed it on July 2, 1863, which was at least nine years before Hutchings climbed the mountain in 1871 or 1872. (Edwards had described *Parnassius behrii* in January or February of 1870.)

Ferdinand Bischoff

Little is known about Ferdinand Bischoff other than his collecting activities on the Wheeler Survey in 1871 (Brown, 1955, 1957). Bischoff was a zoological collector assigned by S. F. Baird of the Smithsonian Institution to Lieutenant William Montague Wheeler, Corps of Engineers in the U.S. Army, who was sent to explore and map the territory west of the 100th Meridian during the seasons of 1869 to 1879. During the years 1865 to 1871, Bischoff collected many specimens new to science from out-of-the-way places in western North America. He collected butterflies in Alaska during 1865 through 1868 and some of these specimens reached Behr, Behrens, and Henry Edwards, as well as William H. Edwards.

His participation in the 1871 Wheeler Expedition extended from the 3rd of May until the first part of December that year. Part of their itinerary included the area near Camp Independence, California, which lasted from July 18 to August 10. Bischoff apparently made at least one trek into the Sierra Nevada to the west of Camp and also probably collected extensively in the bottoms of the Owen's River, possibly as far as Owen's Lake. He also went southward to the vicinity of the present town of Mohave. Among the striking butterflies collected in this area were the types of *Speyeria nokomis apacheana* Skinner, and *Cercyonis pegala wheeleri* (Edwards). Our supposition that Bischoff went into the High Sierras to the alpine area comes from the fact that Mead (1975) lists *Melitaea hoffmannii* Behr as one of the butterflies collected by the expedition of 1871. Bischoff also collected *Colias edwardsii* in the vicinity of Owens Lake.

William Moore Gabb (1839-1878)

Gabb was a professional geologist and paleontologist who was born in Philadelphia, Pennsylvania, on January 20, 1839 and died there on May 30, 1878. He became interested in entomology through his associations with an eminent coleopterist in Philadelphia. When he came to California in 1861 to become a member of the State Geological Survey of California, he joined the California Academy of Sciences and was appointed Curator of Paleontology. In the spring of 1863, he traveled across much of the San Joaquin Valley to Fort Tejon and the Sierra Nevada Range in the Mt. Whitney region. In 1864, he explored northern California and in 1866, he explored the Coast Ranges. In 1867, he explored the White Mountain Range on the boundary of California and Nevada and also made a trip to Baja California. In 1868, he returned to the East and did not return again to California. His explorations throughout California resulted in the collection of many insects which were turned over to the California Academy of Sciences. H. H. Behr named *Euphydryas gabbi* (Behr) after him and W. H. Edwards named *Cercyonis gabbi* Edwards (Essig, 1972).

IV. THE FEDERAL SURVEYS OF THE WEST (1870-1890):

Walter J. Hoffman and the Wheeler Expedition

Dr. Walter J. Hoffman was the contract surgeon and naturalist attached to Lt. Wheeler's expedition of 1871. Brown (1964) noted that he was a good friend of HERMAN STRECKER and that in a letter written from Camp Independence in the Owen River Valley of California, and dated

July 27, 1871, Dr. Hoffman told Strecker that he was collecting butterflies and would give some of his catch to him. FERDINAND BISCHOFF (see Brown, 1957) was one of the field collectors attached to the expedition also and was assigned to Hoffman. Thus we see the origin of the confusion over the naming of one of our extinct California satyrids, *Cercyonis pegala wheeleri*, from the east side of the Sierras. Strecker described (in 1873) the male of *wheeleri* as *hoffmani*. The types of *hoffmani* in the Strecker Collection at the Chicago Natural History Museum are accompanied by a label that reads "S. Hoffmanni / Streck. / Owen's Lake / orig. type Bischoff." WILLIAM HENRY EDWARDS had originally labeled his three type specimens of *wheeleri* with "Arizona" as the site, but he later wrote letters to William G. Wright with the suggestion that Wright visit the Camp Independence-Owen's Lake region to collect eggs of *wheeleri*. Thus as Brown (1964) points out, it seems from these letters that Edwards learned that the type series had come from that region rather than Arizona. Edwards also wrote to Strecker from Coalburg, West Virginia, on July 22, 1873, with the comment "I see you have figured my *S. wheeleri* under the name Hoffmanni [sic]." Apparently, Edwards published the name *wheeleri* in the form of a preprint of his paper by March 1873, because Strecker later (in 1878) accepted the name *wheeleri* as published prior to his own *hoffmani* that had been published in June 1873. Thus he accepted the date of the Edwards preprint as the date of publication of the name *wheeleri*, described from two females as it turned out.

It is of interest to note that the Walter J. Hoffman on the Wheeler Expedition of 1871 is a different person than the **CHARLES FREDERICK HOFFMANN** who came to California in 1858 and joined the California State Geological Survey, serving with the Survey until its termination in 1874. He is believed to have collected the type specimens of *Colias behrii* and other high-altitude or alpine Sierra Nevada butterfly species for William H. Edwards (Farquhar, 1966). Charles F. Hoffmann worked with William H. Brewer, another eminent geologist in the Whitney Survey. Brewer was in charge of the botanical duties and did a considerable amount of plant collecting, laying a good foundation for later botanists exploring the state of California.

John Muir

An early account of butterfly collecting by John Muir is recorded by his biographer, W. F. Bade' in *Life and Letters of John Muir* (1924; see also Garth and Tilden, 1963, page 3):

Muir to Mrs. Ezra S. Carr, August 13, 1871:

"I suppose you have seen Mr. King, who kindly carried some [butter]flies for Mr. Edwards ... I collected most of them up on Mount Hoffman, but was so busy in assisting Reilly that I could not do much in butterflies." (*Op. cit.*, Vol. I, p. 292).

Henry Edwards to John Muir, August 25, 1871.

"In the small box that you sent me [through Mrs. Carr] are four species new to my collection and two of these are new to science ... All the specimens are rare, and are different from those found in the Valley. The two new small species are the bright crimson copper one from Cathedral Peak, and one of the small bluish butterflies. There is a pair of greenish yellow ones,

very rare and interesting. The species was described from a pair only which were taken by the Geological Survey at the headwaters of the Tuolumne River, and strange to say, no others have turned up until you found it now ... It is really very singular that the remove of a few miles from the Yosemite should produce species so very different from those of the Valley itself, and at the same time so characteristic in their forms." (*Op. cit.*, pp. 263-264).

As Garth and Tilden (1963) point out, the bright crimson copper mentioned above is probably *Lycaena cupreus* (W. H. Edwards), while the greenish yellow ones are undoubtedly *Colias behrii* W. H. Edwards.

Collecting in the Yosemite Area

A number of our California butterflies were first obtained by a naturalist somewhere in the Yosemite region. The hermit Lambert (whose name is memorialized in Lambert's Dome in the Yosemite National Park) for many years supplied the entomological world with specimens of Behr's Sulphur (*Colias behrii*) from his hideaway in Tuolumne Meadows, and it was not until the Tioga Road was opened to tourist travel in 1915 that his secret source of this rarity was discovered (Garth and Tilden, 1963).

P.C. Truman: Early Collecting in San Diego

P. C. Truman, of whom nothing else is known, spent two months in the early part of 1889 in southern California. Arriving in San Diego on January 22, he began collecting immediately. The first species noted were overwintering nymphalids and danaids, as one might expect, but he noted that the spring butterflies soon began to fly abundantly on the mesas east of San Diego. Between the date of his arrival and February 23, he found "*Melitea*, *Palla*, *Gabbii*, *Whitneyi*, *Quino*, *Anicia*, *Editha*, and *Chalcedona*...." Allowing for the tendency of the time to recognize every variety as a separate species, it is clear that he found these nymphalids in abundance. He also found *Anthocharis sara reakitii* common in the valleys and canyons east of San Diego and various hairstreaks including "*melinus*, *augustus*, and *dumetorum*." A number of blues were found, including *Philotes sonorensis* on the rocky sides of Point Loma. Today in the 1990's, that Point Loma colony is believed extinct. Towards the end of February, he found *Zerene eurydice* and *Papilio zelicaon* on the sides of the canyons (Truman, 1890).

Lord Walsingham

Butler (1882) gives an account of 74 species of butterflies and skippers obtained by a man named Lord Walsingham during the years 1871 and 1872 in California. Butler notes that compared with other collections from the United States at that time, the Walsingham collection is "by no means poor in species: The first series forwarded by M. Lorquin to Dr. Boisduval contained 83 species of butterflies; but some of these may have been obtained from Mr. Doubleday....of the subsequent collection forwarded by M. Lorquin, it would be impossible to guess the exact number of species; but the list of them, published by Dr. Boisduval in 1868, innumrated 62 species,

probably representing those received since 1852." Butler gives the counties in California and the dates where each species was collected. These are virtually all in northern and central California, including Sonoma, Mendocino, Tehama, Siskiyou, Lake, Shasta, and Colusa counties. Butler describes also the confusion over the naming of *Zerene eurydice* in 1855 by Boisduval when the Secretary of the French Entomological Society inadvertently published a brief comparative description ahead of the formal description by Boiduval. This name of *eurydice* replaced the originally intended name of *wosnesenskii* for this beautiful insect because of its timely publication, as explained earlier in this chapter.

Hans Herman Behr (1818-1904)

Behr was born August 18, 1818, in Germany and graduated as a doctor of medicine from Berlin University on March 23, 1843. By that time he had already displayed a passion for research in the field of entomology and at the urging of Alexander von Humboldt, another distinguished scientific friend, he visited Australia, Java, Brazil, and the Philippines, collecting insects. After these initial travels, he returned to Berlin to practice medicine. But the lure of the tropics was too much to withstand and he left again for the East Indies, collecting until 1851, when he came to San Francisco. In 1853, he returned to Germany briefly to bring his Polish bride to his San Francisco home.

In San Francisco, Behr practiced medicine, studied plants, and worked on his special love of butterflies. He became a member of the California Academy of Sciences early in 1854 and served as Professor of Botany at the California College of Pharmacy in San Francisco, during which time he wrote a flora of San Francisco. By far the best educated and most thoroughly trained scientist in the Academy (Essig, 1972), he served as Curator of Botany in 1855, Vice-President from 1864 until his death, and during the last 12 years of his life (to March 6, 1904), as Curator of Lepidoptera. He amassed a large collection of Lepidoptera which was presented to the California Academy of Sciences around 1893. Unfortunately, this valuable collection was destroyed in the San Francisco earthquake and fire of 1906. A few types were saved by their earlier deposition in the Herman Strecker collection in the Field Museum of Natural History in Chicago.

Although Behr published only 16 entomological papers chiefly on Lepidoptera, he named a good number of species, including such butterflies as *Argynnis coronis*, *A. leto*, *A. rupestus*, *A. montivaga*, and *A. adiate*, *Euphydryas gabbi*, *E. cooperi*, *E. hoffmani*, and *Neophasia terlooti* (from Arizona). On his 80th birthday, the Frederick William University of Berlin conferred an honorary doctorate degree, a distinction never before given to a German-American (Anonymous, 1904). Behr's types in the California Academy of Sciences being all destroyed in the 1906 earthquake, it is very difficult to compare the species he named with those named by Boisduval, particularly because Behr gave very short and inadequate Latin diagnoses of his new taxa (McDunnough, 1914). Some of these problems are addressed and clarified in a recent publication by Emmel, Emmel, and Mattoon (1993b).

Henry Edwards (1830-1891)

Henry Edwards was a great actor and lepidopterist, nationally known for his work in both fields. He amassed a very large collection of butterflies and moths which ultimately went to the American Museum of Natural History. After travels to the tropics in 1853 and a brief visit to California, he resided from 1865 to 1878 in California with his home at San Francisco, where he was associated with the famous old California Theatre. He was elected a member of the California Academy of Sciences in 1867 and became a trustee in 1874, as well as first Vice President from 1875 to 1877. He became a life member in January 1877. During this period in California, he published an important series of papers entitled "Descriptions of Pacific Coast Lepidoptera," in the *Proceedings of the California Academy of Sciences* (especially 1877-1880). After leaving California in 1877, he briefly resided at Boston and then went to New York in 1879 where he became affiliated with the New York Entomological Society and was one of the founders and the editor of the journal *Papilio* from 1881 through 1883. At the time of his death, he was President of the New York Entomological Society. He published an important bibliographic catalog of the described life histories of North American Lepidoptera in 1889. His collection, which consisted of 250,000 specimens of Lepidoptera and was one of the finest in existence at his death, was bought by his friends for the benefit of his wife and presented to the American Museum of Natural History in New York, together with much of his correspondence and notes (Essig, 1972).

Throughout his life, Henry Edwards spent most of his income to increase his collection of insects, and he devoted all his leisure time to his favorite study. His collection contained the types of all the species he described, about 450, except for a few that had reached other collections (Beutenmueller, 1891).

William H. Edwards (1822-1909)

Although William H. Edwards never set foot in the state of California, his influence has been profound because of the large number of species and subspecies he named from specimens collected within California. Additionally, his rearing of western species at his home in West Virginia provided the first insights for most lepidopterists into the value of immature stages and foodplant data in both classification and natural history or ecology of species. Because of his prolific writings, including the tremendous three-volume work, *THE BUTTERFLIES OF NORTH AMERICA*, and his tremendous correspondence with literally almost every active lepidopterist during the latter half of the 19th century, there is an abundance of biographical material on his life and research. William H. Edwards and SAMUEL H. SCUDDER were the two most notable students of the butterflies of North America during the 19th century. As we try today to interpret the evolutionary and ecological relationships of the western butterflies, our efforts were truly foreshadowed by the extensive collecting and rearing discoveries made by Edward and Scudder.

Edwards was born at Hunter, New York, on March 15, 1822. His father had an estate of some 1,200 acres of hemlock forest in the Catskill Mountains where young William H. Edwards was born and brought up, developing a love of nature which continued throughout his life. After graduating from Williams College in Massachusetts in 1842, he studied law in New York and was admitted to the Bar in 1847, residing thereafter at Newburg, New York. Subsequently, he became interested in the coal fields of West Virginia and moved to Coalburgh, West Virginia, where he was President of the Ohio and Kanawaha Coal Company. Though an extensive landowner in both

Virginia and West Virginia, a builder of railroads, a developer of coal mines, and active in the community affairs throughout his life, he always found time to devote to the study of butterflies, and even more remarkably, to the preparation for publication of the results of his investigations.

Edwards' first contribution to the pages of the *Canadian Entomologist* appeared in the third number of the first volume in October 1868, and his 170th contribution to that journal alone appeared in the thirtieth volume in January 1898. He also published many papers describing new butterflies in the *Proceedings and Transactions of the American Entomological Society* and the new, but short-lived, journal *Papilio*, edited by Henry Edwards. These two men were friends and corresponded with each other, Henry Edwards residing mostly in California during this time. There has been some confusion in the literature because of the similarity in names.

W. H. Edwards published his first book in 1847, entitled VOYAGE UP THE AMAZON, which gave an account of a trip that he made up that great river in 1846, not long after he graduated from college. His magnum opus, however, was THE BUTTERFLIES OF NORTH AMERICA. The first part of this great work was published in April 1868 and the exquisite beauty and detail of the plates attracted worldwide attention. In July 1872, the first series of parts forming a large quarto volume with 50 plates was completed. The second series of parts, containing 51 plates, was begun in May 1874, but not finished until November 1884. The first part of the third series was issued in December 1886 and the last (the eighteenth) in 1897, with some 51 plates. The quality of the artwork and the writing increased with every part completed. For example, in the third volume, nearly half of the 51 plates are devoted to the alpine or subarctic species of the Satyrinae, and every species of North American *Oeneis* except *O. taygete* from Labrador, was figured with all the life stages fully described. A wealth of detail on larval characteristics was included, along with the eggs and pupae. Until Edwards began this mammoth work, little or nothing was known of the egg, larvae, or pupae of any except a few of the commonest butterflies in North America. He made the notable discovery in 1870 that eggs could be satisfactorily obtained by combining the female butterfly of any species with the growing hostplant of its larva. He at once began having correspondents from throughout the country send him eggs procured in the field, in West Virginia, he could complete their rearing on substitute foodplants and accurately record egg, larval and pupal characteristics. This work was aided by the general extension of railroads across the continent and he was able to secure eggs with reasonable speed from widely distant localities, including western states and territories. Mr. Edwards employed a number of artist assistants, and one of these, Mrs. Mary Peart, not only drew with extreme accuracy nearly all the plates, but also helped to rear a large number of the caterpillars. The coloring of the plates was done by Mrs. Lydia Bowen.

In the first volume of his great work, Edwards said "It is a matter of regret that, in some instances, I shall not be able to say anything of the larvae. Even among our old and common species, the larvae are but little more known than in the days of Abbot, 70 years ago." In the Preface to the second volume, dated 1884, Edwards said "All this has changed, and today it can be said that the preparatory stages of North American butterflies as a whole are better known than all those of Europe." This was made possible by the important fact that Edwards uncovered about the females, as related above. In his own words: "In 1870 I discovered an infallible way to obtain eggs from the female of any species of butterfly, namely by confining her with the growing food-plant. If the eggs mature, they will be laid" (Anonymous, 1909)

At the age of 75, Edwards gave up his studies of butterflies, feeling apparently that his advanced age precluded him from working with the ability and success that he had so remarkably displayed. However, he continued working in literary areas, on such subjects as Shakespeare and a genealogy of the Edwards family; the latter became his last work, published in 1903. During the period of his active studies on butterflies, new specimens of North American butterflies received by the Smithsonian Institution in Washington were sent to him for description and classification. Additionally, the Imperial Russian Government and the British Museum sent to him for examination and description many North American examples that appeared to be new. As a result, he became the author of a large number of new species, including many whose ranges in western North America include California. The Carnegie Museum purchased the Edwards collections before his death and the specimens were curated by William J. Holland, the director, who used them as the basis for his own book, *THE BUTTERFLY BOOK* (Bethune, 1909). While most of the specimens from the great Edwards collection went to the Carnegie Museum, some ended up in other institutions by exchange or trading for life history material (e.g., Irwin, 1966; Irwin, 1972).

Edwards had extensive correspondence with many of the leading professional and amateur lepidopterists in the United States. Some of this extensive correspondence has been analyzed by his biographer, F. Martin Brown (e.g., 1958, 1959). This being before the days of carbon paper or xerox machines, copies of the letters were frequently made by pressing a moist piece of tissue paper against the original letter, resulting often in smeared copies or (if the tissue was too dry) only a bit of a letter here and there making a bold transfer. Nevertheless, the correspondence between William Henry Edwards and such people as Spencer Fullerton Baird offers considerable help in fixing type localities and distributional records from the early collectors in the western states. In particular, F. M. Brown has published a monumental survey of all the Edwards types and used his indefatigable energy to trace down existing correspondence, hints on specimen labels, etc., to recreate the often obscure story of where these specimens were collected and how they reached Edwards for description.

During his lifetime, Edwards wrote about 265 scientific papers, mostly on butterflies, wherein he proposed some 356 names for nearctic butterflies as well as for some moths (dos Passos, 1951). Cyril F. dos Passos, himself a famous lepidopterist of the 20th century, had the good fortune to discover in 1949 an autobiographical manuscript written by Edwards and completed three months before his 80th birthday. These notes were published by dos Passos (1951) and a reading of them reveals many of Edwards' early experiments with life history rearings, illustrations, and of course his wealth of correspondence. At Edwards' urging, friends experimented with the effect of cold on pupae of *Papilio*, especially *marcellus*, which showed the effects that cold and warmth could have on coloration and pattern development. He also discovered between 1875 and 1878 that the larvae of the blue *Celastrina pseudoargiolus* are attended by ants, and he noted the intimate behavior of the ants in proximity with the last segments of the larvae. Subsequently, he and a colleague discovered the sugar-secreting fluid glands on the back of a larva, which served as signals for the ants to come to segment eleven. Edwards then sought to find out why the ants would be of any use to the larvae, and the following summer he watched the larvae (tended by ants) in the field. He discovered that the ants protected the larva from ichneumonid wasps. These and many other discoveries were made as a result of his exhaustive life history work.

In terms of California species, we know from Edwards' correspondence and publications that in April 1886, he received eggs of *Apodemia mormo* from William Greenwood Wright at San Bernardino, California, and he received eggs of many species from C. F. McGlashan at Truckee, California. In 1889 and 1890, he received eggs of many southern California species from Wright at San Bernardino. Edwards noted in his autobiography that he became a correspondent with the actor Henry Edwards about 1872 and from that time until Henry Edwards' death, they frequently exchanged letters and butterflies. They first met personally in December 1887 at Henry Edwards' home in New York where they spent the morning in his study. What an inspiration it would be to read a transcript of their conversations!

Theodore L. Mead (1852-1936)

Theodore Mead was born in the Catskill Mountains of New York on February 23, 1852. His forebears had immigrated from England over 200 years earlier. His early years were filled with adventures in natural history and when butterflies took his interest, he became acquainted with William H. Edwards. Later, he was to become W. H. Edwards' son-in-law. In 1866, he was elected to the American Entomological Society and he spent the following summer in West Virginia working with Edwards. Apparently, the young man's enthusiasm and ability struck a responsive chord, for in 1871 Edwards arranged that Mead accompany the Wheeler expedition to Colorado as a paying member. Edwards shared Mead's expenses and also received a portion of the catch from Mead (Mead, 1875). After he collected in Colorado, Mead continued westward in the fall of 1871 and visited entomologists in California. He then spent some years at Cornell University earning a degree in civil engineering. In 1877 he sold his collection of butterflies to the Carnegie Museum at Pittsburgh, and from that time on he devoted more of his life to botanical and horticultural work. However, in 1878 he did take a second entomologically-oriented trip to California, arriving in San Francisco in early May and leaving there on May 7 for Los Angeles and the San Gabriel Valley. On this California trip, Mead visited the Mojave Desert, Yosemite Valley, Big Trees, Mariposa County (Essig, 1931), Summit Station on Donner Pass, Lake Tahoe, and Freel's and Talloc peaks, the last area being where he collected the types of *Oeneis ivallda* Mead. On his way home, he collected at Virginia City, Nevada, and at several points in Utah and Wyoming. In 1881, Mead joined Henry Edwards and A. R. Grote in starting the journal *Papilio*, which was published for four years. In 1882, Mead married the daughter of William H. Edwards and after a honeymoon in England, he settled in central Florida to try his hand at orange-growing. From this time on, he pursued botanical interests exclusively and did not publish further on butterflies. He died in Winter Park, Florida in 1936, shortly after publishing his autobiography (New, 1935; Brown, 1955). While most of Mead's lepidopterological fame (Brown, 1934) is from his collecting in Colorado, a period which supplied many specimens to W. H. Edwards for description, he did collect significantly in California and helped launch many papers on the western butterfly fauna in his joint founding of the journal *Papilio*.

Richard H. Stretch (1837-?)

A pioneer lepidopterist on the Pacific Coast, and an associate of H. H. Behr, Henry Edwards, Samuel H. Scudder, and William H. Edwards, Richard Harper Stretch was born November 25, 1837 in England. He developed an intense interest in natural history very early. Following his boarding school years, he became an apprentice in a dry goods shop. In 1861, he received an invitation to visit relatives in Illinois, but returned to England after about a month. In 1862, he visited his uncle once again in Illinois, making extensive collections there, and then in 1863, he joined an emigrant party bound for California. His small band of five persons was able to pass unmolested through hostile Indian country despite the fact that other wagon trains were attacked and wiped out at the same time. Their protection apparently ensued from Stretch's entomological pursuits. When Stretch displayed his preserved insects to a friendly Indian at the outset of the journey, the word was passed among the Indian bands that a big medicine chief was coming and that no harm should befall him.

When he arrived in Utah, Stretch changed his plans and went south into Nevada. He proceeded to begin a career in Virginia City, then a rip-roaring frontier mining camp. First employed as a cook, he later ran a sawmill and after that became associated with a partner in a land office business. His entomological knowledge served him well, for he was able to discriminate minute differences and grade with ease the various types of ore. To his astonishment, he was elected State Mineralogist of Nevada. Soon he became known as the best maker of mining maps in America.

In 1867, Stretch journeyed on to California. En route, he was among the earliest of the emigrants to cross the fearful Death Valley region. He visited San Francisco and also descended into Chihuahua, Mexico. In the winter of 1868-1869, he returned to Nevada to Virginia City for the U.S. Geological Survey to make a study of the famous Comstock Lode. He returned to San Francisco and became city surveyor in 1870. Despite all the pressures of business on these trips, his interest in entomology never flagged and he discovered many new and interesting species in both California and Nevada. His most significant California collecting began in 1875 and continued through 1876, when he lived and collected extensively in the Havilah area in Kern County. Here he discovered the dainty blue *Philotes speciosa*, which was named by Henry Edwards. Henry Edwards also described a number of other butterflies taken by Stretch at Havilah. In 1888, he moved to Seattle, Washington, and from there, various mining jobs took him to nearly every state in the West, as well as British Columbia. Shortly after his wife died in 1885, Stretch donated his entomological library to the Mechanic's Institute in San Francisco and his magnificent collection, replete with many types and rarities and numbering about 13,000 specimens, was given to the University of California at Berkeley (Coolidge and Newcomb, 1920). Essig (1939) later estimated Stretch's collection at Berkeley as numbering about 5,000 specimens.

Stretch is probably most remembered in entomology for his personal work on the moths, including his classic work "Illustrations of the Zygaenidae and Bombycidae of North America," published in 1872-73. While he knew many of the other great early entomologists of the West and people such as Thomas Edison and Mark Twain, Henry Edwards was Stretch's closest friend and companion, and his entomological studies practically ceased when Henry Edwards died in 1891.

Oscar Theodor Baron (1847-1926)

Baron was born on September 9, 1847, in Germany, the son of a schoolmaster. He studied collecting insects at the early age of 13 years. As a young man, he was shipped as a sailor to the Orient and visited India, China, and the Austra-Asian region. From Java, he shipped to the west coast of America where his first job in the New World was as a surveyor. The little we know about Baron's life after that has been augmented by the researches of F. M. Brown who examined the extensive correspondence that Baron had with Henry Edwards and Herman Strecker.

Brown (1965) was able to reconstruct a year-by-year itinerary of Baron from the time he was 28 years old (1876) and working at loading schooners applying between a small mill in Mendocino County and San Francisco. In his spare time Baron was collecting moths, butterflies, and other insects. He knew a fair amount about saturnids and other moths in 1876 and 1877, and apparently began exchanging butterflies with W. H. Edwards at this time (although no account in Edwards' journal survives). He also exchanged specimens with Henry Edwards and H. Neumoegen. In 1879 Baron set out from Navarro in Mendocino County on a long collecting trip, starting in mid-April. By September, he returned with a good catch from the summer season. In subsequent years, he traveled as far as San Diego in southern California, but most of his California collecting was in the north-central counties. In 1882, he met William Greenwood Wright and instructed him in how to collect and preserve Lepidoptera. Letters in the Wright collection and in the Pacific Coast Entomological Society files show that Wright started on his long career as a lepidopterist at this time. In 1884, Baron apparently traveled to Mexico and then later to Ecuador. By 1887, he was back in southern California and also working with a crew of engineers in Pima County, Arizona. He collected some butterflies and butterfly eggs for W. H. Edwards during this time. By 1892, Strecker inquired about purchasing Baron's collection, Baron estimated that there were perhaps 27,000 Lepidoptera, of which 6,000 were from California. Baron did not reach an agreement with Strecker, and sometime in 1893, he returned to Germany, and lived there for the last 30 years of his life. He sold a large part of his collection in England en route to Germany but retained about 100 drawers of American butterflies for his own use.

Some of the specimens that Baron shipped to Strecker are in the Chicago Natural History Museum. Those that remain from Neumoegen's collection are in the United States National Museum, and Henry Edwards' specimens from Baron are in the American Museum of Natural History. Many of the specimens in the W. H. Edwards collection at the Carnegie Museum bear on their labels "O. T. B." in Edwards' handwriting, testifying to their origin (Brown, 1965).

James Behrens (1824-1898)

James Behrens was one of the pioneer collectors in California. Behrens was born in Germany on June 30, 1824, and died at San Jose, California on March 6, 1898, at the age of 74 years. He was considered one of the best early collectors in California, acquiring specimens of all orders but describing few species himself. The Lepidoptera he collected were described by many moth specialists as well as W. H. Edwards. His large personal collection was given to the Museum of Lubeck, Germany, a few years before his death (Essig, 1972). Among the California Lepidoptera named for him is *Argynnis behrensi* Edwards, now called *Speyeria zerene behrensi* (W. H. Edwards).

Herbert Knowles Morrison (1854-1885)

Morrison was a notable insect collector who was born at Boston, Massachusetts on January 24, 1854, and died at a very young age on June 15, 1885. He published principally during the years 1873 through 1875, and chiefly in the *Proceedings of the Boston Society of Natural History*. He made a number of important trips through the western states as well as in the southeastern U.S. In 1874, he collected insects in Colorado, in 1878 in Nevada, Utah and the Black Hills of what was to be South Dakota, in 1879 in Washington territory, and in 1880 in Arizona and southern California in 1882. He returned to Arizona and New Mexico in 1883 and then went back to the Southeast where he died in the spring of 1885 at Key West, Florida, from an attack of dysentery. He was said to be an exceptionally capable professional collector, with great physical strength and stamina. Mann (1885) comments that Morrison would frequently walk forty miles a day in pursuit of insects, and then would take care of them that evening while capturing moths that were attracted to his light. He supplied specimens of principally Lepidoptera for systematicists in both America and Europe. He also personally named a number of species from the western region. Species of Lepidoptera were named for him by Henry Edwards, W. H. Edwards, H. Druce, A. R. Grote, and C. V. Riley. Among the California butterflies, *Anthocharis cethura morrisonni* was named after him by William Henry Edwards, and may still be found today in the San Joaquin Valley (Anonymous, 1885; Essig, 1972; Mann, 1885).

Edward Palmer (1831-?)

Dr. Edward Palmer was born in England on January 12, 1831 (though at various times he gave the date of his birth as late as 1837!), and he arrived in the United States in 1849. He studied homeopathic medicine and also started a career as a botanical collector. When the Civil War broke out, he joined the army in Denver, Colorado, and served as a surgeon in the army at various posts in the Southwest. In 1865, he was posted to Fort Whipple in Arizona and began collecting insects for the Smithsonian Institution and for private collectors. He left the army sometime around 1868 and became a professional field naturalist, often employed by the Department of Agriculture to explore for plants in the Southwest and in Mexico (Brown, 1967). The types of metalmark butterfly, *Apodemia palmerii* (Edwards), were collected on a trip in 1870 through Utah and Nevada, including a visit to the mouth of the Colorado River south of the boundary of California and Arizona in Mexico. In the mid-1870's, he collected in southern California, including the San Diego area. He made a major trip in 1877 into southern Utah and adjacent northwestern Arizona, collecting insects in earnest for the museum at Harvard University. The Lepidoptera collected on that trip came to Samuel H. Scudder at Harvard, including four new species: *Neominois dionysus*, *Anthocharis thoosa*, and *Pholisora libya*, all described by Scudder in 1878, and an unnamed species of *Erynnis*. While no species collected by Dr. Palmer in southern California were named as new species, the ones he collected outside of our state such as *Apodemia palmeri* and *Anthocharis sara thoosa* and *Pholisora libya* reach our territory. In fact, the type locality of *Pholisora libya* and possibly of *Apodemia palmeri* is thought to be Littlefield (the modern name of Beaver Dam, Palmer's locality name), Mohave County, Arizona, about 38 miles southwest of St. George via U.S. Highway 91 in desert country (Brown, 1967).

Samuel Hubbard Scudder (1837-1911)

Born in Boston, Massachusetts on April 13, 1837, Scudder has been regarded as one of the greatest systematic entomologists in American biology. Until he died at Cambridge, Massachusetts on May 17, 1911, he pursued three lines of fundamental work: insect paleontology, systematics of Orthoptera, and systematics and morphology of Lepidoptera. He attended both Williams College and Harvard for his B.S. degree (received in 1866) and had already become an assistant to the great zoologist Louis Agassiz at Harvard some two years prior to his degree, in 1864. In 1879 he became Assistant Librarian of Harvard University and continued in that post until 1882. He was the founder and early editor of the journal *Psyche*, and President of the Boston Society of Natural History from 1882 to 1887. In 1886 through 1892, he was paleontologist for the U. S. Geological Survey and in that position laid the foundation for the study of fossil insects and became the greatest American authority on insect paleontology (Essig, 1972). He described 838 Tertiary insects from the fossil deposits of North America, largely from Florissant in central Colorado. He also named 80 species of beetles from Pleistocene deposits of Canada and Massachusetts as well as nearly 200 species of Paleozoic insects. In 1871, he published the *Index to the Known Fossil Insects of the World* in a 744-page issue of the *U.S. Geological Survey Bulletin*.

His reputation for his work on Lepidoptera began in 1889 when he published the great three-volume work entitled *The Butterflies of the Eastern United States* and followed this treatise with several minor papers on butterflies over the next four years. In all, he published 791 scientific papers while pursuing his three distinct lines of work simultaneously. His output was so prodigious and influential on the growth of American entomology that, although he never personally visited the West, his name is as familiar to every entomologist in the West as it is throughout the entire country (Essig, 1972). He named a number of western butterflies, including *Pieris napi marginalis* (Scudder), *Anthocharis sara thoosa* (Scudder), *Hesperia juba* (Scudder), *Erynnis icelus* (Scudder and Burgess), *E. propertius* (Scudder and Burgess), *E. funeralis* (Scudder and Burgess), *Thorybes mexicana nevada* (Scudder), and *Hesperopsis libya* (Scudder), which occur in California.

Tyrone Reakirt (1844-?)

Tyrone Reakirt was very much a mystery person to most biographically inclined entomologists. The short sketch of his life by Essig (1972) is declared to be complete erroneous by Brown (1964), who made an exhaustive search for letters from Reakirt in order to learn more about the man.

Reakirt was born in Philadelphia, Pennsylvania on April 21, 1844. He went into partnership eventually with his father and brother Daniel in the importing and wholesale drug business. He started a new venture in Delaware in 1868, where he manufactured white lead and, later, lead acetate. He became a member of the Entomological Society of Philadelphia in 1863, at which time he was 19 years old, and he had apparently some financial substance at that time. He

subsequently became well-known as a student of the butterflies of the American tropics and of the Indo-Australian region. He also published the first summary of our knowledge of the butterflies of the Rocky Mountain region in 1866, based on the collections brought back from Colorado by James Ridings in 1864 as well as two earlier collections made by William Wood and Winslow J. Howard that were in the Society of Philadelphia's collection. Interestingly, W. H. Edwards considered Reakirt to be the North American Rhopalocerist most competent to handle the very large collection of butterflies sent to the Smithsonian Institution from Colombia (Brown, 1964). Reakirt's collection ultimately was combined with Strecker's and was deposited in the Field Museum in Chicago.

Reakirt apparently did very little, if any, field collecting and instead purchased his specimens from Lorquin and others. In November 1868, for example, he wrote to Strecker and told him that he was expecting a shipment of 1,000 specimens of butterflies from the Philippines, Molucca and California. During the period of 1866-1868, Reakirt employed Strecker to mount much of the material that he was receiving, and in the summer of 1868 he turned his collection over to Strecker in order to sell it to raise additional funds. The original price was set at \$1,800 and Strecker held the collection for some months under agreement to sell it for Reakirt. Reakirt eventually offered the collection to Strecker but, though Strecker agreed to purchase the collection for \$1,446, he made none of the stimulated payments. Reakirt got into serious financial trouble and his company was forced into bankruptcy, so he fled the country early in 1871 to Lima, Peru. Strecker received 11 letters from the exile during the next year and then nothing further is known about the rest of his life. His name is commemorated in the butterflies he named and that were named after him such as *Papilio indra indra* Reakirt, *Pontia occidentalis* (Reakirt), *Lycaena mariposa* (Reakirt), *Leptotes marina* (Reakirt), *Oarisma garita*, and a patronym, *Anthocharis sara* form "reakirti," the early spring form of our common Californian orange-tip.

James John Rivers (1824-1913)

Rivers was born in England on January 6, 1824, and died in Santa Monica, California on December 16, 1913. During his nearly 90 years of life, he personally knew Charles Darwin, Alfred R. Wallace, Thomas H. Huxley, and other naturalists then active in the Entomological Society of London during their college days. In about 1867, he came to the United States, moving from Kansas to Colorado to finally California sometime between 1875 and 1880. He joined the early group of naturalists associated with the California Academy of Sciences, including H. H. Behr and James Behrens, and served as curator of Organic Natural History in the University of California until 1895, when he moved to southern California to live until his death. While he collected very widely in diverse groups of animals, he was interested in Lepidoptera, particularly the genera *Euphydryas* and *Melitaea* (Essig, 1972).

In California and the other Pacific states, John Adams Comstock was the most famous lepidopterist of the first half of the twentieth century. His life has been recounted by many authors (e.g., Emmel and Emmel, 1973, 1989; Martin, 1971, 1972; Van Doren, 1983), from which the following highlights are taken. During his 87 years, he published more than 200 scientific papers on the life history and taxonomy of western Lepidoptera and published the outstanding seminal work on California butterflies, *Butterflies of California*, in 1927. His early field work throughout California and his extensive correspondence and cooperative endeavors with other outstanding lepidopterists in the United States and around the world richly earned him the title of "Dean" of the California lepidopterists. His 1927 book has stood for more than half a century as the preeminent authority on the biology and ecology of the California butterfly fauna. It is only in the 1980's that several new works have begun to appear and to amplify the outstanding foundations laid by Dr. Comstock in his pioneering book.

It is appropriate to open this account of the life of a great lepidopterist by going back 68 years to Comstock's (1920) preliminary published announcement of his project to prepare a book on the butterflies of California, with the color illustrations to be executed in the outstanding "three-color copper-plate process." The plates for this work were prepared in Los Angeles under the direction of Mr. Raymond Thorpe and at the time they represented "the highest expression of this form of reproductive art. Through their use it will be possible to identify any specimen captured in the state at a glance." Comstock had this announcement and these color plates published with related papers on various butterfly genera in advance of the book in the quarterly issues of the *Bulletin of the Southern California Academy of Sciences* over the subsequent half-dozen years, in order to "stimulate the study of this most fascinating branch of the natural sciences, and bring new recruits into the Academy's 'Outdoor Army.'" But his closing paragraph in his 1920 announcement conveys perhaps better than any other words why his outstanding 1927 book made the marvellous California butterfly fauna have such lasting interest to lepidopterists:

"California is unusually favored as an environment for this study. Within its confines are found nearly two hundred and fifty distinct species of butterflies, not counting the many interesting varieties, local races, and aberrations. The diversity of our cultivated flora gives a footing for many introduced species. Our isolated mountain ranges have developed extremely local forms. In a word, California has compressed in its confines the elements of an entomological empire -- a veritable 'happy hunting ground' for the butterfly enthusiast."

The Comstock family traced their ancestry back to William Comstock, who emigrated to Massachusetts from England in 1635. John Adams Comstock himself was born on January 30, 1883, in Evanston, Illinois. He was one of seven children in a wealthy family. His father, John Adams Comstock, Sr., had been born October 2, 1845, in Franklin, Oakland County, Michigan. His mother was Cornelia Hurd who was the daughter of Judge Harvey B. Hurd, one of the founders of Northwestern University and an eminent scholar and jurist. This maternal grandfather, Judge Hurd, lived with the family for some years and contributed toward making the Comstock home an intellectual and cultural center which resulted in even greater benefit to the young Comstock than his early formal education.

Young Comstock was fully trained in the fine arts of natural sciences by individual tutors coming to his home during high school and college. He also took classes at the Chicago Art

Institute and the Laflin and Field Museums of Chicago. He once said of these early influences, "It was the wish of our family that I should follow art as a vocation, but my tastes were more inclined toward natural history. My insect collection was begun at the age of twelve."

In 1901, John Comstock and his brother Hurd traveled to Lake Josephine and Avon Park, in south central Florida, to collect butterflies. Some of these specimens are still in the collection of the Natural History Museum of Los Angeles County. The following year, in 1902, he and his brother and a Professor Snyder went to Hall Valley in Colorado to collect mountain species. This locality had first been made famous by David Bruce's collecting for Henry Edwards, some thirty years earlier.

By the age of 15, John Comstock was Secretary of the Chicago Entomological Society and became its Recorder at age 19. In 1904, at the age of 21, he became an architectural designer for Myron Hunt in Chicago. During the summers he taught nature study in Lake Geneva, Wisconsin. In the fall of 1905, Comstock moved to East Aurora, New York, with the intention of improving his natural ability as a designer and writer. For the next several years, he joined the Roycroft Arts and Crafts Community. This commune had been founded just prior to the turn of the century by Elbert Hubbard, and the community was based on the teachings and philosophy of John Ruskin and William Morris in England. During this time, he conducted nature study classes and introduced nature-inspired designs into the Roycroft work. He improved on his furniture and bookplate designing as well as bookbinding and illustrations, and also delved into metalwork and jewelry design along with other creative work. The Roycroft Press was a key part of this community and Comstock learned much about book design, bookbinding, illustration, and bookplate design at that time. In his subsequent two books on butterflies and the Comstock genealogy, the influence of this experience in New York is quite apparent. He married Carolyn Townsend in 1905 and they had three children: John Sterling, Jean, and Bette. The family moved to Santa Rosa, California, late in 1906, and by 1908 he and his sister had established the Craft-Camarata arts and crafts shop. He also worked for Luther Burbank as a designer for Burbank's nursery publications. By 1910, he opened another Craft-Camarata shop at Santa Barbara, California. In the summer of 1912, he taught at the Carmel Summer School of Arts and Crafts.

In the fall of 1911, he started medical college in Los Angeles, enrolling in a four-year course at the College of Osteopathic Physicians and Surgeons in Los Angeles. In 1915 he passed the State Boards and was licensed to practice medicine and surgery in California. Here he met and married his second wife, Carolyn, who was also a doctor. Later, Comstock's D.O. degree was changed to an M.D. This license was kept up during the rest of his life, and he practiced medicine to earn sufficient income for the pursuit of his other interests.

His interest in natural science and especially entomology never waived during these years of medical study. He collected whenever time permitted, and especially continued his interest and studies of West Coast Lepidoptera. In the early years of the Southwest Museum, which was placed on a hill overlooking the current Pasadena Freeway in the Highland Park portion of Los Angeles, he became Honorary Curator of Entomology. In 1920, he became the Southwest Museum's Associate Director and then its Director from 1921 to 1926. Comstock simultaneously helped to build the Southwest Museum during years of severe financial trouble, enhance its collections, and establish firm public support for the Museum. In 1926, the natural history sections of the

Southwest Museum, including the Lepidoptera collection built by John Adams Comstock, were transferred to the Natural History Museum of Los Angeles County in Exposition Park.

In 1917 Comstock helped found and was elected the first president of the Lorquin Entomological Club. The first meetings of this club were held at the Los Angeles Public Library, but by late fall of 1919 the meetings were held in the tower of the Southwest Museum. In January of 1927, the Lorquin Club moved from the Southwest Museum to the Natural History Museum of Los Angeles County where it became known as the Lorquin Entomological Society and is still one of the largest and most active amateur-professional regional societies in the United States.

Dr. Comstock served as Secretary, Director, and Editor of the California Academy of Sciences during the 1920's, and also taught anatomy and entomology at Occidental College during this period. When he moved to the Los Angeles County Museum of Natural History, he continued his outstanding work on behalf of the development of science in southern California and built the Los Angeles County Museum of Natural History and its associated Southern California Academy of Sciences, including the *Bulletin of the Southern California Academy of Sciences*, to internationally acclaimed stature.

By 1919, the Royal Entomological Society of London had elected Dr. Comstock as a Fellow. He continued his camping trips throughout the West to collect Lepidoptera and went as far as Yellowstone, Jackson Hole in Wyoming, and Bryce Canyon in Utah. In 1926, he returned to private medical practice in the Edwards-Wiley Building at 6th and Grand in downtown Los Angeles. His medical skill was combined with outstanding social interaction towards his patients and he was an extremely popular and outstanding physician. All during those years, his office shelves were full of rearing cages for Lepidoptera.

On April 14, 1927, his early field work in southern California and his extensive cooperative endeavors with other outstanding lepidopterists around the world culminated with the personally-financed publication of his major book, *Butterflies of California*. Illustrated with 63 exceptionally clear and precise color plates made from original Riker mounts of specimens, the book immediately became the classic and authoritative reference on the butterfly fauna of the state. His twenty years of work on California Lepidoptera had resulted in a landmark publication, copies of which today bring a price in the hundreds of dollars on the rare-book market.

In the following decades, his attention turned to working out greater and greater numbers of life histories of California species of both butterflies and moths. In collaboration with Commander Charles M. Dammers, a retired British naval officer and self-taught artist living in Riverside, California, scores of detailed and beautifully illustrated life history descriptions were published in the *Bulletin of the Southern California Academy of Sciences*. The invaluable permanent records of Comstock's life history studies, in the form of watercolor paintings and pen-and-ink drawings as well as notes, are now deposited at the Natural History Museum of Los Angeles County, along with those of Commander Dammers.

The year after publication of his book, Comstock was made Acting Director of the Los Angeles County Museum of History, Science, and Art, as it was known then. After serving as Acting Director for most of 1928, that fall he was made permanent Assistant Director of the Los

Angeles County Museum of History, Science, and Art. He then served as Director of Science from 1939 to 1942, at which time his title was changed to Chief Curator of the Science Division. He was renowned for his leadership and organizational skills as both Director and Curator of the Natural History Museum, but he always had time for young naturalists who came to the Museum and he greatly influenced several generations of future entomologists. He also served as President of the Southern California Academy of Sciences during 1926-1927, and continued as editor of the *Bulletin* from his election in 1921 until 1962. In 1929 he was elected Fellow of the Academy. The scope and international prestige of the *Bulletin* and the Academy are in large part due to the many years of his close association and hard work for the Museum.

After his retirement from the Museum in November of 1948, he was given the position of Curator Emeritus of Entomology. He continued to be associated with the Museum very closely and was appointed Research Associate in Entomology until his death in 1970. In 1928 he had married Ruth Gard, who remained his close companion for the rest of his life. Simultaneous with retirement from the Natural History Museum in 1948, the Comstocks moved to Del Mar, California. There, he was exceptionally active in civic affairs, and in 1952 served as President of the Del Mar Civic Association. He worked very hard to preserve important California natural areas, particularly in the fight to preserve the remaining coastal Torrey Pine stands in a natural state. He served as president of the Torrey Pines Association from 1955 to 1962. The Comstocks had started their visits to Del Mar in the 1930's and bought their Del Mar property at that time -- several acres on Crest Road, where he built a cabin partway down the chaparral-covered canyon. This would subsequently become his "bug room" and guest house, below their main house which was built in 1948 when they first retired. A visit to their home was a memorable event for those fortunate enough to be invited there, including two of the present authors (T.C.E. and J.F.E.) when they were high-school students. American Indian artifacts and jade cicadas (Chinese tongue amulets), numerous pet cats wandering throughout the immaculate main house, and home-built furniture designed by the doctor himself made it a fascinating experience, and his gracious wife would serve an incredibly delicious, hot formal luncheon in their dining room, treating even the shyest student visitor like a greatly honored guest. Here he continued his scientific contributions by studying the life histories of both moths and butterflies, and publishing resultant papers, right up until the time of his death.

Comstock also helped the San Diego Museum of Natural History in a great many ways during his years of residence at Del Mar. He was elected as President of the Fellows of the San Diego Society of Natural History for 1958, and served as a member of the Board of Directors of the San Diego Museum from 1957 to 1970, when he had to resign because of age and poor health. The Board refused to accept his resignation and instead voted him the unique status of Member Emeritus. The San Diego Museum had also designated him Honorary Curator of Entomology at that Museum in 1969.

The international Lepidopterists' Society elected Comstock as President in 1962, in recognition of his tremendous accomplishments and many professional collaborations in research on the life and cycles of butterflies and moths. In 1968, he was voted an Honorary Life Member of that society, an honor accorded to only ten or fewer living lepidopterists at any one time.

Comstock's legendary collecting trips throughout California were almost innumerable. From 1932 to 1964, he also made many trips to Arizona, collecting tremendous numbers of moths and butterflies which were deposited in the entomological collections of the Natural History Museum of Los Angeles County. Many of these served as voucher specimens for his life history studies in the field in Arizona and for publications illustrating the early stages of many Lepidoptera not previously described. He organized the Channel Islands Survey off the coast of California from 1939 to 1942. He made several extended field trips to southern Mexico and American Samoa which resulted in major scientific publications on the life histories of tropical butterflies. In the spring of 1957, John and Ruth Comstock went to Puerto Vallarta, Mexico, where they spent four months from June to October collecting Lepidoptera. Many of the life-history research findings were published in collaboration with Dr. Leonila Vasquez in Mexican journals. Their stay in American Samoa during the six months of May to October 1961 was facilitated by an invitation to stay in the country home of the former governor. The life history studies resulting from this expedition were published by the Bishop Museum of Hawaii. It is hard to believe that he carried out his trips to Puerto Vallarta in Mexico when he was 74 years of age; yet his research there resulted in notes on *sixty* life histories and *seventy-one* colored illustrations of life histories. He was almost 80 when he spent six months in the tropics of American Samoa, and at 84 he was greatly disappointed at having to cancel a collecting trip to New Guinea because of a heart condition.

Comstock's great contributions to entomology, in the form of more than 200 papers in many scientific journals, were only part of his legacy in laying the foundations of our knowledge of California and other western butterflies. He helped many young entomologists, especially another great southern California lepidopterist, Lloyd M. Martin, and scores of others, who found him to be an outstanding inspiration to initiate their own serious scientific work in the field of Lepidoptera. To quote Lloyd Martin, "His honors, positions, accomplishments, talents, personality, and affection for his fellow man will long be remembered by those who were fortunate to know him. His talents in art, science, medicine, and genealogy, and his qualities for leadership, have been widely recognized." In the words of Robert F. Heilborn, President of the Board of the San Diego Society of Natural History, "He was wise, gentle, always kind. His life touched ours and we were enriched" (Martin, 1972).

Thus the affection and esteem of the several generations of California lepidopterists who were fortunate enough to personally meet or know Dr. Comstock during his long and productive lifetime are perhaps the finest legacy that this great scientist has left behind. A detailed reading of the original edition of *Butterflies of California* (1927), or its re-issued edition with an introduction by two of the present authors (Emmel and Emmel, 1989) will enable the modern reader to gain perhaps some appreciation of the great labor of love and the great scientific erudition possessed by this pioneering lepidopterist of the American West, John Adams Comstock.

Equipped with Comstock's BUTTERFLIES OF CALIFORNIA book, generations of resident and visiting lepidopterists have found that California is indeed a paradise for butterflies. Even more today than six decades ago, despite countless environmental changes wrought by mankind in many areas and thousands of lepidopterists and naturalists actively pursuing research on butterflies and other wildlife here, California remains a state whose Lepidoptera fauna offers

endless possibilities for a lifetime of study and enjoyment -- one as rich and rewarding as that life exemplified by John Adams Comstock's ceaseless activity and permanent contributions.

Lorquin Entomological Society

The predecessor to the Lorquin Entomological Society, the Lorquin Natural History Club, was started in June 1913 and the first meeting was held that August, when nine schoolboys and one adult met at the first regular meeting of the Lorquin Natural History Club (Anonymous, 1916).

Southwest Museum

In July 1914, the Southwest Museum opened in Los Angeles on a 17-acre site at Marmion Way and Avenue 46, with a frontage of 200 feet. The initial cost of the building was \$165,000 and the first appropriation for collections was \$250,000. It was built in a concrete Hispano-American style, commanding a view of 60 miles across to the Sierra Madre Mountains. The 125-foot high caracol tower (42 feet on a side) had a spiral staircase inside with ten floors of room. The entomological department was placed on the top floor, with Fordyce Grinnell, Jr., as Curator. The new museum was supported by an Entomological Club, the Biological Section of the Southern California Academy of Sciences, and to organizations of young naturalists, the Lorquin Natural History Club and the Rivers Natural History Club. The last two organizations were primarily supported by younger lepidopterists, and all cooperated in building up a local collection of insects at the new museum (Anonymous, 1914).

San Diego Natural History Museum

In 1924, when San Diego was a small town on the coast, several naturalists who had been meeting informally at each other's homes decided to found the original San Diego Natural History Society. Among this group was O. M. Sanford, a coleopterist, who became the first Curator at the San Diego Natural History Museum building which was obtained as one of the buildings erected for the Panama-California Exposition in 1915-1916 in Balboa Park. This institution was a private museum and although it received some city funds, it was largely dependent on public donations until 1920, when the Scripps family of San Diego left a substantial foundation. The second curator at the museum was Mr. George Field, a lepidopterist, and he was succeeded by W. S. Wright, a specialist in Geometridae. The entomological activities of the San Diego Museum began in earnest in 1923, when it acquired by donation the Wright Collection of Insects. By 1929, there were approximately 50,000 specimens of butterflies and moths in the mounted collection, including practically all the Lepidoptera from San Diego County (Gunder, 1929a).

Charles Montague Dammers (1878-1956)

Commander Charles M. Dammers was a close associate for many years of John Adams Comstock, with whom he published numerous papers dealing with the life histories of Lepidoptera.

Most of these were illustrated by Dammers' own drawings, executed with great skill and fidelity. He was born in Dorset, England on May 3, 1878. He joined the Royal Navy at the age of 12 years and served on the *H.M.S. Britannia*. He eventually became an authority on mine-sweeping and attained the rank of Commander. After retirement from the Navy, Dammers had even more colorful and active career which led him into many corners of the globe. He took up ranching in Argentina where his properties embraced 27 square miles including one of the highest mountain peaks in South America. There he grew oranges, raised cattle, and hunted wildlife, as well as played polo for recreation. When World War II began, he entered the Royal Navy again and served through the conflict, earning several major awards for valor. Following the war, he and his wife, Ethel Dammers, came to the United States and eventually settled in Riverside, California.

The couple was interested in many avocations, including raising geraniums and violets, but Charles Dammers' special interest was the study of Lepidoptera. He corresponded and exchanged widely with specialists, and a number of butterflies and moths and other insects were named for him. His original paintings and drawings were presented by him to the Los Angeles County Museum of Natural History, where they are preserved to this date. Many of his outstanding renderings of life histories of southern California butterflies were published as text illustrations in Emmel and Emmel (1973). Most of these had been published earlier in the pages of the *Bulletin of the Southern California Academy of Sciences*, but because Dammers' extremely active association with John Adams Comstock developed after Comstock's 1927 publication of *BUTTERFLIES OF CALIFORNIA*, these exceptional life-history illustrations are lacking in the Comstock book (Comstock, 1957).

William Greenwood Wright (1830-1912)

Wright is believed to have been born in about 1830 in Newark, New Jersey, and he died in San Bernardino, California on December 1, 1912, at the approximate age of 83. After several years of education, he was a soldier in the Civil War and emigrated to California soon after the close of the war. Initially, he lived in Los Angeles and then moved to San Bernardino in 1873, where he operated a planing mill until about 1897. His only child had died in infancy and his wife died soon after his retirement. His later years were then entirely devoted to the study of butterflies and moths. When he first began, he was acquainted with William H. Edwards, Henry Edwards, Samuel Scudder, Herman Strecker, H. H. Behr, R. H. Stretch and other lepidopterists of note, but in his later years he worked almost entirely alone (Essig, 1972). He published many papers and sent a great number of eggs to William H. Edwards during the preparation of the latter's work, *The Butterflies of North America*. The most significant publication by Wright was his book, *The Butterflies of the West Coast of the United States*, which was published in San Francisco, California, by The Whitaker and Ray Company in 1905. As stated in the preface to the Second Edition, which was published in 1906 and sold exclusively by the author, "The items going to make up this book *The Butterflies of the West Coast*, including color plates, stereotype plates, and material in the printers' and binders' hands, and the finished goods in the hands of the original publishers, all was destroyed" in the great fire in San Francisco following the earthquake of April 18, 1906. The Second Edition is a facsimile of the First, with the same typeface, identical color plates, same paper and binding, but with the addition of a one-page preface and some modification

of the title page (Tilden, 1975). Wright's particular innovation in this book was the use of color photography in preparation of his plates.

Wright's library and collection of 6,000-7,000 specimens was turned over to the California Academy of Sciences after his death. The original specimens on which the text and illustrations of Wright's book were based are housed in a separate section of the entomological collections at the California Academy and were reviewed by Tilden (1975).

While Wright named a considerable number of new species, most of those published in his book have proven to be merely races or varieties of other species. The one species of butterfly that has remained unreduced in stature is *Strymon avalona* Wright, named from Santa Catalina Island. *Cercyonis pegala stephensi* Wright is still a recognized race in northeastern California. Several butterflies were named after Wright, including *Euphydryas wrighti* (Edwards) and *Melitaea wrighti* Edwards. Wright discovered many other interesting insects in the desert areas of southern California, especially the extraordinary California Palm borer beetle, *Dimapate wrightii*. *Dimapate* was coined from two Greek words meaning "clever deception," probably in reference to Wright's wily tactics of keeping the secret of where he had found his specimens for over eleven years (Jaeger, 1956). Many of his entomological friends tried to follow him into the desert, but since he was selling the beetles to leading museums for extraordinary prices (the first three pairs went for nearly \$1,000 a pair to the British Museum, the Russian Museum at St. Petersburg, and to a museum in Paris), Wright was anxious to keep his "desert gold mine" a secret. He followed the same practice in labeling his unusual southern California butterflies with incorrect or inadequate locality data.

Fordyce Grinnell, Jr. (1882-1943)

Grinnell was born at Pine Ridge Indian Agency in South Dakota on June 17, 1882. He was educated in the public schools of Pasadena, California, and at Stanford University. At an early age, he developed a keen interest in natural history, particularly entomology, and had a natural talent for organizing his friends into study groups. In 1913, he founded the Lorquin Natural History Club in Los Angeles which was the precursor of the Lorquin Entomological Society, today a thriving association of amateur and professional entomologists associated with the Natural History Museum of Los Angeles County. Fordyce Grinnell published many papers on the Lepidoptera and discovered and described 14 of California butterflies as new, including *Anthocharis lanceolata australis*, *Cercyonis behrii*, *Vanessa atalanta edwardsi*, *Vanessa carye intermedia*, *Vanessa carye letcheri*, *Strymon sylvinus desertorum*, *Everes comyntas herrii*, *Plebeius saepiolus hilda*, *Plebeius acmon cottlei*, *Plebeius emigdionis*, *Glaucopsyche lygdamus australis*, *Erynnis persius pernigra*, *Erynnis callidus*, and *Polites sabuleti tecumseh*. Some of those names have been reduced to "form" status or to synonymy.

In addition to his work in southern California, Grinnell lived and traveled in the Hawaiian Islands, the Philippines, Australia, and even Alaska (Comstock, 1943). Grinnell carried on a substantial correspondence with Dr. Henry Skinner in Philadelphia, Pennsylvania, during 1905 to 1916, including many comments on collecting sites, new species and other forms that he had

discovered, etc. Skinner apparently sent him many references and data on various names (Gordon F. Pratt, in litt.).

Jean Daniel Gunder (1888-1948)

J. D. Gunder was born in New York City in 1888, but moved to Pasadena, California, over 25 years prior to his death on November 17, 1948. He was keenly interested in butterflies of western North America, particularly California, and he described some 212 species, races, forms, and aberrations in a series of papers in the leading entomological journals of America. He is most well-known for his outstanding systematic work on checkerspot butterflies, as published in his paper "The Genus *Euphydryas* of Boreal America" in 1929. With extraordinary insight and taxonomic acuity, he managed to reduce the rampant systematic confusion in that genus, with its tremendous geographic variation, into just seven species. He used genitalic structures in this paper to such an extent that it has become one of the landmark papers that has shaped our modern classification and concept of butterfly species, as L. P. Gray (1970) has stated. Gray (1970) also emphasizes that Gunder was doing equally brilliant work with the genus *Argynnis* (now called *Speyeria*), although this work was not finished before his active interest in butterflies was dropped in 1935, when economic conditions forced him to give up his collection and enter a new business (Martin, 1948).

In 1937 Gunder sold his collection of about 28,000 specimens to the American Museum of Natural History in New York, while his outstanding entomological library was acquired by Cyril F. dos Passos. In the latter years of his work, Gunder concentrated on his principal interest of aberrations and "transition forms," a fascination which unfortunately led to his disparagement by certain eastern lepidopterists who dismissed Gunder as a wild amateur (e.g., Gunder, 1927). It is particularly unfortunate that his pioneering systematic revisions of *Euphydryas* and his incipient revision of *Speyeria* were overlooked for some time as a result of that attitude. During Gunder's career, at least six butterflies and two moths were named in his honor by leading entomologists.

John F. Garth (1909-)

For more than 45 years, John S. Garth has been a principal researcher and important contributor on the butterfly fauna of western North America. His books, monographs and scientific papers on the butterflies of California and of our major western national parks are familiar to all American lepidopterists. In 1986, he co-authored a major new work entitled *California Butterflies*, published by the University of California Press, which stimulated additional wide public interest in our butterfly fauna and which encouraged many new students to take up the study of California butterflies. For these and many other accomplishments in lepidopterology, Garth was honored by the Pacific Coast Section of the Lepidopterists Society with the John Adams Comstock Award in 1987.

John Shrader Garth is that rarity of citizen: a native Californian. He was born in Los Angeles, California, on October 3, 1909, and graduated from Long Beach Polytechnic High School in 1927. He began his first butterfly collection at the age of nine, collecting in Bixby Park. His

early interest in southern California Lepidoptera was fostered by contact at the Los Angeles County Museum of Natural History with John Adams Comstock and Lloyd M. Martin, who soon became life-long friends. He was also to meet many others of the early southern Californian lepidopterists through the monthly meetings and field trips of the very active Lorquin Entomological Society.

Following high school, John Garth entered the University of Southern California where he was to take his next three degrees: a Bachelor of Music degree in 1932, a M.S. degree in 1935, and a Ph.D. in Zoology in 1941. He also married Isla L. Detter on June 25, 1940, to whom he is still happily married and who is a frequent participant with John at the Pacific Slope Section meetings each year. Mixed in these academic years of study at U.S.C. were summer sessions at the Yosemite Field School (1933), Cornell University (1937), and the University of Pennsylvania (1940). The multifaceted foundations to Garth's lifelong series of accomplishments and expertise in a diversity of fields -- from music to entomology to crab systematics and biogeography -- were laid during these key years. In fact, it was Garth's outstanding ability in music that gave him his first great opportunity for travel and field research in the tropics.

In 1931, when Garth was a senior at U.S.C. and an instructor at the Long Beach Institute of Fine Arts, he was recommended by the Dean of the U.S.C. College of Music to go with Captain Allan Hancock of Los Angeles on a scientific expedition to the eastern Pacific. Garth was studying piano, and his interest in butterflies was enough to satisfy Hancock who was looking for someone with a background in the natural sciences to play in his shipboard ensemble during the trip. By just such serendipity, events drew John Garth to his life's work and forged his lifelong association with Captain Hancock, a great philanthropist, musician, real estate developer, mariner, aviator, scientist, industrialist, farmer and founder of what became the United California Bank.

Thus in the middle of the Great Depression, Garth left school at the age of 21 to embark on this three-month-long, 12,000-mile voyage with Hancock and his group of research scientists from major universities. The boat was the **Valero III**, a 195-foot motor cruiser which Hancock had outfitted for the first scientific expedition under his auspices. They sailed for the Galapagos Islands off the coast of western South America to study marine life and ocean currents, with some terrestrial field work on the insects as John's planned assignment. Hancock played the cello, and as part of this patron's expedition program, the musical ensemble played classical music each evening after the day's work. This initial voyage started the Hancock Pacific Expeditions, which were conducted annually from 1931 to 1941 aboard the **Valero III**. John's career as a marine biologist started with the first voyage and he assumed increasing shipboard responsibilities with each successive voyage.

In 1940, the Allan Hancock Foundation was established on the University of Southern California campus to serve as a repository for marine collections gathered from Mexico, Central and South America, and the Galapagos Islands, and Garth served successively as Research Associate, Curator of Crustacea (including other arthropods), Associate Professor of Biology, Professor of Biological Sciences, and Chief Curator of all the collections until his formal retirement in 1975. He continued as actively as ever thereafter as Professor Emeritus at U.S.C. He published more than 50 scientific papers and monographs in entomology and crustacean biology, and is widely recognized as a pre-eminent world authority on crab taxonomy, distribution and

ecology. In the course of his academic career, he guided more than 40 graduate students towards advanced degrees, and is known as the key scientist who produced a whole generation of Ph.D.-level carcinologists.

Through the Hancock Pacific Expeditions, John Garth was exposed very early to the riches of the tropics and their bewildering diversity of Lepidoptera and other organisms. He participated in expeditions to the Galapagos Islands in 1931-32, 1933, 1934, 1935, and 1938. He visited mainland Ecuador in 1934, Peru in 1935 and 1938, and the Caribbean islands of Aruba and Curacao (Dutch), Trinidad and Tobago (then British), and Colombia and Venezuela in 1939. Additionally, he visited Mexico, the Marshall Islands, India, Ceylon, and the Maldives from the 1940's to the 1960's. He also travelled to many European museums, Australia, New Zealand, Singapore, Malaysia, Thailand, Hong Kong, and Japan during the course of his scientific researches. With all this field work in exotic places, Garth's first love of Lepidoptera was always centered in the western United States. But it was not easy to immediately start professional work on western Lepidoptera in those days, and though John published several important papers in the early 1930's on Yosemite National Park butterflies and the geographical race concept in Lepidoptera, he looked for additional entomological background in his usual thorough manner.

While John Garth majored in zoology at U.S.C., with a strong emphasis on marine invertebrates, his early interest in entomology had to be carried on as a minor. Unable to obtain graduate-level work in entomology at U.S.C. in the 1930's (entomology was represented on his Ph.D. committee at U.S.C. by John Adams Comstock from the Los Angeles County Museum across the street), Garth sought summer course work in the East, first at Cornell (1937) and later at Pennsylvania (1940). He also met E. O. Essig, a famous western entomologist, as a member of the Yosemite School of Field Natural History in 1933. During the Second World War, John was assigned to the Army Air Corps, where he served as lieutenant/captain at Boca Raton Army Air Base in Florida, with responsibility for mosquito control. Access to a military reconnaissance car allowed him to collect Lepidoptera extensively in Broward and Dade counties, although gasoline rationing permitted only two private collection trips (to Marco Island on the Florida west coast, and to Marathon in the Florida Keys). He also renewed his acquaintance with J. Harold Mattheson in Miami, who showed John many of his choice collecting localities. Earlier during the Hancock cruises, Garth had occasion to visit Barro Colorado Island in Gatun Lake, Canal Zone, where he met many influential scientists of note from the American Museum of Natural History such as Frank M. Chapman (ornithologist and author of well-known books on the tropics), Frank E. Lutz (eastern entomologist and author of *The Insect Book*), James Schwartz (hymenopterist), and Irving Huntington (lepidopterist). Thus, while Garth was "on his own" as entomologist with the Hancock cruises, and at that time had had no formal work in entomology, these contacts with professional entomologists at Barro Colorado (and with medical entomologists at Grogas Memorial Hospital in Balboa) proved helpful in answering questions that arose concerning tropical insects and entomology in general. Some of his first rain-forest collecting was done along the trails of Barro Colorado Island, and it was here that Garth collected his first iridescent blue *Morpho amathonte*.

In the summer of 1933, Garth attended the Yosemite School of Field Natural History with 19 other participants, and his instructors included notable scientists from Stanford, Berkeley, and the National Park Service, including Dr. Harold C. Bryant, co-founder of the school and at that time assistant director of the National Park Service. The School included a high-country trip across

the Sierra Nevada and the first scientific survey of a remote area along Yosemite Creek. Garth's lepidopterological discoveries during this summer were published over the next several years in the *Bulletin* of the Southern California Academy of Sciences.

In the summer of 1935, Garth was appointed seasonal ranger-naturalist in Glacier National Park, Montana. Stationed at the former St. Mary's Lodge on upper St. Mary's Lake, his duties included morning and afternoon nature walks, evening boat trips on the lake, and an evening nature talk each night at St. Mary's Lodge. This pace continued unabated seven days a week for six weeks straight before he was given a week off! He promptly used this time to drive to Great Falls, where Dr. C. C. Albright showed Garth his splendid collection of butterflies and took him to a number of his favorite collecting localities. Among these was King's Hill, where they collected *Argynnis* (now *Speyeria*) *albrighti* at the type locality. Late that season, Garth returned to Glacier Park and obtained many late-flying species of butterflies. An unforgettable memory as the Garths left Glacier Park after Labor Day was of swarms of *Nymphalis j-album* alighting in every sunny patch along the highway near Lake McDonald. Following World War II, Garth was able to return to Glacier Park for vacations in 1949, 1950, and 1954. A Park Service ski cabin was made available, making it possible to explore vast areas of the park inaccessible to tourists, including the remote northwestern lakes, Bowman and Kintla. In 1970 and 1974, the Garths were joined for field work at Glacier by Jens W. Knudsen. John's greatest thrill came that last year when Knudsen and Garth hiked from Lower St. Mary's Lake to the summit of Cathedral Peaks, where they found *Oeneis melissa* flying among mountain goats within two feet of the edge of a mile-high precipice. An illustrated booklet on the butterflies of Glacier National Park was projected, but N.P.S. administrative support waned at the time. Today, these unique collections from Glacier National Park are still to be found at the Allan Hancock Foundation, with representative series from early years in the Nature Workshop at West Glacier, Montana. One hopes that these fascinating surveys of the distribution and ecology of the butterfly fauna of Glacier National Park will be published by John Garth in another venue; his thorough research in the back country there would provide a unique historical perspective by which to judge future faunal changes.

In the middle of the years of his Glacier work, John Garth turned his attention to Arizona and the butterfly fauna of Grand Canyon National Park. His field work began in the Park on the Powell Plateau in 1946, and was strongly supported by his old friend Harold C. Bryant, now Superintendent of Grand Canyon National Park, as well as Louis Schellbach III, chief naturalist. A well-illustrated book entitled *Butterflies of Grand Canyon National Park* was published in 1950 and is still in print. It combines a scientifically detailed approach with a popular writing style that engages the interest of amateur naturalist and professional scientist alike.

John Garth's latest contribution, *California Butterflies*, was published in late 1986 with J. W. Tilden. It was an outgrowth of their joint monographic work on the Yosemite butterfly fauna in 1962, and Tilden's 1965 booklet on the butterflies of the San Francisco Bay region. The two authors were under contract separately to the University of California Press for popular works on the northern and southern California butterfly faunas at the time (1973) that Thomas C. Emmel and John Emmel published *The Butterflies of Southern California* with the Natural History Museum of Los Angeles County. The U. C. Press proposed to Garth and Tilden that they combine forces on a new single book as Guide No. 51 in the California Natural History Guides series. The book illustrates most of the 235 species recorded in the state by Garth and Tilden, usually with one

northern California subspecies and one from southern California. Twenty full-color plates by David Mooney add to the impact of the text of this excellent introduction to the California butterfly fauna, a book that includes much novel information on the history of butterfly collecting in California that only someone of John Garth's great scholarship and meticulously accurate nature could gather.

John S. Garth has had a truly remarkable career, one that has spanned the period from the fabled early lepidopterists of California such as John Adams Comstock himself to the present-day young students who are themselves contributing so much each year to our knowledge of the western Lepidoptera. A man who intensively studied Lepidoptera before most of those reading this book were born, who travelled the West in model-T Fords and rickety metal trailers before the days of Interstate highways, 4-wheel-drive, and fancy motels, and who continues to publish his findings and encourage younger workers today, John S. Garth has made an important and lasting impact on the study of western Lepidoptera.

Robert Grant Wind (1912-1975)

Robert Wind was one of the most active promoters of the study of Lepidoptera on the West Coast. He was born in San Francisco on June 17, 1912, and died in Guatemala on July 4, 1975. He was raised in the community of Berkeley and attended the University of California at Berkeley from 1930 to 1933. As a nature counselor of the Boy Scouts of America Camp Wolfeboro in the Sierra Nevada of Stanislaus County in the summer of 1933, he strongly influenced Thomas W. Davies and William A. Hammer to start butterfly collecting. These men subsequently became leading lepidopterists in central California.

Also in 1933, Wind began a new business, Pacific Coast Biological Company, for sales of all types of biological supplies. He included lists of insect specimens for sale from around the world. In 1938, a year after marrying Clo Mifflin, he sold his business in order to finance and organize his "Papuan-Australian Expedition." Accompanied by his wife, Wind collected from 1938 to 1940 throughout New Guinea, the former Dutch East Indies, and Australia, reportedly returning with a quarter-million specimens of insects. His health was affected by these tropical travels and on his return, he spent some time recovering from tuberculosis and then started a mail-order philatelic business from the sanatorium. He purchased a house in Livermore and continued his philatelic as well as entomological sales, the latter primarily from his extensive Wind Expedition materials. Wind collected frequently throughout Contra Costa County, twice at Strawberry Lake at Pinecrest where the new *Melitaea leanira daviesi* Wind was collected, and at Sonora Pass.

During the period of 1945-1947, Wind actively published on the Indo-Australian Lycaenidae (papers co-authored with Harry K. Clench), as well as on the North American Satyridae and Nymphalidae. Eighteen species and subspecies were described in five papers. From 1950 to 1955, Wind opened and operated the Butterfly Tree Park Museum and Gift Shop in Pacific Grove, associated with a motel and a grove of Monterey Pine where overwintering Monarchs usually stayed. In 1953, the Winds established a business on Fisherman's Wharf in Monterey. Here they sold natural history materials, particularly shells and butterflies. A large warehouse had

to be rented on Cannery Row in Monterey to have room for all the stocks and this led to the establishment of Bob Wind's Butterfly Shop, with floor space of over 20,000 square feet. Insect specimens from all over the world were in stock here. In 1955, the Winds opened another gift shop called the Trade Winds, also located on the wharf at Monterey.

Wind became very well-known nationally because of his promotion of butterflies and insect collecting, and even received awards for his outstanding product developments aiding the growth and welfare of the hobby industry (because of his butterfly-collecting and mounting kits, which started many a youngster in the field of entomology). In May 1959, Wind joined a partnership to open "The Outrigger" restaurant located at 700 Cannery Row on the ocean end of the Old Monterey Cannery overhanging the waters of Monterey Bay. The front end of this cannery was occupied by his wholesale and retail Butterfly Shop, while the restaurant was capable of seating 600 persons with dining on two levels overlooking the Bay. In October 1960, the Winds opened an even larger Tradewinds Gift Shop in the Carmel Plaza area. Financial difficulties in the restaurant business led to a gradual sale of the gift shops and in 1965, Wind moved to Mexico. There, he renewed his activities based on his own collecting of butterflies and insects, particularly in Jalisco and later in the state of Chiapas. In 1975, he was moving from Chiapas to collect in Guatemala when he died on July 4.

Butterfly specimens that Robert Wind collected personally were handled through his wholesale and retail business, and today they are found throughout the world in private and institutional collections. Some 9,600 insect specimens from the tropics were deposited in the California Academy of Sciences collection before his death. Then in 1986, his collection of western North American butterflies, assembled in the 1930's and 1940's, and numbering 3,841 pinned specimens and including many types of the species and subspecies he named, was transferred to the California Academy.

Taxa named after Robert G. Wind include *Incisalia fotis windi* Clench, *Euphydryas anicia windi* Gunder, and an aberration, *Plebejus pardalis windi* Gunder. A listing of the new taxa described by Wind is given in Arnaud and Davies (1976), but the only new taxon named from California was *Melitaea leanira daviesi* Wind, named as a new subspecies in 1947 from Strawberry Lake, Tuolumne County, California. The Wind Collection included eight specimens of the extinct *Speyeria adiaspe atossa* (Edwards) from the Tehachapi Mountains (Arnaud, 1977).

Francis Xavier Williams (1882-1967)

Williams was born in the small town of Martinez, near the northeastern end of San Francisco Bay, California on August 6, 1882. When Williams was about 5 years old, his family moved to San Francisco. He obtained an A.B. degree in 1903 after attending St. Ignathius College, but rather than entering the priesthood as his family hoped, he went to Stanford University where he studied zoology and graduated in 1908. Another future famous lepidopterist, Fordyce Grinnell, was also a student friend there at Stanford. Williams became enthusiastic over entomology by his contact with Dr. Edwin C. Van Dyke, at the California Academy of Sciences. However, Williams had started collecting butterflies at Martinez between the ages of 4 and 5 years, and began serious collecting and study even as a small boy. His father made insect boxes for Francis and he had an

attic room modified as a laboratory where the young scientist could house his collection and carry on his experiments. The family lived close to Lone Mountain in San Francisco and young Francis could also collect in the Presidio area as well. Thus his extensive collections of San Francisco insects were made at a time when there was much natural vegetation and open space in areas later covered by roads and buildings. Historically, his material is "the best sample of the now essentially extinct Lepidoptera fauna of the San Francisco sand dunes" (Powell, 1964). He published a notable paper on the butterflies of San Francisco in 1910, as well as other observations and notes at later times (see Arnaud, 1970, for a complete list of Williams' publications and the insect taxa described by him).

While still a student at Stanford, Williams joined the California Academy of Sciences Expedition to the Galapagos Islands in 1905-1906, on which he served as entomologist. He spent about a year in the archipelago and visited all of the important islands. His important publications on the Galapagos insect fauna remain classic works to this day, and his collection of Coleoptera there was the largest ever made in the Galapagos.

In 1910, when Williams published his article "The Butterflies of San Francisco, California" in *Entomological News*, he listed 43 species of butterflies that were known at that time to inhabit or to have inhabited the area, and he stated that perhaps not more than 30 species could still be found there in 1910. He also prophetically said, "Before a decade has passed away there will be little left of the insect fauna of our city, and therefore the importance and necessity of making local insect lists while the fauna is still extant and in an undiluted condition cannot be too much emphasized." His comments on the vegetation and conditions prevailing in San Francisco in 1910 are invaluable today and in striking contrast to what we now see in the area.

In 1913, Williams went to Harvard to obtain his D.Sc. (conferred in 1915) under Professor William Morton Wheeler, and he subsequently went to Hawaii to work on insect problems in the sugar cane plantations. During the next five years, he traveled to the Philippines in search of parasites and predators, and made extensive notes on the habits of the bees and wasps of the Hawaiian Islands. He continued economically oriented research throughout the tropics until 1948, when he retired and moved to Danville, California, near the base of Mt. Diablo and east of San Francisco Bay. Eventually, the Williams moved to La Mesa, near San Diego, California, where Williams became associated closely with the San Diego Museum of Natural History and continued his study of wasps. While Williams greatest fame is as a hymenopterist, he was an extremely broadly based researcher whose early writings on butterflies did much to record the passing scene in the San Francisco area of California (Zimmerman, 1969; Arnaud, 1970).

William Barnes

Barnes was born in Decatur, Illinois, on September 3, 1860, and died on May 1, 1930 at the age of 70. At this time, Dr. Barnes owned the largest and most important private collection of North American Lepidoptera. Residing in Decatur, Illinois, for most of his life, he was also one of the foremost surgeons in that state.

After graduation from Harvard University (1883) and Harvard Medical School (1886), and a post-graduate medical study period in Germany, Barnes returned to Illinois to begin his career as a surgeon and to carry on his avocational researches in North American Lepidoptera. In the course of this work, he assembled one of the outstanding world-class collections of American Lepidoptera. He hired the best possible curatorial staff, including J. H. McDunnough, F. H. Lindsey, and S. H. Benjamin, all trained entomologists of outstanding ability. His collection was housed in a separate building from his home, with fireproof construction, and oak cabinets containing some 1,200 drawers with over 2,000 additional Schmit boxes arranged on shelves along the wall. The type specimens, including the holotypes, paratypes, and the like, amounted to nearly 7,000 specimens. The entire collection numbered over a half million specimens. As far as California lepidopterology is concerned, Barnes' chief goal was to obtain some of the Boisduval types of California species. Secondly, he purchased California specimens from Ximena MacGlashan and E. J. Newcomer. He also published the copiously illustrated series of volumes, "Contributions to the Natural History of the North American Lepidoptera," which included the taxonomic research by Barnes and his collaborators and consisted of extensive descriptive and revisionary papers, including California material. The Barnes collection was purchased by the United States government through an act of Congress and was deposited in the U.S. National Museum in Washington in 1930 (Engelhardt, 1930; Schaus, Busck, and Heinrich, 1930).

William Nelson Burdick (1887-)

Burdick was born in Denver, Colorado in 1877, the son of a well-known physician. He graduated from the University of California with a degree in entomology which he pursued as an avocation throughout his life. He authored a number of scientific papers on North American butterflies and bequeathed his large collection of over 20,000 specimens to the University of Colorado Museum at Boulder (Anonymous, 1962).

Erich Carl Walter (1903-1990)

Christopher Henne (____-____)

Edwin Ray Hulbirt (1886-1965)

Born in Pennsylvania on April 9, 1886, Hulbirt died in Glendale, California, on March 12, 1965. After receiving his college degree in chemistry from Princeton University, he taught in Oregon and then Azusa, California, helping to organize the Citrus Junior College and serving as its first dean from 1915 to 1918. His chemical research led to his appointment as Chief Chemist for a company that eventually was absorbed by the American Cyanamid Company, in which he served as Chief Chemist from 1920 to 1941 and Administrative Assistant from 1941 to 1947, when he retired. He had a very strong avocational interest in entomology as well as mountain climbing. Between 1909 and 1923, he climbed many of the great peaks in the western United States, including (in California) Mt. Shasta, Mt. San Antonio (Mt. Baldy), Mt. San Jacinto, Mt. Hoffman, Mt. San Antonio, Mt. Whitney, and Mammoth Peak. He collected butterflies throughout the state of California and particularly specialized in the HesperIIDae and LycaenIDae. Two butterflies were named for him, *Hesperia comma hulberti* Lindsay (1939) and *Lycaena dorcas hulberti* Field (1936). His collection of 23,000 Lepidoptera was given to Citrus College in Azusa, California, in 1963 (Comstock, 1965).

After Hulbirt gave his worldwide collection of Lepidoptera to Citrus College in January 1963, the school, faced with a shortage of storage and exhibit space, transferred the entire collection in late 1972 to the Natural History Museum of Los Angeles County as a permanent loan. This collection then consisted of 19,340 specimens (Donahue, 1975).

Charles Henry Ingham (1904-1957)

Born in San Francisco, California, on May 26, 1904, Ingham developed an early interest in Lepidoptera. His family moved to the Los Angeles area in 1917. There, while still attending high school, Charles Ingham became associated with the Western Auto Supply Company in a part-time position, which led finally to a permanent position and later to executive capacity. During his 35 years of work for that firm, he devoted almost every weekend and most of his yearly vacations to field trips, resulting in the compilation of one of the finest private collections of butterflies on the Pacific Coast. He was particularly interested in variations within species, especially aberrations, and he bred many bizarre forms. One of his breeding projects included a series of experiments on *Euphydryas* in order to determine the effects of environment and genetics in creating these aberrant forms. Together with Christopher Henne, Ingham explored many of the more remote areas of the southern California deserts and the Sierra Nevada Range of central California. He described several taxa, including *Anthocharis sara gunderi* Ingham from Santa Catalina Island in 1933 (this was a nice friendly turn, as Jeane Gunder had named *Anthocharis sara inghami* Gunder from southern Arizona in 1932!).

The important part of the Ingham collection was purchased by Yale University after his death on August 15, 1957, including a magnificent series of aberrations of *Euphydryas*, aberrations and hybrids of other genera, and certain groups of research interest at Yale, including *Glaucopsyche xerces*, *Papilio*, *Colias*, *Anthocharis*, *Philotes*, and other genera (Henne, 1957; Remington, 1958).

Carl W. Kirkwood

Kirkwood amassed one of the largest private collections of North American geometrid moths in history, containing 1,220 species or 86% of the known fauna. His collection, which was donated to the Natural History Museum of Los Angeles County after his death, consisted of 33,720 specimens including a number of valuable butterfly records from the Santa Barbara and San Luis Obispo areas of California (Donahue, 1975).

Wilbur S. McAlpine

The bulk of the Wilbur S. McAlpine collection of Lepidoptera was given to the Smithsonian Institution in 1973. While the collection consisted of over 12,000 specimens and was rich in material from Michigan and Alaska, the most important part of the collection consisted of the metalmark genus *Calephelis*, which contained all described species of that genus together with the types of many new species and subspecies described by him. Types of species and subspecies in this genus that are found in California, however, went to either the Carnegie Museum (*Calephelis nemesis bajaensis*) or the Los Angeles County Museum (*Calephelis nemesis dammersi* and *C. n. californica*) (Clarke, 1973).

E. J. Newcomer (18__-19__)

Newcomer, while best known for his work on Washington butterflies in the Pacific Northwest, spent his student days in California at Stanford University, and his summers working at resorts at Lake Tahoe (Newcomer, 1963). He sent William Barnes butterflies from Lake Tahoe, and that famous North American lepidopterist, together with his wife, son, daughter, and his curator, J. H. McDunnough, came to visit the Deer Park area where Newcomer worked, situated in the next small valley south of the now-famous Squaw Valley. Barnes, of course, assembled one of the largest collections in the United States early in the present century. The E. J. Newcomer collection was divided by him between Washington State University and the Smithsonian Institution. The Smithsonian received nearly 3,000 specimens from the West and was particularly strong in the genus *Speyeria* (Clarke, 1973).

Charles Rudkin

Rudkin's chief activity in southern California ranged between 1930 and 1945 when he worked with Christopher Henne and Charles Ingham on joint field work throughout the desert region. He also collected in southeastern Arizona. The Charles Rudkin Collection of Lepidoptera together with Rudkin's field notebooks, was acquired by the Museum of Systematic Biology at the University of California, Irvine in 1974. The collection contained over 10,000 mounted specimens, primarily butterflies, and was housed in Riker Mount. Substantial material from southeastern Arizona was also included with the collection (Orsak, 1974). John Adams Comstock named *Papilio rudkini* after him.

Oscar E. ("Elton") Sette

Sette was one of the most active California butterfly collectors until his death in July 1972. He compiled exhaustively detailed notes on the locality or source of every specimen added to his collection, and cross-referenced the locality labels on the specimens with numbers referring to these notes. He was particularly interested in the Lycaenidae and Hesperidae, and collected in a number of foothill areas that have been destroyed or completely altered by human activities in subsequent years. The Sette collection was donated to the Natural History Museum of Los Angeles County after his death, and consisted of 22,476 butterflies (Donahue, 1975).

John L. Sperry (1894?-1954) and Grace ____ Sperry (18__-19__)

John Sperry was born in Rhode Island and graduated as a Civil Engineer from Brown University; Grace Sperry was born in ____, After 1925, the two naturalists, lived in Riverside, California. The Sperrys collected throughout the American Southwest, especially in the desert areas, and uncovered many interesting records for southern California and Arizona. Butterflies were a side interest, with John Sperry being an outstanding authority on the taxonomy of the Geometridae moths. His collection was deposited in the American Museum of Natural History in New York (Remington, 1954).

Munroe L. Walton

Walton had an absolutely enormous collection of North American land snails, but also had an impressive collection of Lepidoptera. Following his death in Glendale, California, at the age of 84 on July 18, 1974, his 10,472 specimens of Lepidoptera, consisting almost entirely of California material and containing virtually every species and subspecies of butterfly known from the state, was donated to the Natural History Museum of Los Angeles County. Of the 2,037 specimens of Nymphalidae, over a quarter (577) were *Euphydryas*. The 1,795 specimens of Lycaenidae included 73 specimens of the extinct Xerces Blue. Of the 10,472 specimens of Lepidoptera, 6,190 were butterflies (Donahue, 1975).

Bernard H. Weber (____-____)

Bernie Weber was an avid collector in southern California who carried on an extensive exchange program with other lepidopterists. His collection of 43,988 specimens, more than 90% of which were nearctic and which represented the majority of the presently recognized taxa of the region, was donated by his widow, Virginia Weber, to the Allyn Museum of Entomology in 1981 (Miller, 1983). Such rare California species as *Speyeria egleis tehachapina* J. A. Comstock and other California species were well represented.

Charles and Ximena McGlashan

Butterfly farms are becoming relatively common around the world today, from scores initiated on small to large scales in Europe to major recent enterprises in Japan, Australia, Malaysia, the Philippines, and several huge attractions in the United States. But Charles Fayett McGlashan and his daughter Ximena started such a farm in Truckee, California, at the turn of the century and made quite a success of it, reaping great national publicity at that time, long before these relatively late "newcomers."

Charles McGlashan was born in Wisconsin in 1847. After Charles' mother died two years later, his father eventually decided to gather up his family in 1851, load them into a covered wagon and head for California. Consequently, Charles grew up in the rugged mining and timber country of the Sierra Nevada and by 1872, he found himself a job as superintendent of the school system of Truckee, a Sierran town on the road between Sacramento and what was later to become Reno, Nevada. The Central Pacific Railroad had arrived just three years earlier and had helped to transform Truckee from a stopover on the great east-west emigrant wagon trail into a bustling terminus on the new transcontinental railroad run. McGlashan was an ambitious young man who tried his hand at many occupations, including teaching school, studying law, collecting butterflies and moths, making historical notes on regional lore, and serving as a local correspondent for the *Sacramento Daily Record-Union*. By 1875, he was not only a lawyer in Truckee, but also editor of the local newspaper, *The Truckee Republican*. He became famous across the United States in 1879, when he published his book, *History of the Donner Party*. This melodramatic and grisly account was based on actual interviews with the survivors of the Donner Party still living at that time. It told the true story of an emigrant party that started late in the summer to cross the Sierras. They were caught by a snowstorm near Truckee, and the survivors had to resort to cannibalism on the bodies of their friends and relatives to live until rescued.

In 1893, McGlashan built a museum containing collections of baskets made by local Indians, Donner Party relics that he had excavated, and butterflies and moths that he had collected in the local area. McGlashan had first learned how to collect and rear Lepidoptera from an English prospector named Oldfield who was an insect collector. Not long afterwards, he met Henry Edwards, an ardent entomologist who worked the mining-camp entertainment circuit as an actor. For the next dozen years, he shipped Edwards many of the moths that he was able to rear and he also corresponded with other prominent American entomologists of the day. Eventually, he was able to amass a collection of over 20,000 specimens, part of which survive today in the Nevada County Courthouse, in Nevada City, California, not far from Truckee.

In 1912, McGlashan and his seventh daughter, Ximena, hit upon the idea of building a butterfly farm. Two decades earlier in England, a young lepidopterist named Leonard W. Newman had started a successful butterfly farm in England, and it is possible that McGlashan had heard about this farm. The early twentieth century in America was an appropriate time to be starting new enterprises, and McGlashan's farm turned out to be a huge success. During that summer of 1912, Ximena was 18 years old and had just graduated from San Jose Normal School. McGlashan casually remarked to her that he thought she could earn more money catching butterflies than teaching school. He had received an offer from Dr. William Barnes, the wealthy midwestern collector, to purchase any Lepidoptera that he could collect and ship, but Charles was far too busy with his law practice to get involved. Ximena was quick to realize the possibilities of this offer

and within two weeks, after mastering the skills of collecting and rearing, she had shipped Barnes about 1,500 specimens for which he paid her \$75.

By the end of that first summer, Ximena had shipped over 10,000 specimens, being paid at a flat rate of five cents a specimen. This averaged out to about \$50 a week, which was certainly more money than she could have earned teaching school. After a local newspaper article was published on her activities, the Hearst newspaper chain picked up the story of her exotic and unusually profitable business. Soon, she was receiving hundreds of letters from people who wanted to imitate her success. Thus in September 1913, she and her father began publishing *The Butterfly Farmer: A Monthly Magazine for Amateur Entomologists*. This magazine was full of practical information, and consisted essentially of a comprehensive correspondence course in entomology. Suggestions of books to read, equipment needed for collecting (and how to make it or where to buy it), how to care for eggs, larvae, pupae, and adults, how to mount specimens, how to sugar for moths, etc., were all contained in the monthly issues. In September 1914, Ximena enrolled as a student of entomology at the University of California at Berkeley and transferred to Stanford a year later, where she got a degree in botany and entomology. Her success in business continued until World War I. Then, marriage to a professor of military science (who had to move to Fort Leavenworth, Kansas, to train enlisted men) intervened, and she never went back to farming butterflies. This summary of her life is drawn from Oppewall (1979), who interviewed Ximena McGlashan Howard at Berkeley for her definitive biography of this fascinating personality and her father.

Albert and Amy Carter

The next serious butterfly farmers in California had more similarities to present-day butterfly farms and parks, in that they opened their rearing facilities to the public and had a specially landscaped, hillside insect zoo where the public could roam at large for free every Sunday. Albert and Amy Carter began their butterfly farm as a get-rich-quick scheme in 1929, and called their enterprise "Butterfly Park." The first issue of their magazine, *Butterfly Park Nature Club News*, was sent out in March 1929, and it appeared monthly through October, when the great 1929 stockmarket crash began putting a dent in all business enterprises. The Carters' publication then became bimonthly, it became quarterly in 1931, and petered out sometime in early 1932. Their magazine contained essentially the same kind of information as Ximena McGlashan's *Butterfly Farmer*, and the Club managed to attract about 500 to 600 subscribers. The Carters used their reared butterflies to make into such objects as book ends, trays, and jewelry. These artistic creations were sold at the Butterfly Park, located in Roscoe, now called the "Shadow Hills" section of Sunland, in the northern end of the San Fernando Valley in southern California. Lloyd M. Martin, who was to become Associate Curator of Lepidoptera at the Natural History Museum of Los Angeles County, worked for the Carters for five years from 1930 to 1935, the last year being the date that the Park was closed down. Up to that time, however, as many as 100 visitors a Sunday came to wander freely in the 100-square-foot, specially landscaped, screened-in hillside insect zoo where, as the Carters said, "16,000 caterpillars are feeding on foodplants planted especially for them." Cascading waterfalls, inviting picnic tables and strolling peacocks offered touches which we see today, 60 years later, in some of the bigger butterfly parks in the United States and elsewhere in the world (Oppewall, 1979).

VI. THE MODERN AGE OF LEPIDOPTERA STUDY:

RECENT LEPIDOPTERISTS IN CALIFORNIA (1940-Present)

William Hovanitz (1915-1977)

Born in Chicago on November 6, 1915, William Hovanitz died on September 14, 1977. At the age of three, he moved with his family to the San Francisco Bay area of California where his interest in nature, especially butterflies, started. Even in high school while he was working as a delivery boy for a San Francisco drug store, he took time to collect specimens while making his deliveries around the city. These included various *Plebejus* blues that are now rare and threatened, and *Glaucopsyche xerces*, that is now extinct. He obtained his B.S. degree in entomology from the University of California, Berkeley, and in 1938 began advanced study immediately in the graduate program at the California Institute of Technology under Nobel-Laureate Thomas Hunt Morgan, where he received his Ph.D. in Genetics in 1943. Because Morgan died during his graduate work, Hovanitz finished under the eminent geneticist A. H. Sturtevant. Hovanitz spent the next three years (1942-1945) working for the National Research Council in South America, Michigan, and Florida. He then accepted academic appointments at the Laboratory of Vertebrate Zoology at the University of Michigan, Wayne University at Detroit, and finally the University of San Francisco. At the latter institution, he served as Associate Editor of the *Wasmann Journal of Biology*. While teaching summer sessions at the University of California at Santa Barbara in 1949, he met and married his wife, Barbara. In 1955, he returned to Cal Tech with some time spent at U.C.L.A., but finally settled into an academic position as Professor of Biology at the California State University in Los Angeles in 1956. He resigned from that faculty in 1975, and in early 1977, the Hovanitz's moved to Santa Barbara where they planned to build a home and allow Bill to devote his full energies to research. His untimely death cut those expectations short, particularly unfortunate because of the large body of unpublished material that Hovanitz had ready for analysis.

Hovanitz published 131 papers and other publications during his lifetime. Some of his most impressive and significant works were his 1943 paper on the variation on *Argynnis callippe* in California, and his 1940 paper explaining color variation of *Oeneis chryxus* in the Sierras, in particular the occurrence of the dark-colored subspecies *stanislaus* and the light-colored subspecies *ivallda* as related to the distribution of their alpine background substrates. One of his earliest papers, written as a sophomore in college, described the geographic variation in the lycaenid butterfly, *Plebejus icariodes* in terms of its relationship to a *Rassenkreis* ("circle of races"). He was perhaps most famous for his work on *Colias* butterflies, which included several classic papers such as his 1948 treatise demonstrating differences in diurnal activity of genetically different orange and white females with *Colias eurytheme* in the Imperial Valley of California (explained in terms of adaptation to diurnally cyclic environmental factors). He also looked at the influence of complex environmental selective forces in producing color variation in the female dimorphism of *Colias* species across the continent (Hovanitz, 1950). His classic studies on geographic variation in *Euphydryas chalcedona* (Hovanitz, 1943, 1952) revealed the tip of a scientific iceberg of incredible dimensions and complexity in this group, whose details are still being explored by dozens of lepidopterists and evolutionary biologists today. He also contributed very significantly to butterfly biogeography with the first comprehensive review of the

zoogeography of butterflies in the New World, published in 1958 by the American Association for the Advancement of Science. This major paper described the major features of latitudinal and altitudinal distribution of the families and major groups of butterflies in the Nearctic and the Neotropics.

One of Hovanitz's most enduring legacies, of course, was the establishment of the *Journal of Research on the Lepidoptera* in 1963. This effort was not without controversy, as it was viewed by some as competition with the existing *Journal of the Lepidopterists' Society*. But as Mattoni (1979) pointed out in his definitive biography of William Hovanitz, "a clear niche developed for both to the lasting benefit of all lepidopterists."

After 40 years of collecting and studying butterflies before his untimely death in 1977, Hovanitz had desposed of parts of his material to the California Academy of Sciences. The William Hovanitz material still in his family's possession at his death numbered almost 24,000 specimens, and this material was given to the Allyn Museum of Entomology (part of the Florida State Collection of Arthropods) in 1981 (Miller, 1983). Several years later, the more than 4,400 *Colias* and other Pieridae groups from the Nearctic and Palearctic were transferred to the California Academy of Sciences collection. In 1992, the Pacific Slope Section of the Lepidopterists' Society posthumously conferred upon William Hovanitz the John Adams Comstock Award in recognition of his manifold contributions to the study of California butterflies and Lepidoptera in general (Emmel, 1992).

Lloyd Milo Martin (1912-19xx)

Lloyd Milo Martin was born on a homestead near Bayard, Nebraska, on May 24, 1912. After the death of his father in a farm accident four years later, he was raised by his grandparents in Steele City, Nebraska. Trips back to the farm became his first collecting forays as he helped a cousin collect butterflies for her collection. In December 1921, Martin moved to Long Beach, California, with his grandparents, and his collecting activities increased. In his own words, "Many species of butterflies, so different from those of the farm in Nebraska, were caught in California; this was the beginning of a real interest in insects. It was my ambition to get a college degree and, some day, to work in a museum. The depression of the early 1930's put an end to plans for college. After graduation from high school in 1929, I worked for Hal Newcomb in South Pasadena, doing butterfly art work. This work went on for about a year. From May 1930 to October 1935, I worked at Butterfly Park, near Roscoe (now Sun Valley), for Albert Carter. [This commercial effort by Carter to build a showplace of butterflies ultimately failed.] During the summers of 1931 and 1932 I was in the field, collecting butterflies for Jeane D. Gunder of Pasadena. I made two trips to the Catalina Mts. of southern Arizona in the spring of 1931; later in the same year I collected at Pyramid Lake, Nev., in the Cascade Mts. of northern California, including Mt. Shasta. The summer of 1932 was spent in the field in southern California."

On February 19, 1936, Lloyd Martin started working for John Comstock at the Natural History Museum of Los Angeles County as a Student Assistant in Entomology. Like Comstock, he donated his personal collection to the Museum. In 1941 he was promoted to Assistant Preparator, then to Curatorial Assistant in 1943, and on July 1, 1944, to Assistant Curator of Entomology. In 1952 he was promoted again to Associate Curator, in charge of all Lepidoptera at the Museum (some 250,000 specimens at that time). He held this position until his retirement on July 31, 1969, at which time he was given the title of Curator Emeritus. He continued as a Research Associate of the Museum, operating from his home in Prescott, Arizona, where he avidly continued his researches on the moths of that fascinating state until his death on _____, 19__.

During his three decades at the Museum, Lloyd Martin carried out the usual curatorial duties of collecting, classifying, and preparing insects for the museum collection and for exhibition, as well as identifying insects for scientific government agencies and the general public. His greatest source of pleasure, though, was encouraging young collectors through the Lorquin Entomological Society meetings and field trips, and through answering thousands upon thousands of questions from them, especially every Saturday up on the "third floor" of the Museum at Exposition Park. Under Comstock and then Martin, the holdings of the Entomology Section of the museum greatly increased in size and diversity. Comstock and Martin were both active collectors and outgoing individuals who attracted the volunteer cooperation of many amateur collectors, old and young, in the Los Angeles area. This helped to accelerate the growth of the collection.

Lloyd Martin wrote a major paper on the butterfly fauna of the Huntington Lake region in California, published an annotated check list of North American Lepidoptera in the Natural History Museum of Los Angeles County, described several new butterflies including *Papilio indra fordii* Comstock & Martin and *Euchloe hyantis andrewsi* Martin, and wrote a widely-noted article for the general public, "Spectrum on Wings," for the *Arizona Highways* magazine (April 1951 issue),

describing the beauty of Lepidoptera found in the Southwest. He intensified his personal field work in Arizona together with Fred S. Truxal, and the museum rapidly accumulated an outstanding collection of butterflies, moths and other groups from the little-known insect fauna of that state. Martin recounted in an autobiographical sketch that, "My real interest was trying to find out how insects could survive in the semi-arid regions and deserts of the Southwest. I was fascinated by their adaptations to the environment, the changes of color patterns to blend in with the desert, the vast numbers of species of insects that are nocturnal in habit, and the comparatively few diurnals, due to the inclement conditions in which they live." His photographs and vivid descriptions of these studies at many national and regional meetings of the international Lepidopterists' Society, the Southern California Academy of Sciences, and the Lorquin Entomological Society, brought to thousands of budding naturalists and professional biologists the richness of the natural history of the American Southwest.

Despite all the preceding accomplishments, Lloyd Martin always maintained his strongest enthusiasms for helping beginning students of Lepidoptera. His finest legacies are the legions of southern California entomologists and biologists who have been profoundly influenced to go into serious amateur or professional work with Lepidoptera because of his dedicated example and constant encouragement.

Charles L. Remington

Charles L. Remington was one of the two co-founders of the Lepidopterists' Society in 1947 and has served in this Society and in the development of the science of lepidopterology in the United States for more than four decades. His researches in the biology of western Lepidoptera, particularly in Colorado, Texas, northern Mexico, and the Channel Islands of California, have made important contributions to our knowledge of the evolution, ecology, biogeography, and life histories of our western species. His editorship of the *Journal of the Lepidopterists' Society* during its formative years included not only remarkable expansion of its scientific and amateur scope, but also the careful nurturing of many of our western lepidopterist authors and researchers.

Charles Lee Remington was born in Reedville, Virginia, in 1922 and he grew up in St. Louis, Missouri. He pursued his undergraduate work at Principia College in Illinois, receiving his B.S. degree in 1943. He migrated eastward to Cambridge, Massachusetts, where he earned his Masters in 1947, and his Ph.D. at Harvard University in 1948. During those graduate school years at Harvard, he and Harry K. Clench, who knew each other by previous correspondence due to their mutual interests, got together and decided to promote the formation of a union or society of lepidopterists that would encourage the scientific study of Lepidoptera. This joint aim was to be accomplished through distributing a periodical on that insect order and through facilitating the exchange of specimens and ideas by both the professional worker and the interested amateur.

This effort formally started on March 24, 1947, with a letter to the wide circle of friends that each man had in the field. The dues were a modest \$1.00. Charles Remington was the first Treasurer in this founding year of the Lepidopterists' Society. The *Journal* began that year as an inexpensively mimeographed publication. It graduated to photolithography when revenue and membership grew enough to warrant the change. From there, it eclosed to regular printing. As Harry Clench has said in the Society's commemorative volume, Charlie Remington knew what he wanted and how to go about getting it. Lepidopterists, evidently, agreed with him. This Lepidopterists' Society, which he largely shaped, has grown and prospered to major size and influence in the field today. In the beginning, no meetings or elected officials were contemplated. By 1950, however, members realized that formal organization would be in the best interests of the growing group and on July 31, 1950, Charles Remington appointed an organization committee, naming Cyril F. dos Passos as chairman, with the charge to appoint temporary officers and develop the Constitution and By-Laws. The present form of the Society resulted from this committee's efforts, and the first annual meeting of the Society was held 29-30 December 1950 at the American Museum of Natural History. In September 1954, the first Pacific Slope Section Meeting of the Lepidopterists' Society was held in California at the Academy of Science in San Francisco. Pacific Slope Section annual meetings have been held each year since 1954 and occasionally these have been combined with the national meetings of the Society (1962 Santa Barbara, 1970 Carson City, 1974 Los Angeles, 1976 Boulder, 1982 Laramie, 1987 Berkeley, 1989 Albuquerque, 1991 Tucson, 1993 Fort Collins). Though an eastern member, Remington participated on the programs of the 1965, 1974, and 1988 Pacific Slope meetings, and attended others during the 1960s.

Publications of this Society were also heavily influenced by Charles Remington. The Society's first publication, which began in 1947, was known as *The Lepidopterists' News*. Under Remington's editorship, this organ evolved from an initial mimeographed format to a

photolithographed format and finally to a letter press format from Volume 6 onward. With Volume 13 in 1959, at Remington's urging, the name of the Society's major publication was changed to the *Journal of the Lepidopterists' Society*, and the Society initiated a second, more frequent and informal publication, *The News of the Lepidopterists' Society*, which was designed to include matters of more transient interest. Charles Remington served as Editor-in-Chief of the *Journal* and its predecessors from 1947 to 1963.

It is also of great interest to note that the first Annual Field Summary was begun at the same time by C. L. Remington and Harry K. Clench, founders of the Lepidopterists' Society. North America was divided into eight zones in their initial efforts, and by the time of the second annual (1948) summary, each had a corresponding "zone coordinator." Thus, from the very first year of the Society (1947), individual members were encouraged by Remington and his colleagues to contribute to the Summary and to keep careful field notes during each collecting season. In the first year, there were 59 contributors and this has increased to several hundred today. Charles Remington also started the Library of the Lepidopterists' Society, which today is housed at the Natural History Museum of Los Angeles County in California but was started at Yale University. This evolved from the publications being received by Remington in exchange for copies of *The Lepidopterists' News*. The Society Library contains complete or nearly complete sets of some forty periodicals devoted in whole or in part to entomology, and incomplete sets of many more. In addition, there are many reprints and a large collection of books which have been donated over the years by authors and members. From the beginning, the policy has been to make this material available on loan to members upon request.

In addition to his contributions of inestimable value to the founding and evolution of the Lepidopterists' Society, Charles Remington has had a remarkably diverse research career. The range of his specialties extend from evolutionary genetics to speciation theory and experimental and natural hybridization in animals and plants. He has delved into island biology and biogeography, mimicry, insect-plant coevolution, the systematics of Lepidoptera, paleoentomology, and even cytosystematics of insects. Collaborating with K. Maeki, he pioneered the study of chromosomes in the North American Rhopalocera, uncovering many fascinating cytotaxonomic situations, especially in the Megathymidae. In this latter family, he pursued profitable collaborations with Don B. and Viola Stallings, the Turners, and Hugh Avery Freeman throughout the southwestern United States and northern Mexico. His field research has taken him to Australia, Iceland, England, Norway, Italy, Mexico, Canada, the offshore islands of California, the Hawaiian Islands, the Marshall Islands, Nauru, Guadalcanal, the New Hebrides, New Caledonia, New Zealand, Fiji, Tonga, Moorea, Bora Bora, Tubuai, Layte, Hokkaido, Ecuador, the Galapagos Islands, Peru, Brazil, Chile, Venezuela, and 49 states in the U.S.A. He has collected Lepidoptera on all eight of the California Channel Islands, particularly on San Clemente Island in August 1968 and December 1981 and extensively on Santa Cruz Island in all the spring months except February and in July, August and October, between 1967 and 1974. He deployed his son Eric there for about three months in 1970, and many moth records from Santa Cruz in the California Insect Survey come from his efforts. Charles was one of the organizers of the 1978 Channel Islands Symposium at Santa Barbara and presented an overview of the insects in a plenary session paper. He likewise participated in the 1981 Entomological Society of America symposium on Channel Islands insects.

Despite his intensive research program and field travel, he found time to be an outstanding teacher at Yale University from the onset of his appointment there in 1949. He rose through the academic ranks to the highest position as Professor in the Department of Biology, Curator in Entomology of the Peabody Museum, and Professor of Forest Entomology and Museology in the School of Forestry and Environmental Studies.

Among his many academic honors, he was a Sheldon Traveling Fellow at Harvard University in 1947, a John Simon Guggenheim Fellow at Oxford University in 1958-59, was named an honorary Life Member of the Lepidopterists' Society in 1966, was named a Research Fellow in Entomology for C.S.I.R.O. in Australia in 1976, a Research Fellow in Ecology at Campinas University in Brazil in 1981, a Research Fellow in Entomology at the University of California, Berkeley, in 1981, and has been an invited lecturer at many national and international meetings. He has been Secretary (1955-59) and Trustee (1962-63) for the Rocky Mountain Biological Laboratory in Gothic, Colorado, where he has actively pursued field research for more than 20 summers, including work there with Dr. Gary Bernard of Yale on the color vision of butterflies. He has served on the advisory boards of the Connecticut Audubon Society, the IUCN, the Connecticut State Geological and Natural History Survey, and as Counselor of the Xerces Society. He was named Honorary Life Member of the Lepidopterists' Society in 1966.

Dr. Remington has contributed to the development of lepidopterology in California and the western United States not only through his publications and his participation in meetings and as a visiting research fellow at western institutions, but also through his personal encouragement of scores of western lepidopterists who today are highly active in the Society and in Lepidoptera research. His friends and colleagues have long stood in awe of the indefatigable energy, boundless interests, and incredible breadth of knowledge of this "Founding Father" of the Lepidopterists' Society, who has brought so much favorable worldwide attention, from sophisticated scientific research to greatly expanded amateur interest, to this fascinating group of insects (Emmel, 1988).

Paul R. Ehrlich

Dennis R. Murphy

John F. Emmel

Thomas C. Emmel

Sterling O. Mattoon

Richard Arnold

Jerry A. Powell

Fred T. Thorne

Fred Thorne of El Cajon, California, was born on June 25, 1909, in Casper, Wyoming. Educated at San Diego State College (1937-41), he was a life-long resident thereafter in San Diego County and published papers on some of that area's notable Lepidoptera species, such as the endemic *Lycaena hermes*. He also studied the life histories of many southern California butterflies, and was particularly interested in chaparral and desert faunas. *Mitoura thornei*, a hairstreak species on Otai Mountain in Eastern San Diego County, was named after Fred Thorne by John Brown.

Thomas Davies

Gregory R. Ballmer

Gordon R. Pratt

A. Oakley Shields

J. W. Tilden

James Wilson Tilden was born on December 31, 1904, at Philo, California. He obtained his A.B. degree at San Jose State College (1932), and his M.S. (1937) and Ph.D. degrees (1938) at Stanford University. He married Hazel Miller in 1933. He returned to San Jose State College to teach in the Department of Entomology, rising through the academic ranks to Professor. While broadly interested in insect systematics, he particularly focused on the butterflies and especially the family HesperIIDae in the western United States. He published more than 50 papers and several books on the western butterflies, including *Yosemite Butterflies* (1963) with John S. Garth, *Butterflies of the San Francisco Bay Region* (1965), and *A Field Guide to the Western Butterflies* (19__) with Arthur Smith. Several western butterflies have been named after Tilden, including *Hesperia tildeni* Freeman (1958) and *Philotes enoptes tildeni* Langston (1964).

Arthur M. Shapiro**Michael Singer****David Faulkner****John Brown**

Julian P. Donahue

George T. Austin

REGIONAL STUDIES OF CALIFORNIA BUTTERFLIES

In this section, we introduce the reader to previous surveys that have been done on the spatial and temporal distribution of species and subspecies of California butterflies. In some areas of our state, such as the cities of San Francisco and Los Angeles, radical changes in the course of extensive development have changed the distributions of these insects or even caused local extirpation or complete extinction. One of the great uses of these lists and studies from earlier dates is that we have documentation of the different habitats and their butterflies as they both existed at those times.

Publications on California butterflies and skippers began with studies in the San Francisco Bay area, as gold miners like Pierre Lorquin arrived and began sending specimens to Europe or having them described by local naturalists (Boisduval, 1852, 1858, 1869; Behr, 1862). The Bay Area butterflies were further reviewed by F. X. Williams (1910) and J. W. Tilden (1956), each author noting the passing of one or more species since the last published survey. J. W. Tilden (1965) wrote of butterfly fauna of the San Francisco Bay region in popular format, and Paul A. Opler and Robert L. Langston (1968) wrote a distributional analysis of the butterflies of Contra Costa County (Opler and Langston, 1968). Arthur M. Shapiro (1975c) published a regional fauna for the butterflies of Suisun Marsh. John Steiner (1990) wrote a very comprehensive summary of the Bay Area butterfly fauna with extensive documentation of the distribution and natural history of the San Francisco region's butterflies and skippers; he included detailed distribution maps and carefully graphed phenologies.

In southern California, Jean D. Gunder (1930) published the first general account of the butterflies of Los Angeles County. This was followed in 1973 by Thomas C. Emmel and John F. Emmel, with their comprehensive and liberally illustrated book, *The Butterflies of Southern California*. Larry J. Orsak (1978) published an excellent survey of the butterflies of Orange County, and Mattoni (1990) published an outstanding color-illustrated summary of the butterfly fauna of the greater Los Angeles area as it existed in that year.

Elsewhere in the state, the first published lists of the Sierra Nevadan butterfly fauna came early in the twentieth century. E. J. Newcomer (1910) reported on the butterflies of the Lake Tahoe region in a comprehensive listing. Fordyce Grinnell (1915) published his observations on the

butterflies of King River Canyon in the Sierra Nevada; his transect ran from Cedar Grove to Kearsarge Pass during July 20 to August 16, 1914, and included such diverse records as *Neophasia menapia*, *Habrodais grunus*, *Oeneis chryxus ivallda*, *Lycanea cupreus*, and *Colias behrii*. John S. Garth and J. W. Tilden (1963) did a thorough summary and ecological survey of the butterflies of the Yosemite sector of the Sierra Nevada range, while A. M. Shapiro (1975b) published an exhaustive survey of the ecology and host plants of the butterfly fauna of the Sacramento Valley. Further north from the Yosemite region in the Sierra Nevada, T. C. Emmel and J. F. Emmel (1962a, 1962b, 1963a) looked at the species composition and relative abundance of butterflies in the Donner Pass area. Kenneth Davenport (1983) published an excellent account of the geographic distribution and species of butterflies present in Kern County.

The Butterflies of the West Coast by William Greenwood Wright (1906) was the first book with major emphasis on California butterflies, but the text was primarily a list of taxa with sparse distributional data and no biological information. Reviews of the butterfly fauna of the whole state of California have been relatively few. The first other than Boisduval's listings of Lorquin's species was a state publication written for the general public by C. W. Woodworth (1900); it included two halftone plates of the more common species, line drawings of wing venation in all genera, and a listing of 353 species (many forms and many non-California taxa being counted in this list). John Adams Comstock (1927b) published the first and most comprehensive book on butterfly natural history for California, listing some 236 species and subspecies (477 species and varieties in total) and depicting the fauna in 63 excellent color plates. The appearance of this book did much to stimulate interest worldwide in the California fauna, and the author received richly deserved accolades for this seminal work. The next attempts to cover the whole state fauna were published 60 years later. Tilden and Smith (1986), in their *Field Guide to Western Butterflies* (Houghton-Mifflin, Boston), emphasized California species, as the bulk of their experience was with that fauna. Garth and Tilden (1986) concentrated entirely on the California fauna in their book entitled *California Butterflies* (University of California Press, Berkeley) and recognized 236 species as occurring within the state, giving brief information about most of the subspecies known to those authors. Color and black-and-white plates made from paintings executed by the noted artists David Mooney and Gene M. Christman illustrated most of the species. The field guide format, as in Smith and Tilden (1986), did not allow much space for depiction of life history, distribution, or exhaustive lists of foodplants, but essential information was usually included.

THE PRESENT WORK

This brings us to the present book. Conceived in 1974, it has been in gestation for over three decades as the three authors (John F. Emmel, Thomas C. Emmel, and Sterling O. Mattoon) personally combed the entire state for additional distributional records, described scores of newly discovered taxa, and reared and photographed life history stages for all species and subspecies within the state. The invaluable, indeed essential, collaboration and contributions of hundreds of lepidopterists, amateurs and professionals alike, added new data to every section of the book. In its writing and illustration, the three authors have circulated countless check lists and manuscript drafts, borrowed innumerable specimens for examination and illustration, and in general requested and received unstinting help from every museum and individual with substantial collections and

information on California butterflies. This is truly a collaborative and cooperative product. Its aim to present as complete a picture as possible of the California butterfly fauna at the close of the Twentieth Century: its biodiversity, present and past distribution, historical changes in population sizes, ecology, life history, host plants, chromosome numbers, and overall biology. Our success in reaching such a goal will be judged by you, the reader. Doubtless, much remains to be learned about the butterflies of California, and it is the hope of the authors that this book will encourage the present naturalists of the state and elsewhere to work for the preservation of the state's remaining wild areas so that future generations may enjoy what we can still see and study today.

Chapter 2

THE GEOLOGICAL LANDSCAPE OF CALIFORNIA

In this brief chapter, we shall look at the geological history of California and its influence on the vegetation and butterflies of the state. Our understanding of the diversity of the California flora, and the rich butterfly fauna, depends to a considerable extent on an appreciation of the geological forces at work and the timescale involved in creating the present-day physiographic appearance of California. Geology has directly influenced climate, which in turn has dramatically affected plant and butterfly communities in the state. The following discussion is summarized principally from the excellent essay by Daniel L. Axelrod in Munz and Keck (1963).

Early in the Cenozoic Era, which began approximately 63 million years ago, the vegetation across North America was composed of three geofloras. A *geoflora* is a major vegetation unit that has managed to maintain its essential identity through time and space. Throughout the southern half of the continent spread the broad-leaved evergreen *Neotropical-Tertiary Geoflora*. The northern half of the continent was occupied by the temperate *Arcto-Tertiary Geoflora*, composed of mixed deciduous hardwoods and conifers. Between these two geofloras, centered in the area of southwestern North America, the *Madro-Tertiary Geoflora* was making its initial appearance. Composed notably of the sclerophyllous ("hard-leaved") and microphyllous ("small-leaved") plants, the Madro-Tertiary Geoflora contained drought-adapted plants.

During the first several epochs of the Cenozoic Era, the Neotropical-Tertiary Geoflora migrated northward as far as southeastern Alaska on the coast and close to the Canadian border in the interior. Here it came into contact with the Arcto-Tertiary Geoflora which occupied the higher, cooler latitudes. Broad-leaved evergreens of tropical families, including figs and sabal palms, occurred throughout the area -- species that are now at least subtropical in characteristics and occur in regions where rainfall is 80 or more inches annually and where climate is uniformly warm throughout the year. Thus no desert flora yet existed in the Southwest, nor was there any high mountain range in the interior to foster an alpine flora. The distribution of this neotropical forest gradually was restricted towards the south and to the coasts as a cooler and drier climate predominated, and no plants in California today represent direct descendants of this humid subtropical forest. However, a number of California genera and species were derived from that secondarily, as Axelrod (*in* Munz and Keck, 1963) points out.

The western part of the Arcto-Tertiary Geoflora became adapted to a new climate, one typified by winter rain and summer drought. The major communities of this geoflora developed chiefly during the later Pliocene, when more diverse climates developed over the Southwest in response to important topographic changes: chiefly, the elevation of the Sierra Nevada, the Coast Ranges, and the Transverse and Peninsular Ranges.

All of these mountains are part of the great Western Cordilleras belt along the outer continental edge of North America (the Eastern Cordillera is the Rocky Mountain system, along the inner edge of the old North American continent). The Western Cordilleras began forming in the Jurassic Period (about 180 million years ago) of the Mesozoic and continued right on into the

Miocene (about 10 million years ago). At this time, the Sierra Nevadas and the Cascades were initially raised and folded from older Mesozoic conglomerates and coarse sands that had washed into the Pacific Ocean from the central continent area. Intense folding, uplift, and severe faulting followed, especially between 100 and 50 million years ago. Summits in the Sierras eventually reached close to 15,000 feet above sea level.

The Coast Ranges have a less pronounced, more rounded relief that is generally below 3,300 feet elevation, but some peaks rise above 6,000 feet or even up to 11,500 feet (3,506 meters) on Mt. San Geronio in the eastern Transverse Ranges. These young ranges arose in two phases. In the mid-Miocene (about 20 million years ago), earth movements thrust up the Early Cenozoic (60 million year old) layers of sediments that had been washed out along the continental shelf by erosion from the then-existing margin of the North American continent to the east. These upfolded layers were eroded subsequently almost to a plain, and were covered by new layers of younger sedimentary rocks washed down from the east. Then a second phase of mountain-building began in the Quaternary Period, possibly one million years ago, and has continued to the present as the central Coast Ranges and Transverse Ranges are still being built up, deformed, and eroded today.

All these vast mountain ranges along coastal and interior California altered the climate substantially, wringing much of the moisture from the prevailing westerly winds as the air masses flowed up and over the mountain ridges, cooling at the higher altitudes and consequently precipitating their water load previously picked up over the Pacific Ocean. Thus the orogenic (mountain-building) episodes in the vicinity of California initiated a widespread climatic change to cooler and drier conditions.

Van Devender (1977) presents evidence that the shift to non-pluvial climates in the Southwest occurred as recently as around 8,000 years ago. This involved a synchronous change from woodland to desert or grassland across the Chihuahuan, Sonoran, and Mojave deserts because of a shift to the north of the Aleutian low and the winter storm track, which resulted in drastically reduced winter precipitation in these areas. The existence of continental glaciers to the north had modified general circulation patterns and caused the Pluvial (wet) southwestern climates during the Pliocene and Pleistocene (2 million to 10,000 years ago). With a shift from glacial to non-glacial climates, the changes in pluvial climates would lag behind changes in glacial climates as long as the glaciers existed. The relatively xeric woodland found between 11,000 and 8,000 years ago in the Southwest may have occurred in such a lag period. Finally, when heavy winter precipitation diminished in the Southwest and post-pluvial conditions dried the playa lakes, the formation of desert and grassland communities followed.

Regardless of the exact time table, the new mountain ranges caused the Madro-Tertiary Geoflora, named for the Sierra Madre of northern Mexico where many of its relics now survive, to originate in southwestern North America. Here, small-leaved, drought-deciduous, sclerophyllous plants were apparently derived from the more humid tropical groups of the Neotropical-Tertiary Geoflora which were becoming adapted to the expanding dry climate. Some members of the Madro-Tertiary Geoflora, however, apparently are derived members of Arcto-Tertiary groups which also were developing in response to increasing aridity during the middle and later Tertiary times. Plant communities such as Oak-Conifer Woodland, Chaparral,

Thornscrub, Desert Grassland, and Sage, as well as part of the Desert flora, appeared from the middle Eocene through the following epochs.

By the middle Pleistocene, dry climates were rapidly expanding across the area, and Oak-Conifer Woodland and Chaparral vanished from the lowlands of the present central and southern desert regions, as well as from the forest of the northern portions. In the late Pliocene and Pleistocene (1 million years ago), the rapidly elevating Cascades, Sierra Nevada, and the Peninsular Ranges created a drier climate on their interior (rain shadow) sides, and a desert flora of remarkably drought-resistant plants came into existence. The new desert species had been derived principally from the geofloras that had dominated the area earlier in the Pliocene (2-1 million years ago). The higher and colder Great Basin Desert and northern Mojave Desert received floral components from the surviving Arcto-Tertiary Geoflora. The lower and hotter Sonoran and southern Mojave Deserts obtained species from the Madro-Tertiary Geoflora (Axelrod, *in* Munz and Keck, 1963).

The rainfall during this span of time changed from possibly 80 inches or more in the early Eocene, for much of the West, to about 12 to 25 inches during the Miocene, on the western border of the Mojave Desert. A flora new to this region developed as a result. Summer dryness throughout what is now California became important, and the sclerophyllous types of woody plants increased in number. This drought-resistant, small-leaved and deciduous flora stood in strong contrast to the plants typical of the early Tertiary floras. By the Pliocene, the forest and woodland had to move towards the coast or into the mountains, and the lower elevations of what is now desert became dominated by scrub and grassland. Desert species evolved from plants already present, the colder northern deserts getting some species from Arcto-Tertiary sources and the warmer southern deserts from Madro-Tertiary groups. In southern California, chaparral vegetation, adapted to the new Mediterranean climate of cool winters (with some precipitation) and long hot summers, dominated the lower mountain areas.

During the Pleistocene, the cool glaciation periods that left their marks on the California mountains allowed temperate vegetation to advance further southward than at any other period of the Cenozoic Period. The Redwood Forest moved as far south as Carpinteria and Santa Cruz Island, approximately 200 miles south of its present limits. Glaciation during this time not only produced a cooler climate, but probably a wetter climate. We can see support for this theory from the evidence that many lakes existed at that time. Additionally, older present lakes once had greater depths, and even the Mojave Desert shows evidence of many riverbeds that are no longer filled with water. Mono Lake, for example, had obtained a depth of nearly 900 feet during the Pleistocene Epoch. Owens Lake was 250 feet higher and overflowed into the basins of China and Searles lakes, and water from the Searles Basin overflowed into the Panamint Basin to form a lake 930 feet deep, which in turn apparently spilled southward into Death Valley, producing a lake 90 miles long and 600 feet deep!

Southward migrations of plants during such colder and wetter periods, with subsequent periodic northward migrations, undoubtedly had a great influence on both the evolution and distribution of our present vegetation and the butterflies associated with it. Much hybridization along the flowering plants would have occurred as species were brought into contact repeatedly after long periods of isolation. Movement of species would have occurred up and down the

mountains, as well as southward and northward. The persistence of over 300 species of Sierran plants in the pine belt of the southern California mountains can best be explained by the extensive southward migrations of plants during the glacial period (Munz and Keck, 1963). The lack of many widely distributed alpine plants in California, found as far south as Colorado or New Mexico in the Rocky Mountains but not in the Sierra Nevada, was probably a result of the historical influence of summer dryness in California. On the other hand, the evolution of high-altitude species from somewhat lower-elevation genera has been notable, with our alpine flora having many endemics.

Furthermore, and perhaps most significant for the student of butterflies, the whole region has been so broken up into separate mountain ranges and low-lying valleys that a *host* of ecological niches, often quite isolated from each other today, has been created. Such conditions cannot help but favor endemism and the development of many exceedingly local species and subspecies of both plants and insects. Thus California has a flora which is extremely rich in number of forms and has many very large genera. The existence of over 7,000 species of plants here, and nearly 300 species of butterflies with over 700 subspecies, has its roots in the geological history, often orogenically violent and climatically dramatic, that we have traced in this brief chapter. Both plants and animals in California have followed a diverse series of pathways in their evolution, but we can conclude with Munz and Keck (1963) that "all have undergone rather rapid and highly polymorphic differentiation."

Chapter 3

THE RELATION OF THE CALIFORNIA CLIMATE TO THE BUTTERFLY FAUNA

Because of the influence of its coastal position and mountain relief with a wide range of topography in California, the state incorporates several quite different climates, with marked differences occurring within a very few miles. Summer temperatures in the low-elevation southeastern latitude is not the chief determinant of temperature but rather the isotherms which tend to have a north-south trend in this state rather than the usual east-west trend, as they follow topographic contours of the coastal and Sierran mountains.

Most of the United States is marked by sharp differences between summer and winter climates. The midcontinent is flooded by a huge mass of frigid, dry Canadian air in winter, which then moves eastward, often with snow. Winter climate on the West Coast is quite different. A great mass of relatively warmer, moist air moves south from the Aleutian Islands of Alaska, occasionally reaching southern California, which receives nearly all its rain during the winter. This Pacific air brings mild temperatures along the entire coast, and the rain storms are separated by long periods of relatively warm, sunny weather in these winter months.

During the summer, the Pacific weather regime also differs from the humid, hot climate of the eastern states, with their frequent convectional and frontal summer thunderstorms. The moist Aleutian air masses retreat northwards, and are replaced by mild stable air from the cool subtropical Pacific. Virtually no rain falls on the Pacific coast in the summer, except in the mountains. In the intermontane desert areas, temperatures rise to scorching levels. The irregular topography of California shatters any general bioclimatic pattern into an intricate mosaic of small climatic regions that differ drastically according to elevation, exposure direction, and sharp variation in soils and vegetation cover. The following brief summary of California's complex climate is based principally on Sprague (1941).

The Effect of Temperature

Along the immediate coast, the climate is cool and without extreme fluctuation in temperature. This maritime-type climate occurs on the lower seaward slopes of the Outer Coast Ranges in the beach dunes of California, where mild winters and cool summers are the rule. The weather seldom includes freezing temperatures, nor does frost occur on the immediate coast. In fact, on sunny days in January and February, the south-facing slopes and protected sides of the dunes may get quite warm (Langston, 1974). Because of the relatively warm nights, the development of Lepidoptera and other insects can start quite early in most years.

On the other hand, in the summer the coastal slopes and dunes may receive long periods of cold winds and fogs, with the sun not shining for several days to several weeks in a row. During these cool periods, new adult butterflies do not emerge from their pupae and those already in the adult stage may remain quiescent, not carrying on their activities of nectaring,

inating, or ovipositing (Langston, 1974). When the weather becomes clear and sunny again for a short time, the adults resume their activities before the next siege of summer fog.

On the eastern slopes of the Coast Ranges and in the Central Valley occurs a continental climate, with a greater range in temperature. Summer temperatures may exceed 100° F, while winter temperatures will drop below freezing, with snow in northern counties of the Valley.

This Valley-localized continental climate gives way to the mountain climate in the Sierra Nevada and other ranges. Langston (1974) summarizes the Inner Coast Ranges and Sierra Nevada climate as being characterized by cold winters and hot summers, with high temperatures regularly reaching in the 90's (F). The flight season tends to be shorter in length, particularly at the higher elevations. Below-freezing temperatures and winter frost tend to be common in the Inner Coast Ranges, while heavy snows and several months of below-freezing temperatures are characteristic of the Sierra Nevada.

Thus the eastern and western slopes of the Coast Ranges and the Sierra Nevada as a whole rise to sufficiently high elevations for snow; in fact, freezing temperatures may occur in any month of the year. In areas near the coast, there may be 365 days that are frost-free each year, but above 6,000' in California, fewer than 100 frost-free days occur. In the spring, the days may warm up suddenly, even with night temperatures still remaining below freezing. When the days have warmed, it generally stays warm and gets progressively hotter as summer approaches. As a result, a rather synchronous and near total emergence of adults of a particular species will occur. With adequate temperatures occurring daily, the adults nectar, mate and oviposit in a short time frame. With adult activities concluded, the flight period is soon over in such species (Langston, 1974).

The Impact of Precipitation

The amount of precipitation in the state is strongly influenced by the distance from the ocean. It is also affected notably by the elevation, shape, and steepness of the mountain slopes, and their direction of orientation in relation to the moisture-bearing wind. The prevailing wind from the west moderates the climate throughout the state and increases precipitation. Most of the state is characterized by an annual wet season and dry season alternation, the wet season falling usually in the cooler months of the winter. In general, precipitation increases from south to the north, and is heavier on the southern and western slopes. The average annual precipitation throughout the state varies from less than 2 inches (50 mm) in Death Valley to over 109 inches in parts of Del Norte County in the northwest. However, some interior desert areas may see entire years pass without moisture, while a recording station in Del Norte County has received as much as 153.54 inches (3,900 mm) and the village of Honeydew, in the redwoods of Humboldt County, has received as much as 174 inches in a year. Mountain recording stations sometimes receive as much as 10 inches (254 mm) in 24 hours, particularly in southern California, with torrential floods ensuing. Snowfall may range from a trace or none near the southern coast to as much as 449 inches (11,405 mm) in the Sierra Nevada. However, great variability in annual precipitation is the rule in California and long drought periods may occur. Occasional wet years, like 1958, 1966, or 1973, may result in remarkably abundant vegetation, where virtually none

has appeared for years, and great numbers of butterflies, including a number of new records as butterflies fly north from Mexico or Arizona. Cold springs may delay the season as long as three or four weeks in the Sierra Nevada or even in relatively low elevation areas.

An important climatic factor for both vegetation and butterflies along the coast is fog. Summer fogs generally increase with latitude and altitude. Summer fogs are more frequent than in winter along the coast and on windward slopes. However, in winter, fog may be a very important moisture-delivering system for plants in interior areas as in the Central Valley.

HISTORICAL CLIMATES OF CALIFORNIA

The distribution of vegetation and butterflies in California has been anything but static in recent history. Dry periods alternating with wet periods were tied to the advance and withdrawal of the great Pleistocene glaciers during the 100,000 years. These vegetational changes have occurred down to relatively recent times. For example, by studying the fossil fecal material in coprolite deposits of the extinct ground sloth, *Nothrotherium shastense*, and of the remarkably ubiquitous wood-rat middens deposits, containing abundant well-preserved plant macrofossils, Wells and Berger (1967) showed that at the close of the Wisconsin glacial period, there was widespread expansion of the pinyon-juniper zone downward into areas that are presently desert. This paleobotanical record, conveniently kept by sloths and wood-rat middens in protected caves, show that xerophytic juniper-woodlands vegetation descended to an elevation of 1,100 meters around 9,000-10,000 years ago, which is some 600 meters below the present lower limit of woodland (1,700 meters) in the latitude of Frenchman Flat in the Mojave Desert. Desert or semi-desert shrubs co-existed with the woodland trees throughout much of the elevational span corresponding to this weather-lowering of the pinyon-juniper woodland. Joshua Trees, accompanied by desert shrubs, moved down as low as 600 meters at Gypsum Cave, Nevada.

These discoveries of macrofossil evidence for movements of the trees downward during wet periods in Californian history have important implications for butterfly distribution patterns. For example, they show that there was a former continuity of the many disjunct stands of vegetation in the Mojave Desert region, at least along the higher divides connecting most of the ranges. This suggests that some species, such as *Papilio indra* which today exists in highly isolated populations in the higher parts of the Mojave Desert, may have had a more continuous range as recently as 9,000 years ago. Subsequent isolation by the juniper-dominated woodland shifting upward on limestone mountains, as the climate of the area became historically drier, left small, separated populations behind of both larval foodplants and butterflies. In these butterfly colonies, genetic drift and founder effects could operate with relative ease to produce dramatic evolutionary changes in phenotype, resulting in such different subspecies as the narrow-banded *P. indra martini* and the wide-banded *P. i. fordi* being located in mountain ranges only twenty miles apart today.

Chapter 4

PLANT COMMUNITIES OF CALIFORNIA

The plant community concept is a somewhat artificial one because of the continual change in phases of any one community, depending upon which species is or are dominant. Other problems include the transitional ecotone areas between communities, etc. Phillip A. Munz (1959), in his book *A CALIFORNIA FLORA*, presented an excellent scheme, but other authors have identified different divisions, and in fact, there are probably an almost infinite variety of communities that could be defined in a state as geographically large and as topographically diverse as California. Because of its widespread adoption, utility, and ready recognition, the Munz scheme of plant communities has been adopted in the present book to identify the basic plant communities in which the butterflies of California are found.

In each of the following plant communities, we follow an outline of naming the plant community, then listing the dominant plants that characterize that community, the butterfly foodplants that are found in that community, and the characteristic butterflies that usually occur in that plant community. A brief discussion follows in each community section.

1. COASTAL DUNE SAND PLANT

DOMINANT OR CHARACTERISTIC PLANTS

Ammophila arenaria, *Bromus maritimus*, *Elymus* spp., *Poa douglasii*, *Juncus lesueurii* and *Carex pansa*; species of *Abronia*, *Carpobrotus*, *Mesembryanthemum*, and *Cakile*; *Calystegia soldanella*, *Eschscholzia californica* *maritima*, *Fragaria chiloensis*, *Ambrosia chamissonis*, *Artemisia pycnocephala*, *Atriplex leucophylla*, *Camissonia cheiranthifolia*, *Lathyrus littoralis*, and shrubby species of *Lupinus*.

BUTTERFLY FOODPLANTS

Castilleja mollis, *Corethrogyne filaginifolia*, *Eriogonum latifolium*, *E. parvifolium*, *Lotus scoparius* (prostrate ecotype), *Lupinus arboreus*, *L. chamissonis*, *Viola adunca*.

CHARACTERISTIC BUTTERFLIES

Thessalia leanira ssp. (Oso Flaco dunes), *Chlosyne gabbii*, *Speyeria zerene myrtleae*, *S. z.* near *hippolyta*, *Apodemia mormo virgulti* (El Segundo dunes ecotype), *A. mormo* ssp. (Marina dunes, Monterey Co.), *Callophrys dumetorum*, *C. perplexa perplexa*, *Glaucopsyche lygdamus* near *australis* (Marina dunes), *G. xerces*, *Euphilotes battoides allyni*, *E. enoptes* near *tildenii* (Marina dunes).

DISCUSSION

This plant community is confined to sandy beaches and sand dunes scattered along the coast of California. Annual precipitation ranges from moderate to heavy, mostly during the winter months, but considerable fog during the summer months tends to supplement this moisture. Temperature fluctuations tend to be minimal, both seasonally and diurnally. The growing season is 12 months long, and freezes are extremely rare or non-existent.

The butterfly inhabitants of this community tend to have long flight periods because of the mild temperatures and moderating influence of the ocean; most are spring or early summer flying (see Langston, 19).

Because of the extremely restricted geographic area of this particular plant community, most of the endemic butterfly subspecies inhabiting it are restricted in their distribution, and several have been declared endangered species as a result. In fact, one butterfly species and two subspecies within this plant community have become extinct as the result of human encroachment upon it: *Cercyonis sthenele sthenele*, *Glaucopsyche xerces*, and *Icaricia icarioides pheres*. Large areas of this habitat have been destroyed by urbanization and other human activities. In particular, the city of San Francisco has replaced an extremely extensive coastal dune habitat, and the western coastal area of greater Los Angeles has similarly destroyed over 95% of the once extremely extensive sand dune systems in that geographic area. Additionally, other extensive sand dune habitats, such as the Oso Flaco Sand Dunes in San Luis Obispo County and the Marina Dunes in Monterey County, have been extensively altered by such human activities as off-road vehicle activity, military reservations, sand-mining, and encroachment of exotic species of plants such as Ice Plant (*Mesembreanthum* species).

2. COASTAL SALT MARSH

DOMINANT OR CHARACTERISTIC PLANTS *Salicornia virginica*, *S. subterminalis*, *Suaeda californica* and var. *pubescens*, *Distichlis spicata*, *Spartina leiantha*, *Limonium californicum*, *Frankenia grandifolia*, *Triglochin maritima*.

BUTTERFLY FOODPLANTS *Distichlis spicata*, *Suaeda* spp.

CHARACTERISTIC BUTTERFLIES *Brephedum exilis*, *Polites sabuleti sabuleti*, *Panoquina errans*.

DISCUSSION This community consists of salt marshes along the coast from sea level to approximately 10 feet elevation. Rainfall, fog, and temperature patterns are similar to that of the Coastal Dune Sand plant community.

The butterfly fauna of this community is depauperate, with only 3 species regularly associated with it. As with the Coastal Dune Sand plant community, the Coastal Salt Marsh habitat has been greatly reduced in California as a result of human activities. Thus, if the current rate of destruction of this habitat within the state continues, the one butterfly endemic to it, namely *Panoquina errans*, will become an endangered species.

3. FRESHWATER MARSH

DOMINANT OR CHARACTERISTIC PLANTS

Scirpus olneyi, *S. validus*, *S. acutus*, *S. californicus*, *Typha latifolia*, *T. doomingensis* (*T. angustifolia*), *Heleocharis palustris*, *Carex senta*, *C. obnupta*, *Juncus*, *Phragmites australis*, *Sagittaria*, *Sparganium*, with a few dicots like species of *Bidens*, *Cicuta*, *Polygonum*, and *Rumex*.

BUTTERFLY FOODPLANTS

Aster chilensis lentus, *Cirsium hydrophilum*, *Phragmites australis*, *Potentilla egede*; *Rumex* spp.

CHARACTERISTIC BUTTERFLIES

Phyciodes campestris (Suisun Marsh ecotype), *Lycaena hellouides* (Suisun Marsh ecotype), *Ochlodes yuma sacramentorum*.

DISCUSSION

This community is composed of the marshes of the interior valleys such as in the Sacramento River Delta area or the southern San Joaquin Valley in the vicinity of Tulare Lake. Climatic conditions for this community are variable, depending on geographic location within the state, but temperature fluctuations tend to be somewhat moderated by the presence of bodies of water. As in the preceding two communities, the once extensive series of marshes in the Great Central Valley of California have been markedly reduced in extent due to human activities such as farming, ranching and real estate development.

Shapiro (1975b) discusses in detail the butterfly fauna of the Suisun Marsh, in west central California, and the reader is referred to that paper for more detailed discussion of this community and its associated butterfly fauna. Shapiro found a large proportion of weedy or adventive species, and only two species which had locally differentiated populations within the marsh. The absence of species endemic to the freshwater marsh habitat in California is puzzling, in view of the once very great geographic extent of this wetland habitat within the state.

4. VERNAL POOL EPHEMERAL

DOMINANT OR CHARACTERISTIC PLANTS

Marsilea vestita, *Pilularia americana*, *Anagallis minima*, *Gergia texana*, *Damasonium californicum*, *Crassula aquatica*, *Deschampsia danthonioides gracilis*, *Lilaea scilloides*, *Myosurus minimus*, and species of *Alopecurus*, *Blennosperma*, *Boisduvalia*, *Callitriche*, *Downingia*, *Elatine*, *Eleocharis*, *Eryngium*, *Isoetes*, *Juncus*, *Lasthenia*, *Lepidium*, *Limnanthes*, *Lythrum*, *Mimulus*, *Navarretia*, *Orcuttia*, *Orthocarpus*, *Phalaris*, *Plagiobothrys*, *Pogogyne*, *Psilocarphus*, and *Ranunculus*.

BUTTERFLY FOODPLANTS

Lepidium spp., *Mimulus* spp., *Orthocarpus* spp.

CHARACTERISTIC BUTTERFLIES

Pontia protodice, *Junonia coenia*.

DISCUSSION

This plant community is found in scattered localities throughout the cismontane portion of the state, on valley bottoms or flat mesas in the foothills, where winter precipitation forms temporary shallow pools of water which in the course of evaporation in the spring, produce a succession of flowering plants within the basins or depressions in which the vernal pools form. Like the preceding 3 communities, it is a rapidly disappearing one, and only in recent years have such organizations as the Nature Conservancy moved to save some of the more undisturbed and unique vernal pool habitats.

This community has no resident butterfly populations, and is only used incidentally by certain weedy species which utilize certain of the annual plants found in these habitats as larval foodplants.

5. COASTAL BOGGY MEADOW

DOMINANT OR CHARACTERISTIC PLANTS

A mixture of plants from more acid bogs like *Sphagnum* spp., *Blechnum spicant*, *Habenaria dilatata leucostachys*, *Ledum glandulosum columbianum*, *Menyanthes trifoliata*, and *Potentilla palustris*, and from less acid swamps like *Baccharis douglasii*, *Juncus* spp., *Lysichitum americanum*, *Salix sitchensis*, and *Veratrum fimbriatum*.

BUTTERFLY FOODPLANTS

Carex spp., *Lotus formosissimus*, *Trifolium* spp.

CHARACTERISTIC BUTTERFLIES

Lycaeides idas lotis, *Icaricia saepiolus saepiolus*, *Polites sonora siris*, *Euphyes vestris osceola*.

DISCUSSION

This is an extremely restricted habitat in the northern part of the state, confined to only a few small bogs near the immediate coast. Only one such habitat within the state has received any attention from lepidopterists, namely a small boggy meadow near the town of Mendocino in Mendocino County. At this site, the last known population of endangered species, *Lycaeides idas lotis*, has been studied by J. F. Emmel (unpublished data) and Richard Arnold (1980). In contrast to the more montane boggy meadows within the state, which are relatively rich in butterfly species, only a few species are associated with the coastal version of this habitat.

6. RIPARIAN WOODLAND

DOMINANT OR CHARACTERISTIC PLANTS

At lower elevations, the prominent woody species are *Acer macrophyllum*, *A. negundo californicum*, *Alnus oregana*, *Cephalanthus occidentalis californicus*, *Fraxinus latifolia*, *Platanus racemosa*, *Populus fremontii*, *Quercus agrifolia*, *Q. lobata*, and species of *Baccharis*, *Cornus*, *Salix*, and *Vitis*. Common herbs are *Nasturtium officinale*, *Urtica dioica holosericea*, and species of *Juncus*, *Mentha*, *Mimulus*, *Polypogon*, *Stachys*, and *Veronica*. At higher elevations where riparian woodland blends into mixed evergreen forest, the conspicuous riparian species are *Acer macrophyllum*, *Alnus rhombifolia*, *Populus trichocarpa*, *Salix* spp., *Umbellularia californica*, and the herbs *Aralia californica*, *Boykinia rotundifolia*, *Datisca glomerata*, and *Peltiphyllum peltatum* (Thorne, 1976).

BUTTERFLY FOODPLANTS

Amorpha californica, *A. fruticosa*, *Sorbus* spp., *Aristolochia californica*, *Barbarea* spp., *Cardamine californica*, *Carex senta*, *C. spissa*, *Cirsium* spp., *Dicentra formosa*, *Fraxinus* spp., *Phoradendron flavescens* var. *macrophyllum*, *Populus* spp., *Quercus lobata*, *Rhododendron occidentale*, *Ribes divaricatum*, *Salix* spp., *Urtica holosericea*.

CHARACTERISTIC BUTTERFLIES

Papilio rutulus, *P. multicaudatus*, *Battus philenor hirsuta*, *Parnassius clodius clodius*, *P. c. sol*, *Pieris rapae*, *P. napi microstriata*, *Anthocharis sara sara*, *A. lanceolata lanceolata*, *A. l. australis*, *Limenitis lorquini*, *Vanessa atalanta*, *Polygonia satyrus*, *P. faunus rusticus*, *P. f. fulvescens*, *P. oreas*, *Nymphalis antiopa*, *Phyciodes mylitta*, *Satyrium californica* (Sacramento Valley ecotype), *S. sylvinus sylvinus*, *S. s. desertorum*, *S. auretteorum* (Sacramento Valley ecotype), *Atlides halesus*, *Celastrina argiolus echo*, *Euphyes vestris harbisoni*, *Epargyreus clarus californicus*. Shapiro 1974 - Sacramento Valley fauna.

DISCUSSION

This is a rather extensive plant community in the state, found along most permanent streams and springy areas, mostly in cismontane California. It is most conspicuous in the lowlands, particularly in the Great Central Valley where extensive stands of *Quercus lobata* and other trees line the major watercourses. At higher elevations in the mountains, this community blends into the Mixed Evergreen Forest communities, and at elevations higher than this community, it is poorly defined or non-existent.

This community has a high diversity of butterfly species, undoubtedly a result of both the richer flora as well as the extensive contact with the diverse plant communities bordering these riparian forests. Unfortunately, there has been extensive loss of this particular habitat, particularly in the Great Central Valley, but a number of the remaining stands have been preserved by various conservation organizations. Shapiro (1975b) has made the most extensive study of this habitat in the Sacramento Valley.

With further study, this plant community could probably be subdivided into at least two communities, one involving primarily the *Quercus lobata* forests on the valley bottomlands, and the other encompassing the riparian communities of the foothill canyons where different plant species predominate.

7. NORTHERN COASTAL SCRUB

DOMINANT OR CHARACTERISTIC PLANTS

Artemisia californica, *Baccharis pilularis*, *Ceanothus thyrsiflorus repens*, *Diplacus aurantiacus*, *Eriogonum parvifolium*, *Eriophyllum staechadifolium*, *Gaultheria shallon*, *Rubus* spp., *Achillea borealis californica*, *Amsinckia spectabilis*, *Anaphalis margaritacea*, *Angelica hendersonii*, *Castilleja latifolia*, *Erigeron glaucus*, *Grindelia stricta venulosa*, *Heracleum lanatum*, *Iris douglasiana*, *Lupinus* spp., *Sisyrinchium bellum*, *Armeria maritima californica*, *Dudleya farinosa*, *Plantago maritima californica*, and *Spergularia macrotheca*.

BUTTERFLY FOODPLANTS

Aster chilensis, *Anaphalis margaritacea*, *Angelica hendersonii*, *Aster chilensis*, *Castilleja* spp., *Ceanothus thyrsiflorus*, *Diplacus aurantiacus*, *Eriogonum latifolium*, *E. parvifolium*, *Heracleum maximum*, *Lupinus albifrons* ssp. *collinus*, *Scrophularia californica*, *Sedum spathulifolium*.

CHARACTERISTIC BUTTERFLIES

Papilio zelicaon, *Euphydryas chalcedona chalcedona*, *E. editha baroni*, *Phyciodes campestris campestris*, *Incisalia mossii bayensis*, *I. m. doudoroffi*, *Callophrys dumetorum*, *Lycaena heteronea heteronea*, *Euphilotes enoptes smithi*, *Icaricia icarioides missionensis*.

DISCUSSION

This plant community occupies a rather narrow coastal strip from San Luis Obispo County north to the Oregon border, where it is located above the Coastal Dune Sand plant community but below the redwood forest and other coastal forest communities. It is largely below 500 feet in elevation, and average rainfall ranges from 25 to 75 inches, with considerable fog and wind. There is a long growing season, from 10 to 12 months, and temperature fluctuations both diurnally and seasonally tend to be greatly moderated by the proximity to the ocean.

The plants in this community tend to be low-growing but often forming a fairly dense vegetation cover, sometimes with small areas of grassland within it. Because of the frequent location of this plant community on steep slopes near the ocean, there has been somewhat less impact on it by human activities. However, one of the most extensive areas of this plant community, on San Bruno Mountain in San Mateo County, is threatened with encroaching urbanization from the San Francisco metropolitan area.

At least 5 butterfly species have developed distinctive subspecies confined to this plant community: two of these are restricted enough to be classified as endangered subspecies.

8. SOUTHERN COASTAL SAGE SCRUB

DOMINANT OR CHARACTERISTIC PLANTS

Artemisia californica, *Crossosoma californicum*, *Diplacus*, *Encelia californica*, *Eriogonum fasciculatum fasciculatum*, *Galium*, *Haplopappus*, *Helianthemum*, *Lotus*, *Lupinus*, *Malacothamnus*, *Opuntia*, *Malosma laurina*, *Rhus integrifolia*, *Salvia*, *Senecio*, *Solanum*, *Toxicodendron radicans diversilobum*, *Marah macrocarpus*, *Calystegia macrostegia*, and species of *Castilleja*, *Haplopappus*, *Lotus*, *Lupinus*, and *Zauschneria*, and *Eriophyllum confertiflorum*.

BUTTERFLY FOODPLANTS

Astragalus trichopodus ssp. *leucopsis*, *Caulanthus lasiophyllus*, *Descurainaea pinnata*, *Diplacus* spp., *Encelia californica*, *Eriogonum cinereum*, *E. fasciculatum*, *Lotus argophyllus*, *L. scoparius*.

CHARACTERISTIC BUTTERFLIES

Anthocharis cethura catalina, *A. sara gunderi*, *Euphydryas chalcedona chalcedona*, *Charidryas gabbii*, *Apodemia mormo virgulti*, *Calephelis nemesis californica*, *Glaucopsyche lygdamus australis*, *G. l. palosverdesensis*, *Euphilotes battoides bernardino* (*Eriogonum cinereum* ecotype).

DISCUSSION

Under this plant community, we lump 3 of the subdivisions of Farn (1976): Sea-bluff Succulent, Maritime Sage Scrub, and Maritime Desert Scrub. This plant community is found in the southern third of the state on the islands and the immediate coast up to the chaparral belt of the coastal mountains. It is fairly rich in plant species because of the favorable conditions of a long growing season, moderate temperatures, moderate winter rainfall, and the moderating effects of summer fog. Most of the associated butterfly species tend to be spring or early summer fliers, in keeping with the period of time at which the plants in this community are actively growing and flowering.

As is the case with the other coastal California communities, large tracts of this habitat along the coast have been replaced by housing developments. On the California Islands, there has been considerable degradation of this habitat from grazing by feral animals, although programs are now in place to eliminate this source of habitat degradation on all the California Islands.

9. INLAND SAGE SCRUB

DOMINANT OR CHARACTERISTIC PLANTS

Artemisia californica, *Diplacus* spp., *Encelia farinosa*, *Eriogonum fasciculatum*, *Eriophyllum confertiflorum*, *Haplopappus* spp., *Helianthemum scoparium*, *Eriodictyon trichocalyx*, *Lotus scoparius*, *Lupinus* and *Malacothamnus* spp., *Malosma laurina*, *Opuntia littoralis* and *O. parryi*, *Rhus*, *Rhamnus*, and *Salvia* spp., *Solanum xanti*, and *Toxicodendron radicans diversilobum*. In sandy washes, *Cucurbita foetidissima*, *Lepidospartum squamatum*, *Rhamnus* spp., and many annuals.

BUTTERFLY FOODPLANTS:

Bebbia juncea, *Caulanthus simulans*, *Corethrogyne filaginifolia*, *Dudleya lanceolata*, *Eriogonum elongatum*, *E. fasciculatum*, *Lotus scoparius*, *Plantago* spp.

CHARACTERISTIC BUTTERFLIES

Anthocharis cethura cethura, *Euphydryas editha quino*, *Chlosyne gabbii*, *Apodemia mormo virgulti* (inland ecotype), *Calephelis wrighti*, *Callophrys perplexa perplexa*, *Lycaena gorgon gorgon*, *Glaucopsyche lygdamus australis*, *Philotes sonorensis*, *Euphilotes battoides bernardino*, *Hesperia columbia*.

DISCUSSION

This community is closely related to the preceding one, in having a similar species composition, although it tends to be subject to much greater extremes of temperature and lower precipitation as a consequence of its distance from the coast. This community is usually present on sandy, gravelly, or rocky slopes on the coastal side of the mountains from the south Coast Ranges in San Luis Obispo County to Baja California. Elevation ranges from near sea level to approximately 3000 feet, and annual precipitation is 10 to 20 inches, with a growing season of 8 to 12 months. Winter minimum temperatures may reach freezing, although only for brief periods of time, while summer maximum temperatures are often above 90° F.

The dominant plants in this community tend to be small shrubs and form a more open community than that seen in the chaparral communities. Most of the butterflies of this particular community fly during the spring months when the plants are either in bloom or putting out new growth. By summer, most of the plant species are in a dormant state, and likewise there are very few butterfly species flying during this season or in the fall months.

Although much of the real estate development currently taking place in southern California occurs within this plant community outside of the valley bottoms, it occupies a rather extensive geographic area and is not immediately threatened. However, in northern San Diego County, western Riverside County, and southwestern San Bernardino County, real estate development is accelerating at such a pace that within the next few years significant destruction or even virtual elimination of this plant community in that area could take place.

10 COASTAL CLOSED-CONE CONIFEROUS WOODLAND

DOMINANT OR CHARACTERISTIC PLANTS *Pinus muricata* and its variety *remorata*, *P. radiata*, *Cupressus macrocarpa*, *C. abramsiana*, *C. goveniana*, and *C. guadalupensis*.

BUTTERFLY FOODPLANTS *Pinus muricata*, *Horkelia* sp.

CHARACTERISTIC BUTTERFLIES *Incisalia eryphone* near *sheltonensis*, *Pyrgus ruralis ruralis* (Monterey Peninsula).

DISCUSSION This was probably once an extensive community within the state, but is currently confined to only a few scattered locations along the coast and on the California Island. It is dominated by closed-cone conifers, and frequently has an understory of sclerophyllous chaparral shrubs. In Mendocino County a few miles inland from the Pacific coast, there is a dwarfed phase of this community forming a rather distinctive pigmy forest, where trees can bear cones and are only one or two feet tall, as a result of the extremely poor soils on which they grow. There are no butterfly species unique to this community but a small number seem at least loosely associated with it.

11. INLAND CLOSED-CONE CONIFEROUS WOODLAND

DOMINANT OR CHARACTERISTIC PLANTS *Pinus attenuata*, *Cupressus macnabiana*, *C. sargentii*, *C. arizonica*, *C. bakeri*, *C. guadalupensis*.

BUTTERFLY FOODPLANTS *Cupressus guadalupensis* ssp. *forbesii*, *C. sargentii*, *C. macnabiana* (?), *C. nevadensis* (?), *C. bakeri* (?). *Mitoura barryi barryi*, *M. muiri*, *M. thornei*.

DISCUSSION This is the inland representation of the Closed-cone Coniferous Forest, and is usually found on either serpentine or volcanic soils, and is loosely associated with chaparral, oak woodland, or even a sparse yellow pine forest. It is found in several widely scattered locations throughout the state, with the largest stands of these unique conifers in the North Coast Ranges and extreme northern Sierra Nevada and Modoc Plateau regions.

Unique to these stands of conifers are several species of *Mitoura*. The conifer species are all pyrophytic, requiring regular fires for opening of their cones to release seeds; the effect of these recurrent fires on the *Mitoura* populations is unstudied at this time, but may shed some light on the current distribution patterns of these species.

12. SHORE PINE WOODLAND

DOMINANT OR CHARACTERISTIC PLANTS *Pinus contorta contorta*, *Arctostaphylos uva-ursi*, *Garrya elliptica*, *Gaultheria shallon*, *Myrica californica*, and *Vaccinium ovatum*.

BUTTERFLY FOODPLANTS *Pinus contorta*, *Arctostaphylos uva-ursi*.

CHARACTERISTIC BUTTERFLIES *Incisalia eryphon* near *sheltonensis*, *I. augustus iroides*.

DISCUSSION This is a rather limited community within the state, being found only at several locations along the northern coast from near Cape Mendocino northward into Oregon. It is usually found on stabilized sand dunes or coastal bluffs, and consists of a relatively low open woodland dominated by *Pinus contorta contorta*. Within the state, perhaps the best development of this plant community is on the Samoa Peninsula west of Humboldt Bay in Humboldt County. Only two butterfly species seem associated with it, both univoltine spring-fliers.

13. TORREY PINE WOODLAND

DOMINANT OR CHARACTERISTIC PLANTS *Pinus torreyana*.

BUTTERFLY FOODPLANTS Undetermined.

CHARACTERISTIC BUTTERFLIES Undetermined.

DISCUSSION This is a coastal woodland community present in only two very limited stands, one in San Diego County near Del Mar and the other on Santa Rosa Island. This community has not been studied from the standpoint of associated butterfly species and bears investigation.

14. NORTH COASTAL CONIFEROUS FOREST

DOMINANT OR CHARACTERISTIC PLANTS *Abies grandis*, *Chamaecyparis lawsoniana*, *Picea sitchensis*, *Pseudotsuga menziesii*, *Thuja plicata*, and *Tsuga heterophylla*. The dense understory includes *Acer circinatum*, *Rhamnus purshiana*, *Polystichum munitum*, and many other species with *Selaginella oregana* often epiphytic on the moss-hung tree trunks and branches (Thorne, 1976).

BUTTERFLY FOODPLANTS *Calamagrostis purpurascens*, *Cardamine californica*, *Carex* sp., *Pseudotsuga menziesii*.

CHARACTERISTIC BUTTERFLIES *Neophasia menapia melanica*, *Pieris napi marginalis*, *Oeneis nevadensis iduna*, *Euphyes vestris osceola*, *Carterocephalus palaemon robustus*.

DISCUSSION This is a coastal coniferous forest of northern California ranging from scattered localities in Sonoma County northward to the Oregon border, from sea level to approximately 1,000 feet elevation on the outermost Klamath and Coast Ranges. It is a very dense, tall, wet forest dominated by conifers often reaching 150 to 200 feet in height. There is also a dense understory of shrubs. It is found in the area of highest rainfall in the state, with some stations receiving 110 inches of precipitation a year, with frequent summer fog. It has a long growing season, with cool and equable temperatures.

The denser portions of this forest are probably devoid of butterfly species, and most of the species recorded for this particular plant community are found in openings within the forest or along roads, or along watercourses where the forest canopy is absent. Because of marginal weather conditions for observing butterflies in this community for much of the year, little research has been done on it.

15. REDWOOD FOREST

DOMINANT OR CHARACTERISTIC PLANTS

Sequoia sempervirens, *Pseudotsuga menziesii*, *Torreya californica*, *Acer macrophyllum*, *Alnus oregana*, *Arbutus menziesii*, *Quercus densiflora*, *Umbellularia californica*, shrubby species of *Rhododendron* and *Vaccinium*, *Ceanothus thyrsiflorus*, *Corylus cornuta californica*, *Euonymus occidentalis*, *Gaultheria shallon*, *Myrica californica*, *Rosa gymnocarpa*, and species of *Rubus*, herbs such as *Asarum caudatum*, *Oxalis oregana*, *Viola sempervirens*, and species of the *Berberidaceae*, *Ranunculaceae*, *Liliaceae*, and *Orchidaceae*, and ferns like *Adiantum pedatum aleuticum*, *Athyrium filix-femina californicum*, *Blechnum spicant*, *Polystichum munitum*, and *Woodwardia fimbriata* (Thorne, 1976).

BUTTERFLY FOODPLANTS

Cardamine angulata, *C. californica*, *Dicentra formosa*, *Ribes divaricatum*, *Sedum spathulifolium*, *Viola sempervirens*.

CHARACTERISTIC BUTTERFLIES

Parnassius clodius strohbeeni, *Pieris napi sequoia*, *P. n. venosa*, *Boloria epithore epithore*, *Polygonia faunus fulvescens*, *P. oreas*, *Incisalia mossii marinensis*, *Celastria argiolus* ssp. (N. Coast segregate), *Euphyes vestris* near *osceola* (Santa Cruz Mts.).

DISCUSSION

This is another high, dense, coastal forest of the northern half of the state. It is found from southern Monterey County northward to southern Oregon. It is found from near sea level to as high as 3000 feet on the seaward slope of the outer Klamath and Coast Ranges, and receives heavy winter rain and frequent dense, dripping fog during the summer months.

In denser portions of this forest, butterflies are virtually absent, but in clearings and along watercourses, trails, or roads, butterflies may be frequently encountered. The species composition of this plant community is best known through the field work of both J. W. Tilden and O. Elton Sette, resident lepidopterists of the San Francisco Bay region who made frequent collecting trips into the redwood forests of the southern Santa Cruz Mountains. At least one subspecies unique to this habitat (*Parnassius clodius strobini*) has possibly become extinct due to destruction of its habitat in the Santa Cruz Mountains.

16. DOUGLAS FIR FOREST

DOMINANT OR CHARACTERISTIC PLANTS

Dominated by *Pseudotsuga menziesii*; often associated with the Douglas-fir are *Quercus densiflora*, *Chrysolepis chrysophylla*, *Arbutus menziesii*, *Ceanothus thyrsiflorus*, *Diplacus aurantiacus*, *Lonicera hispidula vacillans*, *Rhamnus californica*, and *Toxicodendron radicans diversilobum*.

BUTTERFLY FOODPLANTS

Cardamine californica, *Ceanothus thyrsiflorus*, *Pseudotsuga menziesii*, *Quercus densiflora*, *Rhamnus californica*, *Sedum spathulifolium*.

CHARACTERISTIC BUTTERFLIES

Papilio eurymedon, *Neophasia menapia melanica*, *Pieris napi marginalis*, *P. n. venosa*, *Incisalia mossii marinensis*.

DISCUSSION

This is a forest dominated by Douglas Fir, found in the North Coast Ranges and Klamath Mountains Assemblage generally inland from the redwood forest. It is found up to 4500 feet in elevation, and sometimes forms nearly pure stands of Douglas Fir 200 feet in height. There is an understory of smaller trees and shrubs, but with less diversity than that of the often adjacent Northern Mixed Evergreen forest. This forest has been poorly studied, and what little data we have is the result of field studies primarily in small patches of this forest in Marin and Sonoma counties in the North Coast Ranges.

17. NORTHERN MIXED EVERGREEN FOREST

DOMINANT OR CHARACTERISTIC PLANTS

Pseudotsuga menziesii, *Chamaecyparis lawsoniana*, *Quercus densiflora*, *Arbutus menziesii*, *Chrysolepis chrysophylla*, *Umbellularia californica*, *Acer macrophyllum*, *A. circinatum*, *Quercus agrifolia*, *Q. chrysolepis*, *Alnus oregana*, *A. rhombifolia*, *Corylus cornuta californica*, *Cornus nuttallii*, *Ceanothus* spp., and *Dirca occidentalis*.

BUTTERFLY FOODPLANTS

Cardamine californica, *Ceanothus* spp., *Pseudotsuga menziesii*, *Quercus agrifolia*, *Q. chrysolepis*, *Q. densiflora*, *Rhamnus californica*, *Sedum spathulifolium*.

CHARACTERISTIC BUTTERFLIES

Papilio eurymedon, *Neophasia menapia melanica*, *Pieris napi venosa*, *Adelpha bredowii californica*, *Habrodais grunus grunus*, *Incisalia mossii marinensis*.

DISCUSSION

This northern California forest community is richer in plant species, as a result of a combination of floristic elements from both the wetter and drier forests of the Pacific Northwest. Consequently, its butterfly fauna is somewhat more diverse than the adjacent redwood or Douglas Fir forest, but to date it has been poorly studied and further research is indicated.

18. SOUTHERN MIXED EVERGREEN FOREST

DOMINANT OR CHARACTERISTIC PLANTS

Pseudotsuga macrocarpa, *Calocedrus decurrens*, *Acer macrophyllum*, *Quercus agrifolia*, *Q. chrysolepis*, and *Umbellularia californica* with *Alnus rhombifolia*, *Platanus racemosa*, *Populus trichocarpa*, and *Salix lasiolepis* mainly restricted to the stream sides and beds. Characteristic shrubs are *Aralia californica*, *Ribes californicum*, and *Toxicodendron radicans diversilobum* with the vine *Vitis girdiana*, such herbs as *Boykinia rotundifolia*, *Claytonia perfoliata*, *Datisca glomerata*, and *Stellaria media*, and the ferns *Dryopteris arguta*, *Polypodium californicum*, and *Woodwardia fimbriata* (Thorne, 1976).

BUTTERFLY FOODPLANTS

Arabis spp., *Astragalus douglasii*, *Calocedrus decurrens*, *Ceanothus* spp., *Elymus glaucus*, *Quercus agrifolia*, *Q. chrysolepis*, *Rhamnus californica*, *Salix lasiolepis*, *Viola purpurea*, *V. quercetorum*.

CHARACTERISTIC BUTTERFLIES

Papilio eurymedon, *Anthocharis lanceolata australis*, *Colias harfordii*, *Adelpha bredowii californica*, *Speyeria coronis semiramis*, *Habrodais grunus grunus*, *Mitoura nelsoni*, *Ochlodes sylvanoides sylvanoides*.

DISCUSSION

Like its northern California counterpart, this forest community of the southern part of the state is floristically rich because of a combination of elements of both wet and dry forests. It is found from approximately 1500 to 5500 elevation, largely on the cismontane slopes of the southern California mountains, where it tends to be concentrated along streams or on more mesic canyon slopes. At lower elevations, it blends into Riparian Woodland, while along its margins at the higher elevations, it blends into Mixed Chaparral or Lower Montane Coniferous Forest plant communities.

19. NORTHERN COASTAL PRAIRIE

DOMINANT OR CHARACTERISTIC PLANTS

Calamagrostis nutkaensis, *Danthonia californica*, *Deschampsia caespitosa holciformis*, *Festuca* spp., *Holcus lanatus*, *Pteridium aquilinum*, *Arabis blepharophylla*, *Calochortus* spp., *Chrysopsis villosa bolanderi*, *Dichelostemma pulchellum*, *Grindelia hirsutula*, *Iris douglasiana*, *Lupinus* spp., *Luzula subsessilis*, *Orthocarpus* spp., *Ranunculus californica*, *Sanicula arctopoides*, and *Sisyrinchium bellum*.

BUTTERFLY FOODPLANTS

Danthonia californica, *Festuca* spp., *Viola adunca*

CHARACTERISTIC BUTTERFLIES

Coenonympha californica californica, *Cercyonis pegala boopis*, *C. sthenele behrii*, *Speyeria zerene behrensii*, *Hesperia comma dodgei*, *H. columbia*, *H. lindseyi* (N. Coastal segregate).

DISCUSSION

This grassland community is found in scattered localities in northern California from the San Francisco Bay area to the Oregon border, below 4,000 feet elevation on the coastal slope of the North Coast Ranges and Klamath Mountains Assemblage. Although it once had a rich flora of perennial bunchgrasses as well as perennial and annual herbs, it is now partly replaced by introduced weedy grasses and herbs. This is another habitat which has been poorly studied due to its relatively remote location and frequent unfavorable weather conditions for collecting. This community is threatened by both coastal real estate development, as well as poorly managed grazing practices.

Not surprisingly, due to its rich flora of grasses, this community has a high percentage of grass-feeding Satyrids and Hesperiids.

20. FOOTHILL AND VALLEY GRASSLAND

DOMINANT OR CHARACTERISTIC PLANTS

Perennial bunchgrasses of the genera *Aristida*, *Danthonia*, *Festuca*, *Melica*, *Poa*, and *Stipa*, and introduced Mediterranean annuals of the genera *Avena*, *Bromus*, *Festuca*, *Hordeum*, and *Vulpia*.

Also in years of normal or greater rainfall, colorful wildflowers of many genera, including *Amsinckia*, *Coreopsis*, *Dodecatheon*, *Erodium*, *Eschscholzia*, *Lasthenia*, *Lupinus*, *Malacothrix*, *Orthocarpus*, *Phacelia*, *Plagiobothrys*, *Salvia*, *Trifolium*, and *Viola*.

BUTTERFLY FOODPLANTS

Asclepias eriocarpa, *Astragalus* spp., *Lomatium* spp., *Melica imperfecta*, *Plantago erecta*, *Poa scabrella*, *Viola pedunculata*.

CHARACTERISTIC BUTTERFLIES

Papilio zelicaon, *Danaus plexippus*, *Coenonympha californica californica*, *Euphydryas editha editha*, *E. e. insularis*, *Speyeria callippe callippe*, *S. c. comstocki*, *Everes amyntula*, *Hesperia comma tildenii*, *H. lindseyi*.

DISCUSSION

This was once a vast grassland community of the Great Central Valley and the adjacent foothills, as well as being widespread in some of the cismontane valleys of southern California. It has now been largely replaced by agricultural development or urbanization, while the remaining stands of it have been largely altered through overgrazing, fires, and introduction of numerous weedy species. These grasslands tend to grade rather gradually into the oak woodlands which are found along their higher borders in the foothills.

The original native butterfly fauna of this community will probably never be known, but is undoubtedly similar to that found in the few remaining undisturbed remnants of it in scattered areas of the state. Some species may have been continuously distributed across the Central Valley in the past, and are now perhaps isolated in various islands along the edges of the valley due to the virtual complete agriculturalization of most of the central part of the Great Central Valley.

21. NORTHERN OAK WOODLAND

DOMINANT OR CHARACTERISTIC PLANTS

Quercus garryana, *Q. kelloggii*, *Q. chrysolepis*, *Q. wislizenii*, *Q. lobata*, *Aesculus californica*, *Acer macrophyllum*, and *Arctostaphylos manzanita*.

BUTTERFLY FOODPLANTS

Arabis spp., *Quercus chrysolepis*, *Q. lobata*, *Q. wislizenii*, *Viola quercetorum*.

CHARACTERISTIC BUTTERFLIES

Anthocharis sara sara, *Coenonympha californica californica*, *Cercyonis sthenele behrii*, *Adelpha bredowii californica*, *Speyeria callippe liliana*, *Satyrium auretorum auretorum*.

DISCUSSION

This plant community is found in the inner North Coast Ranges from the San Francisco Bay area to the southern Klamath Mountains Assemblage, and ranges from 3000 to 5000 feet elevation. It is an open, grassy woodland with a number of oak species as well as several other associated characteristic species. As with the foothill and valley grassland community, this habitat has been largely altered by heavy grazing activities which have reduced the native perennial bunchgrasses and have replaced them with weedy annual introduced species.

22. SOUTHERN OAK WOODLAND

DOMINANT OR CHARACTERISTIC PLANTS

Quercus engelmannii, *Q. agrifolia*, *Q. dumosa*, *Q. chrysolepis*, *Q. tomentella*, *Juglans californica*, *Ceanothus* spp., *Rhus* spp., *Ribes* spp., and *Toxicodendron*.

BUTTERFLY FOODPLANTS

Arabis spp., *Brassica* spp., *Quercus engelmannii*, *Q. agrifolia*, *Q. dumosa*, *Q. chrysolepis*.

CHARACTERISTIC BUTTERFLIES

Anthocharis sara sara, *Coenonympha californica californica*, *Cercyonis sthenele* ssp. (Santa Cruz Island), *Adelpha bredowii californica*, *Everes amyntula*, *Erynnis tristis*.

DISCUSSION

Included here is the Island Oak Woodland of Farn (1976). This community is similar to its counterpart in northern California, except that there tend to be fewer species of oak in a given habitat, frequently with one species predominating. Frequently there are chaparral elements mixed in with the stands of oak. This southern California plant community has been also greatly altered by overgrazing, as well as extensive urbanization in some of the lower elevation stands of oaks. In many areas, young oaks do not survive due to grazing or frequent fires, and the remaining oak woodlands are becoming senescent. Most of the butterfly species of this community and its northern California counterpart are spring or early summer fliers.

23. FOOTHILL WOODLAND

DOMINANT OR CHARACTERISTIC PLANTS

"Upslope from the grassland it is a parklike oak woodland ("savanna") dominated by *Quercus lobata*, *Q. agrifolia*, *Q. douglasii*, *Q. wislizenii*, *Q. chrysolepis*, and *Aesculus californica*. At higher elevations the woodland becomes denser with dominance by *Quercus douglasii*, *Aesculus californica*, and *Pinus sabiniana*, and considerable underbrush of such shrubs as species of *Ceanothus* and *Arctostaphylos*, *Eriodictyon californicum*, and *Rhamnus californica tomentella*. In the mesic valleys, it grades into riparian woodland with a rich mixture of shrubs, such as *Calycanthus occidentalis*, *Cercis occidentalis*, *Fraxinus dipetala*, *Myrica hartwegii*, *Philadelphus lewisii*, *Ptelea crenulata*, *Staphylea bolanderi*, *Umbellularia californica*, and even such localized endemics as *Carpenteria californica* (Fresno County)" (Thorne, 1976).

BUTTERFLY FOODPLANTS

Arabis spp., *Arceuthobium campylopodum*, *Cardamine californica*, *Ceanothus* spp., *Collinsia tinctoria*, *Keckiella breviflora*, *K. lemmonii*, *Ptelea crenulata*, *Quercus* spp., *Rhamnus californica*, *Sedum spathulifolium*.

CHARACTERISTIC BUTTERFLIES

Papilio eurymedon, *P. multicaudatus*, *Pontia sisymbrii sisymbrii*, *Pieris napi microstriata*, *Anthocharis sara sara*, *A. lanceolata lanceolata*, *Coenonympha californica californica*, *Cercyonis sthenele silvestris*, *Adelpha bredowii californica*, *Euphydryas chalcedona chalcedona*, *E. c. dwinellei*, *E. editha rubicunda*, *Speyeria callippe rupestris*, *Habrodais grunus grunus*, *Satyrium californica californica*, *S. auretorum auretorum*, *S. saepium saepium*, *Incisalia mossii windi*, *Mitoura johnsoni*, *Ochlodes sylvanoides sylvanoides*, *O. agricola nemorum*.

DISCUSSION

This community is closely related to the Northern and Southern Oak Woodland communities, and forms a transitional woodland between the Grassland and Chaparral communities at its lower edge and the yellow Pine Forest and Montane Chaparral communities at its upper edge. This is a much more floristically rich community than the Northern or Southern Oak Woodland communities, and in fact may be subject to further subdivision as it is studied in greater detail. It is found on the lower slopes of the inner Coast Ranges and the eastern slope of the outer Coast Ranges through the western foothills of the Sierra Nevada and into the northernmost part of the Transverse Ranges. It has a broad elevation range, from 400 to 5000 feet elevation.

There is a much greater number of butterfly species associated with this plant community, due to its rich flora as well as more diverse habitats of canyon bottoms, rocky slopes, and extensive interfaces with adjacent plant communities. As with the Northern and Southern Oak Woodland communities, the butterfly species of this community are largely spring or early summer univoltine species.

24. MIXED CHAPARRAL

DOMINANT OR CHARACTERISTIC PLANTS

The dominant shrubs are usually species of *Adenostoma*, *Arctostaphylos*, *Ceanothus*, *Garrya*, *Quercus*, *Rhamnus*, and *Rhus*, plus *Cercocarpus betuloides*, *Dendromecon rigida*, *Fremontodendron californicum*, *Heteromeles arbutifolia*, *Pickeringia montana*, *Prunus ilicifolia*, *Trichostema lanatum*, and *Yucca whipplei*, but the species composition varies greatly with the various sub-communities (Thorne, 1976).

BUTTERFLY FOODPLANTS

Adenostoma fasciculatum, *Arabis* spp., *Astragalus douglasii*, *Castilleja foliolosa*, *Ceanothus* spp., *Cercocarpus betuloides*, *Eriogonum fasciculatum*, *Fremontodendron californicum*, *Keckiella ternatus*, *Koeleria cristata*, *Lotus scoparius*, *Malacothamnus* spp., *Prunus ilicifolia*, *Quercus dumosa*, *Rhamnus californica*, *R. crocea*, *Tauschia arguta*.

CHARACTERISTIC BUTTERFLIES

Papilio zelicaon, *P. indra pergamus*, *P. eurymedon*, *Anthocharis lanceolata australis*, *Colias harfordii*, *Euphydryas chalcedona chalcedona*, *Thessalia leanira leanira*, *T. l. wrighti*, *Satyrium californica californica*, *S. auretorum auretorum*, *S. a. spadix*, *S. saepium saepium*, *S. s. chalcis*, *S. s. chlorophora*, *S. s. fulvescens*, *S. tetra*, *Incisalia augustus iroides*, *Lycaena hermes*, *Celastrina argiolus echol*, *Glaucopsyche lygdamus australis*, *Euphilotes battoides bernardino*, *E. enoptes cryptorufes*, *Hesperia columbia*, *Ochlodes agricola agricola*, *O. a. nemorum*, *Erynnis brizo lacustra*, *E. pacuvius callidus*, *E. afranius*, *Heliopterus ericetorum*.

DISCUSSION

This community of sclerophyllous shrubs adapted to a Mediterranean-type climate, is widespread on the slopes of the foothills and mountains of California from Shasta County southward into Baja California. It has an annual rainfall of 14 to 25 inches, virtually all of it falling during the cool winter months, and it is subject to hot, dry summers. The community is fire-adapted, and many of its species require fire for seed germination and for rejuvenation of senescent plants. Many of the annuals in this community will only sprout after burns.

This community has a relatively rich butterfly fauna, with many species (particularly the chaparral hairstreaks) being largely associated with it and to a much lesser extent with other communities. Most species are univoltine, with peak flight activity during the spring and early summer.

25. SERPENTINE CHAPARRAL

DOMINANT OR CHARACTERISTIC PLANTS

Quercus durata, *Garrya buxifolia*, *G. congdonii*, *Ceanothus divergens confusa*, *C. ferrisiae*, *C. jepsonii*, *C. pumilus*, *Arctostaphylos montana*, *A. obispoensis*, and certain subspecies of *A. canescens*, *A. hookeri*, and *A. stanfordiana*.

BUTTERFLY FOODPLANTS

Adenostoma fasciculatum, *Arceuthobium campylopodium*, *Ceanothus* spp., *Koeleria cristata*, *Lomatium marginatum*, *Pedicularis densiflora*, *Quercus durata*, *Rhamnus californica*, *Streptanthus* spp.

CHARACTERISTIC BUTTERFLIES

Papilio zelicaon, *P. indra* ssp. (NW California segregate), *Pontia sisymbrii sisymbrii*, *Euchloe hyantis hyantis*, *Euphydryas editha luestherae*, *Satyrrium saepium chalcis*, *Mitoura muiri*, *M. johnsoni*, *Hesperia columbia*, *Erynnis brizo lacustra*.

DISCUSSION

This subcommunity of chaparral is found on stoney, infertile serpentine soils and is readily separable from Mixed Chaparral communities by its constellation of certain serpentine endemic plants which are often accompanied by more widespread chaparral species. Growing with these chaparral plants are also sometimes found the serpentine endemic closed-cone cypresses, such as *Cupressus sargentii* and *C. macnabiana*. It is found primarily in the northern two-thirds of the state, in the Coast Ranges and Sierra Nevada Foothills, at a number of widely scattered localities.

The butterfly fauna of serpentine chaparral habitats in the North Coast Ranges has been studied by Harrison and Shapiro (19). Several butterfly subspecies or ecotypes are virtually completely restricted to serpentine, such as *Mitoura muiri* or *Erynnis brizo lacustra* (at least for the northern California populations of this skipper). The Checkerspot, *Euphydryas editha luestherae*, is largely confined to serpentine habitats, even though its foodplant may be found on non-serpentine substrates as well; this suggests that features of the micro-habitat controlled by the serpentine substrate may be as important as the availability of the foodplant itself for the presence of this butterfly.

The butterflies associated with this plant community are largely univoltine, with most flight periods occurring during the months of April and May.

26. MONTANE CHAPARRAL

DOMINANT OR CHARACTERISTIC PLANTS

Chrysolepis sempervirens, *Quercus densiflora echinoides*, *Q. wislizenii frutescens*, *Q. sadleriana*, *C. chrysolepis nana*, *Q. vaccinifolia*, *Ceanothus cordulatus*, *Arctostaphylos parryana*, *A. patula*, *A. pungens*, *A. pringlei*, and *Chamaebatia foliolosa*.

BUTTERFLY FOODPLANTS

Ceanothus cordulatus, *Quercus chrysolepis nana*, *Q. vaccinifolia*, *Q. wislizenii frutescens*.

CHARACTERISTIC BUTTERFLIES

Papilio eurymedon, *Erynnis propertius*, *E. pacuvius lilius*.

DISCUSSION

This is a relatively high-elevation chaparral community which is usually found within large openings of the montane coniferous forest. The occupation of these open areas by a chaparral community may be the result of recurrent fires, or possibly edaphic factors which prevent colonization by forest trees. Relative to the lower elevation chaparral communities, this one is somewhat depauperate in species, and often stands of it will be composed primarily of one or two species of shrub. Likewise, the butterfly fauna is not particularly remarkable, consisting of species which are also found in the adjacent coniferous forests.

27. DESERT TRANSITION CHAPARRAL

DOMINANT OR CHARACTERISTIC PLANTS *Quercus cornelius-melleri*, *Quercus turbinella*, *Ceanothus greggii*, *Arctostaphylos pungens*, *Purshia glandulosa*, and *Purshia stansburiana*: often accompanied by *Arctostaphylos glauca*, *Ceanothus leucodermis*, *C. crassifolius*, *C. cuneatus*, *Garrya flavescens pallida*, *Fremontodendron californicum*, *Cercocarpus betuloides*, and *Yucca whipplei*.

BUTTERFLY FOODPLANTS *Arabis perennans*, *Ceanothus greggii*, *C. cuneatus*, *Cercocarpus betuloides*, *Dalea searlsiae*, *Descurainia pinnata*, *Dudleya abramsii*, *Eriogonum elongatum*, *E. fasciculatum*, *E. wrightii*, *Fremontodendron californicum*, *Purshia glandulosa*, *P. stansburiana*, *Quercus cornelius-melleri*, *Q. turbinella*.

CHARACTERISTIC BUTTERFLIES *Euchloe hyantis* spp. (Peninsular Ranges segregate), *Anthocharis lanceolata desertolimbus*, *Zerene cesonia*, *Euphydryas chalcedona corralensis*, *E. c. henei*, *Satyrrium saepium fulvescens*, *S. tetra*, *S. behrii*, *Incisalia fotis mojavensis*, *Philotes sonorensis*, *Euphilotes battoides bernardino*, *E. enoptes dammersi*, *Heliopetes ericetorum*.

DISCUSSION This is a chaparral community of the transmontane slopes of the mountains, from the southern Sierra Nevada along the north slope of the Transverse Ranges, and south along the eastern slopes of the Peninsular Ranges. It is also found in the higher mountains of Joshua Tree National Monument and in the higher parts of the eastern Mojave Desert. Its plant species composition is similar to that of the Cismontane Mixed Chaparral community, but some of the dominant species differ as well as the relative percentages of the various species composing it.

The butterfly species composition of this community is similar to that of mixed chaparral but with several distinctive subspecies which show the desert influence on this community. Because of its strategic location between the mountains and the desert, many species are taken in this community which are actually strays from adjacent habitats.

28. SERPENTINE DWARF PINE WOODLAND

DOMINANT OR CHARACTERISTIC PLANTS

Pinus monticola, *Juniperus communis saxatilis*, *Lithocarpus densiflora echnioides*, *Arctostaphylos* spp., *Ceanothus* spp., *Castanopsis*, *Rhamnus*, *Haplopappus lanceolatus* in the drier portions; in moist to boggy areas, *Darlingtonia*, *Phlox*, *Orthocarpus*, *Mimulus*, *Ranunculus*, *Vicia*, and *Viola* spp.

BUTTERFLY FOODPLANTS

Arceuthobium campylopodum, *Castilleja brevilobata*, *Ceanothus* sp., *Collinsia linearis*, *Eriogonum ternatum*, *Rhamnus californica*, *Sedum laxum perplexum*, *Sidalcea* sp., *Streptanthus howellii*, *Tauschia howellii*, *Trifolium* sp., *Viola cuneata*, *V. ocellata*.

CHARACTERISTIC BUTTERFLIES

Papilio zelicaon, *P. indra* spp. (N.W. California segregate), *Euchloe hyantis hyantis*, *Anthocharis lanceolata lanceolata*, *Coenonympha californica eryngii*, *Oeneis nevadensis iduna*, *Euphydryas editha* near *colonia*, *Thessalia leanira* near *oregonensis*, *Clossiana epithore chermocki*, *Speyeria zerene gloriosa*, *Mitoura spinetorum*, *M. johnsoni*, *Euphilotes battoides* near *oregonensis*, *Icaricia saepiolus aehaja*, *Hesperia comma mattooni*, *Thorybes diversus*, *Pyrgus communis*.

DISCUSSION

In the Outer Coast Range of the extreme northwestern corner of the state in Del Norte and Humboldt counties, and in adjacent extreme southwestern Oregon, there is a unique plant community on serpentine substrates characterized as follows: dwarfed individuals of Silver Pine (*Pinus monticola*) are scattered in an open woodland, with interspersed stunted chaparral shrubs and areas of sparse grass and herb growth on gravelly to rocky slopes and flats. There are also seeps, springs and rivulets which support islands of a wet meadow subcommunity within the more extensive dryish portions; the boggiest of these wet meadows support populations of the unique California Pitcher-Plant, *Darlingtonia californica*, and are similar to the boggy meadows on ultrabasic substrates of the Trinity Alps region described by Shapiro *et al.* (1981).

This community is usually bordered by Northern Mixed Evergreen Forest, Douglas Fir Forest, Lower Montane Coniferous Forest, or Mixed Chaparral. Although it receives high winter rainfall and frequent summer fog, the shallow, calcium-poor soil of the serpentine substrate suppresses vegetation growth in all but the more permanently moist portions of it. The result is an admixture of plants from several communities in an open setting on topographically varied terrain, resulting in numerous unique microhabitats and correspondingly a rather rich butterfly fauna.

This unique community was not recognized by Munz (1959) or Thorne (1976).

29. LOWER MONTANE CONIFEROUS FOREST

DOMINANT OR CHARACTERISTIC PLANTS

Pinus ponderosa, *P. jeffreyi*, *P. coulteri*, *P. sabiniana*, *Sequoiadendron giganteum*, *Quercus kelloggii*, *Pseudotsuga menziesii*, *Abies concolor*, *Calocedrus decurrens*, *Pinus lambertiana*, *Cornus nuttallii*; undershrubs of various species of *Arctostaphylos*, *Ceanothus*, *Prunus*, *Ribes*, *Chrysothamnus*, *Eriogonum*, and *Lupinus*, as well as *Chrysolepis sempervirens*, *Chamaebatia foliolosa*, and *Rubus parviflorus*. On the transmontane slopes in the drier forests dominated by *Pinus jeffreyi*, common undershrubs include *Artemisia tridentata*, *Ceanothus cordulatus*, and *Cercocarpus ledifolius*.

BUTTERFLY FOODPLANTS

Amorpha californica, *Arabis* spp., *Arceuthobium campylopodum*, *Artemisia dracunculoides*, *Astragalus douglasii*, *Calocedrus decurrens*, *Ceanothus cordulatus*, *C. velutinus*, *Elymus glaucus*, *Eriogonum fasciculatum*, *E. kennedyi*, *E. marifolium*, *E. nudum*, *E. wrightii*, *Keckiella lemmonii*, *Lotus crassifolius*, *Lupinus albifrons*, *L. andersonii*, *L. formosus*, *L. latifolius*, *Pinus jeffreyi*, *P. ponderosa*, *Ribes roezlii*, *Sedum spathulifolium*, *Streptanthus bernardinus*, *Symphoricarpos* spp., *Viola lobata*, *V. purpurea*.

CHARACTERISTIC BUTTERFLIES

Papilio bairdii bairdii, *P. eurymedon*, *Neophasia menapia menapia*, *N. m. tehachapina*, *Euchloe hyantis andrewsi*, *Colias occidentalis chrysomelas*, *C. harfordii*, *Zerene eurydice*, *Nymphalis californica*, *Euphydryas chalcedona macglashani*, *E. colon colon*, *E. c. wallacensis*, *E. c. sperryi*, *Speyeria zerene zerene*, *S. z. conchylatus*, *S. coronis semiramis*, *Incisalia eryphon eryphon*, *Incisalia mossii hidakupa*, *I. m. windi*, *Mitoura nelsoni*, *M. spinetorum*, *Lycaena arota arota*, *Glaucopsyche piasus piasus*, *Euphilotes battoides intermedia*, *E. enoptes enoptes*, *Icaricia icarioides icarioides*, *I. i. evius*, *I. lupini monticola*, *I. neurona*, *Ochlodes sylvanoides sylvanoides*, *Thorybes pylades*.

DISCUSSION

This plant community combines the subcommunities of Coulter Pine Forest, Yellow Pine Forest, and Mixed Conifer Forest. These are tall Montane Coniferous Forests which are dominated by various species of yellow pine: Forests dominated by *Pinus coulteri* are found from the bay area to northern Baja California, from the Coast Ranges southward through the Transverse Ranges and Peninsular Ranges, at elevations from 1,000 to 7,000 feet. The forests dominated by *Pinus ponderosa* and/or *P. jeffreyi* are found from 1,000 to 9,500' elevation, primarily in the Sierra Nevada, Klamath Mountain Assemblage, North Coast Ranges, and Transverse and Peninsular Ranges of southern California. Where these two yellow pine species are sympatric, there is considerable hybridization. On the west slope of the central Sierra Nevada, from 4,600 to 8,400' elevation, there tends to be a richer mixture of conifer species in addition to the yellow pines, including the Giant Redwood, *Sequoiadendron giganteum*.

Shields (1966) reported on the butterfly fauna of a yellow pine forest community in Tuolumne County in the central Sierra

Nevada. His list of species showed considerable diversity, comparable to that found by Emmel and Emmel (1963) in an Upper Montane Coniferous Forest community at Donner Pass, Placer County, California. The high species diversity of this particular community is due in part to its very extensive range, its diverse flora, and the numerous microhabitats within it which accommodate a wide variety of species. Further study of this particular community may justify subdividing it into 4 or 5 communities, each with its particular floral and faunal composition.

30. UPPER MONTANE CONIFEROUS FOREST

DOMINANT OR CHARACTERISTIC PLANTS

In the Sierra Nevada, largely dominated by *Abies magnifica*, but often accompanied by *A. concolor*, *Pinus contorta murrayana*, *P. monticola*, and *Tsuga mertensiana* from the adjacent communities, also with *Acer glabrum*, *Arctostaphylos nevadensis*, *Lonicera conjugialis*, *Quercus vaccinifolia*, species of *Ribes* and *Symphoricarpos*, *Chrysopsis breweri*, and *Monardella odoratissima*. In the Klamath Mountains assemblage, *A. magnifica* is frequently accompanied by *Abies amabilis*, *A. lasiocarpa*, *A. procera*, *Pinus balfouriana*, *Picea engelmannii*, *P. breweriana*, and *Tsuga mertensiana*. In southern California, the community is dominated by *Abies concolor* and *Pinus lambertiana*, frequently includes *Calocedrus decurrens*, and has a varied flora of understory plants, particularly shrubby species of *Ribes*. On drier rocky slopes and ridges in the Sierra Nevada and Transverse Ranges, there is an open woodland with *Juniperus occidentalis australis*, *Cercocarpus ledifolius*, *Chrysothamnus nauseosus*, *Holodiscus microphyllus*, *Arctostaphylos patula pinetorum*, and *Pinus jeffreyi*.

BUTTERFLY FOODPLANTS

Arabis spp., *Ceanothus cordulatus*, *Chrysopsis breweri*, *Cirsium andersonii*, *Collinsia* spp., *Dicentra nevadensis*, *D. uniflora*, *Eriogonum marifolium*, *E. nudum*, *E. umbellatum*, *Holodiscus microphyllus*, *Juniperus occidentalis australis*, *Pedicularis semibarbata*, *Penstemon newberryi*, *Quercus vaccinifolia*, *Solidago canadensis*, *Viola glabella*, *V. purpurea*, *V. sheltonii*.

CHARACTERISTIC BUTTERFLIES

Papilio eurymedon, *Parnassius clodius baldur*, *P. c.* ssp. (Tulare Co.), *Euchloe ausonides transmontana*, *Anthocharis sara stella*, *Polygonia zephyrus*, *Euphydryas chalcedona sierra*, *E. c. irelandi*, *E. c. trinitina*, *E. editha* ssp. (Generals Highway), *Charidryas palla altasierra*, *Charidryas hoffmanni hoffmanni*, *C. h. segregata*, *Phyciodes orseis herlani*, *Boloria epithore sierra*, *Speyeria hydaspe hydaspe*, *S. h. viridicornis*, *S. a. irene*, *S. a. dodgei*, *Mitoura barryi* ssp. (Sierra Nevada, San Bernardino Mts.), *Euphilotes battoides intermedia*, *E. enoptes enoptes*, *Erynnis propertius*, *E. pacuvius lilius*, *E. p. callidus*.

DISCUSSION

This montane forest community is located above the Yellow Pine Forest but below the Subalpine Forest community in the higher mountain ranges of the state. Thorn (1976) subdivides this into 4 communities, namely White Fir-Sugar Pine Forest, Red Fir Forest, Enriched Conifer Forest, and Mountain Juniper Woodland. Our list of butterfly species and butterfly foodplants is taken almost entirely from the Red Fir Forest and Enriched Conifer Forest subsections of this plant community.

This community shows butterfly species diversity equivalent to that found in the Lower Montane Coniferous Forest, again a result of its occupation of a large geographic area, the high diversity of plant species, and the numerous microhabitats in this community.

31. SUBALPINE CONIFEROUS FOREST

DOMINANT OR CHARACTERISTIC PLANTS

Pinus contorta murrayana, *P. monticola*, *P. flexilis*, *Tsuga mertensiana*, *Pinus albicaulis*, *P. balfouriana*; associated shrubs include *Quercus vaccinifolia*, *Chrysolepis sempervirens*, *Ceanothus cordulatus*, *Arctostaphylos* spp., *Ribes cereum*, and *R. montigenum*.

BUTTERFLY FOODPLANTS

Astragalus whitneyi, *Carex spectabilis*, *Castilleja miniata*, *Dicentra uniflora*, *Draba* spp., *Eriogonum incanum*, *E. nudum*, *E. umbellatum*, *Festuca* spp., *Lupinus arbustus*, *Pteryxia terebinthina*, *Ribes cereum*, *R. montigenum*, *Streptanthus tortuosus*, *Viola purpurea*.

CHARACTERISTIC BUTTERFLIES

Papilio zelicaon, *P. indra indra*, *Parnassius clodius baldur*, *P. c. near menetriesi*, *Pontia occidentalis*, *Euchloe hyantis* ssp. (Sierra Nevada), *Oeneis chryxus ivallda*, *Polygonia zephyrus*, *Euphydryas editha aurilacus*, *Speyeria egleis egleis*, *Satyrium fuliginosum fuliginosum*, *S. f. maculatum*, *Lycaena heteronea submaculata*, *Everes amyntula* (high elevation ecotype), *Icaricia shasta shasta*, *I. lupini lupini*, *Hesperia comma yosemite*, *H. nevada occidentalis*.

DISCUSSION

The Subalpine Coniferous Forest is another montane forest community which lies above the fir forests but below timberline on the higher mountains in the state. Thorn (1976) subdivides this into 3 communities, namely; Lodgepole Pine Forest, White Bark Pine-Mountain Hemlock Forest, and Limber Pine Forest. Again, for the sake of simplification, we prefer to use the all-encompassing community of Subalpine Coniferous Forest. These forests are dominated by Lodgepole Pine, Mountain Hemlock, or the various species of White Pines of timberline, and range from 5,500 to 9,500' in the northern part of the state, and from 8,000' to nearly 11,500' elevation in the southern part of the state. In many areas, this community presents more of an aspect of open woodland than a dense forest, due to the more severe soil and weather conditions at these elevations, which both stunt the trees and also decrease the potentially favorable sites for them to grow. As a result of this open woodland feature, there are many shrubs and perennial herbs scattered on the open slopes and a variety of microhabitats are afforded by the various geologic substrates and varying slope exposures. As a consequence the humidity is relatively high although it does not equal that of the Upper Montane or Lower Montane Coniferous Forest below this community.

Shapiro (1977) describes the butterfly fauna of a combined Subalpine Coniferous Forest and Arctic Alpine Cushion Plant Community at Castle Peak, Nevada County, California. The species composition of this particular locality is somewhat less diverse than that of Subalpine Forest and Arctic Alpine Cushion Plant habitats to the south in the higher Sierra Nevada, or to the northwest in the Klamath Mountains Assemblage, probably a result of its relative isolation and non-granitic substrate.

32. ASPEN WOODLAND

DOMINANT OR CHARACTERISTIC PLANTS

Populus tremuloides, *Salix* spp., *Populus trichocarpa*, *Betula fontinalis*, *Aconitum columbianum*, *Allium validum*, *Delphinium scopulorum*, *Epilobium angustifolium*, *Rosa californica*, and species of *Achillea*, *Arnica*, *Aster*, *Erigeron*, *Senecio*, *Solidago*, as well as numerous grasses and sedges, especially species of *Carex*.

BUTTERFLY FOODPLANTS

Aster spp., *Populus tremuloides*

CHARACTERISTIC BUTTERFLIES

Papilio rutulus, *Phyciodes campestris montana*, *Erynnis icelus*.

DISCUSSION

This community is readily identified by the predominance of Aspen, *Populus tremuloides*, which often forms extensive thickets or even forests from about 7,000 to 10,000' elevation on subalpine eastern slopes of the Sierra Nevada and in the Klamath Mountains Assemblage, the Warner Mountains, and White Mountains. There are small stands in the Sierra San Pedro Matir of Baja California and there is a single small stand in the San Bernardino Mountains. This community is far more extensive in the Rocky Mountain region, and our associated butterfly fauna is extremely depauperate in comparison with that found in the Rocky Mountain region. There are no butterflies in the state exclusively confined to it, and butterfly species taken within this community are usually found in the neighboring forest or meadow communities. Further study may reveal more species associated with it than we have been able to delineate.

33. MONTANE DRY MEADOW

DOMINANT OR CHARACTERISTIC PLANTS

Poa spp., *Festuca* sp., *Muhlenbergia* spp., *Achillea borealis*, *A. lanulosa*, *Horkelia* spp., *Potentilla* spp., annual species of *Polygonum*, *Cirsium* spp., *Vaccinium nivictum*, *Trifolium* spp.

BUTTERFLY FOODPLANTS

Aster spp., *Castilleja breweri*, *C. miniata*, *Cirsium* spp., *Polygonum douglasii*, *P. spargulariaeforme*, *Rumex acetosella*, *R. salicifolius*, *Sidalcea malvaeflora*, *Trifolium* spp., *Urtica holosericea*, *Vaccinium nivictum*.

CHARACTERISTIC BUTTERFLIES

Colias eurytheme, *C. behrii*, *Nymphalis milberti*, *Euphydryas editha augustina*, *Phyciodes mylitta*, *P. campestris montana*, *Lycaena cupreus*, *L. nivalis*, *L. xanthoides xanthoides*, *L. editha*, *Polites sabuleti tecumseh*, *P. sonora sonora*, *Pyrgus communis*.

DISCUSSION

At moderate to high elevations in the mountains, there are numerous meadows, usually located along streams or in open basins where soil moisture or edaphic factors prevent the surrounding forests from occupying those sites. Within almost every meadow, there are both relatively dry and relatively moist areas, with one or the other situation predominating in any given meadow. The drier portions of these montane meadows, which we group here under the plant community category of Montane Dry Meadow, are usually vernal moist, but tend to dry out during the summer months, and tend to have a predominance of grass species rather than the more moisture-loving sedges or other plants of boggy situations. In addition to the grasses, there are numerous flowering herbs, which often provide colorful displays during the late spring and summer months.

Within these drier meadows, the constellation of butterfly species differs from that of adjacent wetter portions of the meadow. As with most other montane communities within the state, the majority of species within this community are univoltine. For some butterfly species found in the meadows, the foodplant may be found in both dry and wet portions of the meadow, but the butterfly will prefer either the drier or wetter portion of the meadow on the basis of a particular microhabitat selection. For example, the foodplant of *Colias behrii*, *Vaccinium nivictum*, grows in both moist and rather dryish portions of the meadows at Tioga Pass, yet the butterfly and immature stages tend to be largely found in the more dryish portions of these meadows, where perhaps overwintering larvae survive the winter by not being drowned or subject to excessive moisture in the early spring when they come out of diapause. Another species, *Nymphalis milberti*, prefers oviposition on patches of its *Urtica* foodplant in more dryish portions of meadows in open sun, and tends to avoid patches of nettle which are found along stream edges, in deep shade, or in moist boggy conditions of the same meadow. Further study of the microhabitat preferences of butterflies in both wet and dry meadows is clearly indicated.

34. MONTANE WET MEADOW

DOMINANT OR CHARACTERISTIC PLANTS

Species of *Carex*, *Eleocharis*, *Glyceria*, *Juncus*, *Aconitum*, *Allium*, *Aquilegia*, *Aster*, *Castilleja*, *Dodecatheon*, *Erigeron*, *Geranium*, *Habenaria*, *Helenium*, *Hypericum*, *Lilium*, *Lupinus*, *Mimulus*, *Pedicularis*, *Perideridia*, *Potentilla*, *Ranunculus*, *Saxifraga*, *Senecio*, *Tofieldia*, *Trifolium*, and *Veratrum*.

BUTTERFLY FOODPLANTS

Cardamine lyallii, *Dodecatheon alpinum*, *D. jeffreyi*, *Lotus oblongifolius*, *Trifolium* spp., *Vaccinium arbuscula*, *Viola adunca*, *V. nephrophylla*.

CHARACTERISTIC BUTTERFLIES

Pieris napi near *pallidissima*, *Coenonympha ampelos* mono, *Cercyonis pegala ariane*, *C. p.* ssp. (Bridgeport-Mono Basin), *Speyeria cybele leto*, *S. nokomis apacheana*, *S. n. carsonensis*, *S. mormonia mormonia*, *S. m. obsidiana*, *Lycaena mariposa*, *Agriades glandon podarce*, *Lycaeides idas ricei*, *Icaricia saepiolus aehaja*, *Polites sonora sonora*, *Euphyes vestris vestris*, *Thorybers mexicana nevada*.

DISCUSSION

As defined here, this plant community designation covers the wet to boggy meadows or portions of meadows in montane habitats, where the substrate is consistently moist throughout the season, even in the early fall months when most plant species are fruiting or becoming sinescent for the year. With further detailed study, this community could probably be further subdivided; in particular, the boggy meadows described by Shapiro (19) in the Trinity Alps region of northern California seemed particularly distinctive. Shapiro found differences in the flora, butterfly fauna, and microhabitats in bogs on granitic substrate versus those on ultra-basic (serpentine) ones.

35. ALPINE FELL-FIELD CUSHION PLANT

DOMINANT OR CHARACTERISTIC PLANTS

Species of *Arabis*, *Arenaria*, *Calyptridium*, *Castilleja*, *Carex*, *Draba*, *Erigeron*, *Eriogonum*, *Festuca*, *Heuchera*, *Hulsea*, *Ivesia*, *Juncus*, *Koeleria*, *Lewisia*, *Luzula*, *Oxyria*, *Pellaea*, *Phlox*, *Phoenicautis*, *Poa*, *Potentilla*, *Polemonium*, *Polygonum*, *Raillardella*, *Ranunculus*, *Sedum*, *Selaginella*, *Silene*, *Sitanion*, and *Trifolium*.

BUTTERFLY FOODPLANTS

Astragalus spp., *Castilleja nana*, *Draba* spp., *Erigeron pygmaeus*, *Eriogonum lobbii*, *E. ovalifolium*, *E. polypodium*, *Festuca brachyphylla*, *Oxyria digyna*, *Penstemon heterodoxus*, *Rumex paucifolius*, *Sedum lanceolatum*, *S. roseum*, *Solidago multiradiata*, *Trifolium andersonii monoense*.

CHARACTERISTIC BUTTERFLIES

Pontia occidentalis, *Oeneis chryxus ivallda*, *O. c. stanislaus*, *Euphydryas editha nubigena*, *Charidryas whitneyi*, *Callophrys lemberti*, *Lycaena phlaeas alpestris*, *L. cupreus*, *L. editha editha*, *Euphilotes battoides battoides*, *Icaricia saepiolus albamontana*, *I. shasta pallidissima*, *I. lupini lupini*, *Hesperia miriamae*, *Polites sabuleti albamontana*, *Thorybes mexicana blanca*.

DISCUSSION

This community occurs in rather extensive areas of higher elevations of the Sierra Nevada, to a lesser extent in the southern Sierra Nevada, and as small limited islands in the northern Sierra Nevada, Mt. Lassen, Mt. Shasta, and in the Trinity Alps. The plants in this community are subject to rather severe growing conditions, usually on poor, rocky soil, exposed to intense insolation, heavy winter snows, frequent high winds, sporadic killing frosts during the summer, and a short growing season. Virtually all the perennial plants in this community form either a low turf or a cushion-like growing habit which help to protect them from these severe conditions.

The butterfly species composition of this community is similar to that found in Arctic Alpine areas of the Rocky Mountains and the far north of North America, and there are several species and subspecies which are endemic to the Sierra Nevada alpine regions. These species are either univoltine or even biennial, as a result of the short growing season and long severe winters.

36. GREAT BASIN CONIFEROUS WOODLAND

DOMINANT OR CHARACTERISTIC PLANTS

Pinus longaeva, *P. flexilis*, *P. washoensis*, *Abies concolor* (Rocky Mountain race), *Cercocarpus ledifolius*, *Artemisia tridentata*, *Chrysothamnus viscidiflorus*, *Chamaebatiaria millefolium*, *Holodiscus microphyllus*, *Ribes cereum*, *R. montigenum*.

BUTTERFLY FOODPLANTS

Chamaebatiaria millefolium, *Chrysothamnus viscidiflorus*, *Holodiscus microphyllus*, *Lupinus alpestris*, *Ribes cereum*, *R. montigenum*.

CHARACTERISTIC BUTTERFLIES

Polygonia zephyrus, *Chlosyne acastus vallismortis*, *C. a. waucoba*, *Celastrina argiolus* near *cinerea*, *Icaricia icarioides panamintinus*.

DISCUSSION

This is a higher elevation woodland community of the Great Basin mountains, which is adapted to a more arid, stringent habitat than the species of the coniferous forest of the Pacific and Sierran regions. Under this plant community category, we include 3 of the subcommunities listed by Thorn (1976): Bristlecone Pine Woodland, White Fir Forest (the Rocky Mountain race of *Abies concolor*), and Washo Pine Forest. In California, only one of these 3 subcommunities (Bristlecone Pine Woodland) is found to any great extent, and is the basis for our list of butterfly foodplants and characteristic butterflies. The White Fir Forest within the state is found only on the highest peaks of the Kingston, Clark, and New York Mountain Ranges of the eastern Mojave Desert, in rather limited stands; there are no butterfly species found primarily in this particular habitat. The Washo Pine Forest, dominated by *Pinus washoensis*, has a rather restricted distribution in northeastern California and extreme western Nevada, from the Warner Mountains southward to the Carson Range in Washo County, Nevada. This community seems to be a somewhat depauperate Great Basin version of the Sierran Yellow Pine Forest, and again we do not know of any particular butterfly species that seem related to it more than to any other community.

The Bristlecone Pine Woodland within the state is found in the highest elevations of the White Mountains, the Inyo Mountains, the Grapevine Mountains, and the Panamint Range. It is an open woodland, with small to medium-sized shrubs, scattered on open rocky to gravelly slopes in these mountains. It is subject to rather severe climatic conditions, similar to the Alpine Fellfield Cushion Plant Community, and has a rather depauperate butterfly fauna. No butterfly species or subspecies seems exclusively confined to it, but several are frequently encountered within it.

37. PINYON-JUNIPER WOODLAND

DOMINANT OR CHARACTERISTIC PLANTS

Pinus monophylla, *P. quadrifolia*, *P. edulis*, *Juniperus osteosperma*, *J. californica*, *J. occidentalis occidentalis*, *Artemisia tridentata*, *Yucca* spp., *Quercus turbinella*, *Q. chrysolepis*, *Cercocarpus ledifolius*, *Purshia glandulosa*, *P. stansburiana*, *Ribes velutinum*.

BUTTERFLY FOODPLANTS

Agave deserti, *Arabis* spp., *Arceuthobium campylopodum*, *Castilleja plagiotoma*, *Eriogonum heermannii*, *E. ovalifolium*, *E. umbellatum*, *E. wrightii*, *Juniperus californica*, *J. osteosperma*, *Keckiella antirrhinoides*, *Lomatium parryi*, *Lupinus argenteus*, *L. excubitus*, *Pinus monophylla*, *Pteryxia petraea*, *Purshia glandulosa*, *P. stansburiana*, *Quercus chrysolepis*, *Q. turbinella*, *Ribes velutinum*, *Tauschia parishii*.

CHARACTERISTIC BUTTERFLIES

Papilio indra phyllisae, *P. i. martini*, *P. i. near nevadensis*, *P. i. panamintensis*, *Pontia sisymbrii nigravenosa*, *Anthocharis sara thoosa*, *A. s. pseudothoosa*, *Cercyonis sthenele masoni*, *C. s. paulus*, *Adelpha bredowii eulalia*, *Euphydryas chalcedona corralensis*, *E. c. kingstonensis*, *E. editha ehrlichii*, *Incisalia eryphon pallidus*, *I. fotis mojavenensis*, *Callophrys comstocki*, *Mitoura siva* (all ssp.), *M. loki*, *M. barryi barryi*, *M. spinetorum*, *Lycaena arota virginiensis*, *Glaucopsyche lygdamus deserticola*, *G. piasus near toxeuuma*, *Euphilotes battoides baueri*, *E. b. euromojavensis*, *E. b. hadrocheilos*, *E. b. panamintensis*, *E. enoptes dammersi*, *E. e. shieldsi*, *Icaricia icarioides panamintensis*, *I. i. near pembina*, *I. acmon texana*, *I. lupini argentata*, *Agathymus baueria* ssp., *Erynnis brizo burgessi*.

DISCUSSION

This is a very extensive community within the state, occurring all along the western edge of the Great Basin and in much of the Mojave Desert and Death Valley region of the state, as well as in scattered areas along the eastern slope of the Peninsular Ranges, the northern and eastern slopes of the Transverse Ranges, and occasionally crossing onto the cismontane slopes of these mountains. This community is subdivided by Thorn (1976) into Northern Juniper Woodland dominated by *Juniperus occidentalis occidentalis*, and Pinyon-Juniper Woodland, which has a mixture of variable percentages of Pinyon Pines and 2 Juniper species. The Northern Juniper Woodland is found mostly on the Modoc Plateau of the northeastern part of the state, while Thorn's subcommunity of Pinyon-Juniper Woodland is found in the southern two thirds of the state. We prefer to lump the 2 into a single category, namely Pinyon-Juniper Woodland.

This is an open woodland of semi-arid regions, which may be dominated by species of Pinyon Pine, species of Juniper, or varying combinations of both. Its elevation ranges from 3,000 to 8,000', and it usually occupies dry, rocky montane slopes, but sometimes occurs on extensive flatlands with deep alluvial soils. For a semi-arid land community, this plant community has a relatively rich flora and butterfly fauna as a result of its strategic location between montane and desert habitats.

38. GREAT BASIN SAGEBRUSH SCRUB

DOMINANT OR CHARACTERISTIC PLANTS

Artemisia tridentata, *Artemisia arbuscula* nova, *Atriplex canescens*, *Ceratoides lanata*, *Chrysothamnus nauseosus*, *C. viscidiflorus*, *Grayia spinosa*, *Purshia glandulosa*, *P. tridentata*, *Tetradymia axillaris*, *Wyethia mollis*, perennial grasses, and many annuals.

BUTTERFLY FOODPLANTS

Artemisia dracunculus, *Astragalus lentiginosus*, *Castilleja chromosa*, *Ceanothus greggii*, *Chrysothamnus viscidiflorus*, *Colinsia* , *Eriogonum kearneyi*, *E. microthecum*, *E. umbellatum*, *Festuca* spp., *Lupinus alpestris*, *L. caudatus*, *L. excubitus*, *L. inyoensis*, *Machaeranthera canescens*, *Purshia glandulosa*, *P. tridentata*, *Stipa* spp., *Viola* spp.

CHARACTERISTIC BUTTERFLIES

Papilio bairdii hollandi, *Colias alexandra edwardsii*, *Cercyonis sthenele paulus*, *C. oetus oetus*, *Neominois ridingsii pallidus*, *Euphydryas anicia wheeleri*, *E. a. near veazieae*, *E. editha monoensis*, *E. e. fridayi*, *Charidryas acastus acastus*, *C. a. vallismortis*, *Speyeria callippe nevadensis*, *Apodemia mormo cythera*, *Satyrrium saepium* ssp. (E. slope Sierra Nevada), *S. behrii*, *S. fuliginosum* near *semiluna*, *Lycaena heteronea immaculata*, *Glaucopsyche lygdamus* near *columbia*, *G. piasus excubitus*, *Euphilotes battoides glaucon*, *E. b. argocyanea*, *E. rita pallescens*, *Icaricia icarioides fulla*, *I. i. eosierra*, *I. i. argusmontana*, *I. i. panamintensis*, *I. i. near pembina*, *I. lupini argentata*, *Hesperia uncas guilianii*, *H. comma harpalus*.

DISCUSSION

This is an extensive semi-desert scrub community, occupying large areas of the Great Basin, and rather extensive areas within California, primarily east of the Sierran-Cascade Axis. It occupies deeper, sandier soils of arid slopes from the Modoc Plateau area southward along the east slope of the Sierra Nevada to the Inyo-White Mountains and Death Valley region, southward to the higher mountains of the eastern Mojave desert and the dryer portions of the higher mountains of southern California.

The dominant shrub in this community, *Artemisia tridentata*, is also found in a number of other semi-desert plant communities, but is here in combination with other shrubs such as *Chrysothamnus* or *Purshia* forms a rather distinctive community. Seasonal precipitation in this community ranges from 8 to 15 inches, some of this falling as winter snow, and it has a growing season ranging from 3 to 6 months, depending on elevation and latitude. It is frequently found adjacent to Pinyon-Juniper Woodland, and frequently there is considerable intermixing of the two communities.

The butterfly species composition of this community is fairly consistent throughout large areas of the Great Basin, and many species or subspecies are found primarily within this community. The butterfly species of this community are largely univoltine, with peak flight activity occurring during the late spring and early summer months.

39. MOUNTAIN SAGEBRUSH SCRUB

DOMINANT OR CHARACTERISTIC PLANTS

Artemisia arbuscula nova, *A. tridentata*, *Eriogonum ovalifolium*, *Leptodactylon pungens*, *Arenaria kingii glabrescens*, *Erigeron clokeyi*, *Hymenoxys cooperi*, *Linanthus nuttallii*, *Koeleria macrantha*, *Sitanion hystrix*, and *Stipa pinetorum*.

BUTTERFLY FOODPLANTS

Castilleja chromosa, *Chamaebatiara millefolium*, *Chrysothamnus viscidiflorus*, *Eriogonum umbellatum*, *Lupinus argenteus tenellus*, *Stipa pinetorum*.

CHARACTERISTIC BUTTERFLIES

Cercyonis oetus oetus, *Neominois ridingsii pallidus*, *Euphydryas anicia wheeleri*, *Chlosyne acastus waucoba*, *Callophrys lemberti*, *Celastrina argiolus near cinerea*, *Glaucopsyche lygdamus near oro*, *G. piasus nevada*, *Lycaeides melissa fridayi*, *Icaricia icarioides albihalos*, *Hesperia uncas macswaini*.

DISCUSSION

This montane scrub community is basically a high-altitude version of Great Basin Sagebrush Scrub, but with differing percentages of dominant plants, as well as a marked decrease in the overall height of the low shrubs which make up the ground cover. This community ranges in elevation from about 8,000 to nearly 13,000 feet, and is found primarily in the White Mountains, the Inyo Mountains, the Panamint Range, the Warner Mountains, and in certain high-elevation localities on the east slope of the Sierra Nevada. It has a short growing season and is subject to rather rigorous weather conditions, including high winds, occasionally deep winter snows, and relatively low seasonal precipitation on the average.

Its butterfly species composition is similar to that of the lower elevation, more mesic Great Basin Sagebrush Scrub, but tends to have fewer species overall.

40. BLACKBRUSH SCRUB

DOMINANT OR CHARACTERISTIC PLANTS

Coleogyne ramosissima; frequently associated species are *Grayia spinosa*, *Larrea divaricata tridentata*, *Lycium andersonii*, *Mendora spinescens*, and species of *Ephedra* and *Yucca*.

BUTTERFLY FOODPLANTS

Arabis pulchra, *Castilleja chromosa*, *Caulanthus cooperi*, *C. lasiophyllus*, *Xylorhiza tortifolia*, *Yucca* species.

CHARACTERISTIC BUTTERFLIES

Pontia sisymbrii nigravenosa, *Euchloe hyantis lotta*, *Anthocharis cethura hadromarmoratus*, *A. c. mojaviensis*, *A. sara thoosa*, *Thessalia leanira alma*, *Charidryas acastus neumogeni*, *Megathymus yuccae maudae*.

DISCUSSION

This community consists of a low scrub dominated by Blackbush, *Coleogyne ramosissima*, and is found on semi-arid, stony soils at moderate elevations in both the Death Valley region and eastern Mojave Desert. The butterfly species associated with it also occur in the adjacent desert plant community.

41. JOSHUA TREE WOODLAND

DOMINANT OR CHARACTERISTIC PLANTS

Yucca brevifolia; frequently associated with it are species of *Cassia*, *Eriogonum*, *Krameria*, *Lycium*, *Salazaria*, *Tetradymia*, *Opuntia*, and other species of *Yucca*.

BUTTERFLY FOODPLANTS

Arabis pulchra, *Bouteloua gracilis*, *Cassia armata*, *Caulanthus cooperi*, *C. lasiophyllus*, *Descurainaea pinnata*, *Lepidium fremontii*, *Stanleya pinnata*, *Thamnosma montana*, *Yucca brevifolia*.

CHARACTERISTIC BUTTERFLIES

Papilio polyxenes color, *Pontia protodice*, *P. beckerii*, *P. sisymbria nigravenosa*, *Euchloe hyantis lotta*, *Anthocharis cethura mojaviensis*, *A. sara thoosa*, *Thessalia leanira alma*, *Charidryas acastus neumoegei*, *Glaucopsyche lygdamus deserticola*, *Euphilotes rita elvirae*, *Megathymus yuccae martini*, *Hesperia pahaska martini*.

DISCUSSION

The tree-like yucca, *Y. brevifolia*, forms a rather distinctive open woodland in the higher deserts of the state, from the mountains of Joshua Tree National Monument northward to the Owens Valley and Death Valley region. Numerous small shrubs are associated with the Joshua Tree, as well as many perennial grasses and numerous annuals. This community is frequently transitional with other desert plant communities, such as Pinyon-Juniper Woodland, Great Basin Sagebrush Scrub, Blackbrush Scrub, etc.

The butterflies associated with this community tend to be spring-fliers, but there is a second peak of flight activity in the late summer and early fall months, particularly in years of summer rainfall.

42. MIXED DESERT SCRUB

DOMINANT OR CHARACTERISTIC PLANTS

Eriogonum fasciculatum *polifolium*, *Larrea*, *Ephedra* spp., *Ambrosia dumosa*, *Atriplex* spp., *Lycium* spp., *Prunus fasciculata*, *Sphaeralcea ambigua*, *Yucca* spp., *Haplopappus linearifolius*.

BUTTERFLY FOODPLANTS

Arabis spp., *Castilleja chromosoma*, *Caulanthus cooperi*, *C. lasiophyllus*, *Cymopterus panamintensis acutifolius*, *Descurainaea pinnata*, *Eriogonum fasciculatum*, *E. pusillum*, *Lotus rigidus*, *Parietaria floridana*, *Sphaeralcea ambigua*, *Thamnosma montana*, *Viguiera deltoidea*, *Xylorhiza tortifolia*, *Yucca schidigera*.

CHARACTERISTIC BUTTERFLIES

Papilio polyxenes coloro, *P. indra fordii*, *Pontia protodice*, *P. sisymbrii nigravenosa*, *Euchloe hyantis lotta*, *Anthocharis cethura* near *hadromarmoratus*, *A. c. mojaviensis*, *Chlosyne californica*, *Charidryas acastus neumogeni*, *Euphilotes battoides martini*, *E. mojave*, *Megathymus yuccae maudae*, *Pyrgus albescens*, *Heliopetes ericetorum*.

DISCUSSION

This name we have coined for a rather extensive desert scrub community which is usually lumped with Creosote Bush Scrub. It is probably similar to the concept of Thorn's (1976) non-basic rock plant subcommunity of his Desert Rock Plant community. But we consider it to cover more extensive habitats. As conceived here, this community consists of a low scrubland community, primarily occupying slopes of the desert mountains, above the Creosote Bush Scrub Community of the flatlands and valley bottoms, but below the other desert plant communities such as Blackbush Scrub, Joshua Tree Woodland, and Pinyon-Juniper Woodland. Creosote Bush (*Larrea*) is usually present in this community, but tends to occur only as scattered plants, in contrast to the "denser" stands of this species on the flatlands below. This community occupies large areas of the Mojave Desert, as well as some of the lower elevations of the Death Valley region, the east slopes of the Sierra Nevada in Inyo County, and the higher elevations of the Colorado Desert.

The butterfly species composition of this community is similar to that of the other desert plant communities.

43. CALCICOLOUS DESERT SCRUB

DOMINANT OR CHARACTERISTIC PLANTS

Agave utahensis nevadensis, *Artemisia bigelovii*, *Buddleia utahensis*, *Cercocarpus intricatus*, *Fendlerella utahensis*, *Forsellesia nevadensis*, *Petrophytum caespitosum*, and *Symphoricarpos longiflorus*, and such herbs as *Arabis perennans*, *Brickellia arguta*, *Cymopterus aboriginum*, *Eriogonum intrafractum*, *Hedeoma nana californica*, *Hofmeistera pluriseta*, *Maurandya petrophila*, *Parietaria floridana*, *Penstemon calcareus*, *Phacelia rotundifolia*, *Salvia funerea*, and *Scophulophila rixfordii*.

BUTTERFLY FOODPLANTS

Agave deserti, *A. utahensis*, *Arabis perennans*, *Castilleja chromosa*, *Caulanthus glaucus*, *Eriogonum heermannii*, *Maurandya antirrhiniflora*, *Petrophytum caespitosum*, *Purshia stansburiana*, *Thamnosma montana*, *Yucca schidigera*.

CHARACTERISTIC BUTTERFLIES

Papilio polyxenes coloro, *Pontia sisymbrii nigravenosa*, *Euchloe hyantis lotta*, *Thessalia leanira alma*, *Incisalia fotis mojavensis*, *Callophrys comstoki*, *Celastrina argiolus near cinerea*, *Euphilotes battoides euromojavensis*, *Megathymus yuccae maudae*, *Agathymus alliaea* ssp., *A. baueri* ssp.

DISCUSSION

This desert scrub community is similar in appearance to the Mixed Desert Scrub community, but has a different plant species composition as a result of its location on Calcareous rock substrates (limestones, marbles, and dolomites). Many of the plants of this community are confined to calcareous substrates, but desert species from other soil substrates are also found mixed with this flora. It is found in scattered localities primarily in the eastern Mojave and Death Valley region mountain ranges, from approximately 3,000 to 8,000 feet elevation. At least one butterfly species (*Agathymus alliaea*) is confined to this community due to the restriction of its foodplant to calcareous substrates, and several other desert butterfly species are found primarily in this plant community as a result of their foodplants growing in abundance on this particular substrate.

44. CREOSOTE BUSH SCRUB

DOMINANT OR CHARACTERISTIC PLANTS

Larrea divaricata tridentata; often accompanied by *Ambrosia dumosa*, *Atriplex* spp., *Ceratoides lanata*, *Dalea* spp., *Encelia farinosa*, *Eriogonum inflatum*, *Fouquieria splendens*, *Grayia spinosa*, *Hymenoclea salsola*, *Lepidium fremontii*, *Lycium* spp., *Menodora spinescens*, *Sphaeralcea ambigua*, along with scattered *Yuccas* and various cacti of the genera *Echinocereus*, *Ferocactus*, and *Opuntia*. Also annuals and perennials in the genera *Abronia*, *Astragalus*, *Camissonia*, *Chaenactis*, *Chorizanthe*, *Coreopsis*, *Cryptantha*, *Eriogonum*, *Eriophyllum*, *Gilia*, *Linanthus*, *Malacothrix*, *Mentzelia*, *Nama*, and *Oenothera*.

BUTTERFLY FOODPLANTS

Amsinckia spp., *Asclepias erosa*, *Caulanthus cooperi*, *C. lasiophyllus*, *Cleome isomeris*, *Cryptantha* spp., *Descurainaea pinnata*, *Eriogonum fasciculatum polifolium*, *E. inflatum*, *E. pusillum*, *E. reniforme*, *Geraea canescens*, *Hilaria rigida*, *Lepidium fremonti*, annual *Lupinus* spp., *Palafoxia linearis*, *Sphaeralcea ambigua*, *Streptanthella longirostris*, *Viguiera deltoidea*, *Xylorhiza tortifolia*.

CHARACTERISTIC BUTTERFLIES

Pontia protodice, *P. beckerii*, *Euchloe hyantis lotta*, *Anthocharis cethura hadromarmoratus*, *A. c. mojavenensis*, *A. c. pima*, *Nathalis iole*, *Danaus plexippus*, *D. gilippus*, *Vanessa cardui*, *V. annabella*, *Chlosyne californica*, *Charidryas acastus neumogeni*, *Apodemia mormo deserti*, *Euphilotes battoides martinia*, *E. mojave*, *Copaeodes aurantiaca*, *Pyrgus albescens*.

DISCUSSION

On the valley floors, flatlands, and bajadas of the California deserts, from near sea level up to approximately 4500' elevation, there is an extensive scrub community dominated by the shrub, *Larrea divaricata tridentata*. Although *Larrea* is the dominant plant of this community, there are numerous small shrubs growing with it, as well as many smaller perennials and numerous annuals which, in years of favorable winter rainfall, can become a mass of color in an extensive spring bloom. Following summer rains, there may also be a similar but less spectacular bloom of summer annuals, which are of different species than those triggered by winter rains. Most rainfall in this community falls during the winter months, and even then tends to be variable and unreliable from year to year. In some dry years, virtually no precipitation whatsoever falls, and that particular season may be devoid of butterfly species. Winters are cool, frequently windy, and summers tend to be very hot and punctuated by only rare thunderstorms.

Not surprisingly, virtually all butterfly flight activity occurs during the spring months, with a peak in late March or early April. For a few species of this community, a late summer or fall brood may be triggered by summer rains.

45. SEMI-SUCCULENT SCRUB

DOMINANT OR CHARACTERISTIC PLANTS

Agave deserti, *Nolina* spp., *Yucca schidigera*, *Ferocactus acanthodes*, *Fouquieria splendens*, *Larrea*, *Encelia farinosa*.

BUTTERFLY FOODPLANTS

Agave deserti, *Yucca schidigera*.

CHARACTERISTIC BUTTERFLIES

Megathymus yuccae ssp. (western edge Colorado Desert), *Agathymus stephensi*.

DISCUSSION

This desert scrub community occurs primarily on the rocky upland slopes of the desert mountains in the Colorado Desert, and is dominated by semi-succulent species in the genera *Agave*, *Nolina*, and *Yucca*. It is more likely to receive summer rain, and in fact approximately half of the rather limited annual precipitation in this community falls during the summer months. The number of butterfly species found in this community is rather limited, with two of the most characteristic skipper species using the *Agave* and *Yucca* species as foodplants. One of these species is a spring-flier, while the other is a fall-flier, and neither seems to be influenced greatly by differences in annual precipitation, in contrast to virtually all other desert butterfly species.

46. DESERT MICROPHYLL WOODLAND

DOMINANT OR CHARACTERISTIC PLANTS

Acacia greggii, *Cercidium floridum*, *Dalea spinosa*, *Olneya tesota*, *Prosopis glandulosa torreyana*, *P. pubescens*, *Chilopsis linearis*, *Hyptis emoryi*, and *Larrea*. Smaller shrubs include *Calliandra eriophyllum*, *Cassia armata*, *Hoffmannseggia microphylla*, *Baccharis sarothroides*, *Condalia lyvioides*, *Hymenoclea monogyra*, and *Lycium andersonii*.

BUTTERFLY FOODPLANTS

Acacia greggii, *Asclepias subulata*, *Bebbia juncea*, *Calliandra eriophyllum*, *Cassia armata*, *Hibiscus denudatus*, *Hoffmannseggia microphylla*, *Justicia californica*, *Palafoxia linearis*, *Phoradendron californicum*, *Prosopis glandulosa*.

CHARACTERISTIC BUTTERFLIES

Eurema nicippe, *Nathalis iole*, *Danaus gilippus*, *Dymasia dymas imperialis*, *Calephelis wrighti*, *Ministrymon leda*, *Atlides halesus*, *Strymon columella*, *Leptotes marina*, *Hemiargus isola alce*, *H. ceraunus gyas*, *Systasea zampa*, *Erynnis funeralis*.

DISCUSSION

This community is characterized by concentrations of Fabaceous desert shrubs located primarily along washes and other desert watercourses or drainageways, and is found primarily in the inter-mountain valleys of both California deserts, primarily below 5,000' elevation. Virtually all the butterfly species associated with this community are also found in the subtropical thorn forests of Mexico, and represent a northern extension of the ranges of those species. Some of these species may not be resident in many of the desert localities in which they have been recorded; considerable fluctuation in abundance occurs from year to year, and undoubtedly some populations are reintroduced by migrants from more permanent populations to the south. There is no high concentration of flight activity in one particular season of the year as there is with the often adjacent Creosote Bush Scrub plant community butterfly species; due to the variations in blooming times of some of the different butterfly foodplants of this community, as well as variations in winter and summer precipitation, as well as considerable fluctuations in numbers of immigrants from populations outside the area, no distinctive pattern of flight activity seems apparent from year to year. In drier years, much of the flight activity seems to concentrate in the late spring and early summer months, whereas in years with heavy summer rains, there may be increasing abundance of species throughout the summer months with a peak abundance reached in the fall months.

47. DESERT RIPARIAN WOODLAND

DOMINANT OR CHARACTERISTIC PLANTS

Platanus racemosa (of western desert margins), *Populus fremontii*, *Salix gooddingii*, *S. laevigata*, *Fraxinus velutina*, *Baccharis sergiloides*, *Washingtonia filifera*, *Pluchea sericea*, *Phragmites australis*, *Arundo donax*, and species of *Typha* and *Baccharis*.

BUTTERFLY FOODPLANTS

Atriplex canescens, *Baccharis glutinosa*, *Phoradendron californicum*, *P. flavescens macrophyllum*, *Populus fremontii*, *Prosopis glandulosa*, *P. pubescens*, *Salix* spp., *Sesbania exaltata*.

CHARACTERISTIC BUTTERFLIES

Limenitis archippus obsoleta, *Apodemia palmerii*, *Calephelis nemesis dammersi*, *Atlides halesus*, *Plebulina emigdionis*, *Erynnis funeralis*.

DISCUSSION

This desert woodland community is found primarily along the Colorado and Mojave Rivers, and to a lesser extent near the Salton Sea and along irrigation canals in the Imperial Valley. Numerous butterfly species, many as strays, have been taken in this type of habitat, but are not "native" to it, having been attracted to it and concentrated around it primarily by the presence of water and therefore nectar sources. However, there are a small number of species which seem regularly associated with it and are dependent on foodplants requiring this habitat. Much of the riparian woodland along the Colorado River has been greatly disturbed by various dam projects and other extensive changes along that particular watercourse, and much of the vegetation which is presently represented there is the result of considerable man-made disturbances.

48. SHADSCALE SCRUB

DOMINANT OR CHARACTERISTIC PLANTS

Atriplex confertifolia, *Grayia spinosa*, *Ceratoides lanata*, *Haplopappus acradenius*, *Kochia californica*, *Artemisia spinescens*, *Menodora spinescens*, *Gutierrezia sarothrae*, and *Coleogyne ramosissima*.

BUTTERFLY FOODPLANTS

Atriplex confertifolia, *Caulanthus cooperi*, *C. lasiophyllus*, *Descurainia pinnata*.

CHARACTERISTIC BUTTERFLIES

Euchloe hyantis lotta, *Anthocharis cethura hadromarmoratus*, *Brephidium exilis*, *Pholisora libya lena*.

DISCUSSION

This is an extensive desert scrub community of primarily alkaline soils, found in extensive stands in the Owens Valley region and in scattered areas within the Mojave Desert. It forms rather monotonous stands on valley bottoms, flats, or gentle slopes, which usually have an alkaline, heavy soil, usually with a shallow hard pan beneath. The average rainfall in these areas ranges from 3 to 7 inches, and elevation ranges from 3,000 to 6,000'.

From a butterfly species' standpoint, this is a rather depauperate community, with only a few species (and their associated foodplants) able to tolerate the adverse environmental conditions.

49. ALKALI SINK SCRUB

DOMINANT OR CHARACTERISTIC PLANTS

Atriplex spp., *Salicornia subterminalis*, *Suaeda depressa*, *S. torreyana*, *Sarcobatus vermiculatus*, *Allenrolfea occidentalis*, *Nitrophila occidentalis*, *Frankenia grandifolia campestris*, *Delphinium recurvatum*, *Heliotropium curassavicum*, *Lepidium dictyotum*, *Sesuvium verrucosum*, and *Wislizenia refracta*. (Beatley, 1971; Hunt, 1966; Ornduff, 1974; Parish, 1913; Twisselmann, 1956, 1967).

BUTTERFLY FOODPLANTS

Atriplex canescens, *A. lentiformis*, *Caulanthus lasiophyllus*, *Sesuvium verrucosum*, *Sphaeralcea* spp., *Suaeda* spp.

CHARACTERISTIC BUTTERFLIES

Anthocharis cethura morrisoni, *Vanessa annabella*, *Brephidium exilis*, *Pyrgus scriptura*, *Pholisora libya libya*, *P. l. joaquina*, *P. l. lena*, *P. graciellae*.

DISCUSSION

This is another desert scrub community found on alkaline soils, generally below the Shadscale Scrub Community. It is found on valley sinks, flats, and playas, or along watercourses where there is very poor drainage and the soil is highly alkaline, from the Colorado and Mojave Deserts northward to the Death Valley region and the San Joaquin Valley. There is more subsoil moisture in this plant community, and it is subject to greater extremes of temperature and lower precipitation than is the Shadscale Scrub Community.

As with the Shadscale Scrub Community, only a few butterfly species are able to tolerate the severe environmental conditions of this community and are able to use as foodplants several of the specially-adapted plant species.

50. ALKALI MEADOW

DOMINANT OR CHARACTERISTIC PLANTS

Distichlis spicata stricta, *Muhlenbergia asperifolia*, *Phragmites australis*, *Sporobolus airoides*, *Juncus cooperi*, *J. mexicanus*, *Scirpus nevadensis*, *S. olneyi*, *S. paludosus*, *Allenrolfea occidentalis*, *Anemopsis californica*; also often present are *Aster frondosus*, *Cressa truxillensis vallicola*, *Hemizonia pungens*, *Cordylanthus canescens*, and *Sida leprosa hederacea*.

BUTTERFLY FOODPLANTS

Distichlis spicata stricta, *Phragmites australis*, *Prosopis glandulosa* and *P. pubescens* (at borders), and *Sida leprosa hederacea*.

CHARACTERISTIC BUTTERFLIES

Cercyonis pegala stephensi, *Apodemia palmerii*, *Pseudocopaeodes eunus* (all ssp.), *Polites sabuleti sabuleti*, *P. s. chusca*, *P. s. alkaliensis*, *Ochlodes yuma yuma*.

DISCUSSION

The desert meadow lands of this community are located on perennially moist, alkaline, heavy soils, usually in valley sinks and near springs and seeps in the desert with relatively poor drainage. These meadows are often dominated by salt grass (*Distichlis spicata stricta*), with a number of other halophytic species present. Such habitats are scattered through the California desert regions, from the Colorado Desert northward to the Mono Basin, as well as in the southern Great Central Valley region. Similar habitats are found in the Modoc Plateau area such as at Honey Lake or in the large alkaline valleys east of the Warner Mountains.

The constellation of associated butterfly species differs from that of the Alkali Scrub communities; frequently species from adjacent plant communities are observed within this community, usually attracted by moisture or nectar sources.

51. AGRICULTURAL

DOMINANT OR CHARACTERISTIC PLANTS

Various agricultural crops, and many introduced weeds.

BUTTERFLY FOODPLANTS

Asclepias eriocarpa, *A. fascicularis*, *Brassica oleracea*, other *Brassica* spp., *Citrus* spp., *Cynodon dactylon*, *Daucus carota*, *Gossypium herbaceum*, *Helianthus annuus*, *Malva* spp., *Matthiola incana*, *Medicago sativa*, *Oryza sativa*, *Phaseolus* spp., *Prunus* spp., *Raphanus sativus*, *Sorghum* spp., *Urtica urens*, *Zea mays*.

CHARACTERISTIC BUTTERFLIES

Papilio zelicaon, *P. cresphontes*, *Pontia protodice*, *Pieris rapae*, *Colias eurytheme*, *Danaus plexippus*, *Vanessa atalanta*, *V. cardui*, *V. annabella*, *Chlosyne lacinia crocale*, *Strymon melinus*, *Hemiargus isola alce*, *H. ceraunus gyas*, *Nastra julia*, *Lerodea eufala*, *Urbanus proteus*.

DISCUSSION

Although this is an artificial, man-made "community," the agricultural areas of the state support various butterfly species, usually weedy or introduced species, but sometimes native species which have flourished as the result of a foodplant being used as an agricultural crop or a plant that has become abundant in agricultural habitats as a result of the frequent soil disturbances, irrigation, etc.

While some of the butterfly foodplants that we list under this community are farm crops, some of them are plants which have become abundant as exotic weeds or native weedy species. An example of this is *Asclepias eriocarpa* and *A. fascicularis*, two native milkweed species which have become abundant in the Great Central Valley in disturbed soils, particularly in areas subject to repeated grazing or certain types of grain farming. As a consequence, the Monarch, *Danaus plexippus*, has probably become more abundant within that general region, at least during the summer months. In the desert agricultural areas such as the Imperial Valley, or in the Blythe region of eastern Riverside County, Bermuda grass (*Cynodon dactylon*) has become abundant along irrigation canals and in other types of watercourses or drainage sinks, or along the edges of irrigated fields. As a consequence, several skipper species which utilize this grass have become more abundant in these regions.

Changes in farming patterns over time can also result in a marked change in species composition in particular agricultural areas. In the early part of this century, farming along the southern California coast was extensive, and at one time there were many acres of bean fields (*Phaseolus* species) in Orange County; at that time, the skipper *Urbanus proteus* was frequently taken in that area. Now that most of Orange County has become urbanized, the skipper is an extremely rare catch in that area.

52. URBAN-SUBURBAN

DOMINANT OR CHARACTERISTIC PLANTS

Mostly various exotic species; rarely natives such as *Ceanothus* spp., *Eriogonum* spp., *Platanus* spp., *Fraxinus* spp., etc.

BUTTERFLY FOODPLANTS

Althaea rosea, *Antirrhinum* spp., *Canna* spp., *Cassia* spp., *Citrus* spp., *Cynodon dactylon*, *Ehrharta erecta*, *Eriogonum* spp., *Festuca* spp., *Foeniculum vulgare*, *Fraxinus* spp., *Hibiscus* spp., *Lippia nodiflora*, *Malva* spp., *Passiflora* spp., *Plumbago capensis*, *Poa pratensis*, *Populus* spp., *Prunus* spp., *Robinia* spp., *Salix babylonica*, *Soleirolia soleirolii*, *Tropaeolum majus*, *Ulmus pumila*.

CHARACTERISTIC BUTTERFLIES

Papilio zelicaon, *P. rutulus*, *Pieris rapae*, *Phoebis sennae*, *Eurema nicippe*, *Junonia coenia*, *Vanessa atalanta*, *V. cardui*, *V. annabella*, *Nymphalis antiopa*, *Phyciodes phaon*, *Dione vanillae*, *Strymon melinus*, *Leptotes marina*, *Hylephila phyleus*, *Polites sabuleti sabuleti*, *Atalopedes campestris*, *Calpodus ethlius*, *Epargyreus clarus californicus*.

DISCUSSION

The urbanized areas of the state support a number of native and non-native butterfly species, as a result of various foodplants being used for landscaping. The numerous lawns of our urban and suburban areas support vast numbers of certain skipper species, particularly *Hylephila phyleus* in the southern two-thirds of the state. This skipper was probably not native to the state before the first settlers came, but it is now one of the most abundant butterflies of the California lowlands.

Changes in landscaping patterns also influence the species composition of butterflies within the urban and suburban areas. In the early part of this century, various *Cassia* species were widely used as ornamentals, and the Cloudless Sulfur (*Phoebis sennae*) was abundant in the Los Angeles area for many years. This particular genus of ornamentals apparently fell into disfavor in the 1930's and 1940's, and other exotic shrubs were more commonly used, and this species has become more and more scarce in the urbanized areas of southern California.

Chapter 5

PATTERNS OF GEOGRAPHY AND SPECIES DIVERSITY IN THE STATE OF CALIFORNIA

In this chapter, we shall attempt to discern the overall patterns of species diversity among the butterflies of California. First, we shall look at the natural landscape and geography of the state, to give us the proper background to understand how these patterns of species diversity correlate with geographical features of the state and surrounding source regions, as well as internal centers of endemism. Second, we shall look at the origins of the California fauna, with particular attention to historical factors and floral biodiversity factors that have undoubtedly contributed to making the California butterfly fauna assume the composition it has today. Third, we shall look at the centers of endemism for butterflies in the state: in other words, the areas that have the largest concentrations of endemic species and subspecies found nowhere else in the United States or the world. Finally, we shall look at the present patterns of distribution and diversity among all the butterfly groups in the state, and map these to ascertain critical habitat areas that should have special attention from conservationists and habitat preservationists.

THE NATURAL LANDSCAPE AND GEOGRAPHY OF CALIFORNIA

California offers incredible contrasts of landscape and physical diversity in its vast geographic extent. One can visit climates here as varied as the Sahara Desert and the Arctic Circle. Rainfall extremes range from 174 inches in the northwest to near traces in the southeastern desert. Yet coastal temperatures and rainfall may be quite moderate, a factor which has led to a concentration of human settlements along the coast for centuries. In such regions, freezing temperatures are rare or absent, and tropical and subtropical plants can be grown with ease.

Coast Ranges

The famous long coastline of California is surprisingly mountainous the intertwined and rather indistinct chains of coastal mountains range from 20-40 miles in width and from 2,000 to 8,000 feet in height. Three major natural harbors, at San Diego, San Francisco and Eureka, are surrounded by hills of lower height. The less-developed northern coast has many creeks and rivers flowing from the Coast Ranges, and this is the home of the coastal redwood forest and Redwood National Park. These coastal redwood trees are among the tallest in the world and have individual specimens that may exceed 300 feet in height, be up to 35 feet in diameter, and exceed 4,000 years in age. Prior to European settlement, the redwoods covered an estimated 1,500,000 acres (607,000 hectares) of California. Most of these redwood forests are gone today, having been cut for lumber, but 109,000 acres of redwoods are still protected in state and national parks.

In southern California, the Coast Ranges move somewhat inland, bordering a valley in the Los Angeles area from 40-60 miles inland. North of Los Angeles, the Coast Ranges move closer to shore and the population becomes sparser until one reaches the San Francisco Bay cities.

Sierra Nevada

On the eastern side of the state, bordering Nevada, lies the majestic Sierra Nevada Range, extending north-south for some 430 miles. The eastern escarpment of this range is sheer, dropping some 10,000 feet within ten miles near Owens Lake. On the western side, however, the range slopes more gently to the Central Valley in gradually declining foothills. Arising near volcanic Lassen Peak in the north, the Sierra Nevada extends south to the fringes of Los Angeles. It is approximately 50-80 miles in width and contains about 27,000 square miles of area in its 430 mile length. Mt. Whitney, the highest point in the continental United States, and ten other peaks exceed 14,000 feet in altitude. Very few passes cross from east to west over the Sierras and several of these occur at more than 9,000 feet elevation. The largest lake in the Sierra Nevada is Lake Tahoe, extending across the California-Nevada border at 6,229 feet above sea level. It is almost 200 square miles in area, and is remarkably deep, with the maximum depth exceeding 1,600 feet. Throughout the Sierra lie hundreds of smaller lakes, many above timberline in regions of tumbled granite and smooth walled canyons. There are three great national parks in these mountains: Kings Canyon, Sequoia, and Yosemite, the last being particularly famous for its glacier-carved valleys of the Merced and Tuolumne Rivers, with their many waterfalls and granite domes.

Central Valley

Between the coastal ranges and the Sierra Nevada, the great Central Valley runs for 450 miles in a north-south arc. Once a paradise of flowers and natural grassland, with scattered oaks, today the Valley constitutes the state's agricultural heartland. Its single exit is the delta through which the Sacramento and San Joaquin Rivers drain into San Francisco Bay. The northeastern edge is bordered by the Cascade Range and the northwestern edge by the Klamath Mountains. In these northern areas, few people live and the terrain is quite rugged and heavily timbered. The coastal sides of the Cascade and Klamath Mountains tend to be wet, while the northeastern sides are drier and more barren of vegetation. At the southern end, the Central Valley is closed off by the several Transverse Ranges, especially the Tehachapi Mountains. The Tehachapis are regarded as a dividing line wall between southern and central California.

Deserts

The deserts of eastern and southeastern California are quite varied in vegetation and topography. The Colorado Desert of southeastern California has summer temperatures of up to 130° F (54° C), with annual rainfall averaging 3-4 inches. Much of this desert area lies below sea level. The inland Salton Sea (300 square miles in area) is entirely below sea level and was created in 1905-1907 when the Colorado River broke out of its channels and poured into an interior desert basin with no outlet. Northward, in the higher Mojave Desert, which can range 3,000 to 4,000 feet on the desert floor and up to 7,000 feet or so above sea level in the mountain ranges there, temperatures are somewhat less extreme. This area of more than 25,000 square miles reaches from the Tehachapi and the Sierra Nevada to the Colorado River, and is still relatively untouched by development. Mining companies, military reservations and aviation test facilities have disturbed some areas. The eastern Great Basin Desert area lying in the eastern rainshadow of the Sierra Nevada Range rises from 2,000 to 7,400 feet above sea level and has temperatures ranging from 75° F (24° C) in the summer to -25° F (-32° C) in the winter.

All of these geographic regions of the state collectively represent a varied natural landscape, one in which butterflies of all groups have found hospitable niches to inhabit and evolve

new and marvelous forms that we find today. The unique geographic diversity of California has thus contributed directly towards generating the exceptional butterfly species diversity found in the state.

ORIGINS OF THE CALIFORNIA BUTTERFLY FAUNA

ORIGINS OF HOSTPLANT FLORAL ELEMENTS

The origins of the California butterfly fauna are related in substantial part to the geoflora sources generating the diverse plant assemblages found in the state. First, as noted in the preceding chapter, many relic plant groups from the Tertiary Period (63 to 2 million years ago) of the Cenozoic Era have survived in the California Floristic Province because of the mild climate of the region and its relative insulation from the extremes of the continental climate for the past million years or so. Additionally, there has been a substantial interplay between the mesic (moisture-loving) floral elements derived from the Arcto-Tertiary Geoflora with the xeric (dry-loving) floral elements associated with the Madro-Tertiary Geoflora. With the great topographic relief and varied soil conditions in this region, many new combinations of plants could evolve in new community relationships. Third, some of the more important genera that are butterfly foodplants, such as *Lupinus* and *Penstemon*, have shown substantial bursts of speciation and clusters of species have been preserved in limited areas of the region. Some of the plants (about 15% of the species in the California Floristic Province) appear to have radiated into our state from the deserts of other, more southern parts of North America (e.g., species of the family Malvaceae). Many families of flowering plants seem to have come in an ultimate sense from South America to North America (Raven and Axelrod, 1974: 627-628; Raven, 1988). These include many of the legumes and such families as the Lauraceae (hosts of some of our swallowtails) and Asteraceae (hosts of a number of our nymphalids). Additionally, there are some similarities existing between the floras of the Mediterranean region and California, which in part have had their origins via differentiation from a common northern flora, including such important butterfly host genera as *Juniperus*, *Populus*, *Prunus*, *Rhamnus*, and even *Pinus* and *Quercus*.

Nonetheless, the unique character of the flora of California has been stressed by many workers. Consider that, within the California Floristic Province alone, some 58 genera (7.5% of the total genera) and 2133 of the 4427 species (48%) are endemic. However, taking a broader view and looking at the ultimate sources of the flora, Raven (1988) feels that "it is clear that the flora of California can be regarded as comprising two elements: a northern, or Arcto-Tertiary, and a southern, or Madro-Tertiary, element." Because the Mediterranean climate had developed after the mid-Pliocene (see Chapter 2) in the broad ecotone area occurring between these fundamentally different vegetation types, a further stimulus for the proliferation of species and even some genera was present. During relatively recent times (the last 10,000 years), additional plants from the drier parts of the Madro-Tertiary region have entered the California Floristic Province and especially colonized the drier valleys of cismontane to southern California, the San Joaquin Valley, and the inner South Coast Ranges, evolving a number of endemic species in that region.

But the influences on the California flora are not restricted solely to those contributing to the origins of plants within the California Floristic Province. After all, while that province comprises about 75% of the state's area (with some 744 of the 875 genera [85%] and 4,119 of the 5,057 species [81%] found in the state), we also have a large number of genera (approximately 131) and 938 species that occur only east of the Sierra Nevada mountains and on the deserts, but still within the boundaries of California. Stebbins and Major (1965) have pointed out that among 10 biotic subdivisions statewide, there are four distinct transmontane regions in the eastern and southeastern portions of California with affinities outside the state. These are shown in Figure 5-

1. These vegetational areas each have had an impact on the influence of extra-California butterfly faunal regions on the state's butterfly fauna, again because of the introduction of larval foodplant elements.

Great Basin Region

The Great Basin Region occupies the northeastern corner of California, including all of Modoc County and portions of Lassen, Shasta, and Siskiyou counties. It also includes the northernmost part of Inyo County above the Owens Valley, and Mono County east of the Sierra Nevada. The flora of this vast region, comprising approximately 22,600 km², is essentially that of the Great Basin, although a number of taxa of the California flora extend beyond the Sierra-Cascade axis to the Warner Mountains and other portions of the Modoc Plateau. While there are only two endemic plants restricted to the northern part of this Great Basin region within California (*Lomatium ravenii* and *Mimulus pygmaeus*), there are at least a dozen or so other endemic species in the southern part. Additionally, both the northern and the southern parts of the Great Basin region in California have over 120 and 147 species, respectively, that do not occur in the California Floristic Province, including 67 and 26 species each that are found nowhere else in the state.

The White Mountains, situated at the southwestern corner of the Great Basin region, contains some 763 native species and varieties (Lloyd and Mitchell, 1973). These latter authors conclude that the White Mountains are a Great Basin Desert range with a flora enriched during the Pleistocene by many boreal elements via the Sierra Nevada Range. These are especially found in alpine and subalpine areas, while other families such as Fagaceae and Ericaceae are absent in the White Mountains. From the south have come various Sonoran and Mojavean taxa.

Inyo Region

The Inyo Region is, as Raven (1988) points out, the richest and most interesting floral region in transmontane California. Here are found some 454 plant species that only occur within this region in California, including at least 43 endemic species. Even some genera are endemic in the Inyo Region, including those in the Death Valley area. Some of the butterfly foodplants and nectar sources occurring in California only in this region include *Buddleia*, *Cowania*, *Enceliopsis*, and *Monarda*. Endemic plants developing on limestone in the deep canyons flanking Death Valley are a particularly important feature of the Inyo Region.

Mojave Desert Region

In the Mojave Desert occur about 757 plant species, of which 22 are endemic. Over 50 of the species in the Mojave Desert are not found in any other part of the state, but range into Nevada or northwestern Arizona. Approximately half of the plant species in the Mojave Desert extend westward to the mountains of southern California, the San Joaquin Valley, or the inner South Coast Ranges, and thus occur in the California Floristic Province as well.

Sonoran Desert Region

The Colorado Desert represents the northwestern arm of the Sonoran Desert, and has about 306 species not found in the California Floristic Province. At least 100 species are included that do not occur elsewhere in the state, and there are at least eight endemic plant species. The Colorado Desert receives summer rain storms, whereas much of the Mojave Desert lacks summer rain, and this factor may restrict a number of desert plants in the California portion of their range to the

Colorado Desert. Accordingly, the butterfly faunas of the Colorado Desert and the Mojave Desert are substantially different, although some butterfly species range northward to the Mojave Desert or even to the Great Basin deserts of Inyo County as well.

ORIGINS OF CALIFORNIA BUTTERFLY FAUNAL ELEMENTS

Paleartic Influence

The butterfly fauna of California contains a sizeable number of species that are very closely related to European butterflies. Many genera and even some species are held in common. For example, the modern genera shared by Europe, northern Asia, and North America include *Papilio*, *Parnassius*, *Colias*, *Pieris*, *Coenonympha*, *Oeneis*, *Vanessa*, *Nymphalis*, *Polygonia*, *Lycaena*, *Ochlodes*, *Erynnis*, and *Hesperia*. We could easily expand this list to include genera which are likely identical, such as *Argynnis*/*Speyeria* and many of the lycaenid groups. The extraordinary similarity among many of the parnassians, fritillaries, ringlets, coppers, hairstreaks and blues is related to the physical connection of the Nearctic (North America) and Palearctic (Europe and northern Asia) regions across the North Pacific by the Bering land bridge and the Aleutian arc islands. All these areas were exposed during Pliocene and Pleistocene periods of lower sea level and heightened glaciation, and butterflies were able to cross from Siberia to Alaska and proceed south down the Cascades and Sierra Nevada Range. The southern limit was reached about the level of the Kern River and Walker Pass. Presumably, many of these species occurred at lower elevations at such times, as glaciers covered much of the high country in the Sierra and the cooler temperatures would have forced hospitable vegetation zones for these northern species lower on the mountains.

Great Basin Influence

Another large element of California's butterfly fauna penetrates from the Great Basin areas. These include many checkerspots of the genera *Euphydryas* and *Chlosyne* (*sensu lato*), *Cercyonis* woodnymphs, the admiral *Limenitis weidemeyerii*, skippers in the genus *Hesperia*, and blues such as *Icaricia icarioides* and *Lycaeides melissa*. These desert-adapted species have frequently undergone phenotypic divergence in both the Great Basin mountain ranges and the elevated desert ranges in California.

Southern Desert Influence

Further to the south, a substantial portion of the butterflies currently in California came in from the Sonoran Desert areas of Arizona and northern Mexico, having foodplant members of the Madro-Tertiary flora. These butterflies, characteristic of desert, grassland, open woodland, and even thorn forests, penetrated the desert regions of southern and eastern California, from the Colorado River west to the cismontane region. Notable faunal elements for the butterflies include the family of giant skippers (Megathymidae). Except for several coastal and interior mountain populations in San Diego County, the megathymids are largely restricted to the Mojave and Colorado deserts in California. Here, too, are found most of the California metalmarks of the family Riodinidae. Only the Mormon Metalmark (*Apodemia mormo*) extends its range as far as the San Francisco Bay area of northern California.

Neotropical Influence

A fourth influence on butterflies has been the invasion of neotropical species, following the introduction of subtropical and tropical plants into California for horticultural use. Our only

representative of the subfamily Heliconiinae, the Gulf Fritillary (*Agraulis vanillae*), has successfully established itself because of widespread plantings of Passionvines (genus *Passiflora*) in landscaping, from the southern border of California to as far north as Redding in the Sacramento Valley. The planting of citrus trees from southeastern California and the Imperial Valley, up into the San Joaquin Valley at least as far north as Porterville in central California, has made possible the expanding introduction of the Giant Swallowtail (*Papilio cresphontes*). Likewise, the planting of *Cassia* shrubs in southern California north to San Jose and Santa Clara County have allowed the range expansion of the Cloudless Sulphur (*Phoebis sennae*) and the Orange Sulphur (*P. agarithe*) from more tropical climes.

Loss of Floral Influences

Concomitantly, the loss of floral elements in certain areas has resulted in extinction of local butterfly fauna. San Francisco on the northern California coast has been extensively surveyed by botanists since the time of the founding of the local Presidio and Mission in 1776. Here was a unique mingling of the north coastal and south interior elements, and a small but impressive group of endemics found nowhere else. Up to 1940, the natural wild areas in San Francisco seemed relatively secure from human destruction, but after World War II, vast housing projects and industrial developments marched up even the steep hillsides of the San Francisco peninsula and much of the floral diversity began to disappear (Howell, Raven, and Rubtsoff, 1958). Far earlier than this, the unique sand dunes areas and their vegetation that supported such unusual endemic butterflies as the Boisduval's Satyr (*Cercyonis sthenele sthenele*) and the Xerces Blue (*Glaucopsyche xerces*) were consumed by the expanding urban areas, and these butterflies became extinct by 1880 and 1941, respectively. Today, other characteristic San Francisco butterflies are going the same way, including the San Bruno Hairstreak (*Incisalia mossii bayensis*) and the Bay Area Checkerspot (*Euphydryas editha editha*).

The unique mild coastal climate of these sand dunes and the shrouded hillsides of the California coastline have given rise to many endemic butterfly species and subspecies. Some are now gone. Others remain, such as the ringlet, *Coenonympha ampelos yontocket*, restricted to a remarkably small area among the coastal sand dunes north of Crescent City in Del Norte County. Consideration of such restricted patterns of distribution and endemism is sufficiently important to be treated in a section of its own.

CENTERS OF PLANT ENDEMISM IN CALIFORNIA

As in the overall distributions of butterfly and plant diversity in California, the centers of endemism for butterflies in the state relate in part to centers of endemism for plants. Stebbins and Major (1965) and Raven (1988) provide excellent summaries of plant endemism in California, from which this overview is taken.

One group of endemic species are the **Paleoendemics**. These plant species are found in relic areas and are the sole representatives of their genera in California or are separated from other species of their genera by considerable geographic distances. The distribution of these relic species is shown in Figure 5-2. Two areas of maximum concentration of relic plant species are obvious. One is in the *Klamath Mountain area* of northern California, adjacent to southwestern Oregon, where Arcto-Tertiary relic plants predominate. The other center for relic species is along the

northern and western margin of the Colorado Desert, from the Little San Bernardino Mountains along the east slope of the San Jacinto and Santa Rosa Mountains, the Borrego Valley area, and southward into Baja California, where Madro-Tertiary relics abound. Axelrod (1966) points out that these two regions represent areas in which relic plant species and genera associated with the Arcto-Tertiary and Madro-Tertiary geofloras have persisted. Thus, as Raven (1988) states, "It has been the interplay between these elements from the Miocene onward that has given the flora of California its richness. Between them, a region of rather low frequency of relic species, compared with the diversity of the flora as a whole, extends from the inner South Coast Ranges to the Tehachapi Mountains. This is an area of active speciation but not of relic endemism."

The other areas of richest endemism in the state identified by Stebbins and Major (1965) in sampling endemic species found in 70 large genera of the California flora. As the numbers on the map in Figure 5-1 show, the areas richest in endemics in these genera are *Southern California*, the *Sierra Nevada*, and the *Central Coast*. The poorest areas are the Central Valley and the desert. A high degree of endemism seems to occur in areas that have a great variety of habitats today and that, during the Pleistocene, at least, were not subjected to such catastrophic changes as glaciation. More endemic plants are found in the low mountain areas than in the very high mountains (Stebbins and Major, 1965; Raven, 1988). Many of the endemics that have developed in California have done so in association with unique edaphic conditions. Thus the restriction of plant taxa to certain soil types is an important feature of the flora in the state of California, and this may be as commonplace as sand dunes along the coast to podsoils in the Pigmy Forest area of Mendocino County or the serpentine and limestone rock regions of the state.

CENTERS OF BUTTERFLY ENDEMISM IN THE STATE

Butterfly endemism in general is associated with the centers of plant endemism in California. These are more finely defined, however, by the fact that butterfly species normally tend to be less widely distributed than their hosts. Thus the Veined Blue, *Icaricia neurona*, is restricted to several localities in the western Transverse Ranges of Southern California, while its larval host, *Eriogonum wrightii*, is a very widely distributed plant. Just to the north of these Ranges occurs another rare endemic blue, *Plubulina emigdionis*, known only from a few colonies; yet its larval host plant, *Atriplex canescens*, enjoys a vast distribution throughout the west. We identify seven centers of butterfly endemism in California.

(1.) First, the *San Francisco Peninsula* had several endemic species and subspecies restricted to the sand dune areas and interior hills along the coast, including *Cercyonis sthenele sthenele* (extinct in 1880), *Glaucopsyche xerces* (extinct in 1941), *Icaricia icarioides pheres* (extinct in San Francisco), and *Parnassius clodius strohebeeni* (last recorded in 1958 from the moist forest areas near the base of the peninsula).

(2.) The second center of endemism was the *El Segundo Sand Dunes and Palos Verdes Peninsula area* of the Los Angeles basin. Here once occurred an extensive sand dune habitat area and coastal mountain-beach interface which supported such species as *Euphilotes battoides allyni* and *Glaucopsyche lygdamus palosverdensis*. At the opposite end of the state in Del Norte and Humboldt counties, and also along the coastline, occur such rarities as the ringlet *Coenonympha*

ampelos yontocket, a relic hairstreak population recently named *Incisalia polios maritima*, and the beautiful dark fritillary *Speyeria hippolyta*

(3.) A third center of differentiation is in the *Transverse Ranges* of southern California. The San Bernardino Mountains represent the site of probable origin for the beautiful California Dogface, *Zerene eurydice*, splitting off in the distant past from the lowland and much more widely distributed North American Dogface, *Zerene cesonia*. The adaptations associated with movement into the cooler mountains and foothills of these inland montane regions may have provided the opportunity for the evolution of this iridescent overlaid pierid. Additionally, *Colias harfordii*, *Euchloe hyantis andrewsi*, hairstreaks such as *Incisalia mossii hidakupa*, *Mitoura thornei*, *Mitoura barryi* subspecies, and *Mitoura loki*, as well as metalmark subspecies of *Apodemia mormo* at various elevations, blues such as *Glaucopsyche piasus gabrielinus*, *Euphilotes battoides vernalis*, all attest to this area's interest as a center of speciation and endemism.

(4.) The fourth center of endemism and evolution for California butterflies has been the *desert mountain ranges of both the Mojave and Colorado deserts*. Virtually every range has its own distinctive subspecies of *Euphydryas chalcedona*. A remarkable number of subspecies and well differentiated populations of *Papilio indra* have developed in these ranges. Many blues and other lycaenids have evolved distinctive subspecies here.

(5.) A fifth center is the *Death Valley region* of California. Here, distinctive subspecies of *Papilio indra* have evolved, along with various desert checkerspots and blues, such as *Chlosyne acastus vallismortis* and *Icaricia icarioides panimentinus*.

(6.) To the north, in the *alpine regions of the White Mountains and Sierra Nevada Range*, we find a sixth center where additional endemic species and subspecies have evolved. Perhaps the most notable is the green-colored sulphur, *Colias behrii*, found nowhere else in the world except in the alpine areas of the highest part of the Sierra. Additionally, the remarkable new species of alpine blue, *Agriades cassiope*, is found nowhere else but in the central and northern Sierra Nevada. The beautiful copper, *Lycaena cupreus periglenes*, is found only on the highest summits of the White Mountains and the Sierra Nevada.

Finally, we should not fail to mention the northeastern corner of California as a seventh center of endemism. Influenced by the Great Basin species fauna but also having unique endemics of its own, the northeastern montane fauna includes the unusual coppers *Lycaena nivalis* and *Lycaena gorgon jacquelinae*, and the checkerspot *Euphydryas editha warnermontana*.

PRESENT PATTERNS OF BUTTERFLY DISTRIBUTION AND DIVERSITY

The present distributional patterns of butterfly species diversity in California are summarized in Figure 5-3. Approximate numbers of endemic species and subspecies found in each area are indicated in parenthesis. This map is derived from the species distributions described in detail in Chapter 8 of the present work.

It is clear from examination of Figure 5-3 with Figure 5-1 that the overall pattern of butterfly diversity approximately parallels the pattern of plant diversity in California. The highest diversity of butterflies is associated with the greatest topographic relief, in the Sierra Nevada Range of northern and central California and the Transverse Mountain Ranges of southern California. The second highest diversity is located along the coast, associated with the various Coast Ranges of the state. A third center of biodiversity is in the northern part of the Great Central Valley of California, well studied by Arthur Shapiro and his students at the University of California at Davis, and Sterling O. Mattoon and a notable group of co-workers, over the years. The fourth center of butterfly biodiversity in the state are the California deserts. Interestingly, the Colorado Desert area has a greater diversity than the Mojave Desert area, perhaps due to the altitudinal restriction and colder winters of the northern desert region. Nonetheless, it is perhaps somewhat surprising that the Great Basin desert regions of Inyo County rank last in biodiversity.

[The above brief discussion is subject to extensive modification after discussion with JFE and SOM, and construction of Figure 5-3 on actual data figures, rather than impressions.]

One area of California not included in the above discussion is the Channel Islands, lying offshore in the Pacific. Their butterfly faunas are sufficiently interesting that we devote a separate short chapter to them (Chapter 6).

CONCLUSIONS

The preceding discussion paints only an overall picture of the patterns of species diversity in the state of California, and formal intensive analysis will occupy future generations of lepidopterists for many years. In one sense, however, it is a race between the developer elements in the state and the naturalists and conservationists to assemble those data before the species are exterminated or extirpated in the more vulnerable regions. Fortunately, generations of lepidopterists who went before us collected across the state and even in early urban areas, such as San Francisco, Los Angeles, and San Diego. By recording their captures in publications and in the form of specimens preserved in public museums today, we can reconstruct the biodiversity present a century ago. Without that huge data base to draw upon, we would have little knowledge of the remarkable species diversity that was once found in the Los Angeles Basin and the San Francisco Bay area.

One does not have to travel to the tropics to see dramatic examples of environmental change and biodiversity loss; they are present right here at home in our own state. The butterflies of California are an eloquent symbol, in many cases, of man's role in changing the natural environment. The great loss to mankind of once-wild places to ill-considered development schemes and environmental degradation is painfully evident even in the loss of this group of colorful wildlife. It is incumbent upon us to not only record what we see today (for who can predict what tomorrow will bring in many of these areas?), but also to work to mitigate the effects of human activities on Lepidoptera populations in California. This last topic is so important that we will cover it in a separate chapter, Chapter 7, when we review extinct and threatened species found in the California butterfly fauna, conservation issues, and prospects for the future.

Chapter 6

THE CALIFORNIA ISLANDS AND THEIR BUTTERFLY FAUNAS

Plant Distribution on the California Islands

The flora of the California Islands is particularly interesting because of the high degree of endemism in 6 major offshore islands as well as smaller islets. Additionally, these islands have served as a refuge for more northern species that extended farther south during the Pleistocene pluvial cycles (Raven, 1963; Raven and Axelrod, 1978). During the late Pleistocene, trees such as Douglas Fir (*Pseudotsuga menziesii*) and the shrub *Ceanothus thyrsiflorus* occurred on Santa Cruz Island whereas today they are restricted to farther north on the mainland.

Several genera particularly reflect a high degree of endemism, most notably the buckwheats in the genus *Eriogonum* (Polygonaceae), the stonecrops in the genus *Dudleya* (Crassulaceae), the Manzanita genus *Arctostaphylos* (Ericaceae), *Malacothris* and *Hemizonia* (Asteraceae), and *Lotus* (Fabaceae), to mention only some of the important foodplants among California butterflies (Wallace, 1985). In the entire Channel Islands group, there are a total of 621 native vascular taxa of plants, including 137 endemics and 227 introduced taxa.

The four principal islands of the northern group include San Miguel, Santa Rosa, Santa Cruz, and Anacapa Island. These islands lie physically closer to each other as well as to the mainland than do the islands of the southern group, which tend to be more widely scattered and further offshore from the mainland of southern California. The characteristics of the flora, the area in square kilometers of the island, and highest altitude in meters above sea level, as well as the distance to the mainland in kilometers, are given in Table 1 for all of the Channel Islands of southern California. Santa Cruz Island, the largest of the Channel Islands of southern California and also very close to the mainland, has 61 native taxa found exclusively on Santa Cruz and the mainland, but it also has 17 of the 19 taxa endemic to more than 1 of the northern islands, showing the close affinities of Santa Cruz to the other islands of the northern group. Santa Rosa Island is also close to the mainland and to Santa Cruz Island. Santa Rosa Island has 27 known endemic native taxa found exclusively on that island and the mainland. In fact, there are only 3 unshared endemic taxa on the island despite its large size, suggesting less isolation than some of the other islands.

In the southern group of islands, San Nicholas lies furthest off shore and has 2 endemic taxa and additional 4 taxa restricted to San Nicholas and the mainland. It shares about 77% of its shared native taxa with Santa Cruz Island and the same percentage with Santa Catalina Island (Wallace, 1985). The affinities of San Nicholas seem to lie equally with the northern and southern islands. In the case of Santa Barbara Island, only the 3 endemic taxa of the 72 native taxa on Santa Barbara Island are not shared by another island. It shares 89% of its shared native taxa with Santa Catalina Island and San Clemente Island, along with 81% shared native taxa with Santa Cruz Island to the north. The largest island in the southern group, Santa Catalina Island, has 58 native taxa exclusive to Santa Catalina and the mainland. It shares 86% of its shared native taxa with Santa Cruz Island to the northwest. There are 37 native taxa of plants common only to Santa Catalina,

Santa Cruz, and the mainland (Wallace, 1985). Floristically, San Clemente Island seems to align itself with Santa Catalina Island. They share exclusively 3 endemic taxa, and 12 additional taxa are endemic to San Clemente and 1 or more of the other islands of the southern group.

Many of the plants in the floras of these Channel Islands represent surviving populations of mainland taxa that have become decreased in range with great disjunctions today because of the drying since the Pleistocene pluvial periods. Today, the insular endemics shared between the islands seems to indicate stronger floristic affinities between islands than sharing of other native plant taxa.

(Note: The figure of 621 native vascular plant taxa is for the Channel Islands of southern California *and* Guadalupe Island, Mexico. Guadalupe Island shares 8% of its shared native taxa with Santa Catalina, 79% with San Clemente, and 76% with Santa Cruz. It shares 10 endemic taxa with 1 or more of the Channel Islands, but has 35 taxa endemic to the island in total. Floristically, there are clear affinities between Guadalupe Island off Baja California in the Channel Islands of southern California.)

Insect Fauna of the Channel Islands

Butterfly Fauna of the Channel Islands

Evolution and Biogeography of the Channel Islands Butterfly Fauna

Chapter 7

EFFECTS OF HUMAN ACTIVITIES ON LEPIDOPTERAN POPULATIONS IN CALIFORNIA

California now has the largest population of any state in the nation. Its great and seemingly limitless wild spaces have rapidly been depleted in the last century by many human activities. The impact of these activities has been substantial, effecting first and foremost the vegetation in diverse areas throughout the state. Changes in the plant cover, air quality, water quality, and other environmental perimeters will effect animal species that depend on a normal environment for their survival, and among these are the butterflies of our state.

The purpose of this chapter is to sketch in a general survey, some of the important types of human impact on the environment in California which have led to changes in the lepidopteran populations of our state. Among the more important types of human impact are the following:

1. urbanization
2. agriculturalization
3. water projects
4. road construction
5. grazing
6. smog and other air pollution
7. pesticides and herbicides
8. mining
9. ski runs and ski areas
10. forest cutting and logging
11. fire
12. recreational vehicles and other motor vehicle activities
13. introduction of non-native vegetation into native habitats

We will examine each of these human impacts in turn, giving examples of some of the suspected or documented impacts on lepidopteran populations in California.

1. Urbanization

Urbanization commonly results in the virtual eradication of the native vegetation and habitat in a settled area. At best, a few islands of natural vegetation are left, as on Twin Peaks in San Francisco. Urbanization was the cause of the first butterfly extinction in California, that of Boisduval's Satyr in the sand dunes of San Francisco. As the city expanded into the dunes in the 1880's, Boisduval's Satyr became extinct, despite its former abundance. Later urbanization would become the documented cause of extinction of the second species of butterfly to become extinct in California, the Xerces Blue (*Glaucopsyche xerces*). This butterfly was once reasonably common in the sand dune habitats of the San Francisco Peninsula but became progressively restricted until by the late spring of 1943 it was found in only a few square yards of sand dune persisting within the Presidio, the United States Army installation near the tip of the Peninsula. It did not survive that year, and in 1944 no more Xerces Blues were found in the state. As noted under the species account in the present book, this butterfly would have made a magnificent subject for observations and experiments on evolution in a highly variable animal species. That opportunity is now forever lost.

The expansion of the Los Angeles City Airport into the El Segundo Dunes with a proposal during the 1980's to build a golf course in the last remaining habitat areas for the El Segundo Blue (*Euphilotes battoides allyni*) has only been stopped by public outcry against the eradication of the last of these dunes for still another golf course in Los Angeles. Standard Oil Company of California has preserved their part of the El Segundo Dunes in an active management program to help the habitat recover and provide a reasonably safe environment for the El Segundo Blue and associated sand dune species to continue their existence on this, our planet.

Yet not all butterflies suffer when urbanization takes place in the original habitat area. *Eurema nicippe* and *Phoebis sennae* were abundant earlier in the 20th century in southern California when ornamental *Cassia* plants were used widely in landscaping. For some unknown reason, perhaps less frequent use of *Cassia* in horticulture, these two sulphur butterflies are less common today than they were 50 years ago (Emmel and Emmel, 1973). The Cabbage White, *Pieris rapae*, has become more abundant in southern California urban areas due to the widespread planting of nasturtium as border flowers.

Some species have been characteristic inhabitants of vacant lots in urban areas, where secondary succession is allowed to progress for at least several years. The various *Vanessa* species of Nymphalids feed on mallows (*Malva* species), while the Red Admiral (*Vanessa atalanta*) feeds on Baby's Tears, used as ornamentals and frequent escapees to vacant lots. The Anise Swallowtail (*Papilio zelicaon*) does very well feeding on fennel or wild anise in the vacant lots of southern to central California.

A number of butterflies have spread in urban areas because of widespread planting of their particular foodplants. Several skipper butterflies, such as the Fiery Skipper (*Hylephila phyleus*) and the Umber Skipper (*Poanes melane*) are particularly abundant in lawns in suburban areas and parks. The latter species, for example, feeds on *Eharharta*, an introduced test grass species at the University of California at Los Angeles Botanical Garden and the Santa Ana Botanical Gardens, surrounded by urban areas.

The Gulf Fritillary (*Agraulis vanillae*) feeds on introduced Passion Flower vines that are grown as ornamentals on trellises and backyard fences in urban areas. When freezes kill these vines back during the winter, the butterfly disappears, only to be reintroduced from Arizona or Mexico the following summer via migrants. Some butterflies have become more abundant in urban areas due to planting of their host shade trees. For example, the Mourning Cloak (*Nymphalis antiopa*) has become relatively abundant in cities due to widespread planting of Weeping Willows, Poplars, and Chinese Elm. The Western Tiger Swallowtail (*Papilio rutulus*) occurs wherever Sycamores and Modesto Ash have been planted as shade trees in parks and along city streets. The Dusky-Wing Skipper (*Erynnis tristis*) has followed its host, Cork Oak, into suburban areas while a Crescent-spot Nymphalid, *Phyciodes phaon*, has followed its host *Lippia* wherever *Lippia* lawns have been planted in urban areas in the desert, particularly at Brawley and Blythe, but it has also been successfully introduced to *Lippia* lawns in Hemet in the western part of Riverside County.

Along with the spread of the *Papilio rutulus*, due to the planting of Sycamore trees in parks, the arrival of parasitic mistletoe on these trees has made possible the wider establishment of the Great Blue Hairstreak, *Atlides halesus*, whose larvae feed on these mistletoes.

Finally, it ought to be noted that not all butterflies have followed plantings of their host plants into urban areas. Canna Lilies are widely used as plantings throughout southern California, yet the Canna Skipper, which has been reported several times as strays in southern California, has not become established to date.

2. Agriculturalization

Like urbanization, the spread of agriculture normally results in the total loss of native habitat. In rare instances, narrow hedgerows of native vegetation are left between fields but normally only by farmers who are seeking to preserve some cover for game birds, an act of wildlife conservation rarely encountered in California. Most native species, of course, will disappear when their habitat and foodplants are removed. However, agricultural practices have introduced some species which serve as excellent hosts for immense populations of certain species. The widespread planting of alfalfa throughout the year in the Imperial Valley and Coachella Valley of southeastern California has made possible tremendous populations throughout the year of the Alfalfa Sulphur, *Colias eurytheme*. In addition, certain lycaenids such as *Everes comyntas*, *Hemiargus gyas*, and possibly *Ministrymon leda* have been more common due to the widespread planting of beans (genus *Phaseolus*) as an agricultural crop in southern California.

Members of the cabbage family have been planted fairly widely and *Pieris* species such as *rapae* and *protodice* may become abundant at times in such areas. This family includes commercially grown mustard (grown for mustard seed and creating mustard spread).

Fields of cotton (family Malvaceae) provide an alternative host for *Vanessa cardui*, the Painted Lady, and the Gray Hairstreak, *Strymon melinus* in both the southeastern California area and the Great Central Valley of California.

In citrus orchards, two species of swallowtails may become a pest at times and have spread throughout new agricultural areas as a result of their ability to switch to citrus from other native foodplants. These include the Anise Swallowtail (*Papilio zelicaon*) and the Giant Swallowtail (*Papilio cresphontes*), the latter being an invader from Arizona which originally appeared in the Imperial Valley along the Colorado River and then moved up into the Bakersfield area and north in the Central Valley.

Extensive plantings of Sorghum grass and corn allowed the population sizes of the skipper (*Lerodea eufala*) to increase, although they have not become of pest proportions.

Irrigation canals in some of the major agricultural areas have provided a disturbed habitat for certain butterfly foodplants. Sunflowers (genus *Helianthus*) do well in such habitats, and the Patch Butterfly (*Chlosyne lacinia*) multiplies abundantly in such favored areas. Likewise, agriculture in the Imperial Valley has favored the growth of Alkali Mallow (*Sida heteranea*??) along the margins of fields. This is the host for several skipper species (*Pyrgus scriptura* and *P. communis*) as well as a hairstreak (*Strymon columella*), and these three butterflies have become relatively abundant in this field margin or hedgerow habitat.

3. Water Projects

Water projects of all types have effected butterfly populations in the state, from dams and reservoirs to harbors and breakwaters, as well as wells that lower the water table, effecting natural surface water emissions.

Dams and reservoirs normally create a total loss of habitat due to its submergence under water. The classic example perhaps is Hetch Hetchy Dam on the Tuolumne River in the Hetch Hetchy Valley just north of Yosemite Valley, inside Yosemite National Park. Shortly after the turn of the century, the city of San Francisco managed to persuade the federal government to allow them to dam the Tuolumne River here inside a national park and flood this great valley (larger than the present Yosemite Valley which is packed with millions of visitors every year). A host of butterfly habitats as well as a great number of other wildlife species were lost by this flooding to create a reservoir for a water supply for San Francisco.

In the western part of the state, closer to the coast, several diversion and drainage projects have effected butterfly populations. There was originally a system of natural marshes in the San Joaquin Valley, which probably had extensive colonies of the skipper *Ochlodes yuma* and its foodplant, the grass *Phragmites communis*. Today these colonies of the grass host and the butterfly have been virtually eliminated in the San Joaquin Valley by widespread drainage projects. Along the Kern River, at Weldon, the skipper butterfly *Pseudocopaeodes eunus*, has been greatly effected by water diversion projects above and below its colonies. These diversion projects effect the species adversely in some years by drying out the habitat, or positively in other years by protecting the habitat against floods. In the Sacramento River Valley, there are many species like this skipper, *Ochlodes yuma*. We have no idea yet what the impact will ultimately be at peripheral canals and the planned diversion of the Feather River water to southern California.

Another common type of water project in California is deep wells to tap underground water supplies. The effect of such wells is to lower the water table as greater and greater amounts of water are withdrawn for human use. Along the San Jacinto River in the San Jacinto Valley, cottonwood trees are being lost due to the dropping of the water table. On these cottonwoods grow mistletoes which are the host plants for the Great Blue Hairstreak, *Atlides halesus*. The dramatic dropping of the water table in the Owens Valley on the eastern side of the Sierra has resulted in the drying up of springs there. This has definitely resulted in the extinction of the satyrid, *Cercyonis pegala wheeleri*, at Owens Lake, and possibly the extinction of colonies of the beautiful fritillary, *Speyeria nokomis apacheana*, south of the current known colonies in Round Valley. The dropping of the water table in desert areas results in the drying up of isolated springs. Thus pupfish populations in Death Valley and elsewhere, especially in Nevada but also in California, have been threatened by the loss of water. Some butterfly species in these areas, dependent on their host plants which in turn are dependent on a constant water supply in these desert springs, will die out like the pupfishes, for example the Phragmites grass and the *Ochlodes yuma* skipper are highly interdependent on each other in these isolated desert canyons where springs have occurred for thousands of years.

Flood control channels built to control occasional flooding by major rivers such as the Los Angeles River in Los Angeles County and the Santa Ana River in San Bernardino County has resulted in extensive loss of riparian habitat and woodland, including willows and other foodplants of *Limenitis lorquini*, *Satyrrium sylvinus*, and *Phyciodes campestris*.

Cloud seeding efforts over the Sierra Nevadas and attempts to increase snow pack may effect butterfly populations by influencing the increased abundance or decline of their respective foodplants. Agricultural activities may effect weather too, by increasing humidity in the Imperial Valley of southeastern California. Originally a desert, this extensively agriculturalized area may have an increasing frequency of summer thunderstorms due to the increased humidity from evaporation of irrigation water, as well as transpiration from the greatly increased plant biomass of these areas. These agricultural and urbanized areas now act as corridors for nectar sources, water, and host plants for larvae for Mexican species to come up into southern California from either Baja California or Arizona. Clearing the vegetation along the Mojave River in the desert has destroyed *Atriplex* foodplants and thus endangered populations of the very rare Desert Blue, *Plebejus emigdiones*.

Along the coast, the construction of breakwaters has stopped the natural creation of sand dunes or has resulted in an increase of dune building, depending on the location of the breakwater. The construction of breakwaters in harbors then may reduce erosion and loss of coastal sand in one area, but by changing coastal currents may cause actual loss in another area. The fragile coastal sand dune habitat which supports various rare and highly restricted subspecies of a number of blues, metalmarks, and fritillaries, can be greatly effected by man's activity offshore in an attempt to preserve beaches that have provided sheltered anchorages for recreational boats.

4. Road Construction

Road construction results in a complete loss of habitat in the immediate area that the road is occupying, of course, but the new roadside environment and roadcuts through hills provide a

disturbed habitat where secondary succession can occur. Richard Arnold (1983) notes that two *Lupinus* hosts for *Plebejus icarioides missionensis* readily colonize roadcuts within a year or so of road construction and rapidly provide a habitat for expansion of the butterfly's range. John Downey (1962?) cites this phenomenon for all *Lupine* hosts of the western *icarioides* subspecies. The natural host biomass for *Papilio bairdii* in the San Bernardino Mountains has been greatly favored by roadcuts where the host sage, *Artemisia dracunculus*, is widespread in such habitats.

A widely used species of wild buckwheat (*Eriogonum fasciculatum*) utilized by *Apodemia mormo* metalmarks and a number of blues is a frequent colonizer of roadcuts, such as on the passes leading from the San Francisco Bay area to the Great Central Valley or on Cajon Pass from the San Bernardino Valley north into the Mojave Desert. Here *Eriogonum fasciculatum* has followed the new highways (such as Interstate Highway 15) out into the desert from the mountains and the San Bernardino Valley. An interesting question for lepidopterists to investigate in the future will be whether butterfly species associated with this foodplant will follow it out into the desert.

Other common plants that increase in roadside habitats are the mustard *Brassica*, which enhances the distribution of *Pieris rapae* and *P. protodice*, and various mallows (*Sidalcea* in the family Malvaceae) which serve as a host for various *Pyrgus* species (including *P. heliopes*) which follow its distribution. According to Richard Arnold (1983), the legume *Lotus formosissimus* is doing well along the roadsides near the only known colony of the Lotus Blue (*Lycaeides idas lotis*) on the Mendocino County coast. The fact that the host plant is spreading may expand the range of this endangered butterfly due to the presence of roadcuts near the sole known remaining colony. A much more common butterfly, the Anise Swallowtail (*Papilio zelicaon*), has followed the expansion of wild fennel (*Foeniculum vulgare*) which does well on roadcuts such as in the San Francisco Bay area.

Roads, particularly in forested areas, act as natural corridors for butterfly flight patterns, much as do canyon bottoms and streams. The existence of a road may also increase runoff of rainwater from the highway along the roadsides, allowing for less vegetation growth there. Both larval host plants and nectar sources may become quite abundant. In the higher mountain areas, where snow plows pile up snow along the roadsides during the winter, the increased snow pack there provides greatly enhanced precipitation for spring and summer plant growth. Even in the desert, plant growth along desert highways is noticeably improved, including such plants as *Sphaeralcea* (family Malvaceae) which serves as a host for the skipper, *Pyrgus scriptura*. In northern California *Sedum spathulifolium* does well along roadsides and the hairstreak, *Incisalia mossii* (various subspecies in different areas), may colonize these abundant hosts. Likewise, buckwheats or *Eriogonum* species in general (*E. nudum*, *parvifolium*, *umbellatum*, etc.) tend to do well on roadcuts and promote the establishment of new colonies of blues and metalmarks.

Finally, the existence of the road increases collecting pressure on the collecting locality. A classic example of this is the fact that the Tioga Pass Highway (right outside the eastern entrance to Yosemite National Park) makes it the most heavily collected spot for alpine species in the state of California. Fortunately, there has been no apparent effect of this heavy collecting pressure each June and July to date.

Finally, two other examples of specific butterfly expansions due to roadcuts may be found in southern California mountains. In the San Bernardino Mountains, the foodplant of the rare marble *Euchloe hyantes andrewsi*, which is *Streptanthus bernardinas*, follows roadcuts and provides an egg and larval substrate, while at the same time the road acts as a natural corridor for the ovipositing marble females (Chris Henne, personal communication). Likewise, the legume *Lotus scoparius* does well on roadcuts and provides the expanding resource for the hairstreak, *Callophrys perplexa*, and the blue, *Glaucopsyche lygdamus australis*.

5. Grazing

Grazing has a number of varied effects on butterfly populations. First, it can cause changes in the grass species composition of the community in the grassland area. The native perennial bunchgrasses tend to be replaced by introduced annual European grasses. This possibly influences the species of skippers and Satyrids that live in these grassland communities, although how much influence is exerted is still unstudied.

A more direct immediate effect is that erosion normally increases with overgrazing. Additionally, certain species of plants poisonous to cattle, such as *Astragalus*, *Lupinus*, or *Asclepius* milkweeds, may proliferate due to the impact of grazing. Butterflies that feed on these poisonous plants may actually become more abundant due to the grazing pressure. Species that are specialized to feed on oak trees, however, may not fair well in oak grassland areas where overgrazing occurs. Oak seedlings are prevented from growing, and the oak trees will eventually die out in such an area.

Natural meadows, particularly in mountain areas such as alpine meadows in the Sierra Nevada and Garner Valley in the San Jacinto Mountains of southern California, may become so overgrazed that they are invaded by weedy species, and today we have no idea what the original flora and fauna was of these rich, wet, boggy meadows, before they were overgrazed by cattle and sheep. Such grazing pressure was observed very early by John Muir in the 1880's and 1890's in the Sierras when he helped herd sheep before becoming an ardent conservationist.

The diversion of water sources for cattle troughs and springs for irrigation projects may cause meadows and grasslands to dry up and essentially disappear from their natural state. Grazing in marginal habitats, such as the eastern Mojave Desert, makes no sense at all. The diversion of natural water sources and the grazing of cattle in a desert environment today impacts heavily on the native desert vegetation and results in very few cattle being raised while creating inestimable damage to the environment. The grazing of wild burros in the western desert mountain ranges in higher desert areas has considerable impact on grasses and brush, as well as greatly disturbing natural springs. (J.F.E.: Look up Kingston Range and Granite Mountains Resource Survey Grazing Report, and report on effective mining on plants for T.C.E. to use or for J.F.E. to modify this section and the later one on mining.)

It also should be noted that changes in the spotting pattern of the Satyrid butterflies, *Cercyonis oetus*, have been noted in Colorado populations living in heavily grazed meadows. Thus, the evolutionary and ecological impact of grazing may effect genetic diversity and phenotypic characteristics of butterflies as well as endanger their very continued existence.

6. Smog and Air Pollution

The effects of air pollution have been reasonably well studied in plants where the deleterious effect on ponderosa pine forests some 60 miles east of the Los Angeles Basin have been noted. But the impact on butterfly populations has not really been studied yet. It has been hypothesized (Emmel and Emmel, 1973) that one factor possibly accounting for the decline in *Phoebis sennae* sulphur populations in the Los Angeles area has been the change in air quality.

7. Pesticides and Herbicides

The widespread use of pesticides in agriculture, mosquito control, and forest insect pest control is done virtually without a thought as to possible side effects on non-target insects and other wildlife. Vast spraying programs to control injurious infestations or outbreaks may result in incalculable effects on wild butterfly populations. To date however, hard evidence from experimental studies is available only from one study (Emmel, 1986, 1988) in Florida where the effect of mosquito control pesticides on the Schaus Swallowtail, a federally endangered species, and the common Giant Swallowtail (*Papilio cresphontes*) in the Florida Keys has been studied. Other chemicals of great concern are herbicides which are used along roadsides throughout the state and in the past, have been used on firebreaks to control vegetation growth. The direct impact can be measured in the loss of larval and adult host and nectar plants, but a lighter impact may be a poisoning of the only populations of many of these butterfly species in an area. As has been noted above, many species follow disturbed habitats along roadsides and as more extensive native habitat is destroyed, roadside habitats may provide the last refuge for a number of these species. Periodic spraying by herbicides to control roadside growth can only result in a threat to the continued existence of these species.

8. Mining

Mining has been rather extensive in many areas in California, starting in the days of the 1849 Gold Rush and continuing to date. One of the classic examples of ecological damage done by mining is that of placer mining in the Sierran foothills. Placer mining created huge piles of gravel tailings which in some cases have remained barren of vegetation for a century and have changed the routes of watercourses as well. Likewise, modified strip mining, as in the Kingston Range of the eastern Mojave Desert (J.F.E. cite that study here.) has created wholesale habitat destruction for the talc mine.

Sand mining in the sandhills of southern Santa Cruz County [ask John Lane for details] is destroying unique ecotypes of the metalmark, *Apodemia mormo*, and the blue, *Euphilotes enoptes*, which feed on *Eriogonum nudum* in the sandhills. A population of the skipper *Polites mardon* on serpentine in Del Norte County is endangered by planned mining activities there [John: Get details from S.O.M.]. Quarry mining on the eastern side of the San Bruno Mountains is destroying the habitat of the endangered hairstreak species, *Incisalia mossii bayensis*.

9. Ski Runs and Ski Areas

The construction of ski areas and ski runs through national forests and other areas maintains a subclimax meadow or open slopes, preventing the regrowth of trees in the cleared areas. There is probably a greater growth of wildflowers in these areas than in climax forests, thereby increasing the number and variety of nectar sources and diversity of larval host species of plants for butterflies. These areas also act as corridors for montane species such as *Chlosyne hoffmanni*, *Papilio indra*, *Parnassius* sp., and *Lycaena* coppers. In particular, *Lycaena cupreus*, *L. nivalis*, and *L. editha* do well in these corridors created for skiing. Thus, the construction of ski areas commonly results in a greater abundance of butterflies during the summer months.

10. Forest Cutting and Lumbering

Selective lumbering introduces second-growth vegetation which provides normally a greater abundance of nectar sources and larval foodplants for butterflies. Clear cutting, on the other hand, creates erosion of slopes and siltation of streams with great effects on riparian habitats downstream as well as the mountain slopes where the forest once stood. It would be particularly interesting to study redwood forests or other areas where clear cutting is taking place, in order to document what happens with species diversity among butterflies. For instance, in a redwood forest *Pieris napi* has a subspecies with very limited distribution in Humboldt County, along with the Anglewing butterfly, *Polygonius faunus fulvescens*. These butterflies are undoubtedly effected by the logging operations in the forest, and it would be valuable to understand how short-term or long-term these effects are.

Lumbering also creates a direct effect on species that use conifers as foodplants. However, in every case in California, the butterflies that feed on conifers in the larval stages are widespread species and lumbering has only a temporary effect in the immediate area on their abundance. On the other hand, any fritillaries in the genus *Speyeria* or other butterfly species that require a shaded forest canopy as a habitat for oviposition activities, may be exterminated or greatly reduced in numbers due to extensive lumbering in an area. The fact of the matter is that no detailed ecological studies of butterfly diversities have been done in lumbered versus unlumbered forests and such research is badly needed in not only our state but also the other western states.

11. Fires

The only study that we know of on the effect of fires on butterfly succession and diversity is that by Richard Kelton (1987, unpublished paper). Kelton studied fire in the chaparral area and listed all the species favored by fire along with their hosts. Fire opens up the habitat to allow both the hosts and the butterflies to increase. For example, the southern California species *Papilio indra pergamus* has a foodplant which does extremely well on burned slopes. In the years following a forest fire, this butterfly greatly expands in number due to the abundance of its foodplant. All the chaparral host species and their butterflies are probably benefited by fire because most of the plants are crayon-sprouters, and new growth would be favored by ovipositing females in any year, let alone following severe fire. The basic question in the case of severe fires is whether there is any survival at all of the butterflies in the area of a fire. Lycaenid and *Papilio indra* pupae are normally placed in sheltered areas and probably survive a fast moving fire without much difficulty. Other species that pupate on dry foodplants, such as Pierids (Orange tips, Whites, etc.) probably have to reinvade fire-burned area from an adjacent unburned habitat.

Besides chaparral fires, we also have forest fires which cause wholesale destruction of an area, but then succession occurs on the burned slopes and, as in slopes cleared by lumbering or for ski areas, butterfly host plants and nectar sources do quite well in the early years of succession. Grass fires in serpentine grassland or other relatively open and sparsely vegetated habitats such as deserts will normally sweep through too rapidly to create long-term problems for butterflies.

In the New York Mountains in the eastern Mojave Desert, there is a very interesting situation that may be the result of fire. Several plants, including *Purshia* and *Ceanothus greggii* may represent relics from earlier burns in this mountain range. Yet, there are no butterflies associated with them (one would expect the hairstreaks, *Satyrium behrii* on the *purshia*, and *Satyrium saepium* on the *Ceanothus* species). On the coast of California, these butterfly species re-establish themselves on the newly sprouting *Purshia* and *Ceanothus* bushes quite readily. In the more isolated New York Mountains, a recolonization may be a relatively rare event for these hairstreak species.

12. Off-Road Vehicles

Recreational vehicles for off-road travel have had a considerable impact on several habitats in California. One of these habitats is the desert, where motorcycle trails and RV trails at Jawbone Canyon in the Mojave Desert and other desert mountain ranges (sites for *Papilio indra* subspecies and other rare desert butterflies) have torn up the desert habitat extensively. At the Marina Dunes in Monterey County and the Oso Flaco Dunes in San Luis Obispo County along the coast, motor vehicles racing cross the dunes have caused the direct destruction of plants which are the hosts of an ecotype of *Euphylotes enoptes tildeni* there at the Marina Dunes on *Eriogonum latifolium*, and a subspecies of the metalmark *Apodemia mormo* on the same plant. At the Marina Dunes exists the only known sympatric populations of the two green hairstreaks, *Callophrys dumetorum* and *C. perplexa*. These have long confused California lepidopterists and taxonomists, and have only recently been differentiated as distinct species by careful examination of their life histories. It would be a tragedy to lose the one natural laboratory where the two species come in contact, and be unable to study possible hybridization and barriers to interbreeding that may exist between these beautiful butterflies. At Oso Flaco Dunes, a beautiful checkerspot subspecies of *Thessalia leanira* is endangered by off-road vehicle activity. The rare blue *Plebejus icarioides moroensis* which inhabits the sand dunes in San Luis Obispo County along the coast, have been mostly destroyed by development and it would seem particularly ironic if the last known populations were destroyed by man's careless use of off-road vehicles in the sand dunes.

13. Introduction of Exotic and Weedy Plant Species into Native Habitats

Under this category of human influence, we mention the alteration of vegetation by the accidental or deliberate introduction of plants from outside the state of California. In some cases, these plants have increased butterfly abundance such as fennel (*Foeniculum vulgare*), which has made possible the increased distribution and abundance of the beautiful Anise Swallowtail. Likewise, the Malva species from Europe have become widely distributed in disturbed areas, roadsides, vacant lots, and agricultural areas greatly effecting the distribution of *Vanessa cardui* and *Vanessa carye*. The distribution of mustards in the genus *Brassica*, especially European

mustards, has greatly increased the numbers of the whites in the genus *Pieris*, especially *P. rapae* and *P. protodice*.

On the negative side of the ledger, Tamarisk has been introduced into the desert areas where it invades desert springs and riparian habitats and replaces cottonwoods, willows, and mesquite (*Prosopis*), all foodplants of native butterflies. Gorse is becoming very abundant in northern California, like Scotch Broom has invaded much of the montane areas of southern California along roadsides. In the Big Sur area, pampas grass has become naturalized and is crowding out virtually everything else. Ice plant on the El Segundo Sand Dunes, as well as a native but introduced buckwheat species, *Eriogonum fasciculatum*, have been crowding out the native hosts of the rare El Segundo Blue (*Euphilotes battoides allyni*). Currently, an active removal program has been initiated in the El Segundo Dunes in order to remove these exotic species.

Even in the remote desert areas, butterfly distributions can be affected by accidental or deliberate introductions. A colony of watercress was introduced some time ago at Paphalka Spring on Clark Mountain in the eastern Mojave Desert, apparently with some eggs of *Pieris rapae* on it. Today, a thriving colony of *Pieris rapae* occurs in this most unlikely desert habitat. Likewise, the widespread distribution of the vine of the morning glory, *Convolvulus arvensis*, may ultimately lead to *Phyciodes picta* becoming established in California. James Scott has found that it feeds on this *Convolvulus* in addition to its native host. The butterfly is common in Arizona and will undoubtedly eventually invade the Blythe area along the Colorado River and find its *Convolvulus* foodplant awaiting it for successful introduction of the butterfly.

Raven (1977) has provided a fascinating summary of the literature on the introduction of exotic plants into California. This began in May 1769, when Father Junipero Serra reached San Diego Bay and founded the first permanent European settlement in what would be ultimately the state of California. At least 16 species of exotic plants were established in California during the Spanish colonization period of 1769 to 1824. During the Mexican occupation, from 1825 to 1848, 63 additional species were introduced. Some 55 more introduced plants arrived during American pioneer settlement from 1849 through 1860. Thus by 1860, at least 134 alien species of plants were established. By 1920, 186 immigrant species excluding odd fugitive plants from gardens and waifs from wind-blown seeds, in southern California alone. In 1925, Jepson believed that 292 species of established exotics were in the California flora. By 1951, 437 introduced species of weeds were listed for the state, and Munz and Keck (1959) listed 797 species of introduced plants. By 1968, Munz added 178 more species of introduced plants, for a total of 975 introduced species in California. Many new weeds are being established in California with each passing decade, but not all are becoming a part of the naturalized flora of the state. The good climate and widespread irrigation during the dry summers allows many species to persist and even reproduce by seed locally but this is due in part to human interference. Raven (1977) concluded that there were actually 654 species of introduced plants in California at that time, ignoring those that were persisting with human assistance. Of these, 544 were of Old World origin and only 110 were of New World origin, the latter including some 50 from the United States, 23 from tropical America, and 37 from South America.

Chapter 8

SPECIES ACCOUNTS

OF THE

BUTTERFLIES AND SKIPPERS OF CALIFORNIA

P A P I L I O N I D A E

The family Papilionidae, or swallowtails and parnassians, contains three recognized subfamilies. The subfamily Papilioninae includes the true swallowtails, with about 517 species worldwide. The subfamily Parnassiinae contains the parnassians, which are found largely in the Holarctic and include 54 recognized species. The third subfamily, Baroniinae, contains only a single species (*Baronia brevicornis*) which is endemic to central Mexico (Heppner, 1991).

The family is separated from its closest relatives, the Pieridae, and the other families of butterflies by having (1) six functional legs in both sexes; (2) a spur called an epiphysis on the tibia of the front (or prothoracic) legs; (3) a larval osmeterium or forked organ that protrudes forward from behind the head when the larva is disturbed; (4) five-segmented feet, with the tarsal claws single and simple in structure; (5) clubbed antennae which are not curved at the tip; (6) a head as wide as the thorax, and bearing short palpi; (7) a central (or discoidal) wing cell between the veins in both the forewings and hindwings which is completely closed (i.e., the veins are joined) at the cell end closest to the body; (8) larvae which are generally cylindrical, although often with an enlarged thoracic region in the younger stages of the true swallowtails. Most of the species of this family in California bear tails, excepting only *Battus polydamus* and the two species of *Parnassius*.

* * * * *

Subfamily **Papilioninae** Latreille

I. *Papilio bairdii* W. H. Edwards

ADULT BEHAVIOR: The males of this western black swallowtail are strong hilltoppers while females are frequently encountered flying in canyon bottoms in search of the foodplant.

Thistles (*Cirsium* spp.) are favored nectar sources in the San Bernardino Mountains. In southern Utah, adults have been observed nectaring on *Cleome serrulata* Pursh (J. F. Emmel, unpublished data).

- LIFE HISTORY:** The eggs are laid on new growth near the tips of the foodplant stems. They are spherical in shape, smooth in texture, and pale yellow in color. The diameter is about one mm. The mature larva is usually green to blue-green in ground color, with a black band across each segment. Each band contains a series of orange spots. The pupa is brown or green and is very similar in morphology to that of *P. zelicaon* or *P. polyxenes*. The species diapauses in the pupal stage.
- CHROMOSOME NUMBER:** Unknown (Maeki and Remington, 1960, used "brucei" to refer to *P. zelicaon* and not *P. bairdii* counts).
- SIMILAR SPECIES:** The only similar species to be confused with black *bairdii* is form "clarki" of *Papilio polyxenes coloro*. The latter is found only in desert areas and occurs earlier in the spring or later in the fall period. Additionally, the eye-spot at the base of the hind wing (at the anal angle) is red-orange in *bairdii*; in f. "clarki", this spot is usually half yellow. The differences between the yellow form "brucei" and other swallowtail species are discussed under *Papilio zelicaon*.
- GEOGRAPHIC AND SEASONAL VARIATION:** Specimens of the summer brood tend to be larger than those of the spring brood, but there are no color pattern differences. The populations in the San Bernardino Mountains do not appear to differ significantly from topotypical *P. bairdii* from Arizona; the White Mountain populations of *hollandi* are very similar to topotypical *hollandi* from Glenwood Springs, Colorado. The White Mountains populations appear to be all of the yellow "brucei" form; in the San Bernardino Mountains populations, most adults are of the typical "bairdii" form, and only about 1 to 4% are form "brucei".
- GENERAL REMARKS:** One of the most curious features of this species is its limited distribution in California, where the foodplant, *Artemisia dracuncululus* L. (Compositae), is abundant and found in seemingly suitable habitats such as the Laguna Mountains and San Jacinto Mountains at elevations similar to those in the San Bernardino Mountains. Perhaps summer rainfall patterns or as yet unknown biological factors limit the distribution of this species to its present, curiously disjunct range.
- SUBSPECIES:** Two subspecies of this widely distributed but usually local species are found within the state.

a) *P. b. bairdii* W. H. Edwards

- DIAGNOSIS:** This is a large swallowtail, with strong sexual dimorphism. The males are black with a prominent yellow post-median band, while the females lack this post-median band or have only a faint development of it, and both sexes have prominent blue scaling in the post-median area of the hindwings, particularly in the females. A rare form ("brucei") has yellow wings with black markings and is very similar to *Papilio zelicaon* and *P. polyxenes coloro*.
- ORIGINAL DESCRIPTION:** W. H. Edwards, *Proceedings, Entomological Society*, Philadelphia, Volume 6: 200 (1869).
- TYPE LOCALITY:** "Arizona," restricted to Fort Whipple, near Prescott, Arizona, by F. M. Brown, *Transactions American Entomological Society*, 101: 14-15 (1975). Neotype in

Carnegie Museum, designated by F. M. Brown, *Transactions American Entomological Society*: 101: 13-15 (1975).

- DISTRIBUTION:** In California, the nominotypical subspecies is confined to a single mountain range: the San Bernardino Mountains. Its restriction to this mountain range alone is curious, in that seemingly suitable habitats occur in adjacent southern California mountain ranges. Outside of California, *P. b. bairdii* ranges from southern Nevada and Arizona eastward to New Mexico and southern Colorado.
- ELEVATION RANGE:** 5,000' to 9,000' elevation, with hilltopping males going as high as 11,500' on the summit of Mt. San Geronio.
- HABITAT AND PLANT COMMUNITIES:** Within the San Bernardino Mountains, the species is largely confined to habitats within the Lower Montane Coniferous Forest and Southern Mixed Evergreen Forest. Here it favors canyon bottoms, streamsides, or roadside situations within the forest.
- PHENOLOGY:** Adult emergence of the first brood begins in mid-May and continues through June. A second and smaller summer brood emerges in July and August. In very wet years, the summer brood may be as large or larger than the spring brood.
- FOODPLANTS:** The sole foodplant in California is *Artemisia dracunculus* L. (Asteraceae) (numerous records from many California lepidopterists, unpublished.).

b) *P. b. hollandi* W. H. Edwards

- DIAGNOSIS:** This is the Great Basin subspecies of *Papilio bairdii*. In these populations, the "brucei" form predominates. In this form, the wings are yellow with black markings and closely resemble adults of *P. zelicaon* and *P. polyxenes coloro*.
- ORIGINAL DESCRIPTION:** W. H. Edwards, *Canadian Entomologist*, 24: 50 (1892).
- TYPE LOCALITY:** "W. Colorado," restricted to Glenwood Springs, Garfield County, Colorado, by F. M. Brown, *Trans. American Ent. Soc.*, 101: 17-18 (1975). Lectotype in Carnegie Museum, designated by F. M. Brown, *Trans. American Ent. Soc.*, 101: 16-18 (1975).
- DISTRIBUTION:** Within California, this subspecies is found in the canyons of the White Mountains in eastern Mono County and northern Inyo County; there is also a single record for Bishop Creek on the east slope of the Sierra Nevada in Inyo County. From here, it ranges eastward across the Great Basin to western Colorado, and then extends northward until it blends with subspecies *oregonius* in the Pacific Northwest and subspecies *dodi* in southern Alberta. Along the southern edge of its range, there is a blend zone with the nominotypical subspecies; these populations show varying percentages of the black and yellow forms, with a gradual increase in the percentage of yellow forms as one goes from south to north.
- ELEVATION RANGE:** From 6,000' to 9,000', with hilltopping males flying as high as 13,145' on the summit of Boundary Peak in the White Mountains.
- HABITAT AND PLANT COMMUNITIES:** In the White Mountains, this subspecies is found within the Great Basin Sagebrush Scrub and Pinyon-Juniper Woodland plant communities. It typically flies along streams in well-watered canyon bottoms in this range of the extreme western Great Basin.

PHENOLOGY: Adults of the first brood fly from mid-May to late June; the second and smaller summer brood emerges in mid-July to mid-August and flies into early September.

FOODPLANTS: The foodplant in the White Mountains (as it is throughout the remainder of its range) is *Artemisia dracunculoides* L. (Asteraceae) (Wayne Dawes, in litt.).

2. *Papilio zelicaon zelicaon* Lucas

The Zelicaon Swallowtail occurs abundantly in the non-desert lowlands of California and flies in the mountains as well. It commonly feeds on the introduced European Fennel (not "Wild Anise," as it has been erroneously called in many popular works) in the larval stages, and has undoubtedly become more abundant in the last 150 to 200 years due to the spread of this weedy umbellifer.

DIAGNOSIS: This is a medium-sized swallowtail with predominantly yellow hindwing and half black-half yellow forewings. Variable amounts of blue scaling occur in the black post-median areas of the dorsal hindwing. There is no sexual dimorphism.

ORIGINAL DESCRIPTION: Lucas, in Guérin-Meneville, *Rev. Zool* (2)4: 136 (1852).

TYPE LOCALITY: "California." Type locality fixed to San Francisco, California by Emmel, Emmel and Mattoon (1998). Lectotype in Museum Nationale de Histoire Naturelle, Paris.

DISTRIBUTION: This common species occurs from the Mexican border to Oregon. It ranges westward from the western edge of the desert in southern California, and westward from the eastern base of the Sierra Nevada-Cascade Range axis to the coast. It is also found in the Warner Mountains of northeastern California, but is curiously absent from the White Mountains where suitable habitat has been reported. From California, it ranges south into northern Baja California, eastward to New Mexico, and northward to western Alberta and British Columbia.

ELEVATION RANGE: This species is found in a remarkably wide elevational range, from sea level to over 14,000' in the Sierra Nevada where males hilltop. It probably breeds as high as 12,000' on native Apiaceae.

HABITAT AND PLANT COMMUNITIES: Because of the remarkable adaptability of this species to various foodplants and habitats, the butterfly is found in a wide range of plant communities in California: these include Foothill and Valley Grassland, Foothill Woodland, Mixed Chaparral, Serpentine Chaparral, Subalpine Forest, Montane Wet Meadow, Arctic-Alpine Cushion Plant, Riparian Woodland, Agricultural, and Urban-Suburban.

PHENOLOGY: Populations in California above about 7,000' appear to be univoltine. Certain low-elevation populations, which feed on native, seasonally restricted foodplants, are also apparently univoltine (see Sims, 1980; Emmel & Shields, 1979; Shapiro, 1975). Lowland populations on the introduced European Fennel (*Foeniculum vulgare* Mill.), which provides some green foliage, flowers, or green seeds virtually 12 months of the year in most lowland areas, are multivoltine; additionally, populations associated with *Citrus* are multivoltine. There are records of adults or immatures in every month of the year for the urbanized areas of southern California. The main spring emergence for lowland populations occurs in March and April. At higher elevations, emergence takes place in May and June, and some first-brood adults may be taken into August in the highest alpine regions.

- ADULT BEHAVIOR:** The males are strong hilltoppers while the females are usually encountered near larval foodplants or nectar sources. The hilltopping behavior has been described in detail by Shields (1967) and Sims (1979). Shields found that males seek the highest points in their surrounding habitat, established territories there, and patrol them in search of virgin females which also ascend to these elevations. He believed that "hilltopping" is an adaptation to bring males and females together in habitats where individuals might otherwise be widely dispersed. Sims has shown that mating frequency is significantly greater (up to three matings with males) in females from montane populations compared to lowland females, apparently resulting from increased mating opportunities with males in "hilltop" areas.
- LIFE HISTORY:** The eggs may be laid on the leaves or the flowers of the foodplant. The spherical eggs of *P. zelicaon* are a delicate lemon yellow when first laid, changing later to a mottled color and then blackish brown before hatching. In general, the eggs of *zelicaon* tend to be slightly smaller than eggs of the *Papilio indra* complex and may be distinguished by their more yellowish color (*P. indra* eggs tend to be a light cream color.) The mature larva is a vivid green, striped with black on each segment and with reddish to yellowish orange spots in each black band. The younger four instars are black, with a white saddle-marking in the mid-dorsal area which makes the larva resemble a bird dropping. Some fourth-instar larvae have a color pattern similar to that of the fifth-instar larva.
- The pupa may be green or brown in color. Sims (1980, 1983a, 1983b) reported on the environmental and genetic factors that influence pupal diapause dynamics, larval color and the final color of the pupa during the pupation process.
- Pupal color dimorphism in *P. zelicaon* is a polygenic trait with a threshold effect. Short days and cool temperatures induce mostly brown pupae regardless of the color of the substrate; these pupae go into diapause. Conversely, long days (as in summer) and warm temperatures facilitate continuous development to hatching of the pupae, and allow cryptic color matching of the pupae to whatever substrate the larvae pupate on, presumably through neuroendocrine control. As regards overwintering, then, this species diapauses in the pupal state. Long days (greater than 14 hr light) prevent pupal diapause while short days (12 hr light) induce diapause (Sims, 1980). Diapause is terminated by a period of chilling, optimally at 11° C.
- FOODPLANTS:** European Fennel (*Foeniculum vulgare* Mill.), *Tauschia parishii* (C. & R.) Macbr., *T. arguta* (T. & G.), *Lomatium dasycarpum* (Nutt.) C. & R., *L. utriculatum* (Nutt.) Coult. & Rose, *L. dissectum* var. *multifidum* (Nutt.) Math. & Const., *L. marginatum* (Benth.) C. & R., *L. californicum* (Nutt.) M. & C., *Pteryxia terebinthina* (Hook.) C. & R. var. *californica* (C. & R.) Math., *Sphenosciadium capitellatum* Gray, *Oenanthe sarmentosa* Presl., *Heracleum sphondylium* L. ssp. *montanum* (Sch. ex Gaud.) Brig., *Angelica arguta* Nutt. ex T. & G., *A. hendersonii* C. & R., *A. lineariloba* Gray, *A. tomentosa* Wats., (all Apiaceae, formerly called Umbelliferae), and *Citrus* species (Rutaceae): *C. sinensis* (L.) Osbeck and *C. limon* (L.) Burm. (see Emmel and Shields, 1979). Additionally, the species uses the cultivated *Ruta graveolens* (Rutaceae) in urbanized areas (J. F. Emmel, unpublished data). Oviposition has also been observed on *Ptelea crenulata* Greene (Rutaceae) and larvae are able to feed through to pupae on this plant, but the resulting adults are much smaller than normal-sized individuals (J. F. Emmel, unpublished data).
- CHROMOSOME NUMBER:** n = 30 (Macki and Remington, 1960a).

- SIMILAR SPECIES:** This butterfly may be confused with either *Papilio polyxenes coloro* of our desert areas or form "brucei" of *Papilio bairdii* in the mountains. During wet years along the western edge of the deserts, *coloro* populations expand and move up into the lower montane regions onto larval foodplants of *Papilio zelicaon* and some ecological overlap of these species occurs (see Ferris and Emmel, 1982). In the San Bernardino Mountains of southern California, one may also expect occasional confusion of *zelicaon* and *bairdii* form "brucei" where the two overlap in hilltopping situations.
- Papilio zelicaon* may be distinguished from *coloro* by the following characters. In *zelicaon* the forewings tend to be more stubby, whereas in *coloro* they are more pointed. The submarginal yellow spots in *coloro* are more rounded, whereas in *zelicaon* they tend to be more crescent-shaped. The tails in *zelicaon* tend to be stubby in comparison to the longer, more slender tails of *coloro*. The yellow stripe along the sides of the abdomen in *coloro* usually has a row of yellow spots along the upper edge, whereas in *zelicaon* it tends to be a straight line with no evidence of yellow spotting. There are also important character differences in the larvae of these two species. Mature larvae of *coloro* tend to be much darker and tend to be more whitish in ground color than *zelicaon* larvae, which tend to be more green. Also, the fourth instar larvae (see text figures) are quite distinctive.
- In distinguishing adults of *Papilio zelicaon* from those of *Papilio bairdii* form "brucei", there are several important character differences. One is the character of the anal eye spot on the hindwing. In "brucei" this tends to be elongated and connected to the margin of the wing, whereas in *zelicaon* it tends to be a round spot not connected to the margin. Also in "brucei," the yellow stripe along the sides of the abdomen tends to be broader and more developed than in *zelicaon*. The size of "brucei" adults tends to be slightly larger than that of *zelicaon* adults.
- GEOGRAPHIC AND SEASONAL VARIATION:** This species is relatively uniform in maculation and size throughout the state, although specimens from higher altitudes tend to be somewhat smaller and darker. Early spring specimens in low elevation populations may resemble these smaller and darker high elevation phenotypes. This phenotypic plasticity in response to environmental factors and phenology is discussed in detail by Shapiro (19).
- GENERAL REMARKS:** This species has probably become substantially more abundant in the state with the introduction of fennel from Europe and the large-scale planting of citrus trees. Today, it is an abundant and familiar swallowtail, even within our largest cities. It has also spread into many agricultural areas where commercial growing of citrus is being affected to a minor degree by the feeding of the larvae on *Citrus* foliage.

3. *Papilio polyxenes coloro*

This desert swallowtail was named *Papilio coloro* by William Greenwood Wright in 1905. It was not recognized by John Adams Comstock (1927) who considered it a synonym of *P. zelicaon*. In 1937, Frank and Ralph Chermock named the yellow desert swallowtails as a new species, *Papilio rudkini* F. & R. Chermock, with a type locality of the Ibanpah [sic] Mountains in San Bernardino County. Subsequently, Clifford Ferris and John F. Emmel (1982) reduced the taxon to a subspecies (using the name of *coloro* Wright on the basis of priority) of *Papilio polyxenes*, the broad-ranging Eastern Black Swallowtail, because hybrids could be created freely in the laboratory between *polyxenes* and *coloro* (=rudkini), and because of the existence of a large blend zone, both ecologically and

phenotypically, between *coloro* and *P. polyxenes asterius* in southeastern Arizona.

- DIAGNOSIS:** A small to medium-sized desert swallowtail, with highly variable extent of black and yellow markings in the basic wing patterns. Three basic adult forms occur in this polymorphism, but only one is sexually dimorphic. Form "clarki" resembles more typical *P. polyxenes* of the eastern U.S., with a narrow band of yellow spots on black wings, and shows the same sexual dimorphism as *asterius*. Form "coloro" resembles *P. zelicaon* very closely with broad yellow markings. Form "comstocki" is intermediate in yellow band width, with broad areas of blue scaling across the black areas on the hindwing.
- ORIGINAL DESCRIPTION:** W. G. Wright, *Butterflies of the West Coast*, p. 86 (1905).
- TYPE LOCALITY:** Colorado desert, southeastern California (from Wright, 1905). Type locality restricted to Whitewater Hill, Riverside County, California by Ferris and Emmel (1982). Type in California Academy of Sciences.
- DISTRIBUTION:** This swallowtail is widespread in our deserts from the Death Valley region south to the Mexican border. Temporary or ephemeral populations become established in the foothills of the western Mojave and Colorado deserts in wet years.
- ELEVATION RANGE:** This species occurs close to sea level near the Coachella Valley to as high as 8,400' on Dry Mountain in the Death Valley region, and perhaps to as high as 11,000' in the case of hilltopping males on Telescope Peak in the Panamint Range.
- HABITAT AND PLANT COMMUNITIES:** *P. p. coloro* flies in desert washes or on open flats or slopes within the following plant communities: Creosote Bush Scrub, Mixed Desert Scrub, Shadscale Scrub, Desert Microphyll Woodland, Pinyon-Juniper Woodland, and Desert Transition Chaparral. These habitats are in marked contrast to the more mesic situations occupied by *P. polyxenes asterius* in the eastern United States.
- PHENOLOGY:** This butterfly flies normally in two main flights, the spring brood flying in February to May and the fall brood in September and October, depending upon the distribution of desert rains in any given year. However, specimens have been taken in every month of the year by collectors, and the occurrence of the species in different parts of the desert will vary depending upon local rainfall patterns from winter or summer storms. Pupae have been known to delay emergence for 4-6 years in the laboratory and are probably capable of doing the same under conditions of low annual rainfall in the desert.
- ADULT BEHAVIOR:** The males are strong hilltoppers while the females are usually found in lower areas (particularly desert washes) in the vicinity of the *Thamnosma montana* foodplants, ovipositing. Nectar sources include *Hyptis emoryi*, *Senecio douglasii*, and *Thamnosma* flowers. Males are attracted to mud.
- LIFE HISTORY:** The eggs are laid on tender new growth of *Thamnosma*. The eggs are lemon yellow when first laid and are about one mm in diameter. Within several days the eggs develop a reddish fertility ring, which is the developing embryo, under the chorionic shell and then turn black before hatching. The first four larval instars are black with a white pattern and red, and yellow or orange spots. The last-instar larvae are highly variable in pattern, ranging from a very light form with a whitishground color and thin black transverse bands across segments with orange spots, to a much darker form which can be almost entirely black with only a vestage of the lighter white areas between the segments and orange spots across

the segments. Larvae of the last three instars drop from the foodplant at the slightest disturbance, in contrast to larvae of *P. p. asterius*, *P. zelicaon*, or *P. bairdii* which cling tenaciously to the host. As with *Papilio bairdii* and *Papilio zelicaon*, there are two basic color phases to the pupae, both a light green one and a light brown (or gray) one. Diapause occurs in the pupal stage.

FOODPLANT: The most commonly used native foodplant is Turpentine-Broom, *Thamnosma montana* Torr. & Frem. (Rutaceae). Native species of Apiaceae are occasionally used by *coloro*, particularly in years of extremely high abundance of adults (see, for example Emmel & Emmel, 1969, and Ferris & Emmel, 1982). Apiaceous species used are: *Cymopterus panimentensis* var. *acutifolius* (Coult. & Rose) Munz, *Tauschia arguta* (T. & G.) Macbr., *I. parishii* (C. & R.) Macbr., *Foeniculum vulgare* Mill., and probably *Angelica lineariloba* Gray. Bauer (19) found *coloro* larvae on cultivated *Daucus carota* at Yuma, Arizona. Larvae have also been collected on cultivated *Ruta graveolens* at Hemet, California (J. F. Emmel, unpublished data).

PARASITES/PREDATORS: The eggs are often heavily parasitized by *Trichogramma* wasp species, as are the eggs of *Papilio zelicaon*, *P. bairdii* and the *P. indra* complex. Natural predators in the desert are unknown at present. The bold color pattern of the larvae on the strongly odiferous foodplant suggests that there may be some distasteful compound sequestered by the larvae to ward off mammalian, avian, or reptilian predators in the area.

CHROMOSOME NUMBER: Unknown for *coloro*, but $n = 30$ and 31 in typical *polyxenes* from Connecticut (Macki and Remington, 1960a).

SIMILAR SPECIES: See the discussion under *Papilio zelicaon* and *P. bairdii* for similar species.

GEOGRAPHIC AND SEASONAL VARIATION: There is considerable geographic change in the percentage of the black form "clarki" in the *coloro* populations of California. In the southern part of the range at the Cargo Muchacho Mountains of eastern Imperial County, the percentage of "clarki" ranges around 50%. In the extreme northern portion of the Death Valley region, the percentage of "clarki" is approximately 5% or less. The adult polymorphism is genetically independent of the equally diverse larval and pupal *coloro* polymorphisms. That is, black larvae do not give rise to adults of form "clarki," nor do brown or green pupae yield adults of a single color form. The form "comstocki," which is intermediate between typical *coloro* and "clarki" in band width and often has extensive sub-marginal blue areas on the hind wings, is scarcer than either of the other two color forms. No seasonal variation has been noted.

GENERAL REMARKS: The adults of this species are remarkably agile and rapid fliers in the desert canyons, and out on the open desert floor, it is almost impossible to net them without a hard chase. It is usually easier to rear specimens by collecting mature larvae in the field and raising them on a substitute foodplant such as fennel.

For many years this species was known as *Papilio rudkini* Comstock, after an early southern California lepidopterist (Charles N. Rudkin) who was honored in the naming by John Adams Comstock (1935). Comstock called this new swallowtail *Papilio bairdii* form "rudkini", on the basis of a series of specimens collected by Rudkin in September 1934 in the Ibanpah [sic] Mountains, which were clearly not identical to the phenotypically similar taxon, *P. bairdii* form "brucei." Comstock at first linked the new desert swallowtail to *P. bairdii* because about 2% of the Ivanpah population (in September 1934) appeared to be typical

bairdii (black with a narrow yellow band, the form to be named "clarki" later). When the Chermocks (1937) raised the name *rudkini* for the light yellow form to a species level, and named the two darker forms as *comstocki* and *clarki*, they received subsequent authors' credit for establishing the new species: *Papilio rudkini* F. Chermock & R. Chermock (see Miller and Brown, 1981). Subsequently, it was found that Wright previously had named this butterfly *coloro* in 1905, and for that reason this name has scientific priority or precedence over the familiar *rudkini* used in most publications (Ferris and Emmel, 1982). The affinity of this swallowtail with the eastern *Papilio polyxenes* has been shown recently by studies of a southeastern Arizona blend zone and laboratory hybridizations and is discussed in detail by Ferris and Emmel (1982). If it were not for the fact that *coloro* and *polyxenes* can form F₁ hybrids readily, which can be bred into the F₃ generation, one would not readily suspect this taxonomic association.

Another interesting fact about this species is the remarkable, occasional abundance of this swallowtail in our deserts. In years of especially good rainfall, when *Thamnosma* bushes produce leaves in abundance and are covered with purple flowers, as many as dozen or more larvae per bush may be found and literally thousands of larvae and adults will be seen across a short desert transect.

4. *Papilio indra* Reakirt

These are medium to large-sized swallowtails which are predominately black in ground color and have a postmedian pale yellow band of variable width. The hindwing tail varies in length among the different subspecies. There is no sexual dimorphism. The abdomen is black with a single lateral pale yellow patch near the tip (sometimes expanded to a lateral stripe).

The many geographically isolated populations of the *Papilio indra* complex have evolved into over a half-dozen distinctive segregates; a number of these found in the southern Great Basin region have yet to be adequately studied and characterized. The species is uncommonly encountered because of its specialized and often remote habitats. It is the most divergent member of the *Papilio machaon* group, based on morphology of the immatures and several hybridization studies. Usually, it is sympatric with another member of the *P. machaon* complex, which may even share the same host plant.

ADULT BEHAVIOR: Males of *P. indra* are strong hilltoppers, but tend to patrol just below the actual summit of a given peak, on the leeward side. Females are usually found flying in a large, slow, zig-zag pattern over the rocky slopes where the foodplants grow.

Nectar sources include *Cirsium* species (all subspecies), *Hyptis emoryi* (*fordi*), *Lycium* species (*fordi*), *Clematis* (*nevadensis*), and *Convolvulus* (*nevadensis*). The males are attracted to mud.

LIFE HISTORY: The ova are cream, ca. 1 mm in diameter, and usually laid on the undersurfaces of leaves near their tips, at the periphery of the foodplant. Females tend to select plants which have adjacent protective rocks, and ova will be laid on leaves nearest the rock's surface.

The first two instars rest on the undersurface near the leaf tip and produce a characteristic nibbled-away pattern on the leaf edges. Third and fourth instars rest on leaf petioles further down in the plant. Last-instar larvae rest between petioles near the plant base, or under rocks or in rock crevices immediately adjacent to the foodplant. Virtually all feeding takes place during the daylight hours and at approximately one-hour intervals; the larva crawls up a leaf from its resting place,

a portion of leaf is very rapidly consumed, and the larvae quickly returns to its hiding place. Third through fifth-instar larvae readily drop from the plant when disturbed.

The early-instar larvae are black with varying degrees of white "saddle" markings characteristic of the *Papilio machaon* group. There are marked differences among the various subspecies in the fourth and fifth-instar larvae (Comstock and Martin, 1955; Emmel and Emmel, 1968, 1974; Emmel, J. F., 1981). Fourth-instar larvae of nominotypical *indra* and *phyllisae* tend to be black with transverse rows of yellow spots on each segment. Those of *fordi*, *martini*, and *panamintensis* are deep black with reduced white spotting. The fifth-instar larvae of nominotypical *indra* are black with transverse orange, yellow, or salmon bands and orange or yellow spots along the posterior border of the lighter bands. *Pergamus* larvae have the black areas so reduced that the dominant ground color is a gray-pink; the spots are yellow. In *fordi*, *martini*, and *panamintensis*, there are approximately equal areas of black banding alternating with lighter banding. The light areas in *fordi* larvae are white to pale pink or pale bluish white, with lemon-yellow dots. In *martini* and *panamintensis*, the light areas are pink or salmon, and the dots yellow to orange. *Phyllisae* larvae have somewhat greater expansion of the light areas, which are bright pink in this subspecies; the dots are yellow-orange.

The pupae of *indra* and *phyllisae* are tan to gray-black, while *pergamus* pupae are mottled tan, dull-gray green, and gray-black. The desert subspecies tend to have mostly tan pupae (in *fordi*), or tan pupae with green-tan wing cases (in *martini* and *panamintensis*). The surface of *pergamus* pupae is much rougher and more irregular than that of the other subspecies.

CHROMOSOME NUMBER: $n = 27$ in one typical *P. indra indra* counted from Colorado (Emmel, Eliazar, and Harris, unpublished).

SIMILAR SPECIES: Males of *Papilio bairdii* are superficially similar to *pergamus* adults, but may be readily distinguished by the rows of yellow spots on the abdomen. Females of *Papilio polyxenes coloro* form "clarki" resemble *P. i. martini* adults, but again can be separated by the abdominal spotting pattern. These similar species all can be distinguished by the combination of abdominal markings, wing shape, and hindwing color patterns.

GENERAL REMARKS: The *Papilio indra* complex has been a subject of particular fascination to many authors (Clark & Sheppard, 1953-55; Emmel & Emmel, 1963b, 1965, 1966, 1968, 1969, 1971b, 1973a, 1973c, 1974; Emmel, J. F., 1981). A recent paper (Emmel & Emmel, in prep.) details the interesting contrast in evolutionary divergence between changes in adult characters and changes in larval characters across the broad geographic range of this species in western North America. For a butterfly that often inhabits remote and desolate areas and is considered a great rarity in most of its subspecific forms, this butterfly has shown a remarkable success story in evolutionary terms. It has colonized tremendously diverse regions, from northwestern New Mexico north to the Canadian border, and then west to the east slope of the Cascades, south to the cool, moist areas of northern California to the hot, dry mountains of the Mojave Desert and the chaparral areas of San Diego County and northern Baja California. Its populations in the desert mountain ranges persist under extraordinarily adverse environmental conditions. The facultative pupal diapause of up to five years allows these desert populations to wait out several years of drought until conditions are better for emergence and reproduction. A similar situation of prolonged pupal diapause has been described for *Papilio alexanor* in arid zones of Palestine in the Middle East (Nakamura and Ae, 1977).

a) *P. i. indra* Reakirt

- DIAGNOSIS: The typical subspecies has a relatively small wing size for the group and very short (almost non-existent in some specimens) tails. The postmedian band of pale yellow spots extends fully across forewing and hindwing without varying substantially in width.
- ORIGINAL DESCRIPTION: Reakirt, *Proceedings of the Entomological Society of Philadelphia*, 6: 123 (1866).
- TYPE LOCALITY: Pikes Peak, Colorado. Holotype in ANSP.
- DISTRIBUTION: Within California, nominotypical *indra* is found in the Sierra Nevada from Tulare County and northern Inyo County northward to the Donner Pass region. It is apparently absent from the Warner Mountains. Outside of California, the species complex is found in scattered areas eastward to the Rocky Mountain region and north to the Canadian border.
- ELEVATION RANGE: 4,000' to 11,000' elevation, with hilltopping males going as high as 14,000' on the higher Sierran peaks.
- HABITAT AND PLANT COMMUNITIES: Populations of typical *indra* may inhabit open rocky slopes, ridges and canyon bottoms, within the following plant communities: Lower Montane Coniferous Forest, Upper Montane Coniferous Forest, Subalpine Forest, Arctic-Alpine Cushion Plant, Great Basin Sagebrush Scrub, and Pinyon-Juniper Woodland.
- PHENOLOGY: The Sierran populations are apparently all univoltine. Emergence begins in mid-May and continues through early July, depending on elevation and snowpack. In some very wet years with heavy snowpacks, adults can be taken into mid-August in the higher elevation localities.
- FOODPLANTS: For nominotypical *indra* in the Sierra Nevada, the following species in the family Apiaceae are used: *Pteryxia terebinthina* (Hook.) Coult. & Rose, *P. petraea* (Jones) Coult. & Rose, and *Lomatium rigidum* (Jones) Jeps.; *L. torreyi* (Coult. & Rose) Coult. & Rose is suspected as a foodplant in Tulare County (J. F. Emmel, unpublished data).

b.) *P. i. shastensis* Emmel

- DIAGNOSIS: The phenotype of these populations is very similar to nominotypical *indra*, except that the postmedian yellow band tends to be somewhat narrower and the adults are generally slightly larger than Sierran *indra*. Additionally, in some of the Klamath Mountains region populations, there may be a small second brood during the summer months, at least in favorable years.
- ORIGINAL DESCRIPTION: Emmel, J. F.
- DISTRIBUTION: This subspecies is found in the North Coast Ranges from Napa and Sonoma counties northward to the Klamath Mountains, and from there southeastward into the Mt. Lassen region. It also extends into extreme southwestern Oregon.
- ELEVATION RANGE: 100' to 8,000', with hilltopping males to as high as 10,457' on the summit of Mt. Lassen and possibly to over 14,000' on the summit of Mt. Shasta.

HABITAT AND PLANT COMMUNITIES: In the North Coast Ranges, the butterfly is found on ridges and slopes within Serpentine Chaparral areas; in the Klamath Mountains and Mt. Shasta region, it is typically found on open rocky slopes within the Lower Montane Coniferous Forest or Great Basin Sagebrush Scrub plant communities. In Del Norte County, it is found in the Serpentine Dwarf Pine Woodland.

PHENOLOGY: The low-elevation populations fly from late March to early May, while the higher elevation ones fly from mid-May to early July, depending on temperature patterns and progression of the season. Populations in the Mt. Shasta region may produce a very small second brood which emerges in July to early August.

FOODPLANTS: The followings species of Apiaceae are used: *Lomatium marginatum* (Benth.) Coult. & Rose, and *L. howellii* (Wats.) Jeps.; in the Mt. Shasta region, *Pteryxia terebinthina* (Hook.) Coult. & Rose is the predominant foodplant.

c) *P. i. pergamus* Henry Edwards

DIAGNOSIS: A somewhat larger subspecies of the higher southern California mountains, distinguished by its long tails and somewhat narrower postmedian band of pale yellow spots.

ORIGINAL DESCRIPTION: Henry Edwards, *Proceedings of the California Academy of Sciences*, 5: 423 (1875).

TYPE LOCALITY: "Santa Barbara, California." This locality undoubtedly in error, as *pergamus* has never been collected in the area. Type locality fixed as Devil Canyon, San Bernardino Mountains, San Bernardino, California by Scott Miller (1984). Holotype in American Museum of Natural History.

DISTRIBUTION: *Pergamus* is found in the higher mountains of southern California, from northwest Los Angeles County in the Sawmill Mountain area eastward to the San Bernardino Mountains, south through the mountains of western Riverside and San Diego counties. It is found along the eastern slope of the Santa Ana Mountains in extreme western Riverside County. The southern limits of its range in northern Baja California are undetermined.

ELEVATION RANGE: Mostly below 8,000'; hilltopping males range to 11,500' (peak of Mt. San Geronio).

HABITAT AND PLANT COMMUNITIES: This subspecies inhabits mostly open slopes and canyons in predominantly granitic areas. The preferred plant community is Mixed Chaparral; it is less common in Lower Montane Coniferous Forest, Upper Montane Coniferous Forest, and Desert Transition Chaparral.

PHENOLOGY: Adults fly primarily in April and May, depending on elevation; some higher-elevation populations fly into June.

FOODPLANTS: *Tauschia arguta* (T. & G) Macbr., *T. parishii* (Coult. & Rose.) Macbr., and *Lomatium lucidum* (Nutt.) Jeps. (all Apiaceae) (Emmel & Emmel, 19).

d) *P. i. fordi* J. A. Comstock and L. M. Martin

DIAGNOSIS: A small *indra* race in the desert mountains, with shortened tails and very expanded pale yellow markings.

- ORIGINAL DESCRIPTION: J. A. Comstock and L. M. Martin, *Bulletin of the Southern California Academy of Sciences*, 54: 144 (1955).
- TYPE LOCALITY: Granite Mountains, north and east of Apple Valley, San Bernardino County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This attractive broad-banded swallowtail is found in the ranges of the west-central Mojave Desert (Calico Mountains, Granite Mountains near Victorville) eastward to the Soda Mountains northwest of Baker, south to the Cottonwood, Eagle, and Coxcomb Mountains of Joshua Tree National Monument, the Granite Mountains southwest of Rice, the Old Woman Mountains, and the Granite Mountains north of Amboy.
- ELEVATION RANGE: Mostly 2,000' to 4,400'; hilltopping males to 7,000' in the Granite Mountains north of Amboy.
- HABITAT AND PLANT COMMUNITIES: *P. i. fordi* inhabits mountain ranges with rocky slopes of granite (most populations), rhyolite, or limestone, within the Mixed Desert Scrub plant community.
- PHENOLOGY: Strictly univoltine. Adults fly primarily from mid-March to mid-April (some late February and May records).
- FOODPLANTS: *Cymopterus panamintensis* C. & R. variety *acutifolius*. (Coult. & Rose) Munz (Apiaceae). On rare occasions during population explosions of this species, larvae will crawl off completely-denuded *Cymopterus* plants and move onto nearby plants of *Thamnosma montana* Torr. & Frem. (Rutaceae), and feed successfully through to maturity on this plant (Emmel and Emmel, 1969).

e) *P. i. martini* J. F. & T. C. Emmel

- DIAGNOSIS: Somewhat larger in size than *fordi*, *P. i. martini* is another desert mountain subspecies that is distinguished by a narrow postmedian band on the forewing, a triangular or greatly reduced postmedian band on the hindwings, and longer tails.
- ORIGINAL DESCRIPTION: J. F. Emmel and T. C. Emmel, *Entomological News*, 77: 57-60 (1966).
- TYPE LOCALITY: Gilroy Canyon, Providence Mountains, San Bernardino County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is restricted to the Providence Mountains in the eastern Mojave Desert, where it has been found on the summits of the highest peaks, in Bonanza King Mine Canyon and Gilroy Canyon, and in the Mitchell Caverns State Park area.
- ELEVATION RANGE: 3,000' to 7,000'.
- HABITAT AND PLANT COMMUNITIES: Canyon bottoms and open slopes, within the Pinyon-Juniper Woodland plant community.
- PHENOLOGY: Adults fly in April and May in the normal single brood. Occasionally in very wet years, there is a small second brood that flies in late June and July.
- FOODPLANTS: *Lomatium parryi* (Wats.) Macbr. (Apiaceae) is the sole larval foodplant in the Providence Mountains (Emmel and Emmel, 1966, 1968).

f) *P. i. panamintensis* J. F. Emmel

- DIAGNOSIS:** A large subspecies from the Death Valley ranges, *P. i. panamintensis* most closely resembles *P. i. martini* to the south. Important points of distinction include: the wings in *panamintensis* have a deep, jet black ground color, whereas in *martini* the ground color is dull black; the light markings on the wings are pale yellow in *panamintensis* and cream in *martini*; the forewing post-median row of markings is much narrower in *martini*, often obsolescent, whereas it is well-developed in *panamintensis*; the submarginal spots on both wings are reduced in *martini* and usually enlarged in *panamintensis*; the blue scaling on the hindwing is more prominent in *martini* than in *panamintensis*.
- ORIGINAL DESCRIPTION:** J. F. Emmel, *Journal of the Lepidopterists' Society*, 35:297-302 (1981).
- TYPE LOCALITY:** Thorndike Campground, Wildrose Canyon, Panamint Range, Inyo County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION:** This subspecies inhabits the mountains of the Death Valley region, including the Panamint, Cottonwood, and Last Chance ranges. Similar but atypical populations occur in the Inyo Mountains, Grapevine Mountains, the Nopah Range, and the Kingston Range in extreme southeastern Inyo County.
- ELEVATION RANGE:** 3,000' to 7,400'; hilltopping males occur from Mahogany Flat at 8,100'-8,300' up to 11,000' on the summit of Telescope Peak in the Panamint Range.
- HABITAT AND PLANT COMMUNITIES:** This race is found in the Pinyon-Juniper Woodland plant community. At the type locality in Wildrose Canyon, a large canyon on the west slope of the Panamint Range in the Death Valley region, the vegetation includes *Artemisia tridentata* Nutt., *Cercocarpus ledifolius* Nutt., *Purshia stansburiana* (Torr.) Jeps., *Eriogonum umbellatum* Torr. var. *subaridum* Munz, and *Lomatium parryi* (Wats.) Macbr. (Emmel, J. F., 1981).
- PHENOLOGY:** Adults fly from late April to mid-June, depending on elevation. A small second brood emerges in mid summer in years of above-average winter rainfall.
- FOODPLANTS:** *Lomatium parryi* (Wats.) Macbr. (Apiaceae) is the sole known host (Emmel, J. F., 1981).

g) *P. i. nevadensis* T. C. & J. F. Emmel

- DIAGNOSIS:** This is a large subspecies of *indra*, with more elongate forewings and hindwings, long tails, and broad and prominent postmedian yellow banding. It superficially appears closest to *P. i. pergamus* from southern California, but *pergamus* adults are smaller with more angular wings and the immature stages differ strongly between the two subspecies.
- ORIGINAL DESCRIPTION:** T. C. Emmel and J. F. Emmel, *Pan-Pacific Entomologist*, 47: 220-222 (1971).
- TYPE LOCALITY:** Jett Canyon, Toiyabe Range, Nye County, Nevada.
- DISTRIBUTION:** This subspecies is typically found in the Toiyabe Range and adjacent ranges in central Nevada. Populations of *nevadensis* grading intermediate to nominotypical *indra* occur in the White Mountains of Inyo County near the California-Nevada

border, such as at Westgard Pass, as well as in the Walker River area of Mono County.

- ELEVATION RANGE: 5,000' to 8,000' usually, with hilltopping males occurring to 14,242' at the summit of White Mountain Peak.
- HABITAT AND PLANT COMMUNITIES: Pinyon-Juniper Woodland and Great Basin Sagebrush Scrub are the principal plant communities inhabited by this subspecies. The vegetation at the type locality of Jett Canyon is typical of its favored habitats, including pinyon, willows (*Salix exigua* Nutt.), sagebrush (*Artemisia tridentata* Nutt.), *Prunus virginiana* L. var. *demissa* (Nutt.) Sart., *Purshia tridentata* (Pursh) DC., and *Holodiscus boursieri* (Carr.) Rehd. The umbelliferous foodplants of this swallowtail grow on the steep, rocky slopes and canyon walls (Emmel and Emmel, 1974).
- Males have been taken feeding on *Cirsium* species (thistles) and at mud or wet sand, and occasionally they visit blooms of *Clematis* vines. Females frequented *Cirsium* flowers at Jett Canyon and one was observed feeding on a *Convolvulus* (morning glory vine); they also fly along the canyon bottom. The summer brood in the Toiyabe Range overlaps with other swallowtails, including *P. zelicaon* Lucas, *P. bairdii hollandi* Edwards, *P. multicaudatus* Kirby, and *P. rutulus* Lucas. Only *P. zelicaon* uses the same larval foodplant as *P. i. nevadensis* there. The ecology of *nevadensis* in the White Mountains is much less well known.
- PHENOLOGY: The White Mountains population flies from mid-May to late June; a small second brood may emerge in July and August in favorable years.
- FOODPLANTS: *Pteryxia petraea* (Jones) Coult. & Rose (Apiaceae) is the sole host reported for this subspecies in both California and Nevada (Emmel and Emmel, 1971, 1974).

h) *P. i. phyllisae* J. F. Emmel

- DIAGNOSIS: A large, widebanded subspecies from the southern Sierra Nevada, *phyllisae* has a medium-length tail, more elongated wings, and wider postmedian spots (often twice as wide) than typical *indra* to the north.
- ORIGINAL DESCRIPTION: J. F. Emmel, *Journal of the Lepidopterists' Society*, 35: 297-302 (1981).
- TYPE LOCALITY: Butterbrecht Peak, Kern County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This distinctive subspecies is found from the Piute Mountains and extreme southern Sierra Nevada of Kern County north to the upper Kern River drainage of Tulare County, and along the east slope of the Sierra Nevada in Inyo County as far north as Whitney Portal (Emmel, J. F., 1981).
- ELEVATION RANGE: 4,500' to 10,000' (mostly 5,000' to 7,000').
- HABITAT AND PLANT COMMUNITIES: Pinyon-Juniper Woodland is the usual plant community for this subspecies. On the slopes of Butterbrecht Peak, located about 22 airline miles northeast of the town of Tehachapi, the vegetation consists largely of sparse Joshua Tree (*Yucca brevifolia* Engelm. in Wats.) and Juniper (*Juniperus californica* Carr.) Woodland, with *Eriogonum fasciculatum* Benth., *Atriplex canescens* (Pursh) Nutt., and *Tauschia parishii* (C. & R.) Macbr. (Emmel, J. F., 1981).

PHENOLOGY: Depending on elevation, emergence of adults begins in mid April or early May, and continues through early to late June. A small second brood emerges in July in very wet years.

FOODPLANTS: *Tauschia parishii* (Coult. & Rose) Macbr. (Apiaceae) is the apparent sole foodplant. It is a large apiaceous species found in the California mountains from the southern Sierra Nevada to San Diego County.

5. *Papilio demoleus* Linnaeus

See **Appendix** for the one California record (in Santa Clara County) of this tropical Old World swallowtail.

6. *Papilio (Heraclides) cresphontes* (Cramer)

The Giant Swallowtail is typically an inhabitant of tropical to temperate woodlands from Mexico north into southern Arizona and the eastern United States. In California, it seems well established in citrus groves of the Colorado River area and Imperial Valley.

DIAGNOSIS: A large dark-brown swallowtail with a band of large yellow spots extending from the forewing tip to the center of the trailing forewing edge and ending in the upper third of the hindwing. There is also a submarginal row of large yellow spots on both wings. The broad tail has a large yellow spot in the center.

ORIGINAL DESCRIPTION: Cramer, *Uitl. Kapellen*, 2: 106-107 (1777).

TYPE LOCALITY: "New York, South Carolina, Jamaica." Location of type not known.

DISTRIBUTION: This southern North American species is found regularly in the Colorado River Valley and in the Imperial Valley. It is also sporadically taken in the regions northwest of the desert, including the San Joaquin Valley and in citrus-growing areas near Hemet and Banning in Riverside County.

ELEVATION RANGE: Most records are near sea level, but it has been taken close to 2000' near Hemet, California.

HABITAT AND PLANT COMMUNITIES: Found in agricultural areas where citrus is grown.

PHENOLOGY: Records in eastern Imperial County show that the flight season extends there from March to October or November (Kilian Roever, personal communication) and it is apparently a breeding resident in at least the areas immediately adjacent to the Colorado River. To the west and north, our records include primarily the late summer and fall months, suggesting that these populations may be still seasonally established by migrants coming in from the Colorado River basin or Arizona each year.

ADULT BEHAVIOR: Adults are usually seen flying through citrus groves or visiting flowers of *Lycium* species (family Solanaceae) along irrigation canals and ditches. At Hemet, adults avidly nectar on *Lantana*.

LIFE HISTORY: The spherical egg, about 1 mm in diameter, is light green. The mature larva is dark brown with creamy white markings on the thorax, the end of the abdomen, and a broad white "saddle" across the mid-dorsal portion of the thorax. The larva

is the largest of California swallowtails. The pupa is also large and mottled brown. Diapause is in the pupal stage.

- FOODPLANTS: Various *Citrus* species (family Rutaceae) in California. To the east and south into the tropics, other native trees such as *Zanthoxylum* species are also utilized as foodplants.
- CHROMOSOME NUMBER: $n = 30$ in Mexico and Florida (Maeki and Remington, 1960a; Emmel and Eliazar, unpublished).
- SIMILAR SPECIES: The only species with which *cresphontes* could be confused is *Papilio thoas*, which occasionally reaches the Arizona border and the Yuma area from Mexico. When viewed from above, the male *thoas* has no space between the valvae at the tip of the abdomen, whereas in *cresphontes* a noticeable gap is visible.
- GEOGRAPHIC AND SEASONAL VARIATION: No geographic or seasonal variation has been noted in our present set of populations and all are classified as one subspecies.
- GENERAL REMARKS: The Giant Swallowtail is a relatively recent arrival to our state, with confirmed records going back only to 1963. The Spanish missions introduced orange and lemon orchard culture two centuries earlier, but the butterfly apparently did not become established until very recently.

7. *Papilio (Pterourus) rutulus rutulus* Lucas

The familiar Western Tiger Swallowtail is found throughout the moister lowlands and mountains of the state, and is abundant in even urban areas wherever Western Sycamores, willows and cottonwoods have been planted. There is only one subspecies, the nominotypical, in California. A second subspecies, *arizonensis* (W. H. Edwards), occurs in Arizona.

- DIAGNOSIS: A large yellow swallowtail with four vertical black "tiger" stripes across the forewing and one across the hindwing. One tail is present on the hindwing.
- ORIGINAL DESCRIPTION: Lucas, in Guérin-Meneville, *Rev. Zool.*, (2)4: 158 (1852).
- TYPE LOCALITY: "California." Type locality restricted to Queen Lily Campground, North Fork Feather River Canyon, Plumas County, California by Emmel, Emmel & Mattoon (1998b). Holotype in Museum Nationale de Histoire Naturelle, Paris, France.
- DISTRIBUTION: This species is found in moist woodland or riparian situations widely across the valleys and mountain ranges of northern, central, and southern California. It occurs from the western edge of the desert westward to the coast, and north through the coastal counties and Central Valley counties to the Klamath Mountains Assemblage and Sierra Nevada; then across the Sierra Nevada to the edge of the Great Basin desert region. It is also found in populations in the White Mountains, Inyo Mountains, and the Warner Mountains of northeastern California.
- ELEVATION RANGE: Sea level to approximately 9,000'.
- HABITAT AND PLANT COMMUNITIES: Typically, the Western Tiger Swallowtail is found along watercourses within the following plant communities: Riparian Woodland (the usual associated plant community), Montane Wet Meadow, and Northern and Southern Mixed Evergreen Forest. It is also found in many suburban

and urban areas wherever one or more of its ornamental tree foodplants are found.

PHENOLOGY: In southern California, this species normally flies from March to October, though early adults have been taken the first week of February or even January. In the northern part of its range and at higher altitudes, the season is somewhat more restricted. There, *P. rutulus* flies in the lower valleys in early April, and in the higher mountains, it is common from May to July. The species goes through one to three broods, usually two in the north, depending on elevation and progression of the season. The last brood overwinters in the pupal stage.

ADULT BEHAVIOR: Adults are typically found flying up and down watercourses or along canyon bottoms. In the drier desert areas or on hot summer days, they may also be seen visiting mudflats and drinking. In urban areas they are a familiar sight flying along the tree-lined streets or visiting ornamental flowers such as hydrangea or *Lantana*. Nectaring of first brood adults of *rutulus* on lilac and on wild mustard (*Brassica nigra*) in urban areas and on *Prunus* fruit trees in agricultural valleys signify the onset of spring in the northern part of the state. There is evidence from a marking study done in the East that tiger swallowtails are rather territorial and will stay in the same area for many days or even weeks (Fales, 1959). Males of the eastern species have not been observed to be hilltoppers, but the Western Tiger Swallowtail will occasionally hilltop.

LIFE HISTORY: The egg, 1 mm in diameter, is flattened at the base (sub-conoidal in shape) and is smooth and deep green in color. The early instar larvae have a "bird-dropping" pattern and rest on a silken map on the upper surface of the foodplant leaf. The mature larva is green to bluish-green; on the trailing edge of the first abdominal segment is a yellow line, edged posteriorly with black. On the metathoracic segment are two yellow eye-spots, bordered with black and pupiled with a blue spot. The pupa is dark brown and looks very much like a chip of wood. There is no dimorphism in the female ground color of this western tiger swallowtail species, unlike the Eastern Tiger Swallowtail (*Papilio glaucus*) which has black and yellow forms.

FOODPLANTS: The principal foodplant below 4,000' elevation in southern California is Western Sycamore, *Platanus racemosa* Nutt. (family Platanaceae). Throughout the state, a number of species from the family Salicaceae are utilized, including various willows (*Salix* species) and members of the genus *Populus* such as Aspen and Cottonwood. J. F. Emmel (unpublished) collected a larva on *Salix* _____ near Mono Lake. Brower (1958) lists these documented specific foodplant records from California for the larvae of this swallowtail: *Salix lasiolepis* Benth. (Arroyo Willow) and *Salix lasiandra* Benth., in the family Salicaceae; *Alnus viridis* var. *sinuata* (Regel) Rydb. (Alder) in the family Betulaceae; *Prunus* ("cherry") in the family Rosaceae. In suburban areas, pupae have been collected in the immediate vicinity of plants of *Prunus* _____ (Flowering Plum) and this is presumed to serve as a foodplant (J. F. Emmel, unpublished data).

P. rutulus has recently become abundant around prune and almond-growing areas of the northern Sacramento Valley. Growers have described *rutulus* larvae found feeding on almond (*Prunus amygdalus* Batsch.) leaves. C. Hageman in Yuba City has observed oviposition on prune (*Prunus* species), and has found overwintering pupae on dormant trees in his orchards during the winter.

CHROMOSOME NUMBER: n = 30 in Colorado *rutulus* (Emmel, Eliazar, and Harris, unpublished).

- SIMILAR SPECIES:** *Papilio rutulus* may be confused with *Papilio multicaudatus*, which has thinner and shorter black stripes than *rutulus* and also has two tails on each hindwing rather than one.
- GEOGRAPHIC AND SEASONAL VARIATION:** In contrast to the eastern *Papilio glaucus*, in which there is considerable geographic variation between populations lying at more northern latitudes and the southern populations of the butterfly, the California populations of *rutulus* seem to show no significant variation between specimens in the northern part of the state and specimens in the southern part of the state, or from high elevations versus low elevations.
No seasonal variation has been noted.
- GENERAL REMARKS:** The Western Tiger Swallowtail is an almost ubiquitous sight in city parks and along tree-lined canyon bottoms in California. Adults are apparently rather long-lived, probably up to a month or so. In contrast to Scott (1986), we consider (along with the great majority of other authorities) *Papilio rutulus* to be specifically distinct from the Eastern Tiger Swallowtail, *Papilio glaucus*, on the basis of abundant morphological and genitalic differences, life history differences, chromosomal characteristics, and the other usual criteria by which one distinguishes species and subspecies in butterflies (see also Brower, 1958, 1959a, 1959b; Scriber, 1982; Ritland and Scriber, 1985).

8. *Papilio eurymedon* (Lucas)

- The Pale Swallowtail resembles the Western Tiger Swallowtail in general size and markings, but is strongly white or cream in ground color with bolder, thicker black stripes. It occurs from the Rocky Mountains to the West Coast states and north into southern British Columbia.
- DIAGNOSIS:** A large swallowtail with a white to cream ground color and four broad "tiger" stripes running vertically across the forewing, with one across the hindwing; one long tail is present.
- ORIGINAL DESCRIPTION:** Lucas, in Guérin-Meneville, *Rev. Zool.*, (2)4: 140 (1852).
- TYPE LOCALITY:** "California." Type locality restricted to Queen Lily Campground, North Fork Feather River Canyon, Plumas County, California, by Emmel, Emmel & Mattoon (1998b). Type in Museum Nationale de Histoire Naturelle, Paris, France.
- DISTRIBUTION:** The Pale Swallowtail is found in the foothills and mountains from the Sierra-Cascade axis westward to the coast, excluding the following areas: Modoc County and the eastern Great Basin edge of Plumas County, the Warner Mountains, the Inyo Mountains and the White Mountains (to date).
- ELEVATION RANGE:** From near sea level to approximately 8,200' elevation; for hilltopping males, to at least 10,800' (peak of Mt. San Jacinto).
- HABITAT AND PLANT COMMUNITIES:** The butterfly is a montane species and tends to be found flying over open shrubby slopes or in coniferous forests, within the following plant communities: Mixed Chaparral, Serpentine Chaparral, Desert Transition Chaparral, Northern and Southern Mixed Evergreen Forest, Lower and Upper Montane Coniferous Forest, and Montane Chaparral.
- PHENOLOGY:** Most records are from April through September, but records as early as January and as late as October have been noted. At lower elevations the butterfly appears

to be multiple-brooded, while at higher altitudes, it apparently is univoltine. Diapause is in the pupal stage.

ADULT BEHAVIOR: The males of this species are strong hill-toppers, in contrast to the behavior of *Papilio rutulus* and *multicaudatus*. Brower (1959) did field experiments in Utah which showed that yellow *Papilio multicaudatus* males were not attracted to white *P. eurymedon* females, but no investigation to date has been done on the extent of interspecific courtship in nature between *P. rutulus* and *P. eurymedon*. The whitish *Papilio eurymedon* is frequently sympatric with the Western Tiger Swallowtail, *Papilio rutulus*, and both species may be quite abundant in the late spring in the same moist canyon. A hybrid between *rutulus* and *eurymedon* was taken by Dale A. Fleischer (*in litt.*) in the San Bernardino Mountains, at a site where both willows and sycamore trees were abundant and both parental species were flying. This location was five miles west of Mojave River Forks and about five miles from Silverwood Lake, in early August 1974.

LIFE HISTORY: The life history of this swallowtail was first described in detail by Dyar (1893). The nearly-spherical egg is yellowish green in color and 1.3 mm in size. It is laid singly on the upperside of the leaves of its foodplant. The first four larval instars are dark brown to velvety black, with a pale brown cervical shield (first instar) and a white saddle-shaped patch over the dorsum. The subdorsal rows of tubercles are black. The mature fifth-instar larva is entirely smooth, uniform soft green in ground color, and minutely but obscurely dotted with yellowish. The thoracic eyespots differ in details of pattern from *rutulus* and *multicaudatus* (see figures). They consist of a rounded triangular orange spot with a black edge; below it is a pale blue dot, then a black edged pyriform spot, very slightly concave in front and convex on its lower posterior side, divided in the middle by a transverse black line (above which it is orange, below yellow) and containing a violet dot in a broad black border. As the fifth instar matures, this mark becomes terra cotta color, except for the lower part of the pyriform spot, which is yellow, shaded with terra cotta. Rows of deep blue dots replace the former tubercles. The osmeterium scent organ is orange. The pupa is dark wood brown and is heavily streaked longitudinally with brownish black on the dorsal half. The wing cases are grayish. The pupa is about 35 mm in length.

FOODPLANTS: *Rhamnus californica* Esch. (California Coffee Berry) (Rhamnaceae) is the primary host at lower elevations (many records). Also at lower elevations, the *Ceanothus* species (Rhamnaceae) *C. sorediatus* H. & A. and probably *C. leucodermis* Greene are used (J. F. Emmel, unpublished data). At mid to higher elevations, *Ceanothus* species are used, particularly *C. integerrimus* H. & A. and *C. cordulatus* Kell. (J. F. Emmel, unpublished data). Noel McFarland (in Emmel & Emmel, 1963b) noted oviposition on *Rhamnus crocea* Nutt. in T. & G. in the Santa Monica Mountains. Also, *Prunus virginiana* L. (J. F. Emmel, unpublished data) and the Holly-leaved Cherry, *Prunus ilicifolia* (Nutt.) Walp. (Rosaceae) (see Emmel & Emmel, 1963b) and occasionally domesticated *Prunus persica* Batsch. (oviposition recorded on peach tree at Costa Mesa in Orange County by James R. Mori and in Hemet by J. Emmel). However, larvae do not survive on domesticated peach. From literature records, Brower (1958b) lists the following additional documented foodplants for *Papilio eurymedon* in California: *Ceanothus prostratus* Benth. (Rhamnaceae), and *Jasminum* species (Oleaceae). Brower noted that *P. eurymedon* appears to be usually limited to plants of the family Rhamnaceae, but that *eurymedon* females seem to be more prone to oviposition error than either close relative, *P. rutulus* or *P. multicaudatus*.

CHROMOSOME NUMBER: n = 30 in Colorado *eurymedon* (Emmel, Eliazar, and Harris, unpublished).

SIMILAR SPECIES:	<i>P. eurymedon</i> could be confused with a very worn specimen of either <i>P. rutulus</i> or <i>P. multicaudatus</i> . In such cases, the <i>P. eurymedon</i> could be distinguished by the wider black borders on the upperside and the heavier black markings in general.
GEOGRAPHIC AND SEASONAL VARIATION:	Some workers have suggested that with increased elevation or increasing latitude in the state, <i>Papilio eurymedon</i> becomes smaller and darker; however, we have found no general trends supporting this claim. Perhaps further careful studies will uncover geographic trends that are not now apparent.
GENERAL REMARKS:	Of the three California species of the <i>Papilio rutulus</i> group, <i>P. eurymedon</i> is the only species that regularly hilltops. Further studies of interspecific courtship between <i>P. eurymedon</i> , <i>rutulus</i> and <i>multicaudatus</i> would be a very interesting area of investigation.

9. *Papilio multicaudatus* W. F. Kirby

The Two-tailed Swallowtail is our largest swallowtail and has a powerful soaring flight in the foothill canyons of the state. It is found across the western United States, from the Canadian border south to Mexico and Guatemala in the lower mountains.

DIAGNOSIS:	A very large swallowtail with a yellow ground color, four <i>thin</i> black stripes on the forewing, and <i>two</i> tails on each hindwing.
ORIGINAL DESCRIPTION:	Kirby, <i>Papilio</i> , 4: 104 (1884).
TYPE LOCALITY:	"Mexico." Type apparently in British Museum. Kirby proposed <i>multicaudata</i> as a replacement name for <i>daunus</i> Boisduval, <i>Spec. Gen. Lepid.</i> , 1: 342 (1836), which was preoccupied by <i>daunus</i> Cramer, <i>Uitl. Kapellen</i> , 2: 44 [1777]. W. J. Holland subsequently pointed out that the specific name should be corrected to <i>P. multicaudatus</i> because <i>Papilio</i> is a masculine noun (Brower, 1958a).
DISTRIBUTION:	This species is found from the San Emigdio Range north through the Sierra Nevada and Cascade foothills to the northern tier of counties. It is scattered across the Modoc Plateau to the Nevada border east of the Warner Mountains; in the Klamath Mountain Assemblage it extends west to the outer edge of the northern redwood forest and thence south through the inner Coast Ranges to Contra Costa County. There is one record for the eastern slope of the Sierra Nevada near Monitor Pass, and another at Highway 70 on Beckwourth Pass, near Hallelujah Junction. This species is apparently absent from the White Mountains despite the presence of a known foodplant, <i>Prunus virginiana</i> L. Occasionally this swallowtail becomes temporarily established in both the Providence Mountains (e.g., 1968) and the Big Pines area of the San Gabriel Mountains, but has apparently failed to establish permanent populations in those two localities. The overall distribution of the species tends to be spotty and is in no way continuous up the western side of the Sierra Nevada or the inner Coast Ranges.
ELEVATION RANGE:	From 300' to 7,000' in California.
HABITAT AND PLANT COMMUNITIES:	The species is usually found along watercourses within the Riparian Woodland plant community.

- PHENOLOGY:** This swallowtail flies in April and May at the lower elevations, and from May to June for the higher populations; a second brood flies in August, at least in the lower elevation areas.
- ADULT BEHAVIOR:** Adults tend to fly along water courses or canyon bottoms. Hilltopping behavior has not been observed in this species. The most commonly used nectar source are *Cirsium* species (thistles) in our experience..
- LIFE HISTORY:** The eggs are greenish yellow and are laid singly at the rate of 6-7 a day (Pronin, 1955) on the host leaves. Pronin (1955) found that females usually produce about 55 eggs, and do not start to lay for two or three days after fertilization. The eggs hatch in as little as 7 days. The mature larva is apple green, with thoracic markings similar to those described for *P. rutulus* and *P. eurymedon*. The larvae of all three species are quite variable in the pattern of the eyespots on the fourth segment, but the general aspect of the eyespot seems to be specifically constant for each species. The band across the front of the second abdominal segment is broad and velvety black, with a narrow yellow band just anterior to it on the posterior side of the first abdominal segment. The pupa is more stout than those of the preceding two species and is dark greenish-brown, with a dark or black shaded dorsal region.
- FOODPLANTS:** The principal foodplant in the San Emigdio Range and Tehachapi Mountains populations as well as the Sierra Nevada foothill and northern populations is *Prunus virginiana* L. var. *demissa* (Nutt.) Sarg. (Rosaceae). In the Inner Coast Range, the foodplant is *Ptelea crenulata* Greene; *Fraxinus* (Ash) species are also probably used in the Sierra Nevada foothills. The temporarily established population in the Providence Mountains would likely have used *Fraxinus anomala* Torr. ex Wats., which is native to the area.
- CHROMOSOME NUMBER:** n = 30 in Colorado material (Emmel and Eliazar, unpublished).
- SIMILAR SPECIES:** See discussion under *Papilio rutulus* and *P. eurymedon*.
- GEOGRAPHIC AND SEASONAL VARIATION:** The phenotypes of the California populations of *Papilio multicaudatus* are generally smaller and more pale yellowish than that of the Mexican and Arizonan nominotypical subspecies, and may be deserving of a subspecific name (George Austin, personal communication).
- GENERAL REMARKS:** This large and attractive species with two tails never fails to thrill the observer when first seen in a canyon. It is our largest and most colorful swallowtail.

10. *Battus philenor* (Linnaeus)

- ADULT BEHAVIOR:** The northern California subspecies of the Pipevine Swallowtail, *hirsuta*, is generally found in close association with its *Aristolochia* foodplants. In the south of our state, typical *philenor* is found as strays, flying in a unidirectional manner, fairly rapidly, or sometimes taken at nectar sources. In Texas, a group of six *philenor* came together in a little group on a mesquite tree at mid-afternoon when a rainstorm threatened (Gillaspy and Lara, 1984); otherwise, the species has only been observed to roost solitarily at night. In courtship behavior, the male is reported to approach from below the motionless female (sitting upright). The male lands upside down on the stem below the female and in a few seconds will curve his abdomen up and lock onto her *in copula*. He immediately hangs free in the usual way. The unusual aspects of this pairing behavior are that there was no fluttering of wings by either individual, and the male approached from below with his body initially parallel to that of the female in the frontal position. The natural curvature of the *philenor* abdomen facilitates copulation in this frontal position.

Hand-pairing in this orientation works quite well for *Battus philenor* (West, 1983).

LIFE HISTORY: In this swallowtail species, the eggs are laid in groups on the foodplant. The spherical egg is rusty orange in color. The distinctive blackish-blue larva has orange fleshy tubercles and "unbranched spines" on each segment, as shown in the accompanying illustration. The oddly-shaped pupa may be green or brown in basic ground color. The pupa is the over-wintering stage in the northern populations.

FOODPLANTS: The northern *hirsuta* populations use *Aristolochia californica* Torr. exclusively as a native host (numerous records, many workers). The southern stray populations of the typical *philenor* subspecies apparently cannot breed at all in the state unless ornamental *Aristolochia* is being cultivated and used as a host. No native *Aristolochia* species are known to grow south of Monterey County in California.

CHROMOSOME NUMBER: $n = 30$ in Mexico (Maeki and Remington, 1960a).

SIMILAR SPECIES: None.

GEOGRAPHIC AND SEASONAL VARIATION: The subspecies *hirsuta* tends to be smaller and is supposed to be "hairier", with longer scales on the anterior portions of the wing adjacent to the body. Additionally, the tails are stubbier in *hirsuta*.

GENERAL REMARKS: The Pipevine Swallowtail is believed to be distasteful to most predators as a result of its larval foodplant, which contains poisonous compounds that are presumably incorporated by the larva while feeding. The bright colors of the larva and iridescence of the adult probably reflects this state in the form of warning coloration. Elsewhere in the range of this species, various other swallowtails, such as the female of the Eastern Black Swallowtail (*Papilio polyxenes*), mimic the appearance of the Pipevine Swallowtail which thus serves as a "model" in Batesian mimicry complexes. Within California, three possible mimics of the Pipevine Swallowtail are the female form "clarkii" of *Papilio polyxenes coloro*, the female of *Papilio bairdii* form "bairdii," and both sexes of *Papilio indra martini* in the Providence Mountains. At present, of course, we have no records for established resident populations of *philenor* in these areas with the possible resident "mimic" species. That does not exclude the possibility that earlier in evolutionary history, the species pairs (model and mimic) were sympatric as resident butterflies in our state. An alternative explanation is that migratory insectivorous birds coming through the state each year from areas where the Pipevine Swallowtail is relatively abundant to the south of us have exercised a selective pressure on desert swallowtails and high mountain swallowtails in the southern California area, placing a selective premium on mutations conferring protective coloration of the mimetic type.

SUBSPECIES: The Pipevine Swallowtail, an attractive subtropical species occurs in two subspecific forms in the State of California; the nominotypical subspecies *philenor* and the subspecies *hirsuta*.

a) *B. p. philenor* (Linnaeus)

DIAGNOSIS: A medium-sized tailed swallowtail with iridescent blue-green scaling across blackish wings on the dorsal surface, and seven large, bright red-orange, submarginal spots on the ventral hindwing surface.

ORIGINAL DESCRIPTION: Linnaeus, *Mantissa, Plant.*, 2: 535 (1771).

TYPE LOCALITY: "America." Type probably lost.

DISTRIBUTION: The Pipevine Swallowtail in the nominotypical subspecific form ranges from southern California south along the west coast of North America to central Mexico, and on the east coast of Mexico from the state of Veracruz north to most of the eastern half of the United States. In southern California it is taken as a stray in both the deserts and the coastal lowlands.

ELEVATION RANGE: From sea level (records from beaches of San Diego and Orange counties) to as high as 6200' (summit of Monument Peak, San Diego County).

HABITAT AND PLANT COMMUNITIES: There are no permanently established populations of nominotypical *philenor* in the state; the strays that have been collected have been captured in the following plant communities: Creosote Bush Scrub, Mixed Chaparral, Coastal Dune Sand Plant, Urban, and Agricultural.

PHENOLOGY: We have records extending from April to October in both the deserts and the coastal beaches. One extraordinary record from January 19, 1986 is in Hemet, in Riverside County.

FOODPLANTS: No native *Aristolochia* species (family Aristolochiaceae) occur in southern California. Thus the scattered individual records for the subspecies here are all believed to be of strays from Mexico and Arizona.

b) *B. p. hirsuta* (Skinner)

DIAGNOSIS: A somewhat smaller race in northern California, distinguished from the nominotypical subspecies primarily by the "hairy" (more elongated scales) covering of the body and the relatively shorter tails.

ORIGINAL DESCRIPTION: Skinner, *Ent. News*, 19: 149 (1908).

TYPE LOCALITY: Plumas County, California. Syntypes in Carnegie Museum.

DISTRIBUTION: This subspecies ranges from extreme northern San Mateo County and San Francisco Bay, eastward across the Sacramento Valley to the northern Sierra Nevada foothills and north to the southern Mount Shasta region.

ELEVATION RANGE: Most records for this species seem to be below approximately 1,500' elevation, and the majority of these are actually below 500'.

HABITAT AND PLANT COMMUNITIES: The butterfly is found primarily in Riparian Woodland communities where its foodplant is abundant.

PHENOLOGY: The spring brood emerges in March and April and records go as late as August, indicating at least two or three broods through the annual flight season. The later broods are much smaller in number than the spring brood.

11. *Battus polydamus* (Linnaeus)

See **Appendix** for discussion of the only California record (at Santa Monica in Los Angeles County) of this neotropical swallowtail.

Subfamily **Parnassiinae** Duponchel

12. *Parnassius phoebus* (Fabricius)

In the Old World arctic areas, the genus *Parnassius* has a number of species. In California we have only two species; for all of arctic North America, there are three species.

Parnassius phoebus is a medium-sized white butterfly that is a primitive member of the swallowtail family. It is divided into two subspecies. Both of the described *phoebus* subspecies can be differentiated from our next species, *Parnassius clodius*, by the fact that the *phoebus* adults have their antennal shafts ringed with alternate black and white bands while the *clodius* adults have solid black antennae. Also, the sphragis structure deposited by the male around the terminal end of the female abdomen during copulation has a characteristic color and form for each species. In *P. clodius*, the sphragis is white; in *P. phoebus*, the sphragis is gray or black. The *phoebus* sphragis is flattened ventrally with a scoop and keel, whereas the *clodius* sphragis is shaped like a pointed hood, ventrally. Generally, *phoebus* males have a pair of crisply black bars in the forewing cell and gray marginal markings reduced to the edge of the forewings, giving a strongly whitish appearance, whereas *clodius* males have the forewing extensively marked with gray and the cell bars are gray as well. The male hindwings in both species are mostly white. Females of *clodius*, on the other hand, have mostly white hindwings, while the females of *phoebus* have hindwings that are strongly covered with gray markings.

ADULT BEHAVIOR: Adult males are usually observed in unidirectional flight patrolling the slopes in search of virgin females. Females tend to have a more soaring zig-zag flight, which is mainly occupied with searching out oviposition sites. Females of *Parnassius* carry a sphragis apparatus on the end of their abdomen after they have been mated for the first time by a male. This hard, external structure prevents multiple matings. In observing adults in an alpine or rocky alpine fellfield, one can occasionally see males engage in a mating sequence. This involves the male driving the female towards the ground, forcing her to alight and then he literally drops on her, pouncing and holding her down while copulating. This has been called "rape" mating behavior by several authors (McCorkle and Hammond, 1985; Drummond, 1986). The females of this species oviposit rather haphazardly on debris and other plants near the larval foodplant, a behavioral trait which has given rise to erroneous records for supposed "foodplants" for many *Parnassius*.

LIFE HISTORY: The egg is a chalky white. The species can apparently overwinter as either an unhatched egg or a very young first-instar larva. In the laboratory, fall hatching has been observed or the larvae may not emerge from the eggshell until early spring under conditions of prolonged refrigeration. The young larvae are mostly black and hide under vegetation or rocks near the foodplant during the daylight hours, between periods of feeding. The mature larva is black with many short hairs and has yellow spots on each segment. The pupa is reddish brown to yellowish-brown and is quite rounded in shape compared to most butterfly pupae (almost approaching a lycaenid pupa or noctuid pupa). The pupae are quite rounded in contrast to those of the preceding subfamily, Papilioninae.

CHROMOSOME NUMBER: n = 30 in Colorado (Macki and Remington, 1960a).

- SIMILAR SPECIES:** The second species of *Parnassius* in California, *P. clodius*, occurs sympatrically with this species in most of its range. They can be differentiated by the antennal coloration, in that *phoebus* has alternating black and white segments on the antenna while *clodius* has all-black antennae. Also, the female of *phoebus* bears a keel-shaped sphragis whereas the *clodius* sphragis is more hood-shaped.
- GEOGRAPHIC VARIATION:** Within their respective ranges, subspecies *behrii* and *sternitzkyi* are remarkably constant in their size and wing pattern.
- GENERAL REMARKS:** Adults often visit the flowers of Compositae, especially the genus *Senecio*. *Parnassius phoebus* can be one of the most common butterflies in its favorite areas in the Arctic Alpine zone above Tioga Pass during the short mid-summer flight season.

a) *P. p. behrii* W. H. Edwards

- DIAGNOSIS:** A medium-sized butterfly with very reduced gray markings on the forewing of the male and prominent black forewing cell bars in both sexes. This is the only North American subspecies of *phoebus* in which the costal and median spots on the hindwing are normally yellow instead of red. It occurs above timberline in the Sierra Nevada.
- ORIGINAL DESCRIPTION:** W. H. Edwards, *Trans. American Ent. Soc.*, 3:11 (1870).
- TYPE LOCALITY:** Near summit of Mount Lyell, Yosemite Valley, California. Neotype from Tioga Pass, California, is in the Carnegie Museum and was designated by F. M. Brown, *Transactions American Entomological Society*, 101: 12 (1975).
- DISTRIBUTION:** This subspecies occurs from just south of Donner Pass south to the Mt. Whitney region, generally at high elevations.
- ELEVATION RANGE:** 8,000' to 12,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** Typically, *P. b. behrii* is found on open gravelly to rocky slopes in the Arctic-Alpine Cushion Plant community.
- PHENOLOGY:** Adults are recorded for the months of July and August in California. We have two records for September, one for September 12th from Half Moon Lake and one for September 5th in the Kings Canyon National Park, Fresno County. Conceivably this subspecies (and *sternitzkyi*) could be biennial, with ova overwintering the first year and partly grown larvae the second; field studies are indicated to determine this.
- FOODPLANTS:** The subspecies *behrii* utilizes the following two species of *Sedum* (family Crassulaceae): *S. lanceolatum* Torr., and *S. rosea* (L.) Scop. (J. F. Emmel, unpublished data). Curiously, *P. p. behrii* does not seem to utilize *Sedum obtusatum* Gray ssp. *obtusatum* in the Sierra Nevada despite the range of the plant overlapping that of the butterfly in certain areas.

b) *P. p. sternitzkyi* McDunnough

- DIAGNOSIS:** This larger subspecies, strongly white with prominent large red markings in both sexes, occurs in Siskiyou, Shasta, and Trinity counties. In the male, the anal and submarginal gray hindwing markings are weak to absent, while both the costal and median ocelli on the hindwings are red with white centers. There are also two

to three red subapical spots on the forewing and one black anal spot. In the female, the anal spot on each wing is red (occasionally, two red or black spots). The submarginal gray markings are red with white centers, and there are three red subapical spots on the forewing.

- ORIGINAL DESCRIPTION: McDunnough, *Canadian Entomologist*, 68:273-274 (1936).
- TYPE LOCALITY: Castle Lake, Siskiyou County, California. Holotype in Canadian National Collection, Ottawa, Ontario.
- DISTRIBUTION: Populations of *sternitzkyi* are scattered throughout the Klamath Mountains assemblage in Siskiyou, Shasta, and Trinity counties; it extends northward into the Mt. Ashland area of extreme southern Oregon.
- ELEVATION RANGE: 5,000' to 7,000'.
- HABITAT AND PLANT COMMUNITIES: This subspecies prefers open gravelly or rocky slopes surrounded by Upper Montane Coniferous Forest or Subalpine Forest.
- PHENOLOGY: The single brood flies from the first of July to late August, with the main flight taking place during mid to late July.
- FOODPLANTS: The subspecies *sternitzkyi* uses *Sedum obtusatum* Gray ssp. *boreale* Clausen (J. F. Emmel, unpublished data). It may possibly also use *S. lanceolatum* Torr. in certain areas of the Klamath Mountains assemblage.

13. *Parnassius clodius* Menetries

Parnassius clodius, a species limited to northwestern North America, reaches its greatest diversity of subspeciation in California, where a number of distinctive segregates have evolved. It has a much wider altitudinal range than the preceding species, and several races are even found in moist Redwood forests and other habitats quite different from those of *phoebus*.

- ADULT BEHAVIOR: Males of the low-and mid-elevation subspecies in California patrol along watercourses, whereas males of the higher-elevation *baldur* patrol on open slopes. Females are usually found near the foodplants. Oviposition takes place haphazardly on or near the foodplant. In courtship, the males grab the females in mid-air and both fall to the ground and mate.
- LIFE HISTORY: The life history and biology of *P. clodius* in the Pacific Northwest has been described in detail by McCorkle and Hammond (1985). Females oviposit the tan or pinkish eggs on or near the *Dicentra* foodplants. The indiscriminate oviposition by the females on other plants near the foodplant has resulted in several erroneous foodplant records for this species. The young larvae hide in debris or under rocks near the base of the foodplant much of the time. Feeding takes place at regular intervals and occurs very rapidly so that the larva spends most of the time in hiding.

There are two types of prominent color markings on *P. clodius* larvae. In the form which predominates at lower elevations, the body is black with a lateral row of bright yellow spots on each side of the body. This pattern supposedly mimics the poisonous millipede, *Harpathe haydeniana*, and affords the larva protection against mice and other mammalian and avian predators. The other color form of the larva is gray-brown or pinkish-gray, with creamy yellow lateral spots and

dorsal rows of narrow chevron markings, which tends overall to be a more cryptic pattern, superficially resembling that of many nondescript noctuid larvae. This color form predominates at the higher elevations, in most (if not all) *P. c. baldur* populations. Some populations at the interface between *baldur* and the lower elevation *sol*, such as in the Klamath Mountains region, tend to be polymorphic for both color forms of the larvae.

The pupa is dark brown, is short and rounded, and is very similar to a saturniid moth pupa. It is enclosed in a silken cocoon which, in contrast to that of *P. phoebus*, is rather well-formed and strong.

The species diapauses in the egg stage. For low-elevation populations, development is completed in a single year and the eggs emerge in the spring. However, for the higher-elevation populations, it is possible that partly grown larvae may overwinter, making the species biennial.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: See discussion under *Parnassius phoebus*.

GEOGRAPHIC VARIATION: See discussion under the various subspecies. Some specimens from near the Oregon border in the Klamath Mountains region, particularly near the coast, show tendencies towards the Pacific Northwest subspecies *claudianus*.

GENERAL REMARKS: This is the only species of *Parnassius* endemic to North America. Other New World *Parnassius* species all have subspecific relatives in the Old World near the Arctic region. *P. clodius* seems most closely related to *Parnassius eversmanni* Menetries, which also feeds on host plants in the family Fumariaceae. *P. eversmanni* is found in extreme northwestern North America and Alaska and in Asia, including Japan.

a) *P. c. clodius* Menetries

DIAGNOSIS: This subspecies inhabits the coastal mountains of northern California, north of Marin County. Both sexes are white to creamy in color and have solid black antennae. In the males, the anal hindwing spot is usually absent or much reduced and the submarginal markings are weak or present only as a trace. The median (central hindwing) ocellus is red. In the female, the anal spot is black with sometimes a trace of red, the submarginal markings are gray, and the median ocellus is red.

ORIGINAL DESCRIPTION: Menetries, *Enum. Corp. Anim. Mus. Petropolitana*, 1: 7 (1855).

TYPE LOCALITY: "California," restricted to Bear Valley, Marin County, California, by J. and S. Shepard, in Howe, *Butterflies of North America*, p. 404 (1975). Type may be in Leningrad.

DISTRIBUTION: Nominotypical *clodius* is found along the coastal margin of California, from Marin County to northern Mendocino County.

ELEVATION RANGE: Below 2,000' elevation.

HABITAT AND PLANT COMMUNITIES: Typically found in North Coastal Coniferous Forest and Redwood Forest, this subspecies flies near watercourses.

PHENOLOGY: Emergence begins in late May and continues through mid-June. The butterfly is single-brooded.

FOODPLANTS: The nominotypical subspecies *clodius* uses *Dicentra formosa* (Andr.) Walp (family Fumariaceae) as the larval host (J. F. Emmel, unpublished data).

b) *P. c. strohbeeni* Sternitzky

DIAGNOSIS: This subspecies, possibly now extinct, is found only in the Santa Cruz Mountains. It is characterized by its much smaller spots. In the males, the anal spot is absent, the submarginal markings are present only as traces or are absent, the median ocellus is small with a trace of red, and the hind marginal spot is absent. In the females, the anal spot is a thin black line, the submarginal spots are weak, and both the median and costal ocelli are small with only a trace of red.

ORIGINAL DESCRIPTION: Sternitzky, *Proc. N. England Zool. Club*, 23: 82-83 (1945).

TYPE LOCALITY: Santa Cruz, California. Holotype in Museum of Comparative Zoology, Harvard University.

DISTRIBUTION: This subspecies was confined to the southwestern Santa Cruz Mountains in Santa Cruz County, and is now possibly extinct. The last recorded specimen was taken on July 3, 1956 at 2,300' at Vicente Creek. There is a more recent sight record for this species in Big Basin State Park (John Lane, pers. comm.), where there is a chance that it may still exist in a small population.

ELEVATION RANGE: Below 2,500' elevation in the Santa Cruz Mountains.

HABITAT AND PLANT COMMUNITIES: Primarily found in Redwood Forest, *strohbeeni* occurs in a habitat virtually identical to that of nominate *clodius*.

PHENOLOGY: The recorded specimens taken between 1918 and 1956 were collected between June 10th and July 15th. The majority of specimens were taken in mid-June. Only one annual brood occurs.

FOODPLANTS: By association in the former adult habitat, *Dicentra formosa* (Andr.) Walp (Fumariaceae) is believed to have been the sole available host.

c) *P. c. sol* Bryk and Eisner

DIAGNOSIS: This subspecies of the northern California mountains and Sierra Nevada is much larger than the preceding two medium-sized forms. In the male, the anal spot is absent, the submarginal spots are present only as traces or are absent, the median and costal ocelli are red with black margins, the hind-marginal spot is present and the grayish black on the basal darkening of the hindwing is weak. In the female, the anal spot is black or has two red spots margined by black, the submarginal spots are medium-sized, and both the median and costal ocelli are red with black margins.

ORIGINAL DESCRIPTION: Bryk and Eisner, *Parnassiana*, 2: 97 (1932).

TYPE LOCALITY: "Nevada" (Sierra Nevada?). In a later publication, Bryk and Eisner decided that the type locality of "Nevada" actually referred to the Sierra Nevada and that the phenotype of their specimens most nearly resembled material taken at Baxter in Placer County. Holotype in Rijksmus. Nat. Hist. (Leiden).

- DISTRIBUTION:** We apply the name *sol* to most of the lowland to mid-elevation *P. clodius* populations in California whose larvae feed primarily on *Dicentra formosa* and whose adults have a medium to large-sized wingspan. These populations extend from the Sierra Nevada foothills in Tulare County northward, and become more frequent from Yosemite and the entire west slope of the Sierra Nevada northward into the Klamath Mountains region. From there, populations occur southward in the inner coast ranges to Lake County.
- ELEVATION RANGE:** 2,000' to 7,000', with most populations between 3,000' and 5,000'.
- HABITAT AND PLANT COMMUNITIES:** This species is typically found along watercourses in the Lower Montane Coniferous Forest.
- PHENOLOGY:** Most captures are recorded from mid-May to mid-July, the majority being in June; all emergence dates are dependent on elevation, the later ones being at higher altitudes. Only one annual brood occurs.
- FOODPLANTS:** This subspecies uses *Dicentra formosa* (Andr.) Walp (Fumariaceae) as a primary host. Some populations of *sol* in the Klamath Mountains region and extreme northern Sierra Nevada may also use *D. pauciflora* Wats. and *D. uniflora* Kell. (J. F. Emmel, unpublished data).

d) *P. c. baldur* W. H. Edwards

- DIAGNOSIS:** Found at high elevations in the Sierra Nevada, this subspecies is characterized by its smaller size. The male is similar to *sol* except that it is smaller and the basal darkening of the hindwing is strong. The female is also smaller than *sol* and the anal spot usually has well-developed red centers; otherwise, it is similar to the preceding subspecies.
- ORIGINAL DESCRIPTION:** W. H. Edwards, *Trans. American Ent. Soc.*, 6: 12 (1877).
- TYPE LOCALITY:** "Yosemite, Sierra Nevada, California", restricted to Tioga Pass, California by F. M. Brown, *Trans. American Ent. Soc.*, 101: 5 (1975). Lectotype in Carnegie Museum, designated by F. M. Brown, *Trans. American Ent. Soc.*, 101: 5 (1975).
- DISTRIBUTION:** *Baldur* is a small, high-elevation subspecies of *clodius* in California, primarily found in the higher elevations of the Sierra Nevada. Specimens resembling *baldur* can also be taken in the highest elevations of the Klamath Assemblage of mountains. These populations all feed on *Dicentra uniflora* Kell. Where there is some overlap of the two *Dicentra* species, *D. uniflora* and *D. formosa*, individuals intermediate between *baldur* and *sol* can be taken.
- ELEVATION RANGE:** *Baldur* populations occur between 7,000' and 12,000'.
- HABITAT AND PLANT COMMUNITIES:** In contrast to the low and mid-elevation *clodius* populations in California, *baldur* prefers open gravelly or rocky slopes within the Subalpine Forest and Arctic-Alpine Cushion Plant communities.
- PHENOLOGY:** Our records for the single brood span between late June and mid-August, with the majority of records in early to mid-July.
- FOODPLANTS:** High-elevation *baldur* populations use *Dicentra uniflora* Kell. as a host and possibly *Dicentra pauciflora* Wats. in some areas (J. F. Emmel, unpublished data).

e) *P. c. near menetriesi* Henry Edwards

- DIAGNOSIS:** The Warner Mountains *Parnassius clodius* have their closest affinities with the lightly marked subspecies *menetriesi* from northeastern Utah. In the males, the two cell bars on the forewing are quite narrow and the postmedian dark band is restricted to the post-cell area. The submarginal band is broken or incomplete. The two red hindwing spots are small, with the central lower one frequently reduced to a black dot. The basal and inner margin dark scaling on the hindwing is light. In the females, the marginal markings on the hindwing are nearly obsolete, and on the forewing, both the marginal and submarginal dark bands are quite narrow.
- ORIGINAL DESCRIPTION:** Henry Edwards, *Proc. California Acad. Sci.*, 7: 164-165 (1877).
- TYPE LOCALITY:** Bear Valley, Lake Tahoe and Downieville, California, Mt. Nebo, Utah. Type locality restricted to Mt. Nebo, Utah by Ferris (1977). Syntypes in American Museum of Natural History.
- DISTRIBUTION:** Ferris (1977) restricted the name *menetriesi* to the Utah populations of *P. clodius*. In California, specimens from the Warner Mountains in Modoc County approach the Utah phenotype of *menetriesi* and are referred here as being closest to that taxon.
- ELEVATION RANGE:** 5,000' to 8,300'.
- HABITAT AND PLANT COMMUNITIES:** This subspecies is primarily found on open slopes within Upper Montane Coniferous Forest or Subalpine Forest in the Warner Mountains.
- PHENOLOGY:** Capture dates range from mid-June to mid-July for the one annual brood.
- FOODPLANTS:** The Warner Mountain populations are associated with *Dicentra uniflora* Kell. (Fumariaceae), the presumed foodplant.

f) *P. c. ssp. (Tulare County, high elevations)*

- DIAGNOSIS:** This unnamed segregate is a set of high-elevation populations in Tulare County which utilize *Dicentra nevadensis* as a larval foodplant. The adults are large and much like subspecies *sol* in facies.
- DISTRIBUTION:** This parnassian is found on the west slope of the Sierra Nevada in the northern part of Sequoia National Park, north in Tulare County to the Fresno County line.
- ELEVATION RANGE:** 7,500' to 10,000'.
- HABITAT AND PLANT COMMUNITIES:** This subspecies flies primarily in Upper Montane Coniferous Forest near watercourses, where its foodplant grows in abundance.
- PHENOLOGY:** Most specimens have been taken from early July to late August, with the majority of specimens in mid-July. There is one annual brood.
- FOODPLANTS:** The Tulare County high-elevation segregate is closely associated with *Dicentra nevadensis* (Eastw.) Munz (Fumariaceae).

PIERIDAE

The family Pieridae is a diverse group of generally small to medium-sized butterflies which are rather closely related to the Papilionidae. There are four recognized subfamilies. Two of these, the Pseudopontiinae (one known species from West Africa) and the Dismorphiinae (with about 100 species in the Neotropics and one genus in the Palearctic) do not occur in our area. The third subfamily, Pierinae, is cosmopolitan but has its greatest diversity in the tropics, with approximately 700 species worldwide. We have seven species in California. The fourth subfamily, Anthocharinae, is often included with the subfamily Pierinae. There are five species in California. The last subfamily, Coliadinae, is cosmopolitan, but has its greatest diversity in the tropics, with approximately 250 species being known. This group includes the sulfurs.

The family is characterized by having (1) fully developed prothoracic legs in both sexes, but with no tibial epiphysis as found in the papilionids; (2) distinctly bifid (split into two parts) tarsal claws on the end of the five-segmented feet; (3) clubbed antennae, with no curve in the tip; (4) a head almost as wide as the thorax, and bearing short palpi; (5) almost all genera have the first medial vein moved forward as a branch off a radial vein, whereas in other butterflies, the three medial veins arise directly from the discal cell; (6) wing scales containing pterine-type pigments; (7) a small, slender, cylindrical larva rarely having tiny spines on the surface; (8) larval osmeteria and fleshy filaments are lacking in this family; (9) the crochets on the prolegs of the larval abdominal segments are arranged in a single row; (10) the pupae are supported by a silk girdle, as in the Papilionidae, and often have the wing cases greatly developed in the form of a prominent arched keel, along with a single conical projection on the head which may be quite long. The adults of this family, with about a thousand species worldwide, are usually orange, yellow, or white with dark marginal markings. Several species are known migrants, while most species are often quite numerous in favored habitats. They may also congregate around mud puddles and other moist areas to drink.

* * * * * * * * * * *

Subfamily Pierinae Duponchel

14. *Neophasia menapia* (C. and R. Felder)

ADULT BEHAVIOR: The Pine White is noted for its very characteristic, lazy, slow, weak fluttering flight around its various Pinaceae foodplants. It tends to stay fairly high above the ground and often out of the reach of the collector's net. Males are attracted very readily to other *Neophasia* adults and also to any white object, such as a piece of white paper placed on a pine branch. Adults of both sexes are avid flower visitors, and are most readily collected when nectaring.

LIFE HISTORY: The bluish green egg has a white crown. The eggs are laid in a single row of three to 22 eggs, at an angle and glued together on a needle near the top of the host conifer. While the young larvae feed gregariously, the older larvae feed alone. The mature larvae is green with a purplish tinge, a white lateral band, and a white sub-dorsal band. Two short tails protrude from the rear. The larvae pupate on bark or twigs or on nearby ground vegetation. The pupa may be either yellowish green or dark brown, with whitish yellow bands as markings. This species hibernates in the egg stage. In terms of parasites and predators, this species has been well studied because of its economic importance in coniferous forests. Kohler found twelve species of predators and twelve species of parasitoids feeding on the early stages.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: None in our fauna. This species occasionally becomes a forest pest in Colorado and the Northwest. In California, the Pine White rarely reaches any significant

abundance. Essig (1926) describes vividly historic outbreaks of *Neophasia menapia* populations in California in the early part of the twentieth century, which defoliated yellow pine and douglas fir forests.

SUBSPECIES: The Pine White butterfly, *Neophasia menapia*, is one of two species of this primitive genus in North America. The other species, *Neophasia terlootii* Behr, is found only in southeastern Arizona and has a brilliant brick-orange female form. The genus as a whole is interesting because it is the only pierid to overwinter in the egg stage. The larvae feed on conifers and the adult structures indicate that this butterfly is a more primitive pierid than the rest of the Whites in our state. Within California, *Neophasia menapia* has developed three subspecies.

a) *N. m. menapia* Felder & Felder

DIAGNOSIS: A medium-sized pierid, typical *menapia* has a white ground color in the male and a creamy ground color in the female. The male and female have a distinctive black band (3-4 mm wide) along the front margin of the forewing which terminates in a downward-pointing black bar at the end of the discal cell. The apical tip of the forewing is bordered by a black marking 4-6 mm wide. Hindwing markings are absent or very faint on the male, while the female hindwing always bears an irregular submarginal black band connected by black scaling at each vein to a dusky wing edge. Ventrally, reddish-orange markings occur on the margins and angle of the hindwing.

ORIGINAL DESCRIPTION: C. and R. Felder, *Wiener Ent. Monats.*, 3: 271 (1859).

TYPE LOCALITY: "Utah," restricted by Miller and Brown (1981) to west of Pyramid Lake, Nevada. Lectotype in British Museum. Further restricted by Emmel, Emmel and Mattoon (1998d) to north end Lake Tahoe, California-Nevada border.

DISTRIBUTION: The nominotypical subspecies of *Neophasia menapia* is found in the Sierra Nevada, from Tulare County north to the Klamath Mountains assemblage, and then south as far as Napa County in the inner Coast Ranges.

ELEVATION RANGE: 1,500'-7,000' elevation.

HABITAT AND PLANT COMMUNITIES: Lower Montane Coniferous Forest is the typical plant community for this subspecies in California; the adults stay in close proximity to the pine tree hosts, preferring rather open forests to denser ones.

PHENOLOGY: Captures range from the end of June to early September, with the majority of records in August. One annual brood occurs.

FOODPLANTS: *Pinus jeffreyi* Grev. & Balf. in A. Murr serves as at least one host in our state (J. F. Emmel, unpublished). Outside California, the conifer host plants that have been recorded include the following species in the family Pinaceae: *Pinus ponderosa* Dougl. ex P. & C. Lawson, *P. contorta* Dougl. ex Loud, *P. jeffreyi* Grev. & Balf. in A. Murr., *P. edulis* Engelm., *P. monticola* Dougl.; *Pseudotsuga menziesii* (Mirb.) Franco, *Tsuga heterophylla* (Raf.) Sarg., *Abies balsamea*, *A. grandis* (Dougl.) Lindl., and *Picea sitchensis* (Bong.) Carr. (Scott, 1986). Some of these foodplants may refer to subspecies other than nominotypical *menapia*.

b) *N. m. melanica* J. Scott

- DIAGNOSIS:** This subspecies is found in the outer Coast Range of Sonoma and Mendocino counties. The forewing black submarginal band is broader (about 5-6 mm wide, as opposed to 3-4 mm wide in typical *menapia*) and is only 2-3 mm from the end of the discal cell in most specimens (versus 5-6 mm in *m. menapia*). The black bar at the end of the forewing discal cell is narrower, being a black linear dash rather than expanded into a club as in typical *menapia*. The hindwing pattern resembles typical *menapia*, although the black submarginal band of *melanica* is slightly thicker toward the apex. Male and female genitalia are similar in the two subspecies (Scott, 1981).
- ORIGINAL DESCRIPTION:** J. A. Scott, *Papilio New Series* #1: 2-3. (1981).
- TYPE LOCALITY:** 6 miles west of Willits, Mendocino County, California. Holotype in California Insect Survey, Berkeley, California.
- DISTRIBUTION:** This subspecies is restricted to the outer Coast Range of California in Sonoma and Mendocino counties. The typical subspecies occurs in the inner Coast Range.
- ELEVATION RANGE:** Below 1,500'.
- HABITAT AND PLANT COMMUNITIES:** This subspecies typically occurs in the Northern Mixed Evergreen Forest, Coastal Coniferous Forest, and Douglas Fir Forest plant communities.
- PHENOLOGY:** The type series was taken between mid-June and mid-July.
- FOODPLANTS:** Douglas Fir, *Pseudotsuga menziesii* (Mirb.), is the recorded host to date for *melanica* (Scott, 1981).

c) *N. m. tehachapina* Emmel, Emmel and Mattoon

- DIAGNOSIS:** This distinctive subspecies, restricted to the Tehachapi Mountains of Kern County, has much reduced black markings compared to nominotypical *menapia*. On the male, the black bar at the end of the forewing discal cell is narrow and only half the width of that in *m. menapia*; the black apical margin markings are narrower by half, and the black markings and red lines on the hindwing are nearly absent. On the female, the dark markings are similarly reduced in extent on both wings.
- ORIGINAL DESCRIPTION:** Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 127-128 (1998g).
- TYPE LOCALITY:** Canyon on north slope of Double Mountain, 6,000-7,000', adjacent to Tehachapi Mountain Park, Tehachapi Mountains, Kern County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION:** This subspecies is confined to the Tehachapi Mountains in Kern County. Populations of *N. menapia* just to the north in the southern Sierra Nevada of Tulare County are typical *N. m. menapia*, with no evidence of a cline between the nominotypical subspecies and *tehachapina*.
- ELEVATION RANGE:** 5,000' to 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** *N. m. tehachapina* is typically found in open yellow pine forests within the Lower Montane Coniferous Forest.

- PHENOLOGY: Flying in one mid-summer brood, specimens have been taken from July 9th to 30th and the flight period probably extends into early August.
- FOODPLANTS: *Pinus ponderosa*, is the suspected host for this subspecies, on the basis of adult association.

15. *Pontia protodice* (Boisduval and Leconte)

This butterfly, aptly called the Common White, ranges across the United States, and flies from the desert and coastal lowlands up to the Canadian Zone in the higher mountains. There are no subspecies, but two seasonally different forms are produced by photoperiod length and temperature acting on the late-instar larvae and pupae, respectively.

- DIAGNOSIS: A medium-sized white pierid, the summer-form male is lightly marked with a black or brown bar (whitish center) at the outer end of the forewing cell and several diffuse submarginal spots, as well as small dark patches of scales at the terminus of each of the first five forewing veins. The hindwings are almost pure white. The female is heavily marked with dark brown dorsal patches and mottling, and yellowish-brown veins on the ventral surface of the hindwing. In the spring or at higher elevations, the adults are smaller with darker veins on the underside, and much sharper and heavier markings on the upperside. Some individuals are difficult to distinguish in wing pattern from *Pontia occidentalis*.
- ORIGINAL DESCRIPTION: Boisduval and Leconte, *Hist. Lepid. Amerique sept.*: 45 (1829).
- TYPE LOCALITY: Probably Screven County, Georgia. The type specimen probably never existed; the name is based on a drawing by John Abbot.
- DISTRIBUTION: The Common White is widespread through the state, with the exception of the highest elevations and the northwest coastal areas. The species is prevalent in the Central Valley and in the desert regions, as well as cismontane southern California. It only rarely overlaps the range of the closely related *P. occidentalis*. When this occurs, it is usually in hilltopping situations when *P. protodice* is flying up from much lower elevations.
- ELEVATION RANGE: From sea level to over 14,000' for hilltopping males in the Sierra Nevada and the White Mountains. The species breeds principally below 7,000' elevation. Two gravid females were reported dead in mid-June 1980 and again in 1982 on a snowbank near Barcroft Laboratory at about 12,400' in the White Mountains of Mono County, showing remarkable altitudinal dispersal in this species (Shapiro, 1982).
- HABITAT AND PLANT COMMUNITIES: This species flies and breeds in almost every plant community in California, excluding only the Arctic Alpine Cushion Plant community and areas just below timberline. It seems to do best in the desert regions and in agriculturally disturbed areas.
- PHENOLOGY: Captures are recorded for every month of the year. The main spring flight appears to be in March and April, with a succession of broods following into late fall.
- ADULT BEHAVIOR: The adults move extensively in the course of their lifetime and apparently experience a normal life-span of about one week in nature, although this may last longer in cool weather (Shapiro, 1979). Shields (1967) found only a 15% recapture rate among adults marked on hilltops, indicating a high dispersal rate of adults. Hilltopping behavior only temporarily draws both males and females to hills and

even high mountaintops for mating. The males of the species use ultra-violet reflectance patterns instead of pheromones to identify their mates; they lack androconial scales on their wings, according to Shapiro and Rutowski ().

LIFE HISTORY: The spindle-shaped egg is yellow, but soon turns orange with maturation. The eggs are laid singly on the foodplant inflorescence or leaves, with a preference for the inflorescence. The mature larva varies in ground color from deep to pale blue-green, but always bears four longitudinal stripes of yellow. Black dots are thickly distributed over the entire body. The pupa is light bluish-gray and is speckled with black. This species diapauses as a pupa.

FOODPLANTS: The common native foodplant in the deserts is *Lepidium fremontii* Wats. (Brassicaceae) (Emmel, Shields, and Breedlove, 1971; Emmel and Emmel, 1973), and many other mustard species (*Cleome*, *Brassica*, *Sisymbrium*, etc.) are used in the state, including crucifers introduced from Europe. Known southern California desert and mountain hosts are: *Stanleya pinnata* (Pursh) Britton, *S. viridiflora* Nutt., *Caulanthus pilosus* Wats. (on the east slope of the Sierra Nevada, and in the Darwin Mesa area of Inyo County) (all Brassicaceae); *Cleomella obtusifolia* Torr. & Frem. along the Mojave River, and *Oxystylis lutea* Torr. & Frem. in the eastern Mojave Desert near Shoshoe, Inyo County (both in the family Capparidaceae) (J. F. Emmel, unpublished). In northern California, *P. protodice* is known to utilize the following Brassicaceae: *Brassica geniculata* (Desf.) J. Ball., *Lepidium latifolium* L., rarely *Brassica nigra* (L.) Koch. and *B. kaber* (DC.) Wheeler, and *Raphanus sativus* L., all in low-elevation areas of the Sacramento Valley (Shapiro, 1975c, 1977b); *Rorippa curvisiliqua* (Hook) Bessey in the Trinity Alps and Mount Eddy region (Shapiro et al., 1981); *Lepidium virginicum* L. var. *pubescens* (Greene) Thell. and *Sisymbrium altissimum* L. at Truckee around 6,000' elevation in the central Sierra Nevada (Shapiro, 1975e).

CHROMOSOME NUMBER: n = 26 (Macki and Remington, 1960b).

SIMILAR SPECIES: This butterfly has been frequently confused with *Pontia occidentalis* in the western United States. Chang (1963) showed the distinction between the two species on morphological grounds. The black spot at the ventral forewing corner is large in summer *protodice* (3 mm in width) and small in *occidentalis* (1.5 mm), and genitalia parts (the male saccus, the aedeagus, and the hardened plate on the female bursa copulatrix) are all smaller in *protodice* than in *occidentalis*. Shapiro (1976) has provided further useful color and pattern differences between the two species; he points out that both sexes characteristically are more heavily and completely marked in *P. occidentalis* than in *P. protodice*. Also, the wings of *P. occidentalis* appear thicker and more heavily scaled, and the body is proportionately larger and usually more hairy in *occidentalis*.

GEOGRAPHIC AND SEASONAL VARIATION: While no significant geographic variation is found, there is substantial seasonal phenotypic variation with successive broods. The spring form, "vernalis," tends to be smaller and more heavily marked, with a heavily mottled underside. Arthur Shapiro found that it is caused by the older larvae being exposed to short photoperiod (long nights) regardless of temperature. Later broods are much more lightly marked, both on the upper and lower surfaces. Pupae from larvae raised under long-day (summer) conditions will produce the spring form *vernalis* if exposed to cold temperatures (as in the winter months).

GENERAL REMARKS: This species is one of our weedy butterflies, having invaded agricultural and disturbed habitats throughout the state. It has readily adapted to larval use of the

many introduced mustard species from the Mediterranean and European countries that now occur throughout California.

16. *Pontia occidentalis occidentalis* (Reakirt)

The Western White is restricted to western North America, from the southern Great Basin and the central California mountains north to Alaska and perhaps into the Palearctic (if it is identical to the Old World species, *Pontia callidice*). It closely resembles *P. protodice* in appearance and may be sympatric with it in some areas. Two subspecies have been identified; the typical race occurs in the U.S. and Canada, while *P. o. nelsoni* (with smaller spots) is found in Alaska.

- DIAGNOSIS:** A medium-sized white pierid, the Western White is normally distinguishable from *protodice* specimens by the heavier markings on the ventral surfaces of both sexes, the considerably larger marginal forewing markings on the male, and the black coloration of the dark forewing spots in the female (those of *protodice* females are brown).
- ORIGINAL DESCRIPTION:** Reakirt, *Proc. Ent. Soc. Philadelphia*, 6: 133 (1866).
- TYPE LOCALITY:** "Rocky Mountains, Colorado territory." Restricted by Miller and Brown (1981) to vicinity of Empire, Clear Creek County, Colorado. Holotype in Carnegie Museum.
- DISTRIBUTION:** This species is found from the higher elevations of the Sierra Nevada in Tulare County north to the Klamath Mountains assemblage and the northern Coast Ranges as far south as Mendocino County, eastward into the Warner Mountains and thence south to the White Mountains of Inyo County. It is absent from the higher elevations of the Inyo Mountains and the Panamint Range in Inyo County. It is also absent from the mountains of southern California.
- ELEVATION RANGE:** Mostly 4,000' to as high as 14,500' for hilltopping males. Specimens have been recorded at lower elevations by Shapiro; these are apparently strays.
- HABITAT AND PLANT COMMUNITIES:** The species is typically found on open rocky or gravelly slopes, or slopes with low vegetation, usually within the following plant communities: Upper Montane Coniferous Forest, Subalpine Forest, Arctic Alpine Cushion Plant, Great Basin Pine Woodland, and Mountain Sagebrush Scrub.
- PHENOLOGY:** Records extend from mid-June to early October, with the majority of records for the month of July. It is probably univoltine at the highest elevations, but at least partially bivoltine in the lower elevation populations.
- ADULT BEHAVIOR:** Adults are seen flying rapidly over open slopes, often in unidirectional flight. Males are strong hilltoppers and occur on the summits of some of the highest mountains in the state.
- LIFE HISTORY:** The eggs are usually laid on the inflorescences of the foodplants. The egg is yellow when first laid and subsequently turns orange. The larvae feed on the flower heads, preferring flower buds and petals and fruits. The mature larva is very similar to that of *Pontia protodice*, with a bluish-gray ground color that is somewhat darker than that of *protodice*. It bears black dots and yellow lateral and subdorsal stripes on the body. The pupa is shaped like that of *protodice*, and is light bluish-gray with a few black speckles on the wing veins and body. This species hibernates in the pupal stage.

- FOODPLANTS:** As with *Pieris protodice*, a wide variety of crucifer plants in the family Brassicaceae are utilized, including the following species: *Arabis drummondii* Gray, *A. glabra* (L.) Bernh., *A. platysperma* Gray, *A. holboellii* Hornem. (vars. *pinetorum* [Tids.] Roll., and *retrofracta* [Grah.] Rydb.), *A. breweri* Wats., *A. platysperma* Gray, *Barbarea vulgaris* R. Br., *Brassica nigra* [L.] Kech., *Chorispora tenella* (Pall.) DC., *Caulanthus* species, *Athysanus pusillus* (Hook.) Greene, *Phoenicaulis cheiranthoides* Nutt. in T. & G., *Descurainia richardsonii* (Sweet) O. E. Schulz (and ssp. *viscosa* [Rydb.] Detl.), *D. sophia* (L.) Webb, *Draba cuneifolia* Nutt. ex T. & G., *D. howellii* Wats., *D. crassifolia* Grah., *Lepidium campestre* (L.) R. Br., *virginicum* L. (and var. *pubescens* [Greene] C. L. Hitchc.), *L. densiflorum* Schrad. var. *bourgeanum* (Thell.) C. L. Hitchc., *Sisymbrium altissimum* L., *Streptanthus tortuosus* Kell., *S. barbatus* Wats., *Thlaspi alpestre* auth. *T. californicum* Wats.(=*T. glaucum* A. Nels var. *hesperium* Pays.), *Thelypodium lasiophyllum* (H. & A.) Greene, and *Draba cuneifolia* Nutt. ex T. & G. (Shields, Emmel & Breedlove, 1970, Shapiro, 1975e, 1977a; Shapiro *et al.*, 1981; J. F. Emmel, unpublished). *Draba* species appear to be the preferred foodplants at the highest elevations. Flower buds of *Thlaspi arvense* L. are used in the Santa Rosa Range of Humboldt County, Nevada (Emmel, Shields, and Breedlove, 1971).
- CHROMOSOME NUMBER:** n = 26 (Maeki and Remington, 1960b [1960b]).
- SIMILAR SPECIES:** See *Pontia protodice* for discussion of differences between *P. occidentalis* and *P. protodice*.
- GEOGRAPHIC AND SEASONAL VARIATION:** No notable geographic variation has been found within the state; however, there is variation due to elevational influence of temperature and photoperiod. Individuals from lower-elevation populations in the spring are called form "vernalis," and this phenotype also appears as the predominate form of the univoltine higher-elevation populations (Shapiro, 1976). In this form "vernalis," as in the early-spring form "brunellis" in *Pontia protodice*, the markings are strongly distinctive and present a more heavily mottled appearance. This phenotype on the underside differs from the more lightly-marked broods of the late spring and summer at low elevations, which are considered the "typical" form, *occidentalis*.
- GENERAL REMARKS:** Some authors (e.g., Higgins, 1953; Higgins and Riley, 1970; Scott, 1986) have treated *occidentalis* as a subspecies of the Old World *Pontia* (*Pieris*) *callidice*, considering it to be a circumpolar pierid species. This view is critically discussed by Shapiro (1976), who noted that the Old World populations of *callidice* have characters that are unknown in any North American population of *Pontia* or *Pieris*. Additionally, Shapiro (1980) obtained the first genetic data that bear on the relationship by crossing *P. callidice* from the French Alps with the phenotypically similar *P. occidentalis nelsoni* from Fairbanks, Alaska. Egg hatching for the cross *nelsoni* male x *callidice* female was zero, while the reciprocal cross and parental stock crosses had normal egg hatch. In the reciprocal cross, however, most larvae soon died. The several hybrid pupae and the single hybrid adult were intermediate between the parents. Shapiro concluded that there was a high degree of genetic incompatibility between the Palearctic and Nearctic species.

17. *Pontia beckerii* (W. H. Edwards)

Becker's White ranges from the southern Great Basin deserts north to British Columbia, and from the western side of the Rocky Mountains to southern and eastern California. Its principal haunts are the open deserts and arid foothills.

- DIAGNOSIS: Becker's White is readily distinguished from the preceding two species by the strongly marked green veins on the ventral hindwing surface, combined with the heavy, nearly continuous green suffusion on the inner half of that wing. Dorsally, *beckerii* has a very broad vertical band across the vein at the end of the forewing cell, and marginal black markings that expand *inwardly* from the forewing edge rather than outwardly to the edge as in *P. occidentalis* and *P. protodice*.
- ORIGINAL DESCRIPTION: W. H. Edwards, *Butterflies of North America*, 1: [30]-[31] (1871).
- TYPE LOCALITY: Virginia City, Nevada.
- DISTRIBUTION: Becker's White is found in the western edge of the Great Basin, east of the Sierra-Cascade axis, southward into the Mojave and Colorado Deserts, approaching the coast only in San Diego County.
- ELEVATION RANGE: From near sea level in San Diego County to as high as approximately 8,000' elsewhere.
- HABITAT AND PLANT COMMUNITIES: In our desert areas, this species is found in washes, canyon bottoms, near springs, or on open flats or slopes, within the following plant communities: Creosote Bush Scrub, Mixed Desert Scrub, Pinyon-Juniper Woodland, Great Basin Sagebrush Scrub, Shadscale Scrub, and Desert Microphyll Woodland.
- PHENOLOGY: We have records for every month of the year. The spring brood flies principally in March and April, or May and June in the more northern populations, with a succession of broods (depending on rainfall) following into the fall months. In the desert, the numbers of individuals in the summer and fall broods tend to be quite small in relation to the much larger spring brood.
- ADULT BEHAVIOR: Males of this species do not hilltop, but spend most of their time patrolling the slopes and washes of the open desert in search of females. Adults of both sexes are often seen in the immediate vicinity of the foodplants: females in ovipositional behavior, and males searching for freshly-emerged females.
- LIFE HISTORY: The egg is lemon-yellow in color, changing to orange soon after oviposition. The eggs are laid on flower buds, stems and leaves and the newly hatched larvae prefer feeding on flower buds and fruits. The mature larva is greenish-white, with a marbling of gray dots and a bright orange belt between segments. Numerous (16 or 18) jet-black tubercles with black bristles occur on each segment. The pupa is gray with white wing cases and resembles a bird dropping.
- FOODPLANTS: Bladderpod, *Cleome isomeris* Greene (= *Isomeris arborea* Nutt.) (Capparaceae) is one of the principal hosts in southern California, along with *Stanleya pinnata* (Pursh) Britton (family Brassicaceae). In addition, the following Brassicaceae are used (J. F. Emmel, unpublished): *Stanleya elata* Jones, *S. viridiflora* Nutt. (at the Adobe Hills, Inyo County), and *Caulanthus pilosus* Wats. (on the east slope of the Sierra Nevada in the Lower Rock Creek area, Inyo-Mono counties).
- CHROMOSOME NUMBER: $n = 26$ in western Colorado material (Maeki and Remington, 1960b).

SIMILAR SPECIES:	None in California. The species can be readily distinguished from the other white pierids by reference to the color plates.
GEOGRAPHIC AND SEASONAL VARIATION:	There is no noted geographic variation in California, but the spring form is more lightly marked than the later brood.
GENERAL REMARKS:	This species has been included by some authorities in the Old World Palearctic species <i>Pontia chloridice</i> , which is found across the southern Palearctic area from Turkey to Mongolia. We find that <i>beckerii</i> is specifically distinct from the Old World butterfly and hence follow that treatment here.

18. *Pontia sisymbrii* (Boisduval)

ADULT BEHAVIOR:	Males of <i>sisymbrii</i> are strong hilltoppers, while females are seen flying over open slopes or along canyon bottoms in search of the foodplants. The larvae of this pierid species feed on inflorescences and infructescences of their hosts, and the females assess the egg load already present on individual host plants prior to ovipositing. Shapiro (1981c) has shown that in the northern California lowland populations that feed on <i>Streptanthus breweri</i> Gray and <i>S. glandulosus</i> Hook., both hostplants produce orange-pigmented bodies on their stem leaves which are similar in size, shape, and color to <i>Pontia sisymbrii</i> eggs and which appear to decrease the attractiveness of mature plants to ovipositing females, thus preserving their flowers and seed pods for their own reproduction. When Shapiro experimentally removed the egg-mimics from plants, the likelihood of oviposition on the plants promptly increased. This was the first quantitative demonstration of the efficacy of egg-mimicry by a plant against an herbivorous insect. It was also the first documented instance of egg-mimicry by a plant outside the tropics, where several examples are known among <i>Heliconius</i> butterflies and <i>Passiflora</i> plant species.
LIFE HISTORY:	The long conical egg is yellowish or bluish-green, soon turning orange, and it bears many longitudinal ribs with cross ribs between them. The eggs are laid singly almost anywhere on the host-plant, but usually on the stems; the larvae prefer the inflorescences and fruit. The mature larva is basically light yellow, with a black lateral line and two broad wavy black transverse stripes on each segment with white between them. The head is black, dotted with white, and bears an inverted white "V" on the face. The pupa is dark brown to light tan, with many darker spots and granulations scattered across the surface. The species hibernates in the pupal stage. The pupation site is likely under rocks or in rock crevices, as opposed to being on the foodplant. Diapause occurs in the pupal stage.
CHROMOSOME NUMBER:	Unknown.
SIMILAR SPECIES:	As can be seen by reference to the color plate, <i>sisymbrii</i> can be distinguished from the other <i>Pontia</i> species in our state through its smaller size and prominent veining pattern on the underside.
GEOGRAPHIC VARIATION:	The low to mid-elevation nominotypical subspecies tends to be the most lightly marked and has the largest individuals. The high elevation populations near subspecies <i>elivata</i> are small and more darkly marked, and the darkest markings occur in individuals of the subspecies <i>nigravenosa</i> in the desert regions. These three subspecific phenotypes are not well-defined geographic segregates in that there are broad blendzones between them; many populations can not be readily assigned to a particular subspecies name.

GENERAL REMARKS: This is the only *Pontia* species in our area which is strictly univoltine.

SUBSPECIES: This butterfly's common name is the California White, though the species ranges from the Yukon Territory and British Columbia eastward to South Dakota and south to New Mexico and Baja California. Within our state, three subspecies are found.

a) *P. s. sisymbrii* (Boisduval)

DIAGNOSIS: A somewhat smaller white than the preceding species, typical *sisymbrii* has blackish or dark brown (not green or tan) markings along the veins on the underside of the wings. The black dorsal markings are sharply defined.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 284 (1852).

TYPE LOCALITY: "Californie." Type locality restricted to 1 mile NE of Storrie, North Fork Feather River Canyon, Plumas County, California, by Emmel, Emmel, and Mattoon (1998a).

DISTRIBUTION: For nominotypical *sisymbrii*, the butterfly is found in the inner Coast Ranges from Stanislaus County north to the Klamath Mountain Assemblage, thence east to the Sierra Nevada foothills and south to the cismontane areas of southern California and the western borders of the Mojave and Colorado deserts.

ELEVATION RANGE: Largely below 6,000' elevation.

HABITAT AND PLANT COMMUNITIES: The typical subspecies inhabits generally open, rocky, or gravelly slopes or canyon bottoms within the following plant communities: Mixed Chaparral, Serpentine Chaparral, Desert Transition Chaparral, Foothill Woodland, and Lower Montane Coniferous Forest.

PHENOLOGY: This subspecies is strictly univoltine, with most records in March and April.

FOODPLANTS: The following species of Brassicaceae are recorded for this subspecies: *Caulanthus coulteri* Wats. (J. F. Emmel, unpublished); *Streptanthus glandulosus* Hook., *S. breweri* Gray, *S. barbatus* Wats., *S. tortuosus* Kell. (Shapiro, 1981a, b, c; Shapiro *et al.*, 1981); *S. polygaloides* Gray (Scott, 1986); *Arabis glabra* (L.) Bernh., *A. perennans* Wats., *A. pulchra* Jones, *A. holboellii* Hornem. var. *retrofracta* (Grah.) Rydb., *A. sparsiflora* Nutt. in T. & G., *A. shockleyi* Munz. (J. F. Emmel, unpublished).

b) *P. s. elivata* (Barnes and Benjamin)

DIAGNOSIS: This higher elevation subspecies is characterized by smaller size and somewhat more strongly marked veins on the ventral hindwing surface. It is found in the Rocky Mountains, northern Nevada, and the higher mountains of eastern and northern California.

ORIGINAL DESCRIPTION: Barnes and Benjamin, *Bull. Southern California Acad. Sci.*, 25: 88 (1926).

TYPE LOCALITY: Glenwood Springs, Colorado.

DISTRIBUTION: Within California, this subspecies occurs in the higher elevations of the Sierra Nevada, the Warner Mountains, and the Klamath Mountains Assemblage.

- ELEVATION RANGE: Largely above 7,000', to as high as 12,000' elevation.
- HABITAT AND PLANT COMMUNITIES: Subspecies *elivata* prefers open rocky, or gravelly slopes within the following plant communities: Upper Montane Coniferous Forest, Subalpine Forest, Montane Chaparral, Arctic-Alpine Cushion Plant, Great Basin Pine Woodland, Great Basin Sagebrush Scrub, Mountain Sagebrush Scrub, and Pinyon-Juniper Woodland.
- PHENOLOGY: This race is univoltine, with records from mid-June to the first of August. Most records are concentrated in July.
- FOODPLANTS: The following species of Brassicaceae have been recorded as hosts for subspecies *elivata*: *Streptanthus barbatus* Wats., *S. tortuosus* Kell. (Shapiro, 1981 a, b, c; Shapiro et al., 1981); *Arabis holboellii* Hornem. var. *retrofracta* (Grah.) Rydb. and *Arabis divaricarpa* A. Nels. (in the Siskiyou Mountains) (J. F. Emmel, unpublished).

c) *P. s. nigrovenosa* Austin and Emmel

- DIAGNOSIS: This recently described subspecies is immediately recognized by its very dark (nearly black) and crisply defined pattern on the ventral hindwing, and the breadth of the dorsal markings. The ventral pattern is caused by a restriction of pale yellow scaling to 2-4 rows centered on each vein; there is no scattering of similarly colored scales among the black scales which outline the veins and make them stand out from the cream ground color.
- ORIGINAL DESCRIPTION: Austin and Emmel, *Systematics of Western North American Butterflies*, pp. (1998a).
- TYPE LOCALITY: 2 mi. N. Red Cloud Mine, Spring Range, Clark County, Nevada.
- DISTRIBUTION: This is the small and more darkly marked subspecies of *sisymbrii* that flies in our northern and eastern desert areas, from north of Death Valley south to the eastern Mojave Desert in our state; outside of California it is found in the desert ranges of southern Nevada.
- ELEVATION RANGE: From approximately 4,000' to 8,000' elevation, but with most records from below 6,000'.
- HABITAT AND PLANT COMMUNITIES: This subspecies is usually found in canyon bottoms or on open flats or slopes within the following plant communities: Pinyon-Juniper Woodland (most populations), Joshua Tree Woodland, Shadscale Scrub, and Mixed Desert Scrub.
- PHENOLOGY: Univoltine, flying from mid-March to mid-May, with most records in the month of April.
- FOODPLANTS: For subspecies *nigrovenosa*, the following foodplants in the family Brassicaceae have been recorded by J. F. Emmel (unpublished): *Arabis perennans* Wats., *A. pulchra* Jones, *A. shockleyi* Munz, *A. inyoensis* Roll., *Caulanthus lasiophyllus* (H. & A.) Greene, *C. crassicaulis* (Torr.) Wats. (at Hunter Mountain in Inyo County), and *Streptanthus cordatus* Nutt. (in Grapevine Mountains, California-Nevada border).

19. *Pieris rapae* (Linnaeus)

The Cabbage White is one of our most familiar butterflies, yet it reached California only in relatively recent historic times, certainly not earlier than two centuries ago. It has been amazingly successful in spreading throughout the state at virtually all elevations.

- DIAGNOSIS: A medium-sized white, *Pieris rapae* has blackish forewing tips and unmarked yellowish ventral hindwings. The male bears one dorsal forewing spot beyond the cell, while the female bears two dorsal forewing spots. Ventrally, the female has two black spots on the forewing and the male may have one or two spots there.
- ORIGINAL DESCRIPTION: Linnaeus, *Syst. Nat.*, ed. 10, 1:468 (1758).
- TYPE LOCALITY: Designated as "Sweden" by Verity.
- DISTRIBUTION: Found throughout the entire state, with the exception of the Arctic-Alpine zones, and only a few localities in the deserts. The Cabbage White is largely a butterfly of urban, suburban, agricultural, and disturbed areas, although found in virtually every plant community.
- ELEVATION RANGE: Below 8,000' throughout the state.
- HABITAT AND PLANT COMMUNITY: As noted above, this species has been reported for nearly all the plant communities in our state. In montane habitats, it is usually found in a riparian association; in the deserts, it has become established at permanent springs where watercress (*Nasturtium officinale*) has been introduced, such as at Pachallca Spring on Clark Mountain or at Brewery Spring in the Panamint Range.
- PHENOLOGY: The Cabbage White has been recorded from January to December. For the more northern or higher elevation populations, most records seem to be clustered from May to September. Shapiro (1975c) notes six broods flying in the Sacramento Valley (in 42 weeks during 1972 and 49 weeks in 1973).
- ADULT BEHAVIOR: A very weedy species that is not found in localized colonies, *Pieris rapae* is capable of moving long distances of at least several kilometers from day to day (see, for instance, Emmel, 1973). This butterfly reaches tremendous abundance at times in areas of profuse growth of mustards and other crucifers. Occasionally, interspecific matings between *Pieris rapae* and *Pontia protodice* have been observed in such areas in California (e.g., Priestaf, 1972). These matings are presumably infertile as no hybrid adult captures have been reported.
- Pieris rapae* has also colonized Australia, and McFarland (1971) has reported that *P. rapae* in South Australia have been observed to communally roost in a small *Pittosporum* tree with whitish-green leaves each evening. He suggested this was an unusual situation and that aggregations for nocturnal roosting were not the rule in open circumstances. Considerable experimental work has been done by various investigators on the mechanism of female choice in host plants and on other aspects of behavior of this occasionally important economic pest.
- LIFE HISTORY: The conical egg is white or pale yellow, is strongly ribbed longitudinally, and is usually laid singly on the host leaves. The mature larva is pale green, with a yellowish dorsal stripe and a row of pale yellow spots on each side. The surface is finely dotted with black spots. The pupa varies from pale green to quite mottled gray or brown and speckled with fine black dots.

- FOODPLANTS:** This butterfly uses a number of native and introduced Brassicaceae: in the Sacramento Valley, *Brassica nigra* (L.) Koch, *B. kaber* (DC.) Wheeler, *B. napus* L., *B. oleracea* L. cultivars, *B. geniculata* (Desf.) J. Ball., *Cardaria draba* (L.) Desv., *Sisymbrium officinale* (L.) Scop., *S. irio* L., *S. altissimum* L., *Raphanus sativus* L., *Lepidium latifolium* L. (Shapiro, 1975c, 1977b); Watercress, *Nasturtium officinale* R. Br. (= *Rorippa nasturtium-aquaticum* Schinz. and Thell.) (Shapiro, 1975d); in the Sierras, *Barbarea orthoceras* Ledeb., *Erysimum perenne* Abr., *Rorippa curvisiliqua* (Hook.) Bessey, *Lepidium virginicum* L. var. *pubescens* (Greene) Thell.; *Streptanthus tortuosus* Kell. (Shapiro, 1975e, 1981b, and J. F. Emmel, unpublished); in the desert colonies (e.g. Surprise Canyon in the Panamints or Pachalka Spring at Clark Mountain) on introduced ("naturalized") Watercress, *Nasturtium officinale* R. Br., and in the Granite Mountains northeast of Apple Valley, on *Caulanthus lasiophyllus* (H. & A.) Greene var. *utahense* (Rydb.) Jeps. (J. F. Emmel, unpublished); occasionally on *Arabis glabra* (L.) Bernh. (Tower-Mustard) (J. F. Emmel, unpublished); in southern California urban areas, on cultivated Stock, *Matthiola incana* (L.) R. Br., and all the introduced *Brassica* species previously listed above, as well as one introduced species in the family Tropaeolaceae: Garden Nasturtium, *Tropaeolum majus* L. (many unpublished records, various workers; Emmel and Emmel, 1973; J. F. Emmel, unpublished); in "naturalized" populations in the mountains of southern California, an introduced ("naturalized") Watercress, *Nasturtium officinale*, and *Barbarea orthoceras* Ledeb. (J. F. Emmel, unpublished).
- CHROMOSOME NUMBER:** n = 25 in Connecticut material (Maeki and Remington, 1960b).
- SIMILAR SPECIES:** The species may be confused with *P. napi* in flight, but captured individuals may be readily distinguished by reference to the color plates.
- GEOGRAPHIC AND SEASONAL VARIATION:** No significant geographic variation has been noted within the state. Winter and early spring individuals tend to be more lightly marked than late spring through early fall specimens.
- GENERAL REMARKS:** This butterfly was introduced into Quebec in approximately 1860 and possibly into California in the late 1700's or early to mid-1800's by the Spaniards. Reakirt in 1866 described a *Pieris yreka*, with a type locality of California, from a specimen supplied by Lorquin. This specimen may have been a French specimen which was erroneously labeled (Miller and Brown, 1981) or could have represented an authentic California specimen of a possible second introduction of the species (Shapiro, 1975d) into North America, other than the Quebec arrival referred to earlier. Essig (1926) thought that the earliest California record for *Pieris rapae* was "about 1883." The species is an agricultural pest on certain brassicaceous crops such as cabbage or broccoli, but also feeds on brussels sprouts, cauliflower, horse radish, kale, mignonette, mustard, nasturtium, radish, rape, sweet alyssum, turnip, and other crucifers that have been cultivated commercially in California in the past (Essig, 1926) or present. Potential competition between the native *Pieris protodice* and the introduced *Pieris rapae* has probably been minimized by the fact that regardless of their sympatry or allopatry, *protodice* larvae feed on the inflorescence of various mustards while the *rapae* larvae feed on the leaves and the species are thus ecologically segregated, or displaced from each other when they come into sympatry. Within ten years of the invasion of eastern North America by *Pieris rapae* at about 1860, it had completely replaced a native North American pierine, *Pieris napi oleraceae* Harris, as a domestic species in southern New England (Scudder, 1889). However, *P. rapae* apparently has not had any serious impact on or displacement of *P. protodice* in North America (Hovanitz, 1962; Shapiro, 1975g). In South America, another European pierine, *Pieris brassicae* (L.) was introduced into

Chile about 1970, probably in shipments of potatoes, and it has since spread over much of the densely-populated central part of the country. The native pierine fauna of central Chile, which feeds on the same plant families (including crucifers) as *P. brassicae*, has remained unaffected because it is specialized on small, patchily distributed native hosts in canyon habitats while *P. brassicae* has moved into the "vacant niche" of lowland introduced (since 1800 A.D.) crucifers (Kellner and Shapiro, 1983).

20. *Pieris napi* (Linnaeus)

- ADULT BEHAVIOR:** Adults of both sexes of *napi* are typically found flying along watercourses within forested areas, often in deep shade. Males are readily attracted to other white butterflies and will fly with them briefly, apparently to see if they are potential mates. Adults readily go to nectar; *Arabis holboellii* Hornem. and *Gaultherim shallon* Pursh are recorded sources (S. O. Mattoon, unpublished data).
- LIFE HISTORY:** The eggs are spindle-shaped, white or pale yellow in ground color, and tinged with green. These eggs are laid singly on most occasions, usually on the leaves or on the stems of the host. Young larvae bore into the succulent leaves of the foodplant whereas larger larvae tend to consume the entire leaf edge as they feed. The mature larva (of all California subspecies) is green with black points scattered over the body, and it bears a green mid-dorsal stripe as well as a whitish lateral stripe. The pupa may be green, tan, or light bluish-green, dotted with black and additional light dorsal and lateral strip-like markings. The species overwinters as a pupa.
- CHROMOSOME NUMBER:** $n = 25$ in Colorado *P. napi macdunnoughii* (Maeki and Remington, 1960b).
- SIMILAR SPECIES:** The only butterfly in our range with which *napi* may be confused is a very lightly marked adult of *Pieris rapae*. But with experience, even the adult flight characteristics will be noticed to differ slightly.
- GEOGRAPHIC AND SEASONAL VARIATION:** As can be seen from the figures on the color plates, there are considerable differences between the spring phenotype and the summer phenotype of the subspecies occurring within California. Spring-brood specimens are darker and more heavily marked, in contrast to summer specimens which are always lighter, sometimes almost devoid of markings. The Warner Mountains populations tend to be quite pale in spring and almost immaculate in summer broods. From the standpoint of geographic variation, the subspecies in the Coast Ranges tend to be darker at the southern end of the range and more lightly marked as one goes north or inland away from the coast. Darker phenotypes seem to be associated with cooler environments, which may account for more boldly marked populations within the distribution of *castoria* (= *microstriata*) that are found at higher colder elevations, such as at Mt. Lassen. The distinctive subspecies *sequoia* in the redwood forest of Humboldt County is particularly unusual in that it has very yellow females. *P. n. resedae* populations in the Warner Mountains are much like the Utah subspecies *pallidissima*, and may be consubspecific. Shapiro (1975f, pers. commun.) has shown that the color differences between (1) first and second broods in each subspecies, and between (2) the second-brood phenotypes in each subspecies, are due to (1) photoperiod and (2) genetic bases.
- GENERAL REMARKS:** If this species is identical with the European *napi*, its range is one of the most extensive of any butterflies in the world: from Europe across North Africa and

Asia to Japan, north to Alaska and Canada and south to central California, over to the mountains of Arizona and east to the Atlantic Ocean. It has adapted to shady woodlands, open forest tundra, taiga and even the open Arctic.

SUBSPECIES: This species is either identical to the *Pieris napi* of the Palearctic or represents a complex of several closely related New World species. The taxonomic status of the Nearctic members of this group is currently being studied by Shapiro and his associates; until their studies are completed, we prefer to treat all the California taxa as subspecies of *P. napi*. We have five subspecific segregates within the state of California.

a) *P. n. marginalis* (Scudder)

DIAGNOSIS: This subspecies is characterized by well-defined veins on the upper wing surfaces and strongly outlined veins on the ventral hindwing surface. However, these are not as heavy as in *venosa*.

ORIGINAL DESCRIPTION: Scudder, *Proc. Boston Soc. Nat. Hist.*, 8: 182 (1861).

TYPE LOCALITY: "Gulf of Georgia" (Victoria, B.C., Vancouver, B.C., or northwest shore of Washington) and "Crescent City, California." Holotype in Museum of Comparative Zoology, Harvard University.

DISTRIBUTION: This subspecies is found in the outer Coast Ranges, limited to northern coastal Del Norte County and extending inland in the northwest corner of the county, where blending with *castoria* form vern. "microstriata" appears to take place. Some genetic influence may extend into *castoria* populations in the western Klamath Mountains Assemblage. North of California, *marginalis* extends through the coastal mountains to southwestern British Columbia.

ELEVATION RANGE: From 50' to 2,000'.

HABITAT AND PLANT COMMUNITIES: This *napi* subspecies occurs primarily in Coastal Redwood Forest, but it is also found in Mixed Evergreen Forest and Coastal Coniferous forests in logged and cutover areas or away from the coast in areas of blending. Usually found along sheltered areas along watercourses where its foodplant is locally common, *marginalis* can be relatively abundant at the height of adult emergence.

PHENOLOGY: Two broods fly annually, one in April and May, and the second (smaller than the first) in July and August.

FOODPLANTS: *Cardamine californica* (Nutt.) Greene and *C. angulata* Hook. (Brassicaceae) are both suspected for the Del Norte County populations of *marginalis* (Ken Hansen, personal communication) on the basis of adult association.

b) *P. n. castoria* (Reakirt)

The name *castoria* has been used heretofore as an infrasubspecific name for the second-brood phenotype of *Pieris napi venosa* in most works (see review in Shapiro, 1977c). The name *Pieris napi microstriata* J. A. Comstock (1925) has been applied by Shapiro (1975; 1976a, b) to the interior California *P. napi*, as opposed to coastal *venosa*, with a second-brood form "*castoria*" phenotype. However, when Shapiro discovered that *castoria* actually refers to the interior subspecies, he asked (Shapiro, 1977) that the name *castoria* be suppressed in

favor of continuing with name *microstriata* for those populations. The International Commission on Zoological Nomenclature failed to accept that recommendation. Thus *microstriata* falls back into synonymy, and *castoria* is the oldest available subspecies name for the interior California populations.

- DIAGNOSIS: In this subspecies of the interior mountains, the black veining and markings are greatly reduced and the ventral surface is nearly immaculate pale yellow. The upperside of the male is pure white.
- ORIGINAL DESCRIPTION: Reakirt, *Proc. Acad. Nat. Sci. Philadelphia*, 18: 238 (1866).
- TYPE LOCALITY: "California;" types apparently lost. The types were probably collected at or near a town called Castoria, which existed from 1850 to 1859 (precisely when Lorquin collected Reakirt's types) at a place now called French Camp, San Joaquin County. The headquarters of French beaver trappers on the San Joaquin River, it lies on the floor of the San Joaquin Valley at an elevation of less than 3 meters. In Lorquin's time, marshland and dense riparian alder-cottonwood-willow forest surrounded it. Today, *napi* is extinct in the area (see Shapiro, 1977c, Pp. 224-225 for discussion).
- DISTRIBUTION: This subspecies is found throughout the northern Coast Ranges extending to near the ocean north of the San Francisco Bay. North of Mendocino County, *castoria* is primarily confined to the inner Coast Range, then extends throughout the Klamath Mountains Assemblage below 4000 feet elevation and around the upper end of the Sacramento Valley, and south through the Cascade Range and Sierra Nevada foothills to Mariposa County.
- ELEVATION RANGE: From approximately 12' to 5,500' elevation, but mainly in the 2,000' to 4,000' range except in the San Francisco Bay area.
- HABITAT AND PLANT COMMUNITIES: *P. n. castoria* inhabits moist canyons which are mainly within Foothill Woodland and Lower Montane Coniferous Forest.
- PHENOLOGY: Most populations of this subspecies seem to be univoltine, with the adults flying in April and May. This first brood has been referred to as form "microstriata" (generation vern.). However, a small summer brood of typical *castoria* may emerge in cool, wet years, flying in late June or July. In some locations of regular second brood occurrence, an introduced larval host species may be involved.
- FOODPLANTS (All Brassicaceae) *Cardamine californica* (Nutt.) Greene and *Arabis glabra* (L.) Bernh. are used in the Sierra Nevada foothills (J. F. Emmel, unpublished data); Shapiro (*in litt.*) has also recorded *Barbarea* sp. and *Nasturtium officinale* R. Br. (Watercress).

c) *P. n. venosa* (Scudder)

- DIAGNOSIS: These coastal populations in the summer fog-belt are characterized by heavy black veining on the ventral hindwing and the apex of the forewing. A black spot on the central area of the forewing is also usually present.
- ORIGINAL DESCRIPTION: Scudder, *Proc. Boston Soc. Nat. Hist.*, 8: 182-183 (1861).
- TYPE LOCALITY: San Mateo and Mendocino, California. Holotype in Museum of Comparative Zoology, Harvard University.

- DISTRIBUTION:** This subspecies is found in the fog-belt areas of the Coast Ranges from northern San Luis Obispo County north to central Humboldt County.
- ELEVATION RANGE:** From near sea level to approximately 2,500'. Most populations occur below 1,000' elevation. Some blendzone populations with *castoria* extend upward to over 5,000' along the outer Coast Range fog break zone.
- HABITAT AND PLANT COMMUNITIES:** This butterfly is found along shaded watercourses in Redwood Forest, Northern Mixed Evergreen Forests, and Coastal Coniferous Forest plant communities.
- PHENOLOGY:** This subspecies is bivoltine, with the first brood flying from late February to early May and the second brood flying in June, July and August. The first-brood phenotype of these coastal populations is unambiguously *venosa* as per the type description (Scudder, 1861).
- FOODPLANTS:**

d) *P. n. resedae* Boisduval

Although the name *resedae* has been considered a synonym of *P. n. castoria* (Miller & Brown, 1981), examination of the holotype female specimen in the U.S. National Museum has revealed that it is a typical representative of a set of high elevation California *P. napi* populations which are associated with *Cardamine cordifolia* var. *lyallii* Wats. These populations are currently known from several localities in the Klamath Mountains Assemblage and the Warner Mountains; we strongly suspect that as yet undiscovered populations will be found in the Sierra Nevada of Placer County, California, and extreme western Washoe County, Nevada, where *Cardamine cordifolia* is known to occur. No specific type locality should be fixed for this taxon until *C. cordifolia* colonies in the Sierra Nevada have been thoroughly investigated; if *P. napi* occurs in Placer or Washoe counties, this would have been the most likely source of the type of *resedae*, as Lorquin travelled through the area on the way to Carson City. The scant locality information given by Boisduval (1869) in the original description, "sur les bords da Sacramento" ["on the banks of the Sacramento (River)"], is almost certainly erroneous (as were a number of Boisduval's "localities") as the species is not found on the floor of the Sacramento Valley, and Lorquin, the collector of the type, did not travel to the upper Sacramento River drainage as far as is known.

- DIAGNOSIS:** This subspecies is extremely pale, being practically immaculate in both sexes on both surfaces. The ventral surface is tinged with pale yellow on the hindwings and the apex of the forewings, and the female bears faint traces of a black spot on the dorsal forewing. The female differs from *castoria* females in the reduction of the black spots dorsally.
- ORIGINAL DESCRIPTION:** Boisduval, *Ann. Soc. Ent. Belgique*, 12:39 (1869).
- TYPE LOCALITY:** "sur les bords du Sacramento", [California]. Holotype in U. S. National Museum.
- DISTRIBUTION:** This subspecies is found in scattered colonies in the Marble Mountains, the Siskiyou Mountains, on Ball Mountain [in Siskiyou Co.] and in the Warner Mountains. Its distributional limits to the north, east, and south remain undetermined; possibly it is synonymous with the *P. napi* populations of the

northern Great Basin and Rocky Mountains, many of which are associated with *Cardamine cordifolia*.

ELEVATION RANGE: From 4,200' to 8,400'.

HABITAT AND PLANT COMMUNITIES: *P. n. resedae* flies along watercourses and seeps within the Pinyon-Juniper Woodland and Great Basin Sagebrush Scrub communities, in the Lower and Upper Montane Coniferous Forest and Subalpine Forest (Warner Mountains). In the Klamath Mountains, it is found in wet meadows and similar openings in the Montane Wet Meadow and Upper Montane Coniferous Forest plant communities.

PHENOLOGY: This butterfly is bivoltine, with the first brood flying in June and early July, and the second, smaller brood flying in August and early September.

e) *P. n. sequoia* Emmel, Emmel, and Mattoon

DIAGNOSIS: A resident of the deep redwood forests of the northern California coast, this subspecies exhibits very dark wing venation coupled with strongly yellow wings (in first-brood females and both sexes of the second brood). The second-brood adults, especially the males, are very similar to *Pieris rapae* adults.

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 128-131 (1998g).

TYPE LOCALITY: Prairie Creek Redwoods State Park, 50' elevation, Humboldt County, California. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This subspecies is distributed locally in northern Humboldt County. Blending occurs eastward with subspecies *castoria*, but no contact is known with *marginalis* to the north. At the time of the type description, this subspecies was known only from a short coastal strip of approximately 5 miles, between Prairie Creek Redwood State Park and Fern Canyon Road to the north.

ELEVATION RANGE: From 35 to 50' above sea level, with *castoria-sequoia* blendzone populations in adjacent coastal mountains occurring to 1,000'.

HABITAT AND PLANT COMMUNITIES: The favored habitat is on open flats or along watercourses within dense, climax Redwood Forests. The understory is crowded with ferns and other substory growth as well as fallen redwood trees, making it very difficult to follow the adult butterflies in flight.

PHENOLOGY: The spring brood of this butterfly flies in April, May, and June, with the exact timing of the flight dependent on the temperature and rainfall pattern of the season. In wet, cool years, the flight period extends from late May to early June. In very dry, warm years, adult emergence starts in April. A summer brood occurs in reared material, but has not yet been observed in the field.

FOODPLANTS: The sole recorded foodplant for *P. n. sequoia* is the vine-like *Cardamine angulata* Hook. (Brassicaceae) (S. Mattoon and Ken Hansen, unpublished data).

Subfamily Anthocharinae Tutt

21. *Euchloe ausonides* (Lucas)

- ADULT BEHAVIOR:** This species does not hilltop, unlike its close relative *hyantis* which does hilltop frequently. Adults are found either flying along watercourses or across open fields. Adults in the lowlands may feed occasionally on mustard flowers.
- LIFE HISTORY:** The eggs are light green, turning orange after the first 24 hours. They are laid singly on clusters of flower buds. The mature larva is a dark bluish-green, with dorsal and lateral yellow-green stripes and many fine black spots. The underside is green. The pupa is light brown to whitish-gray, with darker wing covers and a brown lateral dorsal line. This species hibernates in the pupal stage.
- CHROMOSOME NUMBER:** n = 31 in Colorado material (Maeki and Remington, 1960b).
- SIMILAR SPECIES:** Within North America are four other species of *Euchloe*; one other species (*E. hyantis*) is found within California. *E. ausonides* is quite similar to *E. hyantis* but it can be distinguished immediately by counting the number of white scales in the black bar at the end of the discal cell on the upper side of the forewing; *ausonides* has 20 to 120 white scales, while *hyantis* has fewer than 8.
- GEOGRAPHIC AND SEASONAL VARIATION:** In the lowland populations, individuals of the second brood tend to be somewhat larger than individuals of the first brood. As noted above, these nominotypical lowland populations are more heavily marked and larger than the smaller, lighter, more lightly marked individuals of subspecies *transmontana*. There do not appear to be any intermediate populations between the two subspecies.
- GENERAL REMARKS:** Two European authorities, Higgins and Riley (1970), consider *ausonides* to be a subspecies of a European marble, *Euchloe ausonia*. We do not support that supposition. Opler (1966a) likewise considered the Nearctic members of the genus to be distinct from the Palearctic species.
- Both males and females of typical *E. ausonides* at Point Richmond in Contra Costa County were shown by Scott (1975) to engage in long-range flights of hundreds of meters daily, apparently due to a necessity for females (and searching males) to colonize new habitats for oviposition.
- SUBSPECIES:** This widespread *Euchloe* marble flies from Alaska south to southern California and east to the Rocky Mountains and even the Great Lakes region. In our area, two subspecies occur.

a) *E. a. ausonides* (Lucas)

- DIAGNOSIS:** The typical butterfly is a large subspecies with a broad black apex on the forewing and a broad bar at the end of the cell on the dorsal forewing. The bases of both wings have relatively heavy black scaling. Males are a creamy white while females have a creamy white forewing and a strongly yellowish hindwing. The forewing costa of the female is heavily spotted with black, and usually there is a black smudge at mid-costa.
- ORIGINAL DESCRIPTION:** Lucas, *Rev. Mag. Zool.*, (2)4: 340 (1852).
- TYPE LOCALITY:** "California". Restricted by Opler (1966c) to San Francisco, San Francisco County, California. Re-restricted by Emmel, Emmel, and Mattoon (1998b) to vicinity of Sacramento, California.

- DISTRIBUTION:** The butterfly is found in the San Francisco Bay area, from Monterey County northward to Sonoma and Napa counties. From there, it extends eastward across the Sacramento Valley to the lower Sierra Nevada foothills. While it regularly uses introduced mustards in this northern range, the butterfly does not follow the southward extensions of distributional range of these hosts into the rest of California; the precise southern distribution limit in the Central Valley remains to be determined.
- ELEVATION RANGE:** Sea level to 2,000'.
- HABITAT AND PLANT COMMUNITIES:** Valley bottoms in agricultural and disturbed areas, as well as flats, slopes, and ravine bottoms in Northern Coastal Scrub, Foothill Woodland and Foothill and Valley Grassland plant communities.
- PHENOLOGY:** Bivoltine, with the first brood flying in March, April and early May, and the second brood flying in June. The second brood is markedly smaller in numbers than the first.
- FOODPLANTS:** *Arabis glabra* (J. F. Emmel, unpublished) is the only known native host for nominotypical *ausonides*. The following introduced species have been recorded by Shapiro (1974): *Raphanus sativus* L. (preferred); *Brassica nigra* (L.) Koch.; *B. napus* L.

b) *E. a. transmontana* Austin and Emmel

- DIAGNOSIS:** This is a smaller, more lightly marked subspecies of *ausonides* which is found in the inter-mountain region of Nevada and Utah and enters our area from the east. It has a narrower black apex on the forewing, less of a creamy cast to the white wings (even females have only a slight yellowish cast to the hindwing), the forewing costa is less heavily dotted with black, and a black smudge is never present. The ventral surface of the hindwing has broader and deeper green mottling, often obscuring the wing veins.
- ORIGINAL DESCRIPTION:** Austin and Emmel, *Systematics of Western North American Butterflies*, pp. - (1998a).
- TYPE LOCALITY:** Kingston Canyon, 6600-6800', Toiyabe Range, Lander County, Nevada. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION:** The subspecies *transmontana* is found at higher elevations in the mountains. It occurs in the Sierra Nevada from Tulare County northward to the Klamath Mountains assemblage and eastward to the Warner Mountains. It is apparently absent in the White Mountains. Within this area, distribution is spotty.
- ELEVATION RANGE:** From approximately 4,000' to 9,000' elevation, with one record for 3,000'.
- HABITAT AND PLANT COMMUNITIES:** Within the Sierra Nevada, the higher-elevation populations tend to occur along watercourses in Lower and Upper Montane Coniferous Forest. Along the east side of the Sierra Nevada and in the Warner Mountains, populations occur along watercourses within Great Basin Sagebrush Scrub community and Lower Montane Coniferous Forest.
- PHENOLOGY:** These populations are apparently all univoltine, with the butterflies flying from late May to mid-July, depending on elevation or latitude.

FOODPLANTS: In the family Brassicaceae, *Arabis divaricarpa* A. Nels. (J. F. Emmel, unpublished data) is used (Marble Mountains); *A. glabra* is suspected in most of the Sierra Nevada populations. At the type locality in the Toiyabe Range, Nevada, larvae have been taken on *Sisymbrium loeseli* L., an introduced species. In the Warner Mountains, Paul Opler (*in litt.*) has found larvae on the introduced *Isatis tinctoria* (Dyer's Woad).

22. *Euchloe hyantis* (W. H. Edwards)

ADULT BEHAVIOR: The marbles of this species commonly "hilltop" in both desert and foothill areas, as well as on the mountains of southern California. Males frequently patrol most of the day on hilltops in search of females. The flight of both sexes is usually unidirectional and very rapid.

LIFE HISTORY: The life history was described by Comstock and Dammers (1932) for the desert subspecies *lotta*. The eggs are laid singly and are lemon-yellow in color when first laid. In the lowland subspecies, the eggs hatch three days after oviposition. The mature larva is green and is covered with raised purplish or blackish punctae, each bearing a short dark bristle. There is a wide lateral line, creamy white in color and bordered above with a purplish or off-green band. A faint brownish or purplish mid-dorsal stripe is also present. Larvae of all subspecies feed on both flowers and fruits, with larger larvae feeding exclusively on the fruits. The pupa varies in color from a light straw to a dark wood-brown. The head is lengthened into a cone and the wings are expanded downward to a blunt point. This species hibernates in the pupal stage. In the Mojave Desert, the life stages pass through in about 20 days from the hatching of the egg to pupation. Some pupae are known to have passed four or five years in diapause before hatching (J. F. Emmel, unpublished), a strategy which enables this species to survive several drought years in succession in the deserts.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: See discussion under *Euchloe ausonides*.

GEOGRAPHIC AND SEASONAL VARIATION: Because the butterfly is strictly univoltine, there is no seasonal variation. The nominotypical subspecies (North Coast Ranges and Sierra Nevada) and the southern *austromontana* subspecies (Mt. Pinos Block, eastern San Bernardino Mountains and Peninsular Ranges) tend to be lightly marked. Populations referable to *lotta* have a very heavy black mark at the end of the discal cell on the forewing but vary considerably from locality to locality. The subspecies *andrewsi* is the most lightly marked of the subspecies within the state and superficially resembles *Euchloe ausonides*, which led to it being described as a subspecies of *E. ausonides* originally.

GENERAL REMARKS: A series of papers by Opler (1966a, b, c, d, 1970, 1971, 1974, and Opler and Clench, 1983) have reviewed the genus *Euchloe* in recent years and clarified many of the outstanding problems in this interesting group. In 1986, a new species of *Euchloe* was named from northwestern Mexico and it is not impossible that some lucky lepidopterist will discover a new species of this genus within the United States with further searching (Opler, 1986).

SUBSPECIES: While *Euchloe ausonides* has a broader range in North America, *Euchloe hyantis* has developed at least four subspecific segregates in the state of California and it has the broadest altitudinal and ecological range in our state. This geographic variation in phenotype is considerable. Opler (1966a) was the first to straighten

out the relationships of *ausonides* and *hyantis*, and to clarify the placement of the various subspecies known to that date. He stated that six subspecific segregates were present in California, but did not describe them. We have combined his west slope Sierra Nevada segregate with nominotypical *hyantis* of the North Coast Ranges, as we are unable to distinguish them phenotypically. We have also combined the Mt. Pinos Block segregate with the Peninsular Ranges segregate in the interior montane regions of southern California; this entity has been named recently as subspecies *austromontana* (Emmel, Emmel, and Mattoon, 1998).

a) *E. h. hyantis* (W. H. Edwards)

- DIAGNOSIS: This nominotypical subspecies is found in the North Coast Ranges and on the west slope of the Sierra Nevada. The overall wing pattern is similar to that of the preceding species, *E. ausonides*. However, *hyantis* is characterized by its smaller size and the lack of yellowish overscaling found in *ausonides*, such that both sexes are a chalky white in dorsal ground color. The white scales in the black bar at the end of the dorsal forewing discal cell number fewer than 8. The ventral surface is chalky white, with marbling composed of black and yellow scales that make it appear olive green. This subspecies is more heavily marbled than the several segregates in southern California.
- ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Entomological Society*, 3: 205 (1871).
- TYPE LOCALITY: "Mendocino County, California", restricted to vicinity of Ukiah, Mendocino County, California by F. M. Brown, *Transactions American Entomological Society*, 99: 35 (1973). Lectotype in Carnegie Museum, designated by F. M. Brown (1973).
- DISTRIBUTION: The distribution for the nominotypical subspecies is in the North Coast Ranges, from Sonoma County north to Trinity and southern Siskiyou counties, through the Klamath Mountains Assemblage, and on the west slope of the Sierra Nevada, from Tulare County northward to Plumas County.
- ELEVATION RANGE: From 1,000 to 6,000' in the North Coast Ranges, and from approximately 3,000' to 9,000', with most records below 8,000', on the west slope of the Sierra Nevada.
- HABITAT AND PLANT COMMUNITIES: The species is typically found on open gravelly or rocky slopes, frequently in serpentine areas in the North Coast Ranges. Plant communities include Serpentine Chaparral, Mixed Chaparral, and Foothill Woodland in the Coast Ranges, and Lower and Upper Montane Coniferous Forest, Subalpine Forest, and Mixed Chaparral in the Sierra Nevada. In Del Norte County, it is found in the Serpentine Dwarf Pine Woodland plant community.
- PHENOLOGY: This species is strictly univoltine, with records ranging from early March to early June or early July in the North Coast Ranges and Klamath Mountains, depending on elevation and latitude. In the Sierra Nevada, the flight period ranges from late March to mid-July, depending primarily on elevation.
- FOODPLANTS: In the North Coast Ranges, this subspecies uses *Streptanthus glandulosus* Hook. (J. F. Emmel, unpublished data); probably other *Streptanthus* and possibly some *Arabis* species (all family Brassicaceae). In the Sierra Nevada segregate of this subspecies, *Streptanthus tortuosus* Kell. is the favored foodplant (Shapiro, 19).

b) *E. h. andrewsi* Martin

- DIAGNOSIS: This subspecies is primarily restricted to the western end of the San Bernardino Mountains. It is characterized by the greatest reduction of the black scaling on the forewing apex of any subspecies, and the strong narrowing of the black bar at the end of the discal cell. Ventrally, the olive green marbling is the most reduced of any California segregate. It feeds on *Streptanthus bernardinus* primarily.
- ORIGINAL DESCRIPTION: Lloyd M. Martin, *Bulletin of the Southern California Academy of Sciences*, 35: 94 (1958).
- TYPE LOCALITY: Crestline Highway, near Lake Arrowhead, San Bernardino County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is confined to the San Bernardino Mountains, primarily in the southwestern part of the range.
- ELEVATION RANGE: 5,000' to 8,000'.
- HABITAT AND PLANT COMMUNITIES: *E. h. andrewsi* is found on open slopes, often rocky or gravelly or along roads, within the Lower Montane Coniferous Forest plant community.
- PHENOLOGY: Dates of capture range from early May to late June, for the single brood.
- FOODPLANTS: *Streptanthus bernardinus* (Greene) Parish is the principal host in the type locality (Chris Henne, *in litt.*). Ova and larvae have also been collected on *Thelypodium stenopetalum* Wats. (endemic to the "pebble plans" of the Bear Valley area, San Bernardino Mountains) (J. F. Emmel, unpublished), and on *Arabis holboellii* Hornem. (J. F. Emmel, unpublished; G. Ballmer, unpublished); and on *Caulanthus major* (Jones) Pays. (J. F. Emmel, unpublished).

c) *E. h. lotta* Beutenmuller

- DIAGNOSIS: This subspecies has the heaviest black markings of any subspecies on the apex of the forewing, and the widest and most pronounced black bar at the end of the discal cell. The ventral marbling on the hindwing is also heaviest in this subspecies. There is tremendous variation in the black on the forewing and the green marbling throughout the range of *lotta* in California and the Great Basin, but the large black forewing bar is a fairly consistent character. It feeds on many crucifer species in the desert.
- ORIGINAL DESCRIPTION: Beutenmuller, *Bull. American Mus. Nat. Hist.*, 10: 24 (1898).
- TYPE LOCALITY: "Colorado, Arizona, Utah, southern California". Syntypes in American Museum of Natural History.
- DISTRIBUTION: Within California, specimens of *E. hyantis* with the *lotta* phenotype occur from the entire Mojave Desert northward along the east slope of the Sierra Nevada through the western edge of the Great Basin into Modoc County. This subspecies does not apparently occur within the Colorado Desert areas.
- ELEVATION RANGE: Approximately 2,000 to 8,500', with the majority of records below 6,000'.
- HABITAT AND PLANT COMMUNITIES: The adults are found in washes or canyon bottoms, or on open flats or slopes within the following plant communities: Creosote Bush Scrub, Mixed Desert Scrub, Shadscale Scrub, Great Basin Sagebrush Scrub, Joshua Tree Woodland, and Pinyon-Juniper Woodland.

PHENOLOGY: Most records for this univoltine subspecies are for the months of March and April, with a few May and early June records.

FOODPLANTS: The following species of Brassicaceae are utilized in the Mojave Desert and in the Coachella Valley: *Descurainea pinnata* (Walt.) Britton (very commonly used), *Caulanthus crassicaulis* (Torr.) Wats. (commonly used at Hunter Mountain; Inyo-White Mountains; Clark Mountain), *Caulanthus major* (Jones) Pays. (frequently used, e.g., Grapevine, New York Mountains); *Caulanthus glaucus* Wats. (frequently used, e.g., in northern Death Valley region); *Lepidium fremontii* Wats. (occasionally used); *Caulanthus lasiophyllus* (H. & A.) Greene (occasional); *Lepidium perfoliatum* L. (introduced, at Rabbit Dry Lake) (all J. F. Emmel, unpublished). *Stanleya viridiflora* Nutt. is used in the Adobe Hills area (Mono County) and *Caulanthus pilosus* Wats. in the Darwin Mesa area of Inyo County and on the east slope of the Sierra Nevada (J. F. Emmel, unpublished). Opler (*in litt.*) reports this *hyantis* as well as *Euchloe ausonides* and four other pierids using an introduced plant, Dyer's Woad (*Isatis tinctoria*), in June 1969 at Buck Creek Ranger Station, northeast of Alturas in Modoc County.

d) *E. h. austromontana* Emmel, Emmel, and Mattoon

DIAGNOSIS: This *Descurainea*-feeding southern montane subspecies is characterized by the ventral marbling being intermediate in development between typical *hyantis* and *andrewsi*, and the dorsal black markings being generally similar to those on typical *hyantis*. In some of the adults, an extra black marking is added to the margin of the forewing at the base of the apical pattern.

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. - (1998).

TYPE LOCALTY: , Laguna Mountains, San Diego County, California.

DISTRIBUTION: The Mt. Pinos Block segregate of this subspecies is found from the Tejon Range westward to the vicinity of the Cuyama Valley, northward into extreme southern San Luis Obispo County. A second set of populations of this subspecies is found in the Peninsular Ranges in southern California: namely, the San Jacinto Mountains and the Santa Rosa Mountains, southward through the Laguna Mountains into the mountains of extreme northern Baja California; it also is found along the eastern base of these mountains, at the western desert edge. A third set of populations is found at the eastern end of the San Bernardino Mountains, and is phenotypically more similar to *austromontana* than to *andrewsi* of the same mountain range.

ELEVATION RANGE: From 4,000 to 6,000' elevation in the Mt. Pinos Block segregate, from 1,000 to 7,000' in the Peninsular Ranges, and from 3,000 to 8,000' for the eastern San Bernardino Mountains populations.

HABITAT AND PLANT COMMUNITIES: This marble is found on open rocky or gravelly slopes or on open flats in Great Basin Sagebrush Scrub and Pinyon-Juniper Woodland in the Mt. Pinos Block area, and within several plant communities in the eastern San Bernardino Mountains and Peninsular Ranges, including Lower Montane Coniferous Forest, Mixed Chaparral, Creosote Bush Scrub, Great Basin Sagebrush Scrub, and Pinyon-Juniper Woodland.

PHENOLOGY: Most captures in the Mt. Pinos Block area are reported from the month of May, with one record in early April and another in early July to define the extremes of

the flight period. Depending on elevation in the eastern San Bernardino Mountains and Peninsular Ranges, records there range from March through June, with two records from January and February. As for the other *E. hyantis* subspecies, *austromontana* is univoltine.

FOODPLANTS: *Descurainia pinnata* (Walt.) Britton (J. F. Emmel, unpublished; probably the principal host), and *Arabis holboellii* Hornem. (J. F. Emmel, unpublished) are used in the Peninsular Ranges. This subspecies is also closely associated with *Descurainia pinnata* at Cuddy Valley near Mt. Pinos (J. F. Emmel, unpublished).

23. *Anthocharis cethura* C. and R. Felder

ADULT BEHAVIOR: Adults visit flowers of the host plants as well as other plants, particularly *Amsinckia* and *Cryptantha* species. Males are noted for patrolling on hilltops to seek females, and virgin females are known to fly to hilltops to mate (Oakley Shields, 1967). Marked males have been recaptured on the same hilltop as long as 14 days after marking, showing some degree of sedentary behavior.

LIFE HISTORY: The egg is bluish-green when first laid, and it soon turns orange. Eggs are deposited singly on the host, usually on the stems or cauline leaves. The egg is spindle-shaped and bears about 17 straight, sharply elevated, longitudinal ribs with numerous cross lines between the ribs. The first instar larvae frequently begin feeding on the cauline leaves, then move to the inflorescence by the second or third instar and feed on the flowers and fruits. The mature larva is beautifully marked in a complicated pattern of broad white lateral patches and rows of shiny black dots on crossbands of orange-yellow and green. There are progressive changes in coloration with maturation of the last instar larva (Comstock and Dammers, 1932). The pupa is light brown to mottled blackish gray, with many darker striations and a long conelike or beak-like palpal case on the front of the head. This species diapauses in the pupal stage, and has been known to delay as long as seven years before emergence in laboratory rearings (J. F. Emmel, unpublished).

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: As noted earlier in the discussion of *A. c. cethura*, the occasional form "deserti" Wright has a much reduced or absent orange spot and may resemble *Euchloe hyantis*, but the apical markings on the tip of the forewing differ between the two species, as seen in the plates. The tip of the forewing and ventral marbling pattern also more rounded in the orange-tip than in the *Euchloe* marble.

GEOGRAPHIC AND SEASONAL VARIATION: Because the species is strictly univoltine, there is no seasonal variation. As noted above, there is a tremendous amount of geographic variation in the species and blend zones occur where the two phenotypes of different named subspecies come in contact.

GENERAL REMARKS: Further careful study of this species, particularly the immature stages, may lead to a resurrection of the genus *Tetracharis* Grote (1898, *Proc. American Phil. Soc.*, 37: 37). The pupal morphology is closer to that of *Euchloe hyantis* than it is to that of *Anthocharis sara* or *A. lanceolata*. Its larval morphology and coloration also seems to differ considerably from these two *Anthocharis* species.

SUBSPECIES: This colorful little orange-tip butterfly is typically an inhabitant of our desert areas. It has differentiated into a number of subspecies across California.

a) *A. c. cethura* C. and R. Felder

- DIAGNOSIS: Nominotypical *cethura* is a lightly marked subspecies of *cethura* in which both sexes are white in ground color, with usually no yellow individuals in the populations. Males have prominent orange apical areas on the forewings, while females may or may not have orange tips.
- ORIGINAL DESCRIPTION: C. and R. Felder, *Reise...Novara, Lepid. Rhop.*, 2: 182 [1865].
- TYPE LOCALITY: "Sonora". Type locality fixed to Los Angeles, California, by Emmel, Emmel, and Mattoon, 1998d. Lectotype in British Museum.
- DISTRIBUTION: This subspecies in its typical form is found in cismontane southern California from Los Angeles County, southwestern San Bernardino County, and western Riverside County, south to San Diego County and probably to extreme northwestern Baja California. Populations to the north in the extreme western Mohave Desert form a blend zone with the subspecies *morrisoni* and *hadromarmoratus*. To the east, the populations form a blend zone with subspecies *pima* and *mojavensis*.
- ELEVATION RANGE: From sea level to approximately 4,000'.
- HABITAT AND PLANT COMMUNITIES: The typical subspecies flies over slopes or mostly in Inland Sage Scrub or at the lower edges of Mixed Chaparral; along the desert margins, it flies in Creosote Bush Scrub, Mixed Desert Scrub, or Desert Transition Chaparral.
- PHENOLOGY: Adults are recorded primarily during the months of March and April, with a peak in late March. There are some January and February records for the species.
- FOODPLANTS: *Caulanthus simulans* Pays. (J. F. Emmel, unpublished) and *Streptanthus heterophyllus* Nutt. (G. Ballmer, unpublished) in the family Brassicaceae. Probably *Caulanthus lasiophyllus* (H. & A.) Greene is also used. C. H. Dammer's record of *Sisymbrium* is very likely based on a misidentification of *Descurainaea pinnata* (Walt.) Britton. J. F. Emmel has searched thousands of *Sisymbrium* (an introduced genus, also) plants in *cethura* territory in the deserts, and has yet to find a single *cethura* immature stage on it or see even pre-oviposition behavior by females towards it.

b) *A. c. morrisoni* (W. H. Edwards)

- DIAGNOSIS: This is a lightly-marked subspecies, with virtually all females of the subspecies lacking any orange scaling on the forewing tips. It inhabits the southern San Joaquin Valley region.
- ORIGINAL DESCRIPTION: W. H. Edwards, *Papilio*, 1: 43-44 (1881).
- TYPE LOCALITY: "Southern California," restricted to Kern River, Kern County, California, by F. M. Brown, *Trans. American Entomological Society*, 99: 47 (1973). Lectotype in Carnegie Museum, designated by F. M. Brown, *Trans. American Entomological Society*, 99: 49 (1973).
- DISTRIBUTION: This subspecies is found in the southern San Joaquin Valley region, from southeastern San Luis Obispo County and extreme northeastern Santa Barbara County eastward to the Kern County River drainage in the southern Sierra Nevada

foothills. It extends northward in the Valley to approximately the latitude of Fresno.

- ELEVATION RANGE: From approximately 300' to 3,500' elevation, with the majority of records below 2,000'.
- HABITAT AND PLANT COMMUNITIES: This subspecies flies mostly on open flats in the Alkali Sink Scrub community of the Valley floor. It also occurs in Foothill Woodland, Foothill and Valley Grassland, and Pinyon-Juniper Woodland around the edges of the San Joaquin Valley.
- PHENOLOGY: This subspecies flies primarily during March, with some records into early April.
- FOODPLANTS: *Caulanthus lasiophyllus* (H. & A.) Greene and *C. coulteri* Wats. (J. F. Emmel, unpublished data).

c) *A. c. catalina* Meadows

- DIAGNOSIS: This subspecies is closest to nominotypical *cethura*. It is distinguished by a chalky white dorsal surface. The apical spot on the forewing tends to be a paler creamy yellow, rather than orange-yellow, and the butterfly has lighter ventral markings.
- ORIGINAL DESCRIPTION: Don Meadows, *Bulletin Southern California Academy of Sciences*, 35: 177 (1937)("1936").
- TYPE LOCALITY: "Catalina Island, California", restricted by Miller & Brown (1981) to ridge between Renton Mine and Jewfish Point and head of Pebbly Beach Canyon, on Santa Catalina Island. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is confined to Santa Catalina Island. It is absent from the Channel Islands to the north. It is possible that the subspecies will also be found on San Clemente Island to the south of Santa Catalina Island.
- ELEVATION RANGE: From near sea level to 1,800'.
- HABITAT AND PLANT COMMUNITIES: The Catalina Orange-tip flies over open slopes in the Coastal Sage Scrub.
- PHENOLOGY: This subspecies flies from late February to mid-April, the precise dates depending annually on rainfall patterns and the progression of the seasons in terms of warming temperatures.
- FOODPLANTS: *Descurainia pinnata* (Walt.) Britton (*fide* Lawrence F. Gall); *Caulanthus lasiophyllus* (H. & A.) Greene strongly suspected (J. F. Emmel, unpublished data).

d) *A. c. pima* (W. H. Edwards)

- DIAGNOSIS: The distinguishing feature in this subspecies is the yellow coloration in both sexes, combined with relatively light markings on the undersides. It is typically a Sonoran Desert butterfly, barely entering our area in extreme southeastern California.
- ORIGINAL DESCRIPTION: W. H. Edwards, *Canadian Entomologist*, 20: 158-159 (1888).

- TYPE LOCALITY: [Pantano], Pima County, Arizona, according to F. M. Brown, *Trans. American Entomological Society*, 99: 45-46 (1973). Lectotype in Carnegie Museum, designated by F. M. Brown, *Trans. American Entomological Society*, 99: 47 (1973).
- DISTRIBUTION: In our area, this subspecies enters California only in eastern Imperial County and extreme southeastern Riverside County. To the east, it is found through much of southern Arizona, extreme southern New Mexico and extreme western Texas in the El Paso region. From there, it goes south into Sonora, Mexico.
- ELEVATION RANGE: Within California, from approximately 140' to 2,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This rich yellow subspecies is found typically flying either in desert washes, particularly for the females, or on hilltops, for the males, within the Creosote Bush Scrub or Desert Microphyll Woodland plant communities.
- PHENOLOGY: The emergence begins in mid- to late February and continues through March, with some adults straggling into April.
- FOODPLANTS: The most widely used host is *Caulanthus lasiophyllus* (H. & A.) Greene. *Streptanthella longirostris* (Wats.) Rydb. is also used. *Descurainaea pinnata* (Walt.) Britton is probably used on occasion (all Brassicaceae; J. F. Emmel, unpublished data).

e) *A. c. mojavensis* Emmel, Emmel, and Mattoon

- DIAGNOSIS: A subspecies of the eastern Mojave Desert in which both sexes are yellow, with heavier green mottling on the underside and a tendency towards a smaller size than in *pima*.
- ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 131-133 (1998g).
- TYPE LOCALITY: Bonanza King Mine, Providence Mountains, San Bernardino County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is widely distributed in the eastern Mojave Desert, from eastern San Bernardino County to extreme southeastern Inyo County, and extending eastward across southern Nevada to extreme southwestern Utah and northwestern Arizona.
- ELEVATION RANGE: Approximately 500' to 6,000', with the majority of records between about 2,000 and 5,000'.
- HABITAT AND PLANT COMMUNITIES: Most populations are found on open desert flats or on small hills, within the following plant communities: Creosote Bush Scrub (most populations), Mixed Desert Scrub, and Desert Microphyll Woodland. The females are found primarily flying along open desert washes where the foodplants are concentrated.
- PHENOLOGY: Most emergence begins in mid-March, extending through early April, with a few late April records for some of the higher elevations; in some years the flight season has begun as early as mid-February.

FOODPLANTS: The primary host is *Caulanthus lasiophyllus* (H. & A.) Greene; this subspecies also uses *Descurainaea pinnata* (Walt.) Britton, and *Caulanthus cooperi* (Wats.) Pays. (J. F. Emmel, unpublished).

f) *A. c. hadromarmoratus* Emmel, Emmel, and Mattoon

DIAGNOSIS: This subspecies inhabits the lower elevations of the western Great Basin region and has a white ground color in both sexes, with heavy marbling on the underside. Females usually have orange forewing apices, but some populations (particularly in Inyo County) have varying percentages of orange- and white-tipped females.

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 133-134 (1998g).

TYPE LOCALITY: Along U.S. Highway 95, 6.0 road miles north of the Lyon County line, Churchill County, Nevada. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: In our area, this subspecies occurs in the Death Valley region, from the Argus and Panamint Ranges north along the east slope of the Sierra Nevada, through the foothills of the Inyo and White Mountains northward into west-central Nevada.

ELEVATION RANGE: From approximately 2,000' to 5,000'.

HABITAT AND PLANT COMMUNITIES: This subspecies is usually found on open flats or on low hills, within the Creosote Bush Scrub and Shadscale Scrub plant communities.

PHENOLOGY: Adults of this subspecies begin flying in early to mid-April in most years, with some records as late as mid-May.

FOODPLANTS: *A. c. hadromarmoratus* uses *Streptanthella longirostris* (Wats.) Rydb. (probably the main host) and *Caulanthus lasiophyllus* (H. & A.) Greene (J. F. Emmel, unpublished). Possibly *Thelypodium flexuosum* Rob. in Gray is also used (W. L. Swisher, personal communication). *Caulanthus inflatus* Wats. was recorded as a host by C. M. Dammers (see published life history of *cethura* in Comstock and Dammers, 1932).

24. *Anthocharis sara* Lucas

ADULT BEHAVIOR: Adults of the various subspecies of the Sara Orange-tip may be found in canyon bottoms or hillsides, flying with a rather rapid, fairly direct flight and with occasional brief stops for nectar-feeding or oviposition. In contrast to the *Cethura* Orange-tip, there are no records of hilltopping for this species. Evans (1952) has studied the behavior of typical *sara* along southern California canyon bottoms and noted that males seem to patrol a regular route, frequently returning to the same spot. Males are rather pugnacious and fly in brief encounter spirals when another male is encountered in the course of their flight.

LIFE HISTORY: The freshly-laid egg is yellow and soon turns to a deep orange by maturity. It is about 2 mm tall and spindle-shaped, with 16-18 longitudinal ridges and very fine crossridges (Comstock, 1931). The eggs are laid mainly on stalks and petioles near the top of the plant, but also on host leaves and inflorescences. The mature larva is basically green in ground color, with a poorly defined mid-dorsal green line and a dorsal surface tinged with dirty yellow and numerous black blotchings. Transverse rows of black papillae extend to the wide, yellowish-white, lateral line, which is bordered below by a darker green area. The lateral line extends onto the

head capsule, a feature which does not occur in the larva of *Euchloe hyantis* which the *sara* larva otherwise superficially resembles. The pupa is light brown, with darker brown spots and markings. A dark mid-dorsal band is present, with a brown and white line above the spiracles and a brown lateral line as in the figure. The pupa resembles *Euchloe* pupae in having a long beak-like conical head. This species diapauses in the pupal stage.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: This species may occasionally be confused with *Anthocharis cethura*, but a careful examination of the underside markings will help to rapidly differentiate between the two species.

GEOGRAPHIC AND SEASONAL VARIATION: In the bivoltine populations, second-brood specimens tend to be much larger and much more lightly marked than the smaller, darker, first-brood specimens. There is no apparent blend zone nor are intermediate specimens known between the montane *stella* and lowland nominotypical *sara* populations. Similarly, on the east slope of the Sierra Nevada in the Lake Tahoe region, occasional specimens of subspecies *pseudothoosa* and subspecies *stella* can be taken in the same locality, with no evidence of intergradation.

GENERAL REMARKS: Geiger and Shapiro (1986) have recently suggested that the taxa *Anthocharis sara* and *A. stella* in northern California are differentiated at the species level, by reason of electrophoretic differences between them in both allopatric and parapatric populations. While the samples used in this study are quite small, these detectable genetic differences suggest the need for further study as regards a decision to rank them as species rather than as subspecies. The data suggest a lack of gene flow between the taxa, although the opportunity for contact exists, at least in the South Yuba River country and probably elsewhere.

SUBSPECIES: One of our most beautiful springtime butterflies, the Sara Orange-tip occurs throughout California in the foothills of the mountains and even across portions of our deserts. Over this broad range, it displays considerable color variation and five named subspecies occur within our state.

a) *A. s. sara* Lucas

DIAGNOSIS: The early spring brood of typical *A. sara sara*, named form "reakirtii" by Edwards, flies from February to early April. It is a small orange-tip, with heavy green mottling on the ventral surface. The late spring brood, showing the phenotype of the typical subspecies *sara*, flies in May and June. It is larger, with reduced green mottling beneath and lighter black markings above.

Evans (1952, 1975) showed that "sara" is the late spring brood, resulting in as little as 16 days from a portion of the eggs laid earlier that spring by "reakirtii" females; the larvae from the rest of the eggs develop to pupation, but then diapause as pupae until early the following spring, when they emerge as new "reakirtii" adults.

ORIGINAL DESCRIPTION: Lucas, *Rev. Mag. Zoo.*, (2)4: 12 (1852).

TYPE LOCALITY: "California". Type locality restricted to San Francisco, California, by Emmel, Emmel and Mattoon (1998b). Lectotype in Museum Nationale de Histoire Naturelle, Paris, France.

- DISTRIBUTION:** Nominate *sara* is widely distributed through the state in the foothills and mid-elevations of the mountains west of the Sierra Cascade axis, from the Oregon border south to Baja California. It is absent from most of the Great Central Valley. It is found along the western edge of the deserts, from southern Inyo County to the mountains of Joshua Tree National Monument, thence south to the Mexican border. Typical *sara* is also found on Santa Cruz and Santa Rosa Islands.
- ELEVATION RANGE:** From near sea level to approximately 5,000', with some records going as high as 7,000'.
- HABITAT AND PLANT COMMUNITIES:** This butterfly usually occurs in canyon bottoms, particularly along streams, but also on open grassy slopes or fields, within a number of plant communities, including Coastal Sage Scrub, Inland Sage Scrub, Mixed Chaparral, Riparian Woodland, Foothill Woodland, Foothill and Valley Grassland, Southern Oak Woodland, Northern Oak Woodland, Northern Mixed Evergreen Forest, Southern Mixed Evergreen Forest, and Lower Montane Coniferous Forest.
- PHENOLOGY:** Nominotypical *sara* is bivoltine, with the first brood emerging in February, to early April, and a small second brood appearing from late April to early June. There are a few, very early records for late December and January.
- FOODPLANTS:** The family Brassicaceae provides a number of foodplants in California for this subspecies. Those recorded include: *Arabis glabra* (L.) Bernh., *A. sparsiflora* Nutt., *A. perennans* (Wats.), *A. pulchra* Jones, *Barbarea verna* (Mill.) Asch., *Cardamine californica* (Nutt.) Greene (an occasional host), *Brassica campestris* L., *Thysanocarpus curvipes* Hook., and *Caulanthus simulans* Pays. (all J. F. Emmel, unpublished data). Opler (1968) records *Arabis sparsiflora* Nutt. var. *arcuata* (Nutt.) Roll. in Ventura County, *Barbarea vulgaris* (L.) in Contra Costa County, *Brasica kaber* (D.C.) in Alameda County, and *Sisymbrium officinale* (L.) Scop. in Solano County. Shapiro (1975c) records *Brassica napus* L., *B. geniculata* (Desf.) J. Ball, and *Raphanus sativus* L. in the Sacramento Valley.

b) *A. s. thoosa* (Scudder)

- DIAGNOSIS:** This is a desert subspecies, with generally darker or more extensive black markings and heavier mottling on the underside.
- ORIGINAL DESCRIPTION:** Scudder, *Bull. U.S. Geol. Geogr. Surv. Terr.*, 4(1) (x): 257 (1878).
- TYPE LOCALITY:** Mokiah Pass, Mohave County, Arizona. Holotype probably in Museum of Comparative Zoology, Harvard University.
- DISTRIBUTION:** This subspecies is found in the higher mountain ranges of the eastern Mojave Desert, from the Old Woman Mountains north to the Kingston Range. From there, it extends eastward across much of the southern half of the Great Basin as far east as southwestern Utah, and from there into northwestern Arizona. Significantly, it is absent from the Panamint and Argus Ranges in Inyo County.
- ELEVATION RANGE:** 3,000' to approximately 7,000', but mostly 4,000-6,000'.
- HABITAT AND PLANT COMMUNITIES:** This subspecies primarily flies in Pinyon-Juniper Woodland, but it also occurs in Joshua Tree Woodland, Blackbush Scrub, Mixed Desert Scrub, and the upper edge of the Creosote Bush Scrub communities. The adults typically fly along canyon bottoms or washes within these communities.

PHENOLOGY: Emergence begins in March and continues through April. This subspecies is strictly univoltine.

FOODPLANTS: *Arabis perennans* Wats. is the most commonly used host. This subspecies also uses *A. pulchra* Jones, *Descurainia pinnata* (Walt.) Britton, and *Caulanthus cooperi* (Wats.) Pays. It rarely uses *Caulanthus lasiophyllus* (H. & A.) Greene (all J. F. Emmel, unpublished data).

c) *A. s. pseudothoosa* Austin

DIAGNOSIS: A subspecies of the northern desert areas and western Great Basin, *A. s. pseudothoosa* is similar to *thoosa* but has reduced black markings and somewhat lighter mottling ventrally. *A. s. pseudothoosa* usually has five radial veins on the forewing, while *thoosa* usually has four.

ORIGINAL DESCRIPTION: Austin, *Systematics of Western North American Butterflies*, pp. - (1998).

TYPE LOCALITY: Nevada: Douglas County; Sweetwater Mountains, Jackass Creek, 0.5-2 miles southwest of Desert Creek, 2195 m.

DISTRIBUTION: In California, this subspecies flies in the Inyo and White Mountains, and extends northward to the Benton Range, Walker River area, and Sweetwater Mountains in Mono County. It is also present in Lassen and Modoc counties at moderate elevations; at higher elevations in the Warner mountains there are *A. sara* populations which are phenotypically closer to the Sierran subspecies *stella*. In Nevada, *A. s. pseudothoosa* is found in the western half of the state north of the Mojave Desert.

ELEVATION RANGE: 4,000' to 9,000' elevation.

HABITAT AND PLANT COMMUNITIES: This subspecies is usually encountered flying along canyon bottoms or along watercourses, within the following plant communities: Pinyon-Juniper Woodland, Great Basin Sagebrush Scrub, and Great Basin Coniferous Woodland.

PHENOLOGY: Emergence begins in early to mid April, and extends to early June, depending on elevation. As with *A. s. thoosa*, this subspecies is univoltine, in contrast to the partially bivoltine nominotypical *sara*.

FOODPLANTS: *Arabis inyoensis* Roll. and *A. pulchra* Jones are recorded for the White Mountains populations (J. F. Emmel, unpublished data). Undoubtedly other *Arabis* species are used in other parts of the subspecies' range. Opler (*in litt.*) reports this orange-tip using introduced Dyer's Woad, *Isatis tinctoria* L., at Buck Creek Ranger Station northeast of Alturas in Modoc County in June 1969, along with five other pierid species.

d) *A. s. stella* (W. H. Edwards)

DIAGNOSIS: A montane subspecies of the Sierra Nevada and Warner Mountains, *stella* has a distinctive yellowish cast to the wings in both sexes.

ORIGINAL DESCRIPTION: W. H. Edwards, *Canadian Entomologist*, 11: 87-89 (1879).

- TYPE LOCALITY: "Nevada", restricted to Marlette Peak, Carson Range, Washoe County, Nevada, by F. M. Brown, *Trans. American Entomological Society*, 99: 41 (1973). Lectotype in Carnegie Museum, designated by F. M. Brown, *Trans. American Entomological Society*, 99: 43 (1973).
- DISTRIBUTION: This beautiful orange-tip occurs throughout the higher elevations of the Sierra Nevada from Fresno County north to Sierra County, and also flies in the higher elevations of the Warner Mountains.
- ELEVATION RANGE: From 6,000' to 8,000' elevation.
- HABITAT AND PLANT COMMUNITIES: *A. s. stella* is found either along watercourses or flying over open slopes within the Lower and Upper Montane Coniferous Forest community.
- PHENOLOGY: This race is strictly univoltine. Emergence takes place in mid May to early June at the lower elevations, and continues into early July at the higher elevations.
- FOODPLANTS: This subspecies utilizes *Arabis platysperma* Gray, *A. holboellii* Hornem., and *A. lyallii* Wats. (all J. F. Emmel, unpublished data).

e) *A. s. gunderi* Ingham

- DIAGNOSIS: A subspecies endemic to Santa Catalina Island, *gunderi* is characterized by heavier black markings on the upper sides and increased density of the greenish-black marbling on the underside of the hindwings. Frequently, there is also a flush of greenish-yellow tinge on the upperside of the hindwings, primarily occurring in the females but sometimes in the males.
- ORIGINAL DESCRIPTION: Ingham, *Pan-Pacific Entomologist*, 9: 75-76 (1933).
- TYPE LOCALITY: Middle Ranch, Santa Catalina Island, California. Holotype in California Academy of Sciences, San Francisco.
- DISTRIBUTION: This subspecies is confined to Santa Catalina Island. Emmel & Emmel (1973) also listed its occurrence on Santa Cruz Island. Subsequent careful study of these latter populations reveals that they are essentially identical with nominotypical *sara*.
- ELEVATION RANGE: From near sea level to 1,800' elevation.
- HABITAT AND PLANT COMMUNITIES: This insular subspecies is found flying along canyon bottoms along roads, and on open slopes within the Coastal Sage Scrub community on Santa Catalina Island.
- PHENOLOGY: Emergence begins in February to March, and extends into April. A very small second brood of somewhat larger adults occurs in May to June.
- FOODPLANTS: *A. s. gunderi* feeds on the following larval hosts: *Caulanthus lasiophyllus* (J. F. Emmel, unpublished data), *Descurainaea pinnata* (Walt.) Britton, and *Brassica* spp. (Glenn Gorelick, personal communication).

25. *Anthocharis lanceolata* Lucas

- ADULT BEHAVIOR: *Anthocharis lanceolata* is principally found in wooded canyons with high rocky walls. It is never found hilltopping and is usually taken solitarily. Males patrol

the canyon bottoms in search of females, while females seek out the *Arabis* foodplants on the rocky canyon walls for oviposition.

- LIFE HISTORY:** Coolidge (1910) has described the egg and young larva, and the mature larva is described in Comstock (1927a) as well as Emmel & Emmel (1973). The egg is laid singly on hostplant inflorescences and leaves, usually on the flower pedicels; the larvae preferentially eat flowers and fruits. The mature larva is green, with minute flecks of white and a wide white lateral line. A pair of green papillae occurs dorsally on each segment. The pupa is slaty gray-brown and has a palpal case strongly curved above the head. The species diapauses in the pupal stage, sometimes for several years.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** This butterfly is rather unique in appearance, and is not easily confused with any other pierid.
- GEOGRAPHIC AND SEASONAL VARIATION:** All subspecies are univoltine, so there is no seasonal variation. There is subtle geographic variation throughout the state and with the populations we have included under the nominotypical name *lanceolata*, there are perhaps several distinctive segregates; further study of larger samples of specimens from the various populations is indicated.
- GENERAL REMARKS:** The entity *Anthocharis dammersi* J. A. Comstock (1929)[J. A. Comstock, *Bulletin of the Southern California Academy of Sciences*, 28:33 (1929), with type locality of White Water Canyon, Riverside County, California, has been listed as a separate species by Miller and Brown (1981). In addition to the type specimen, two other similar individuals have apparently been reported (Shields & Mori, 1979). All have been taken in areas where *Anthocharis sara* and *lanceolata* are sympatric, and this entity is believed to represent an occasional wild hybrid between the two species (Emmel and Emmel, 1973). This apparent hybridization prompts us to consider *lanceolata* and *sara* as congeneric and therefore we do not use the subgenus *Falcapica* for *lanceolata* (cf. Miller & Brown, 1981, p. 176).
- SUBSPECIES:** This rather scarce, delicately-marked white *Anthocharis* may often be found flying with another species in the genus during the spring months. There are three geographic subspecies located within our state.

a) *A. l. lanceolata* Lucas

- DIAGNOSIS:** A medium to large-sized and white-tipped *Anthocharis* species. In nominotypical *lanceolata*, the markings tend to be lighter, and the underside has somewhat of a brownish cast, as contrasted to the more olive-green cast of the subspecies *australis*.
- ORIGINAL DESCRIPTION:** Lucas, *Rev. Mag. Zool.*, (2)4: 338 (1852).
- TYPE LOCALITY:** "Californie". Type locality restricted to Highway 70 at Chips Creek, 1 road mile W. of Belden, North Fork Feather River Canyon, Plumas County, California, by Emmel, Emmel and Mattoon (1998b). Type in Museum Nationale de Histoire Naturelle, Paris, France.
- DISTRIBUTION:** The nominotypical subspecies occurs in a wide distribution, from the southern Sierra Nevada in Tulare County and southwestern Inyo County, northward to the Warner Mountains, westward into the Klamath Mountains assemblage, and

southward into the North Coast Ranges. It is also found along the east slope of the Sierra Nevada as far south as extreme northern Mono County.

- ELEVATION RANGE: From 500 to 7,000', with the majority of populations found between about 1,000 and 4,000' elevation.
- HABITAT AND PLANT COMMUNITIES: Most populations occur along watercourse bottoms in a number of other plant communities, including Riparian Woodland, Lower Montane Coniferous Forest, Northern Oak Woodland, Foothill Woodland, Mixed Chaparral, Northern Mixed Evergreen Forest, and Serpentine Dwarf Pine Woodland.
- PHENOLOGY: This species is strictly univoltine, with records extending from mid-April to mid-June, depending on elevation and latitude. The majority of records are in early May.
- FOODPLANTS: *Arabis sparsiflora* Nutt. in T. & G. is probably the primary host in most areas (J. F. Emmel, unpublished data). On the west slope of the Sierra in Nevada County, *Streptanthus tortuosus* Kell. is used (Shapiro, 1981b). Opler (*in litt.*) reports *lanceolata* using introduced Dyer's Woad, *Isatis tinctoria*, along with five other pierid species, at Buck Creek Ranger Station northeast of Alturas in Modoc County in June 1969.

b) *A. l. australis* Grinnell

- DIAGNOSIS: A subspecies of the mountains of southern California, *australis* is similar in size to nominotypical *lanceolata* but has somewhat heavier black markings on the upperside and an olive-green cast to the marbling markings on the underside. The latter character is in contrast to the somewhat more brownish cast to these markings in nominotypical *lanceolata*.
- ORIGINAL DESCRIPTION: Grinnell, *Canadian Entomologist*, 40: 72 (1908).
- TYPE LOCALITY: Arroyo Seco and Millard Canyons, Los Angeles County, California. Syntypes in Grinnell and Clemence collections.
- DISTRIBUTION: This subspecies occurs in southern California from northern Ventura County and Kern County southward through the San Gabriel and San Bernardino Mountains to the San Jacinto Mountains, southward into the Laguna Mountains. It is generally found on the coastal side of the mountains, at low to moderate elevations.
- ELEVATION RANGE: From 2,000 to 8,000' elevation. Populations mostly occur below 5,000' elevation.
- HABITAT AND PLANT COMMUNITIES: Usually found along canyon bottoms or watercourses within the following plant communities: Mixed Chaparral, Lower Montane Coniferous Forest, Southern Mixed Evergreen Forest, and Riparian Woodland.
- PHENOLOGY: Univoltine, with emergence starting in mid-March at the lower elevations and extending to early June at the higher elevations.
- FOODPLANTS: The primary hosts are *Arabis sparsiflora* Nutt. in T. & G., varieties *arcuata* (Nutt.) Roll. and *californica* Roll. It also utilizes *A. perennans* Wats., *A. pulchra* Jones, *A. holboellii* Hornem., and *A. glabra* (L.) Bernh. to a lesser extent (all J. F. Emmel,

unpublished data). Opler (1968) reports *Arabis sparsiflora* Nutt. var. *arcuata* (Nutt.) Roll. as being used in Ventura County.

c) *A. l. desertolimbus* Emmel, Emmel, and Mattoon

- DIAGNOSIS: This subspecies occurs in the foothills along the western edge of the desert in southern California, and is characterized by generally smaller size and lighter markings than the nearby subspecies *australis*.
- ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, p. 135 (1998g).
- TYPE LOCALITY: One mile west of Scissors Crossing, San Diego County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is found along the western edge of the Colorado Desert in the eastern foothills of the San Diego County Mountains, and along the east base of the Santa Rosa Mountains and the San Jacinto Mountains in western Riverside County.
- ELEVATION RANGE: From 2,000 to 3,500' elevation.
- HABITAT AND PLANT COMMUNITIES: *A. l. desertolimbus* is found along washes and desert canyons in Pinyon-Juniper Woodland, Desert Transition Chaparral, and Mixed Desert Scrub.
- PHENOLOGY: Most captures are recorded from the month of March, with some records as early as February 1st and several records in early April.
- FOODPLANTS: *Arabis perennans* Wats. (family Brassicaceae) is the primary host (J. F. Emmel, unpublished data).

Subfamily Coliadinae Swainson

26. *Colias eurytheme* Boisduval

- DIAGNOSIS: A small to medium-sized *Colias*, with a yellow-orange to orange ground color except for albinic females. This species is found in a wide variety of habitats throughout the state.
- ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 286 (1852).
- TYPE LOCALITY: "toute de Californie." Type locality restricted to Sacramento, California, by Emmel, Emmel, and Mattoon (1998a). Holotype in U. S. National Museum.
- DISTRIBUTION: This species is found throughout the entire state in virtually every plant community and at all elevations, although it is decidedly scarcer at the higher elevations and in habitats such as redwood forests.
- ELEVATION RANGE: From below sea level in the Coachella and Imperial Valleys to approximately 12,000' in the Sierra Nevada and White Mountains.
- HABITAT AND PLANT COMMUNITIES: The Orange Sulfur is most abundant in agricultural areas where alfalfa is being cultivated. Otherwise, it is found in virtually every plant

community in the state, including the urban and suburban areas. This species is very weedy and tends to invade new habitats readily.

PHENOLOGY: The main flight period of this multivoltine species is from March through November, although captures are recorded for every month of the year.

ADULT BEHAVIOR: *Colias eurytheme*, also known as the Orange Sulfur or Alfalfa Butterfly, is a common sight in many agricultural areas due to the widespread cultivation of some of its legume foodplants as crops. Originally, it was primarily a southern species, but it has invaded the northern latitudes and in the process has encountered another species, the Common Sulfur, *Colias philodice*. Where they come in contact, there is frequent hybridization, yet the two species remain distinct because of their chromosome structure. The genes controlling mating pheromones, the ultraviolet reflection pattern on the male wings, the orange or yellow color of the species, the width of the black forewing border, and the wing size and development rate are all located on the *X* chromosome, forming a giant "super gene" (Grula and Taylor, 1979, 1980a, 1980b). Because the two species have basically different *X* chromosomes, and because the female (XY) hybrids produced in crosses preferentially mate with a male (XX) of their father's species, the hybrid's *X* chromosome stays associated with an *X* chromosome of the original species and does not end up in the other species in the way (by introgression) that the other non-sex chromosomes may (Scott, 1986). Thus, although one can observe interspecific courtship and other adult behavior in overlapping range areas, the two species remain distinct.

Outside of courtship, the Orange Sulfur has a relatively direct, straight-line flight which involves substantial movements as far as a mile or more. Most movements are of much less distance. Males recognize females visually. They are attracted to the greenish-yellow underside of the female, and are repelled by the ultraviolet reflectance of other *eurytheme* males. Females accept either orange or yellow male color; however, they do choose the *eurytheme* males over *philodice* males because those males of their own species are reflecting ultraviolet. In addition, *eurytheme* males have a distinctive male pheromone apart from that of *philodice*, and females will mate only with males having the right pheromone (under normal conditions). Most hybrids result from matings between males of *philodice* and young *eurytheme* females (less than an hour old) which cannot distinguish between the two species very well. This cross is known to usually produce sterile and inviable female offspring, however, whereas the cross between *eurytheme* males and *philodice* females produces very fertile and viable offspring.

In Pennsylvania, Clench (1970) has observed several conspicuous communal aggregations of this species in an open meadow; these appeared to be gathered for the purpose of passing the night together in roosts in dense grass.

LIFE HISTORY: The eggs are creamy or greenish-white in color, turning to crimson in a few days. They are laid singly on host leaves. The egg, which tapers from a broad central portion toward either end, bears the usual longitudinal ribs and cross-ribs of our pierids. Females in the laboratory can lay up to 1,300 eggs, but average around 700 eggs. Females may live up to 39 days. The mature larva is dark green, with a basal white line (enclosing a narrow crimson line) and a sub-dorsal white line (sometimes obsolescent) running along each side. Minute white hairs cover the entire body. The pupa is green, with lateral yellow dashes and black markings in a yellow lateral band. Diapause may take place in either the third or fourth instar larvae.

- FOODPLANTS: Alfalfa, *Medicago sativa* L.; *Lotus scoparius* (Nutt. in T. & G.); clover species in the genus *Trifolium* (Emmel and Emmel, 1973); other species used within California include *Hoffmannseggia densiflora* Benth. ex Gray, *Astragalus lentiginosus* Dougl., *Petlastemun searlsiae* Gray, *Robinia neomexicana*, *Amorpha californica* L., *Lotus crassifolius* (Benth.) Greene, *Lupinus* species (all Fabaceae) (J. F. Emmel, unpublished). Priestaf (1974) found larvae on *Astragalus antiselli* Gray in Santa Barbara County.
- CHROMOSOME NUMBER: n = 31 in Connecticut material (Maeki and Remington, 1960b).
- SIMILAR SPECIES: *Colias philodice* differs from *eurytheme* in having a clear lemon-yellow ground color. Also, *eurytheme* adults are slightly larger than *philodice* adults, and the underside of the hindwing has one silver spot, with two red rings and a satellite spot, as well as brownish sub-marginal dots. In *philodice*, the same hindwing underside spotting pattern is found but the adults are yellow, the males do not reflect ultra-violet, and in the females the black upperside forewing border is narrower with smaller light spots than in *eurytheme*. The white females of the two species are sometimes impossible to distinguish.
- GEOGRAPHIC AND SEASONAL VARIATION: There is no significant geographic variation within our state; however, seasonal variation can be rather pronounced. The spring brood (form "ariadne") has narrow black borders and is almost entirely yellow, with a small central orange patch on each wing. The late summer brood (form "amphidusa") has heavy black marginal borders and is deep orange in both sexes. At any time of the year, one may encounter white females (form "alba") along with the normal yellow-orange females forms. This white color is controlled by a dominant gene (expressed only in the female).
- GENERAL REMARKS: The complicated genetics of color pattern in this species as well as other *Colias*, has been studied in recent years by Charles L. Remington at Yale University, Orley R. Taylor at the University of Kansas, Ward B. Watt at Stanford University, and their students. Earlier work by William Hovanitz in California showed important flight time differences and geographical-distribution differences between the white and orange female morphs in *eurytheme* which seemed correlated with environmental variables such as temperature and degree of insolation. Watt (e.g., 1968, 1969, 1983) has shown that white females of *eurytheme* use the nitrogen that goes into orange pigment of normal females to develop faster, produce more fat, and lay larger eggs -- all characteristics that would give them a reproductive advantage in cooler climates, and may help to explain the greater prevalence of white females in more northern and altitudinally higher populations discovered by Hovanitz.

27. *Colias philodice eriphyle* (W. H. Edwards)

- DIAGNOSIS: This *Colias* species possess a pure yellow ground color, a rather broad black border, and a more northern range as a whole in North America than *eurytheme*. In California, it occurs as one subspecific form, *eriphyle* W. H. Edwards, which is found in several of our eastern and northern counties.
- ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Entomological Society*, 5: 202-204 (1876).
- TYPE LOCALITY: Lake Lahache (misspelled as "Labache"), British Columbia. Lectotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Entomological Society*, 99: 87 (1973).

- DISTRIBUTION:** This species has been found on the eastern side of the Sierra Nevada in Inyo and Mono County and north into Nevada, Placer, Modoc, Siskiyou, and Shasta counties in scattered locations. One bred series from Riverside County was recorded by C. M. Dammers in 1933. In 1963, Richard Funk collected *C. philodice* in the Holtville area in Imperial County. These southern California populations are apparently only transient introductions, as subsequent records are lacking.
- ELEVATION RANGE:** From sea level to 10,000' (e.g. at Rock Creek, Inyo County), with most records below 7,000'.
- HABITAT AND PLANT COMMUNITIES:** In our state, this species is found either in the open agricultural fields of northeastern California or in meadows within the Great Basin Sagebrush or Lower Montane Coniferous Forest communities.
- PHENOLOGY:** Most records indicate a flight period from May to September, probably involving at least two or three broods.
- ADULT BEHAVIOR:** Adults are known from marking studies in Colorado to move more than a kilometer (Watt, Han, and Tabashnik, 1979). Within alfalfa fields, however, movements are usually less than 100 meters. Adults live an average of only 2 to 3 days in nature in Colorado, although the maximum life span is up to 2 weeks. Adults feed on both flower nectar and mud flats. See discussion of *Colias eurytheme* for comparative aspects of mating behavior and hybridization.
- LIFE HISTORY:** The egg is cream-colored, turning crimson in a day or two. Eggs are laid singly on the host, starting within two to four days after female emergence. The mature larva resembles that of *Colias eurytheme*. It is grass-green with a whitish or pinkish stripe running along each side and a faint, darker green mid-dorsal stripe. Occasionally, the body is pale yellow along the sides. The head is green. The pupa resembles that of *Colias eurytheme*. The larvae hibernate in the third or sometimes the fourth instar.
- FOODPLANTS:** Alfalfa, *Medicago sativa* L., and various clover species of the genus *Trifolium* (family Fabaceae) (many sources).
- CHROMOSOME NUMBER:** n = 31 in Connecticut material (Maeki and Remington, 1960b).
- SIMILAR SPECIES:** See discussion under *Colias eurytheme*.
- GEOGRAPHIC AND SEASONAL VARIATIONS:** Early-spring specimens tend to be smaller with darker undersides. All specimens taken so far within California are referable to the subspecies *eriphyle*. No specimens of nominotypical *philodice* are yet confirmed for extreme southern California; however, it is possible that the typical subspecies may enter the state in Imperial County from Arizona, as there are *philodice* populations fairly close to the California border in Arizona.
- GENERAL REMARKS:** See further discussion under *Colias eurytheme*.

28. *Colias alexandra edwardsii* (W. H. Edwards)

- DIAGNOSIS:** A large bright lemon yellow *Colias* with ventral surfaces often dusted with grayish green scaling. The wing fringes contain pink hairs, especially toward the apical area of the forewing. The dorsal black borders in the males are relatively

narrow. The females are generally clear yellow, sometimes with a very slight orange flush and occasionally with a faint partial border on the dorsal forewing (Ferris, 1988). This species occurs primarily in the Great Basin and Rocky Mountain regions but enters the eastern edge of our state.

- ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Entomological Society*, 3: 11 (1870).
- TYPE LOCALITY: Vicinity of Virginia City, Nevada. Lectotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Entomological Society*, 99: 67 (1973).
- DISTRIBUTION: In California, the species is found in the Mono Basin and then again to the north in eastern Lassen and Modoc counties. From there, it goes eastward to the Rocky Mountains, southward to northern Arizona and northern New Mexico, and northward into much of western Canada and extreme eastern Alaska.
- ELEVATION RANGE: From 4,000' to 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is typically found in the Great Basin Sagebrush Scrub plant community, where it flies over open flats or hillsides.
- PHENOLOGY: Records are for July and August, with most records clustering around mid-July. In our area, the butterfly is apparently univoltine; however, in at least some areas of the Rocky Mountain region, the nominotypical subspecies (*C. a. alexandra*) is reported to be bivoltine (Scott, 1986).
- ADULT BEHAVIOR: The male has a very rapid flight, and many males fly up to a kilometer or more in the course of the day away from their original sites of capture. Some adults are recorded to move up to 8 kilometers (in Colorado). Females fly more slowly in a zig-zag flight, searching for oviposition sites. Adults of both sexes sip flower nectar in the morning hours and late afternoon (1600 hours; Ellis, 1974) and drink water at mud flats in the early afternoon (Ellis, 1974). Males are known to live up to a month, but average only 6-12 days of life in nature. Females have a somewhat shorter life. Oviposition occurs most often between 1000 and 1330 hours. The butterfly occurs most frequently in widely dispersed populations.
- LIFE HISTORY: The egg is yellow-green or cream colored, later turning to crimson. The eggs are laid singly on the upper side of the host leaves. Females may lay up to 600 eggs in nature. The larva is yellow-green, with tiny black dots and a white lateral band interrupted with orange dashes. The head is yellow-green, with small black points scattered across it. The pupa is yellow-green with a somewhat darker dorsal aspect, and bears small reddish spots on the ventral side of the abdomen next to the wing cases. The larvae hibernate apparently in the third instar in all subspecies.
- FOODPLANTS: This sulfur is restricted to Fabaceae, but uses a wide variety of species within this family throughout its range in the western United States and Canada. In the Mono Basin, this species uses *Astragalus lentiginosus* Dougl. var. *floribundus* Gray (J. F. Emmel and G. Pratt, unpublished data). Outside the state, the species feeds on a variety of *Astragalus* species, *Lathyrus leucanthus*, *Medicago*, *Oxytropis*, *Trifolium*, and *Vicia* (Ellis, 1974; Scott, 1986).
- CHROMOSOME NUMBER: Unknown for this subspecies. $n = 31$ in typical *alexandra* in Colorado (Maeki and Remington, 1960b).
- SIMILAR SPECIES: This pure yellow Sulfur is larger than either *Colias philodice* or *C. harfordii*. It is superficially similar to *C. occidentalis*, but the ranges are completely separate

in our state. To the north, *alexandra* and *occidentalis* meet in Oregon to British Columbia and hybridization apparently occurs fairly regularly.

GEOGRAPHIC AND SEASONAL VARIATION: In our state, *alexandra* is univoltine and no seasonal variation occurs. Mono Basin material is virtually identical with nominotypical *edwardsi* from Virginia City, Nevada. Northward through Lassen and Modoc counties, *C. alexandra* populations are still referable to subspecies *edwardsi*.

GENERAL REMARKS: Ferris (1973, 1988), followed by Scott (1986), lumped *Colias harfordi* as a subspecies of *C. alexandra* on the basis of shared ultraviolet reflectance patterns. John Burns (*in litt.*) has carried out extensive electrophoresis studies on the isoenzymes of entities in the genus *Colias*, and his results suggest that *harfordi* is best considered a distinct species.

29. *Colias occidentalis chrysomelas* Hy. Edwards

DIAGNOSIS: A medium-large yellow *Colias* species of the forested areas in northwestern California, the males have a broad black border and a ventral surface which is saturated golden-yellow in color. Females are yellow in ground color, with a lightly marked black marginal and submarginal pattern on the forewing. Females are rarely white. Both sexes have a large orange discal spot in the center of the dorsal hindwing, which is pearly and red-rimmed on the ventral surface. The fringes are pink.

ORIGINAL DESCRIPTION: Henry Edwards, *Pacific Coast Lepidoptera*, (24): 8-9 (1877).

TYPE LOCALITY: Napa County, California. Holotype in American Museum of Natural History.

DISTRIBUTION: This species is found in the North Coast Ranges, from Napa and Lake County northward to the Oregon border.

ELEVATION RANGE: From 2,000 to 4,000' elevation.

HABITAT AND PLANT COMMUNITIES: This butterfly prefers open forest within the Lower Montane Coniferous Forest and Douglas Fir Forest plant communities. It is usually not seen in meadows. In the Trinity Alps and Mount Eddy region, Shapiro *et al.* (1981) encountered it frequently in lower montane coniferous forest among Yellow Pine and Douglas Fir.

PHENOLOGY: Most records are from the latter part of May to late June, with a peak at approximately the end of May; some Humboldt County populations near the fog-break zone fly from mid June to late July. The species is apparently strictly univoltine, at least in our area.

ADULT BEHAVIOR: This large and beautiful sulfur is rather local and considered uncommon to rare. It prefers forest glades and clearings in the Coast Ranges, especially in Douglas Fir forests. Unlike several of the other *Colias* species in our state, it does not readily invade disturbed areas.

LIFE HISTORY: The life history of this species is undescribed.

FOODPLANTS: Oviposition has been observed on *Lupinus latifolius* J. G. Agardh. (Fabaceae) in our area (Shields, personal communication and Sims, personal communication). Shapiro *et al.* (1981) found *chrysomelas* associated with *Lupinus albicaulis*

Dougl. ex Hook. and *Lathyrus pauciflorus* Fern. ssp. *browni* (Eastw.) Piper in the Trinity Alps.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: See discussion under *Colias alexandra* and General Remarks below.

GEOGRAPHIC AND
SEASONAL VARIATION: None in our state.

GENERAL REMARKS: While superficially similar to *Colias philodice* or even some *C. alexandra* specimens, *C. occidentalis* is clearly distinct from these taxa (Ferris, 1988). *Colias occidentalis* adults have no ultraviolet reflectance, whereas the other two species are strongly UV-reflective. Also, the two larger species (*occidentalis* and *alexandra*) can be separated by differences in wing shape, pattern, and ventral color. Ferris emphasizes that the outer wing borders of *occidentalis* are rounded, while those of *alexandra* terminate in an acute angle at the apex of the forewing. Ventrally, *occidentalis* has a saturated bright burnt golden yellow tone, while *alexandra* has a softer yellow, often with a greenish cast produced by melanic over-scaling. Male *occidentalis* have wide black wing borders, while *alexandra* males have narrower borders crossed along the veins by yellow lines. Males of *occidentalis* completely lack the specialized UV-reflecting scales found in *alexandra*.

Albinic females of *C. occidentalis* seem decidedly scarce in collections. On Grouse Mountain in Humboldt County, there is a higher percentage of albinic females than in *C. occidentalis* populations more inland (Ken Hansen, personal communication).

30. *Colias harfordii* Hy. Edwards

DIAGNOSIS: This butterfly is a medium-sized, rich lemon yellow *Colias* of the higher mountains in southern California. Males of *harfordii* have a UV reflectance pattern, whereas similar-appearing *philodice* males are not UV-reflective. Females of *harfordii* have a notably more diffuse dark border on the forewing than the relatively crisp markings on female *philodice*.

ORIGINAL DESCRIPTION: Henry Edwards, *Pacific Coast Lepidoptera*, (24): 9 (1877).

TYPE LOCALITY: Havilah, Kern County, California. Holotype in American Museum of Natural History.

DISTRIBUTION: This butterfly is found in cismontane southern California, generally in the mountains but approaching the coast in several areas. It occurs from the southern border of San Diego County northward through the Santa Rosa and San Jacinto Mountains, northwestward through the San Bernardino and San Gabriel Ranges and from there north into southern Kern County and eastern Ventura County and northeastern Santa Barbara County. There is also one record for extreme southern San Luis Obispo County and one record for extreme southern Tulare County. It is recorded from Santa Cruz Island; none of the other Channel Islands seems to harbor the species.

ELEVATION RANGE: From near sea level to approximately 8,000'.

HABITAT AND PLANT
COMMUNITIES: This butterfly is typically found in open grassy or meadowy areas, or along roads, within the following plant communities: Mixed Chaparral,

Southern Mixed Evergreen Forest, Lower Montane Coniferous Forest, Desert Transition Chaparral, Coastal Sage Scrub, and Montane Dry Meadow.

PHENOLOGY: The earliest specimens appear in March and April, with an occasional February record, and the butterfly is then recorded for every month after that up through November. Peak flight seems to be in June and July. The butterfly is thus multivoltine. Later summer broods may depend on summer rainfall patterns.

ADULT BEHAVIOR: Adults are rapid and erratic fliers, and may be collected best while nectaring at flowers. Favored nectar sources include *Eriasturm* species and *Helianthus* species. A wild hybrid (male) between *C. harfordi* and *C. eurytheme* was captured near Cachuma Creek, San Rafael Mountains, in Santa Barbara County on May 1, 1970 (Priestaf, 1974); adults of both species fly in the San Rafael Mountains and larvae of both species have been found on *Astragalus antisellii* Gray in Oso Canyon.

LIFE HISTORY: The egg is yellow-green and similar in shape to others in the genus. The mature larva is green and bears a lateral white stripe enclosing a vermilion line. Minute black tubercles bearing short hairs are scattered over the body. The pupa is basically yellow-green in color, with a yellowish abdomen and a bright yellow band (enclosing a red line) on the sides of the abdomen. This species diapauses as half-grown larvae.

FOODPLANTS: The usual hosts are Rattleweed, *Astragalus douglasii* (T. & G.) Gray, and *A. douglasii* (T. & G.) Gray var. *parishii* (Gray) Jones (Fabaceae). There is also a record for larvae on *A. antiselli* Gray in the San Rafael Mountains (Priestaf, 1974). The species also uses *Lotus crassifolius* (Benth.) Greene and *L. scoparius* (Nutt. in T. & G.) Ottley (many records, J. F. Emmel, unpublished data). Along the western edge of the Colorado Desert, populations are closely associated with *Astragalus palmeri* Gray and this species is strongly suspected to serve as a host.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: Refer to sections under *Colias alexandra*, *occidentalis* and *philodice*.

GEOGRAPHIC AND SEASONAL VARIATION: Early spring specimens of *harfordii* tend to be smaller and darker on the underside than later spring and summer specimens. Aside from *Colias eurytheme* and *Colias philodice*, this is the only species of *Colias* in North America known to regularly have more than a single annual brood (Hovanitz, 1951). On the driest mountain slopes in southern California during the summer, one can still find these golden yellow butterflies, sipping nectar from mints and thistles.

GENERAL REMARKS: John Burns (unpublished) found that the enzymatic arrays of esterases in *harfordii* and *alexandra* differ significantly. Additionally, the adults of *harfordii* bear an orange spot on the upper hindwing and the same wing surface reflects ultraviolet, while the upperside of the forewing reflects only a trace of ultraviolet. In *alexandra*, the yellow populations reflect ultraviolet on the upper forewing only narrowly inside the black border, while the orange populations of *alexandra* outside our state as well as some of the yellow ones in northeastern California tend to reflect ultraviolet extensively on the upper forewing, also. *C. harfordii* is multivoltine; *alexandra* is univoltine except for one bivoltine *C. a. alexandra* population on the high plains near Parker, Colorado, with the first brood from May 25 to June 22 and the second brood from July 25 to August 19 (Ellis, 1973). Despite these differences, Scott (1986), following Ferris (1973, 1988), classifies

harfordii and *alexandra* as the same species. This position is unique in recent major faunal works; A. B. Klots (in Howe, 1975), Pyle (1981), Emmel and Emmel (1973), Miller and Brown (1981), etc. continue to recognize their specific distinctness.

31. *Colias behrii* W. H. Edwards

- DIAGNOSIS:** A small *Colias* species with green wings that is found only in the upper regions of the Sierra Nevada and can be confused with no other *Colias* in our area. The two female forms (normal and albinic) are less distinct from each other than in most *Colias*. Males do not reflect ultraviolet from their wings.
- ORIGINAL DESCRIPTION:** W. H. Edwards, *Proceedings Entomological Society Philadelphia*, 6: 201 (1866).
- TYPE LOCALITY:** "Yosemite mountains", restricted to vicinity of Tioga Pass, Tuolumne-Mono counties, California, by F. M. Brown, *Transactions American Entomological Society*, 99: 52-52 (1973). Lectotype in Carnegie Museum, designated by F. M. Brown (1973).
- DISTRIBUTION:** This beautiful green sulfur is found in higher elevations of the Sierra Nevada from Tulare County (Mineral King area) northward to northern Tuolumne County (Emigrant Wilderness area).
- ELEVATION RANGE:** From 9,500' to 12,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** This species is found in open alpine meadows within the following plant communities: Montane Dry Meadow, Montane Wet Meadow, Arctic-Alpine Cushion Plant, and Subalpine Forest. Most populations occur in meadows which are vernal quite moist, but which dry out significantly by mid-summer.
- PHENOLOGY:** Recorded from early July to mid-August, in a single brood.
- ADULT BEHAVIOR:** To collect this butterfly, one must hike into the high country of the Sierra Nevada range in mid-summer and seek the glacial flower-strewn meadows. The adults fly low to the ground, usually within a half a meter, and the males patrol in strong unidirectional flights searching for females. Because of the green wings and small size, *behrii* adults tend to be less conspicuous than the brighter-colored *Colias* species.
- LIFE HISTORY:** The egg is greenish-white in color, spindle-shaped, with low longitudinal and transverse ridges; it is usually placed on the leaf upper surface. The mature larva is green in ground color, with a fine pinkish-white dorsal line that is finely bordered with black, and a broader sub-dorsal line which is nearly white on the edges, salmon colored centrally, and bordered above by black lunate spots, one on each segment. A similar, very even sub-stigmatal band, pinkish in the center, and with a black border, extends above to surround the spiracles. The pupa is similar in shape and marking to other members of the genus, being yellowish-green with a pale lateral line on the abdomen (Dyar, 1893; Grinnell, 1913; Comstock, 1927a).
- FOODPLANTS:** The larval foodplant is *Vaccinium nivictum* (Ericaceae). J. Emmel and O. Shields () report an oviposition record and an attached pupa on *Salix* (Salicaceae); this probably represents a fortuitous observation, as *Salix* frequently grows in close proximity to *Vaccinium nivictum*; further field observations of ovipositing females as well as rearing studies are indicated.

CHROMOSOME NUMBER:	Unknown.
SIMILAR SPECIES:	None in California. In the Arctic and south to British Columbia the Arctic Green Sulfur, <i>Colias nastes</i> , occurs and has a basically green wing with white spots in the black upper forewing border of both males and females. This species does not reach our area, however.
GEOGRAPHIC AND SEASONAL VARIATION:	None discovered to date. This species is univoltine.
GENERAL REMARKS:	One of our most interesting pierids and very rarely photographed or collected, <i>Colias behrii</i> actually flies in considerable numbers during its summer flight period in the Sierras and may be easily found by those who penetrate its alpine strongholds.

32. *Zerene eurydice* (Boisduval)

DIAGNOSIS:	A large orange or yellow pierid, distinctively marked in the orange male with a broad black border pattern resembling a "dog face", and with a violet sheen on the forewings. The yellow females lack the "dog face", having very narrow dark borders. White females are extremely rare. The freshly emerged male has a particularly beautiful iridescent violet sheen on its forewings.
ORIGINAL DESCRIPTION:	Boisduval, <i>Ann. Soc. Ent. France</i> , (3): xxxii (1855).
TYPE LOCALITY:	"Mountains of California". Lectotype in U. S. National Museum.
DISTRIBUTION:	The California Dog Face ranges from the North Coast Range and southern Mt. Shasta region southward through the coast ranges and Sierra Nevada foothills to the southern California mountain ranges west of the deserts. Its distribution as a whole is very spotty but correlates well with the distribution of the principal foodplant, <i>Amorpha californica</i> .
ELEVATION RANGE:	From sea level to approximately 7,000' near Barton Flats in the San Bernardino Mountains of southern California.
HABITAT AND PLANT COMMUNITIES:	This pierid is found in canyon bottoms and near watercourses, or sometimes on open slopes or along roads, within the following plant communities: Riparian Woodland, Foothill Woodland, Coastal Prairie, Northern Oak Woodland, Southern Oak Woodland, Lower Montane Coniferous Forest, Southern Mixed Evergreen Forest, and Mixed Chaparral.
PHENOLOGY:	<i>Zerene eurydice</i> flies from March to October in two broods. The spring generation flies mainly in April and May, while the summer brood flies abundantly from late July to September. A few late-emerging specimens are caught into October and November. This species is strongly suspected to diapause as an adult; fresh adults may be taken in mid-October in the mountains, when the foodplant leaves are too senescent to sustain larvae, and adults are seen on warm days in February in the lowlands, fully two months before the <i>Amorpha</i> plants begin to leaf out (J. F. Emmel, unpublished data).
ADULT BEHAVIOR:	Adults will begin flying about 6:30 a.m. and continue until about 4:00 p.m. They often roost for a while inside bushes, especially manzanita which have yellowish dying leaves in the interior branches. The adults are rather fast-flying pierids, but

they occasionally stop to sip nectar or drink from moist mud flats near streams, when they can be more easily observed. Favorite flowers include *Senecio*, a little blue gilia (*Navarretia* species), thistle blooms, and wild sunflowers (Riddell, 1941).

LIFE HISTORY: The spindle-shaped egg is yellow-green, and the eggs are laid singly on the host plant leaves, usually on the upper surfaces. The early instar larvae rest on the upper surfaces of the leaves, above the midrib. The mature larva is dull green in ground color and is marked with a white lateral line, edged centrally with orange and dorsally with a black spot or thin crossband on each segment. The head is dull green, with tiny black points. The pupa is pale green and the abdomen is marked with a whitish lateral line. Recent field observations by J. F. Emmel (see remarks under Phenology) indicate that the adults likely go into diapause in the fall and overwinter until the spring. European *Gonepteryx rhamni* pierids go through similar adult hibernation to pass the winter (Higgins and Riley, 1970). In fact, the phenotypic similarity between *eurydice* females and *rhamni* adults initially led Boisduval (1852) to assume that Lorquin had sent him specimens of "*rhamni*" with his California collections and he failed to describe it as a new species until 1855, when he corrected that oversight (Boisduval, 1855).

FOODPLANTS: False Indigo, *Amorpha californica* Nutt. (Family Fabaceae), is the sole foodplant for most populations. In the lower elevations of San Diego and Riverside counties, *A. fruticosa* L. var. *occidentalis* (Abrams) Kearn. & Peeb. is also used (J. F. Emmel, unpublished data).

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: The California Dog Face, *Zerene eurydice*, resembles the Southern Dog Face, *Zerene cesonia*, in general markings in the male, but the orange male of *eurydice* has a strong violet sheen which is lacking in the yellow *cesonia*. Additionally, the females of *eurydice* have very light dark-border markings, in contrast with the heavier "dog-face" markings of *cesonia*.

GEOGRAPHIC AND SEASONAL VARIATION: In southern California populations of *Z. eurydice*, there is a tendency of some females to have increased black markings on the wings, suggestive of the females of *C. cesonia*, with a full spectrum of variation between the females of the two species. This is believed to have resulted from occasional hybridization of *eurydice* with invading *cesonia*. In the males, there is also an apparently increased tendency in the more southern populations to show development of a black marginal band on the hind wings. Again, this may be related to contact with *Zerene cesonia*. We are not aware of any seasonal variation between the spring broods and summer broods. However, Riddell (1941) thought that the form "*bernardino*" (with black margins extending onto the hindwings in the male) was most abundant at the start of the second brood (30:1 over typical *eurydice*) at 5,000' in the San Bernardino Mountains. By the end of the season, she believed most specimens were typical *eurydice*. Further field studies are indicated to confirm these observations.

GENERAL REMARKS: The California Dog Face is the official State butterfly of California, designated as such by the California legislature. Riddell (1941) has illustrated a number of aberrant forms of *eurydice*. She also mentions that the greatest enemies of the larvae in the wild are grasshoppers (*Dissosteira carolina* (Linn.)), which hunt over the shrubs of *Amorpha californica* and seize the larvae to eat. Lizards and these grasshoppers also prey on adults.

33. *Zerene cesonia cesonia* (Stoll)

- DIAGNOSIS: A large yellow sulfur butterfly with "dog face" markings on the forewings, showing less sexual dimorphism than *Zerene eurydice*. Females always show some black markings on the forewings and hindwings.
- ORIGINAL DESCRIPTION: Stoll, *Aanhangs. Werk Uitl. Kapellen Pieter Cramer*, 176 [1790].
- TYPE LOCALITY: "Georgia". Location of type not known.
- DISTRIBUTION: The butterfly occurs as a stray in our state, perhaps temporarily becoming established in some areas. It is taken primarily in the deserts, with occasional specimens being taken in the southern mountains or even in central California.
- ELEVATION RANGE: From near sea level to approximately 7,000'.
- HABITAT AND PLANT COMMUNITIES: In the deserts, this species has been taken in the Creosote Bush Scrub, Shadscale Scrub, Pinyon-Juniper Woodland, and Great Basin Sagebrush Scrub communities. In the San Bernardino Mountains, it has been taken in the Lower Montane Coniferous Forest. Because of the somewhat migratory nature of the strays that come into our area, undoubtedly other plant communities are involved, although less frequently.
- PHENOLOGY: Our records are scattered from March through December, with no real concentration of records during any particular month or season.
- ADULT BEHAVIOR: Adults are seen flying rapidly and erratically over flat areas in the deserts. In the mountain areas they are usually taken in situations similar to those preferred by *Zerene eurydice*, as along watercourses or in forested areas where *Amorpha californica* is abundant. Most of the specimens taken in our area are quite worn, indicating that they have probably travelled some distance.
- LIFE HISTORY: The egg is yellow-green when first laid and turns crimson as it matures. The eggs are laid singly on the underside of terminal host leaves. The larva is green or yellow-green in color and is densely covered with small blackish tubercles, each bearing many short hairs. The green ground color may be unmarked, or it may bear either crossbands or lengthwise stripes of yellow and black. The head is yellow-green, with black points. The pupa is bluish-green or yellow-green, with whitish streaks, black dots subdorsally and a lateral gray line which becomes white on the abdomen. The wing covers are darker green with yellow veins. The species has been said to diapause in the pupal stage (Klots, 1951). However, in northern Florida, adults are seen throughout the winter months and the species is known to pass the dry season in the tropics as an adult in reproductive diapause (T. C. Emmel, unpublished). Roy Kendall (personal communication) has also observed this species in adult reproductive diapause in southern Texas during the winter months.
- FOODPLANTS: Three members of the family Fabaceae have been documented as larval foodplants in California. In the mountains, the species uses *Amorpha californica* Nutt. and in the lower mountain foothills it uses *Amorpha fruticosa* L. (J. F. Emmel, unpublished data; Paul Tuskes, *in litt.*). Tuskes found larvae of both *Z. eurydice* and *Z. cesonia* on the same *Amorpha fruticosa* bush near El Capitan Lake, San Diego County. In the eastern Mojave Desert, larvae have been taken on *Petalostemon searlsiae* (= *Dalea searlsiae*) (G. Ballmer & G. Pratt, pers.

	comm.). It would be of interest to know if other <i>Dalea</i> species are used in the deserts.
CHROMOSOME NUMBER:	n = 31 in northeastern Mexico populations (Macki and Remington, 1960b).
SIMILAR SPECIES:	See discussion under <i>Zerene eurydice</i> .
GEOGRAPHIC AND SEASONAL VARIATION:	No variation has been noted in the specimens collected in different parts of the state, either on a seasonal or a geographic basis.
GENERAL REMARKS:	As mentioned above, the species <i>cesonia</i> and <i>eurydice</i> apparently are able to occasionally hybridize. This situation is perhaps facilitated by the fact that both species sometimes use the same larval foodplant in the same locality.

34. *Phoebus sennae marcellina* (Cramer)

DIAGNOSIS:	A large yellow sulfur butterfly, virtually devoid of dark markings in the males and with mottled dark markings along the wing edges in the females.
ORIGINAL DESCRIPTION:	Cramer, <i>Uitl. Kapellen</i> , 2: 103 [1779].
TYPE LOCALITY:	"Mexico". Type believed to be lost (Miller and Brown, 1981).
DISTRIBUTION:	The butterfly does not seem to be permanently established in any California locality, but is periodically introduced to the area through migrant individuals. It does become temporarily established on both native and ornamental foodplants, primarily in the deserts and occasionally in the urban and suburban areas where ornamental cassias are planted.
ELEVATION RANGE:	From sea level to approximately 6,000'.
HABITAT AND PLANT COMMUNITIES:	Most specimens seen or taken in the deserts have been in the Creosote Bush Scrub plant community. In the coastal localities, it is found typically in urban or suburban settings.
PHENOLOGY:	We have records for most months of the year, from February through December, with an apparent predominance of records in September and October.
ADULT BEHAVIOR:	The adults are strong and rapid fliers, although in the vicinity of the <i>Cassia</i> foodplants, they often show a much more hovering flight, as the males are searching for females and the females are searching for oviposition sites. In open desert areas, adults are frequently seen in rapid unidirectional flight. In the summer of 1984, when there was a huge population explosion of this species in the deserts of southern California, a unidirectional flight in a west-northwesterly direction was noted for several weeks. In the eastern United States, the species migrates in great numbers to the north in the spring from southern Florida and the tropics. Adults move south again in the fall (from September to the end of October) from most of the eastern U.S., down to at least the southern end of the Florida peninsula. Adults of both sexes readily visit red tubular flowers, such as <i>Penstemon</i> , or in our urban garden areas, <i>Impatiens</i> or <i>Salvia</i> . Clench (1970) has reported a late afternoon assemblage of 11 <i>P. sennae</i> (9 males, 2 females) that were apparently forming a communal roost for the night in Florida. This roost was in a hollow pocket between a densely growing vine and a palm trunk, about six feet above the ground. Nocturnal roosting habits of our <i>sennae</i> have not been reported.

- LIFE HISTORY:** The cream-colored egg turns orange with maturity, and is somewhat spindle-shaped. Eggs are laid singly on the very newest unfolding growth of the host plant or on flower buds. The mature larva may be either green or yellow, with minute black nodules densely scattered over the surface. A yellow lateral stripe, bordered above with blue points, runs the length of the body. The pupa varies from a sheer pink to a vivid green to pale yellow, and bears a yellow lateral stripe bordered ventrally with green. The antennal sheaths are yellow and the wing veins are outlined in green. The head is pointed and the wing cases are greatly expanded ventrally. The species is believed to diapause in the adult stage in areas with a severe dry season in the tropics, and in cool-winter areas such as northern Florida. Otherwise, this tropical butterfly apparently cannot survive winters in the United States north of the extreme southern portions of Texas and central Florida.
- FOODPLANTS:** *Cassia* species (Fabaceae), introduced from the American tropics into our urban areas, as well as native species in the deserts, serve as foodplants. In the deserts, *Cassia armata* Wats. is the principal foodplant; it is likely that *C. covesii* Gray also serves as a host (J. F. Emmel, unpublished data). Introduced species which are used by *P. sennae* in urban gardens include *C. didymobotrya*, *C. tomentosa*, *C. bicapsularis* and *C. leptocarpa* (J. F. Emmel, unpublished data).
- CHROMOSOME NUMBER:** n = 31 in Trinidad material and elsewhere in the Caribbean, South America, and Florida (Wesley and Emmel, 19 ; Emmel, unpublished).
- SIMILAR SPECIES:** This species cannot be readily confused with any other in our state.
- GEOGRAPHIC AND SEASONAL VARIATION:** No significant geographic or seasonal variation has been noted in the United States populations of this species.
- GENERAL REMARKS:** In the earlier part of this century, *Phoebis sennae* was apparently a fairly common butterfly in the suburban and urban areas of southern California (see Comstock, 1927b). Comstock also noted that the Cassias were frequently used as ornamental shrubs in gardens and parks at the time. Once the sensitivity of these sub-tropical and tropical species to the occasional frosts in southern California was appreciated, they fell into disfavor as ornamentals and were replaced by cold-hardy species. With this change in horticultural preference, it apparently became much more difficult for the species to become established in the developed areas of southern California and this probably explains why it tends to be a rarity there today. Perhaps if planting of more hardy species of ornamental Cassias was encouraged, particularly along the freeways of Los Angeles, then this butterfly could once again become a familiar sight in these urban areas.

35. *Phoebis agarithe agarithe* (Boisduval)

- DIAGNOSIS:** A large, pure orange *Phoebis* species found rather commonly in southern Arizona and Mexico, rarely straying to the eastern deserts of California.
- ORIGINAL DESCRIPTION:** Boisduval, *Hist. Nat. Ins., Spec. gen. Lepid.*, 1: 623 (1836).
- TYPE LOCALITY:** "Mexico". Locations of types unknown.
- DISTRIBUTION:** This species has been recorded from the Providence Mountains in San Bernardino County (September) and the Bard area in Imperial County (early October). There is one old record for Santa Barbara. The butterfly is not a breeding resident at present.
- ELEVATION RANGE:** From 200' to 5,000' elevation.

HABITAT AND PLANT COMMUNITIES:	The strays in the deserts have been observed in the Creosote Bush Scrub plant community.
PHENOLOGY:	All specimens in our area have been taken in the fall.
ADULT BEHAVIOR:	In areas to the east where this species is more abundant, the butterfly flies very similarly to <i>Phoebis sennae</i> , stopping frequently at foodplant bushes. Otherwise, it is a very strong fast flier.
LIFE HISTORY:	The following life history description is based on material collected by Ron Boender in the Florida Keys and reared by J. F. Emmel. The egg is cream-white in color, turning orange-red with maturation. As with <i>sennae</i> , the larvae feed on tender young leaves of the host. The mature larval stage is polymorphic in ground color; it may be green or yellowish-green with lighter lateral bands or orange patches on each segment, and blackish points. At least one yellowish-white lateral band edged with dark green is found across all segments. The head is yellowish green with four black dots across the front. The pupa is either green or mottled with purple shading and a purple mid-dorsal line; both forms bear a yellow lateral line, and three white irregular spots on each side of the abdomen. Diapause likely occurs in the adult stage.
FOODPLANTS:	In southern Texas, <i>Acacia rigidula</i> is used (Noel McFarland, personal communication; Roy Kendall, personal communication). To the south through Mexico to Costa Rica, species of <i>Pithecellobium</i> , <i>Cassia</i> , and <i>Inga</i> are recorded as hosts (Fabaceae).
CHROMOSOME NUMBER:	n = 31 from tropical American material (T. C. Emmel, unpublished).
SIMILAR SPECIES:	No similar species in our area.
GEOGRAPHIC AND SEASONAL VARIATION:	None recorded in the United States specimens.
GENERAL REMARKS:	This is a rare stray in our area, with the most consistent area for records being the extreme southeastern corner of Imperial County (Kilian Roever, personal communication).

36. *Phoebis philea philea* (Johansson)

See **Appendix 2** for the one record of this species in California.

37. *Eurema दौरа* (Godart)

See **Appendix 2** for the one August 1981 record of this species (two adults) in Monterey County, California.

38. *Eurema mexicana* (Boisduval)

DIAGNOSIS:	A medium-sized sulfur with black "dog face" markings on the forewings and single, blunt, tail-like protrusions on the hindwings. This pierid is a sub-tropical species which enters our area as a stray.
ORIGINAL DESCRIPTION:	Boisduval, <i>Hist. Nat. Ins., Spec. gen. Lepid.</i> , 1: 655 (1836).
TYPE LOCALITY:	"Mexico." Type in Museum Nationale de Histoire Naturelle, Paris, France.

DISTRIBUTION:	Records for this stray from Mexico and Arizona are scattered over the desert regions in the southern mountains, at mid-elevations and in several of the coastal valleys, and all in southern California.
ELEVATION RANGE:	From near sea level to approximately 6,000' elevation.
HABITAT AND PLANT COMMUNITIES:	Strays have been taken in a variety of plant communities, including Creosote Bush Scrub, Lower Montane Coniferous Forest, and suburban areas.
PHENOLOGY:	Our records are for April, May, August, September, October, November, and December, with no particular concentration in any given month. Diapause is probably in the adult stage.
ADULT BEHAVIOR:	<i>Eurema mexicana</i> is a relatively weak, erratic flier that flies close to the ground and frequently visits flowers. Males patrol throughout the day in search of females.
LIFE HISTORY:	The following life history description is based on material reared from a female collected by J. F. Emmel in El Paso County, Colorado. The slender, spindle-shaped eggs are deposited on the foodplant leaves; they are cream when first laid, turning orange with maturity. The mature larva is [T.C.E.: Describe from Kodachrome slides; describe pupa also.]
FOODPLANTS:	In southeastern Arizona, in the Huachuca Mountains, this species is known to utilize <i>Acacia angustissima</i> (Noel McFarland, personal communication). Scott (1986) also lists <i>Cassia</i> , <i>Acacia hirta</i> , and <i>Robinia neomexicana</i> .
CHROMOSOME NUMBER:	n = 31 in Mexican material (Maeki and Remington, 1960b) and in Central American material (T. C. Emmel, unpublished).
SIMILAR SPECIES:	This phenotype is unique and cannot be confused with other species in our areas.
GEOGRAPHIC AND SEASONAL VARIATION:	None in our area.
GENERAL REMARKS:	This species is a rare stray in our area and apparently is unable to utilize the only native acacia, <i>A. greggii</i> Gray. In the central United States, the species migrates as far north as Saskatchewan, but does not overwinter there. In fact, this species seems confined to extreme southern Arizona, New Mexico and Texas, as well as Mexico, during the winter months.

39. *Eureme lisa lisa* (Boisduval and Leconte)

See **Appendix** for description of the one record of this species in California.

40. *Eureme nicippe* (Cramer)

DIAGNOSIS:	This species differs from other <i>Eurema</i> in our state by its uniformly bright-orange wings and broad black forewing and hindwing borders on both sexes.
ORIGINAL DESCRIPTION:	Cramer, <i>Uitl. Kapellen</i> , 3: 31 [1779].
TYPE LOCALITY:	"Virginia." Location of type uncertain (Miller and Brown, 1981).

- DISTRIBUTION:** Found throughout the southern California counties, from San Diego to San Bernardino, Los Angeles, and Santa Barbara counties, northward to Kern and Inyo counties. There is one record from Palo Alto in Santa Clara County. It is found from the lower deserts to the mid-elevations of our mountain ranges.
- ELEVATION RANGE:** From 100' to 6,400' at Barton Flats in San Bernardino County.
- HABITAT AND PLANT COMMUNITIES:** This species is commonly encountered in urban areas, wherever *Cassia* is planted as an ornamental. In the deserts, it is found in wahses, on open flats, or in canyon bottoms within the Creosote Bush Scrub plant community. The species is commonly seen as a stray in the following plant communities: Lower Montane Coniferous Forest, Southern Oak Woodland, Foothill Woodland, Foothill and Valley Grassland, Desert Transition Chaparral, Pinyon-Juniper Woodland, Mixed Desert Scrub and Joshua Tree Woodland.
- PHENOLOGY:** Most records extend from March to November, in an apparent succession of multiple broods. This species has been most commonly recorded in April and May, July and August, and from the month of October to as late as mid-November, suggesting three successive broods. The species has been recorded for every month of the year in Huntington Park, Los Angeles County (Robert Langston, pers. comm.). It overwinters as an adult.
- ADULT BEHAVIOR:** Adults have a jerky, meandering flight pattern, preventing easy capture of this species. This butterfly is occasionally taken as a stray in unusual locations such as high elevations in the mountains, especially in late summer.
- LIFE HISTORY:** The spindle-shaped egg is slightly ribbed with longitudinal lines and is light greenish-yellow in color, turning reddish with maturity. The eggs are laid singly on the undersurface of host leaves or occasionally on flower buds. The mature larva is velvety green to grayish green, with tiny black points and a thin whitish-yellow lateral stripe. The head is yellow-green. The pupa is olive-green to black, these color extremes potentially occurring within a single brood. The species overwinters as an adult in the southern parts of its range.
- FOODPLANTS:** *Cassia* species (Fabaceae) and possibly other genera in the family (*Trifolium* has also been mentioned as a host outside the state). In California, both *C. armata* Wats. and *C. covesii* Gray are used in the deserts (J. F. Emmel, unpublished data). Introduced *Cassia* species used in the state include *C. didymobotrya*, *C. tomentosa*, *C. artemisoides*, and *C. bicuspidata* (J. F. Emmel, unpublished data).
- CHROMOSOME NUMBER:** $n = 31$ from Mexican material (Maeki and Remington, 1960b) and from Florida, Central America and Caribbean samples (T. C. Emmel, unpublished).
- SIMILAR SPECIES:** No similar species of *Eurema* occur within our state.
- GEOGRAPHIC AND SEASONAL VARIATION:** Elsewhere in the southern United States, a seasonal winter color form "*rosa*" has a redder underside than the summer-emerging adults. Occasionally, females are taken that are yellow on the upperside rather than pale orange. No geographic variation has been noted within the southern United States populations.
- GENERAL REMARKS:** The northern limit of the range of *Eurema nicippe* is the Santa Barbara area. The species used to be quite common in Los Angeles until about 1960, and seems to

have been reduced in number since that date. In the cities, its foodplants are introduced *Cassia* species. On the desert it probably uses two native *Cassia* species; perhaps with increased planting of ornamental Cassias, the species will become a familiar sight again in urban areas. Sometimes, large fall broods occur in the deserts, following summer rains.

41. *Kricogonia lyside* (Godart)

- DIAGNOSIS: An extremely variable butterfly, the males are white with a yellow patch on the upper surface of the forewing. Females may be completely yellow. The distinctive wing shape will distinguish it from other pierids in our state.
- ORIGINAL DESCRIPTION: Godart, *Enc. Meth.*, 9: 98 [1819].
- TYPE LOCALITY: Not stated in original description, but designated as "Haiti" by Riley, *Field Guide to the Butterflies of the West Indies*: 131 (1975). Holotype in Museum Nationale de Histoire Naturelle, Paris, France.
- DISTRIBUTION: This species is a rare stray in our area, having only been taken once in southern Imperial County and once (three specimens) in Mono County.
- ELEVATION RANGE: From near sea level to 7,000', in the two sites recorded for California.
- HABITAT AND PLANT COMMUNITIES: The Imperial County record was in an agricultural area. The Mono County location was in a wet meadow near Great Basin Sagebrush Scrub, about two miles west of U.S. 395 off Highway 183 near June Lake (July 7, 1972): about a dozen individuals were seen here, in somewhat worn condition, and three were collected by Professor Everett C. Olson of U.C.L.A.
- PHENOLOGY: All records are during the summer months. It is likely that future records will coincide with times of mass migrations north into Arizona from Mexico. The Mexican migrations of this species, which often orient directly into prevailing winds, may be of tremendous size and duration. One such migration involved densities as high as 10,000 adults crossing each 30-foot section of road per minute, and continuing for days (Welling, 1973). It becomes locally abundant in northern Mexico at times, and strays north as far as Colorado, Nebraska, and Illinois (Ehrlich and Ehrlich, 1961; Byers, 1971).
- ADULT BEHAVIOR: We have no notes on the behavior of individuals taken within California.
- LIFE HISTORY: The larva is described as dull green with a silver dorsal line which is bordered with brown. The sides are yellow with a silvery lateral line edged with brown, and the head is green. The larvae are said to feed at night and hide under bark by day. The pupa is bluish-gray, with a whitish bloom.
- FOODPLANTS: Two species in the family Zygophyllaceae have been recorded in the tropics. These species are *Porlieria angustifolia* and *Guaiacum officinale*.
- CHROMOSOME NUMBER: $n = 31$ in Dominican Republic material (T. C. Emmel, unpublished) and in Mexican material (Maeki and Remington, 1960b).
- SIMILAR SPECIES: Although this butterfly is quite distinctive in the hand and cannot be readily confused then with other white butterflies in our area, it may be mistaken for one of the more common whites before it is captured and while it is still flying.

GEOGRAPHIC AND SEASONAL VARIATION: This species is known to be extremely variable in the Caribbean and tropical America, but the nature of the variation is probably a complicated combination of seasonal and polymorphic genetic factors.

GENERAL REMARKS: Collectors are urged to sample any white butterflies in the Imperial and Colorado River valleys, to be certain they are not missing such a unique species as *Kricogonia lyside*.

42. *Nathalis iole* Boisduval

DIAGNOSIS: This very diminutive sulfur is easily recognized by the small size, the black bar on the trailing edge of the pale yellow dorsal forewing, and the black bar on the front of the upperside of the hindwing.

ORIGINAL DESCRIPTION: Boisduval, *Hist. Nat. Ins., Spec. gen. Lepid.*, 1: 589-590 (1836).

TYPE LOCALITY: "Mexico." Holotype in Museum Nationale de Histoire Naturelle, Paris, France.

DISTRIBUTION: This species is not permanently established in California but frequently becomes temporarily established in the state, particularly during very wet years in the desert. It then becomes widespread throughout much of the southern half of the state. During these times, it is found in many plant communities and over a wide elevational range, from the Mexican border north to approximately Mono County, then into the Sierra Nevada and the Central Valley and sometimes even in the southern coast ranges. It is not uncommonly encountered in the mountains during these years of unusual abundance, sometimes at relatively high elevations.

ELEVATION RANGE: From below sea level in the Coachella Valley to 10,600'.

HABITAT AND PLANT COMMUNITIES: This species seems to breed most characteristically in the Creosote Bush Scrub community of the desert, particularly where annual Asteraceae are abundant. It also becomes temporarily established in lowland habitats on the coastal side of the mountains in southern California, apparently in disturbed or weedy areas where again it utilizes certain weedy annual composites. Elsewhere in the state, it is found in virtually every plant community within the distribution described above, but usually as a stray in these communities.

PHENOLOGY: There are California records for this species for every month of the year, with no particular cluster of dates. Once it does become temporarily established, there is a continual succession of generations until weather conditions either terminate its ability to continue to utilize that habitat or help to maintain it. That is, in years with a wet winter and abundant annual growth in the spring, followed by a good summer rain in the desert, the species would probably continue to propagate itself in these areas. With the onset of drought conditions, individuals would then either die out or migrate to other more favorable areas.

ADULT BEHAVIOR: The Dainty Yellow, *Nathalis iole*, is known to migrate extensively in other parts of the United States. Each spring it moves north from south Florida through northern Florida and the southern states to as far north as the southern border of Canada. In California the same set of annual repopulation efforts probably originate in Arizona and Mexico, so that by early spring, the first individuals arrive in our state and by late fall the wave has proceeded north to sometimes the San Francisco Bay area or beyond. The southward fall flight of the species in our state has not been documented yet, but should be sought by field collectors in September or October.

The flight of this butterfly is quite weak and low to the ground, with males exhibiting constant searching behavior for females during the course of the day and the females searching for the low-growing foodplant. The adults readily visit yellow composite flowers for nectar and are sometimes found in the flower heads, where, because of their small size and buried heads, they are easily caught with the fingers.

LIFE HISTORY: The egg is lemon-yellow or orangish-yellow in color, and is deposited singly on leaves of the hostplant. The mature larva is generally dark green to whitish-green, covered with dark hairs, and bears adjacent blackish and yellow stripes along each side together with a broad purple dorsal strip. A pair of short, reddish conical tubercles covered with bristles project forward on the prothorax. The green pupa lacks the frontal projection from the head that is characteristic of our other yellows and sulfurs. There appears to be no true diapause stage in the species. The adults overwinter in inactive reproductive diapause in northern Florida, flying only on warm winter days (T. C. Emmel, unpublished).

FOODPLANTS: The most commonly used native foodplant in the deserts is *linearis*. In disturbed sites, beggar-tick or burr marigold, *Bidens pilosa* L. is used. Elsewhere, it is known to feed on a variety of composite plants in the family Asteraceae.

CHROMOSOME NUMBER: $n = 31$ in Florida and tropical America (T. C. Emmel, unpublished).

SIMILAR SPECIES: None in our area.

GEOGRAPHIC AND SEASONAL VARIATION: The spring form tends to be darker underneath, with a greenish underside on the hindwing, whereas summer adults are lighter with a yellowish underside on the hindwing. This color difference is apparently related to photoperiod, and the darker coloration in the spring brood is a thermoregulatory adaptation allowing faster warming and therefore northward range expansion, according to Douglas and Gula (1978).

GENERAL REMARKS: This species may often be overlooked because of its weak flight and tendency to stay close to the ground. Also, because of its small size, it may be momentarily mistaken for a lycaenid. Clench (1976) has suggested that *Nathalis iole* is divisible into three geographic segregates in America north of Mexico. The Southeastern segregate is centered in Florida and southern Georgia; it was formerly absent from this region, but invaded the southern Florida peninsula, probably from Cuba, sometime before 1913. It then spread northward at an average rate of about 42 miles per year. The Central segregate extends from Mississippi to Arizona, and from Mexico as far north as Ontario, Manitoba, North Dakota, southeastern Wyoming, most of Utah, and Nevada (see also Austin and Austin, 1981). These populations are probably re-established annually as the result of repeated immigration. This segregate can tolerate temperatures below freezing, however, and has been found flying at Colorado Springs as late as early December (F. M. Brown, *in litt.*). The range of the Central segregate extends south to Guatemala and lowland and montane southern Mexico. The Pacific segregate occurs from Baja California north to central California, and within the state, appears to be an annual migrant. Nothing in its known range suggests that it is cold tolerant (Clench, 1976).

DANAIDAE

The family Danaidae is often combined as a subfamily of the great family Nymphalidae. There are about 150 species worldwide, with the greatest diversity occurring in the Asian tropics. A few species occur in the New World tropics as well as in the temperate zones of both hemispheres.

The butterflies of this family are characterized by having: (1) greatly reduced front legs, leaving four walking legs; (2) the adult male possessing a greatly reduced tarsal foot, whereas the female protarsus has four segments on the front leg which end in a peculiar spiny knob or club; (3) a strongly clubbed antenna, with no curve in the club and no scales occurring on the shaft of the antenna (all other butterflies in our fauna have scaled antennae); (4) a head that is almost as wide as the thorax, and bears short palpi; (5) leathery, tough wings; (6) generally smooth and cylindrical larvae with (in our fauna) two or three pairs of fleshy filament-like tubercles protruding from the top of the thorax; (7) male adults with notable abdominal hairpencils that can be extruded in courtship.

The Danaids form a distinct group of slow-flying, ruddy red or orange-winged, large, conspicuous butterflies. The larvae are strongly and conspicuously striped when seen on their milkweed foodplants, and depending on their foodplant's secondary chemistry, may be quite distasteful to birds and other potential vertebrate predators. One of our species, the Monarch, moves southward every fall in great numbers and overwinters along our coast or in the interior desert valleys. Another species, the Queen, moves north in the spring and south in the fall in our state in less conspicuous numbers, and remains reproductively active in the adult stage in southeastern California desert valleys all year.

* * * * *

Subfamily **Danainae** Duponchel

43. *Danaus plexippus* (Linnaeus)

DIAGNOSIS: A large, reddish-orange butterfly with black veins and a black border around the forewings and hindwings marked by double rows of white spots. This butterfly is famous for its migratory habits and occurs throughout our distributional area during the summer months.

ORIGINAL DESCRIPTION: C. Linnaeus, *Syst. Nat.*, ed. 10, 1: 471 (1758).

TYPE LOCALITY: "Pennsylvania", designated by I. C. Z. N. (Op. 282) (1954). Neotype in U. S. National Museum, designated by I.C.Z.N. (Op. 282) (1954).

DISTRIBUTION: In the winter months, Monarch butterflies congregate along the California coast line from Mendocino County south to the Mexican border, in colonies of several hundred to thousands or even perhaps millions of individuals in approximately 45 selected areas. Additionally, overwintering colonies (which are possibly only temporary aggregations) occur in Saline Valley in Inyo County, and in the southern San Joaquin Valley in the vicinity of Bakersfield. In the deserts, clusters have been found in shrubs overhanging permanent bodies of water (persistent at least in the winter); these shrubs include *Baccharis*, *Larrea*, *Salix*, and *Prosopis*. Documented sites to date include Willow Creek (2,300'), McElvoy Canyon (1,700'), and Hunter Canyon spring (1,500'), all on the eastern slope of the Inyo Mountains (Donahue, 1985). From early spring to early fall, the adults can be found in virtually every plant community or habitat of California, as they disperse looking for their foodplants. They tend to be more abundant in areas where *Asclepias* is common.

ELEVATION RANGE: Sea level to at least 11,000' elevation in the mountains.

- HABITAT AND PLANT COMMUNITIES:** As noted above, the adults are found in virtually all plant communities. The overwintering colonies occur in most instances along the immediate coast in Closed Cone Pine Forest to Riparian Woodland within Coastal Sage Scrub.
- PHENOLOGY:** The adult stage may be found in every month of the year. During the winter the adults are relatively immobile and hang quiescently from roosting trees along the coast or in their other overwintering areas. They are also in reproductive diapause at this time, with the male showing no sperm production and the female showing no egg production. In the spring, around March 21st, the Monarchs become active again in their overwintering colonies, mate, and disperse and from then until October, go through a series of overlapping generations. In the late fall, the Monarchs begin migrating to their overwintering sites again, these individuals being the grandchildren or great-grandchildren of the ones that previously dispersed in the past spring.
- Monarchs are generally believed (Urquhart, 1960) to overwinter in the United States either as free-flying, non-roosting individuals or as roosting colonies. As noted earlier, individuals in both categories are in reproductive diapause with no sperm or egg production. Monarchs have been observed, however, to breed throughout the year in south Florida. Additionally, in 1965-66, Richard Funk (1968) discovered that the monarch population at Yuma, Yuma County, Arizona, was producing eggs, larvae, pupae and fresh adults throughout the winter period of December-March. While copulation was not observed among the 54 fresh adults, oviposition by females was seen on 16 January and 18 and 27 February. Temperature conditions at Yuma would seem favorable to the continual breeding and development of Monarchs during the winter months. Because Yuma is directly across the Colorado River from the equally hospitable Imperial Valley in southeastern California, there may be an overwintering breeding area of Monarchs in our state as well.
- ADULT BEHAVIOR:** The most spectacular example of migratory behavior in butterflies is found in this species, which has been briefly described in the preceding section. Within the state of California, butterflies move hundreds of miles in fall months to the coastal enclaves where they change from the rapidly-moving, searching adult butterfly to one that hangs motionless most days in eucalyptus or Monterey Pine trees (or creosote bush and other shrubs in the desert overwintering areas). Monarchs frequently may be seen nectaring at a variety of flowers during their active period from spring to fall and may live up to nine months or more in the adult phase. The courtship behavior of the Monarch deserves further study. The courtship of a close relative, the Queen (*Danaus gilippus*) has been studied in Florida (Brower *et al.*, 1965) but a similarly intensive study of the Monarch remains to be done, amazingly enough. The best existing description is in Urquhart (1950).
- LIFE HISTORY:** The egg is delicate pale green and is laid on the leaves or flower buds of the *Asclepias* foodplants. The mature larva is greenish in ground color, with transverse bands of black and yellow and two dorsal pairs of fleshy black filaments. In most instances, the larvae feed on the leaves of the foodplant, but in the case of two desert *Asclepias* species which are virtually leafless, namely *A. subulata* Dcne. in A.DC. and *A. albicans* Wats., the larva feed entirely on the flowers and/or fruit of these two species. The pupa, which hangs vertically from the cremaster at the tip of the abdomen, is pale green with raised metallic gold spots.
- FOODPLANTS:** Milkweeds in the genus *Asclepias* (Asclepiadaceae). In California, the following species have been recorded: *A. fascicularis* Dcne. in A.DC., *A. eriocarpa* Benth.,

A. subulata Dcne. in A.DC., *A. albicans* Wats., *A. asperula* (Dcne.) Woodson, and *A. erosa* Torr. (J. F. Emmel, unpublished data).

CHROMOSOME NUMBER: n = 30 or 31 from the Dominican Republic (T. C. Emmel and P. J. Eliazar, unpublished).

SIMILAR SPECIES: The closest relative of the Monarch, the Queen (see species description below), is readily distinguished by its smaller size, more brownish-orange coloration, and general confinement to the deserts of the state. Our only representative of the *Limenitis archippus* complex, *L. a. obsoleta*, is involved in a mimicry complex with the Queen rather than the Monarch in southeastern California.

GEOGRAPHIC AND
SEASONAL VARIATION: None in our state.

GENERAL REMARKS: The Monarch is one of the best studied butterflies in the world, having been the subject of many biogeographic and systematic, physiological, and biochemical studies. Fred Urquhart (1960 and other publications) and his collaborators across the United States have documented the remarkable migrations of this butterfly by tagging literally tens of thousands of butterflies and observing their recapture in other points in the U.S. and Mexico. Lincoln Brower and his collaborators have intensively studied the heart poisons in the foodplants and the Monarch larvae and adults that repel most vertebrate predators (e.g., Brower *et al.*, 1982), and have made many important experimental observations on the relative palatability of Monarchs reared on different hosts, as well as the ecology of the overwintering populations in Mexico and California.

In late 1974, the amazing and immense overwintering colonies of the Monarchs occurring east of the Rocky Mountains in North America were discovered in central Mexico, in the mountains of the state of Michoacan. There, the winter colonies may cover many acres and include literally hundreds of millions of adult butterflies, which spend the winter at elevations of 10-11,000' in fir forests surviving in temperatures just above freezing. Despite the intensive study which has been paid to Monarch migration by Urquhart and his collaborators and to the physiology of the Monarch's defensive compounds by Lincoln P. Brower and his colleagues at the University of Florida, there is much still to be learned about the mating behavior of the butterfly, the physiology of each of the larval instars, and the ecology of the Monarch's foodplant relationships with the 108 species of Asclepiadaceae in the United States.

44. *Danaus gilippus strigosus* (Bates)

DIAGNOSIS: A medium-large, reddish-brown butterfly with one row of white spots on the forewing and two rows (often indistinct) on the hindwing. The Queen has no heavy black lining of the veins as in the Monarch, nor is a black crossbar present on the forewing as in the former species.

ORIGINAL DESCRIPTION: Bates, *Ent. Mo. Mag.*, 1: 32-33 (1864).

TYPE LOCALITY: "Guatemala." The syntypes are in the British Museum.

DISTRIBUTION: The Queen occurs throughout the desert regions of southern California, and occasionally flies as far north as the Mono Basin. It is also found in the southern San Joaquin Valley, with occasional strays to the cismontane areas of southern California.

- ELEVATION RANGE:** From sea level to approximately 6,000', with most specimens taken at the lower elevations, especially in the low desert valleys.
- HABITAT AND PLANT COMMUNITIES:** This species is most frequently found in desert valley bottoms or along washes in the open desert valleys. It is found primarily in the following plant communities: Creosote Bush Scrub, Desert Riparian Woodland, and Mixed Desert Scrub.
- PHENOLOGY:** The adults have been taken in every month of the year, with a peak of abundance in late summer and fall. There is apparently a succession of broods throughout most of the season, with early stages being found in the lower desert elevations such as along the Colorado River in every month of the year. However, a period of adult reproductive diapause in the mid-winter months may be possible, at least in some years. Overwintering congregations like those seen in the Monarch are not known for the Queen, and whether there is a southward migration for the winter is not clear. This would be an excellent subject for investigation by California lepidopterists.
- ADULT BEHAVIOR:** The behavior of the Queen in a different subspecies, *D. gilippus berenice*, has been studied extensively in south and central Florida, but little work has been done in our own area. Among the interesting behavioral phenomena found in Florida is interspecific competition in fields with natural populations of the Monarch and the Queen butterflies. Egg cannibalism is sometimes found among the larvae. The courtship and mating behavior of the Queen butterfly in that subspecies has been extensively studied by Brower, Brower, and Cranston (1965). This study remains one of the most thorough analyses of the courtship of a butterfly species yet done.
- LIFE HISTORY:** The subconical egg is pale green or white. The mature larva is whitish-violet, with adjacent transverse stripes of a deeper purplish, reddish-brown and yellow. The three pairs of brownish-purple filaments arise dorsally from the mesothoracic, second and eighth abdominal segments. The green pupa has gold dots between the fourth and fifth abdominal segments. Occasionally pupae are pink.
- FOODPLANTS:** The following species of Asclepiadaceae are all utilized in California. The two preferred hosts seem to be *A. albicans* Wats. and *A. subulata* Dcne. in A.D.C. These two virtually leafless milkweeds produce rather large inflorescences, upon which the larvae feed. Additionally, the Queen uses *A. erosa* Torr., *A. asperula* (Dcne.) Woodson, and *A. fascicularis* Dcne. (all J. F. Emmel, unpublished data). The asclepiadaceous vines *Sarcostemma hirtellum* (Gray) R. Holm and *S. cynanchoides* Dcne. ssp. *hartwegii* (Vail) R. Holm are also used, although somewhat less frequently than the *Asclepias* species (Emmel & Emmel, 1973).
- CHROMOSOME NUMBER:** $n = 30$ for *D. g. strigosa* from Texas (T. C. Emmel and P. J. Eliazar, unpublished). Maeki and Remington (1961a) give $n = 29$ for *D. gilippus* from Mexico and $n = 30$ for *D. eresimus*, a second queen species.
- SIMILAR SPECIES:** The Arizona Viceroy, *Limnitis archippus obsoleta*, is similarly marked and may at first glance be mistaken for the Queen. See the discussion under General Remarks for a description of the mimetic situation between these species.
- GEOGRAPHIC AND SEASONAL VARIATION:** There is no apparent seasonal variation in adult phenotypes and all specimens from our area represent the same geographic subspecies.
- GENERAL REMARKS:** The Queen, *Danaus gilippus strigosus*, is believed to be distasteful to potential predators in the Colorado River and Imperial Valleys. A completely unrelated

butterfly species, the Arizona Viceroy, *Limenitis archippus obsoleta* (family Nymphalidae), occurs in the same areas and is an excellent mimic of the distasteful Queen. The larvae of the Viceroy feed on *Populus* species and willows of the genus *Salix*, which have been considered to be non-toxic plants in the past. Recent evidence (David B. Ritland, Marian Rothschild) suggests otherwise. Thus, it is currently uncertain as to whether the Viceroy is a harmless Batesian mimic of the Queen or is a Mullerian mimic, being equally distasteful. Research currently underway by David B. Ritland (unpublished) may clarify this question.

SATYRIDAE

The family Satyridae, or the woodnymph butterflies, is a large family (Miller, 1968) of around 3,000 recognized species worldwide, including many special groups found in the temperate zones as well as other localized taxa in the tropics. If treated as a subfamily within the great family Nymphalidae, as done by some authors (e.g., Ehrlich and Ehrlich, 1961), it is the second largest subfamily. We have nine species in California.

The family is characterized by (1) great reduction of the forelegs in both sexes, more so in the male; (2) the forefeet (tarsus of the foreleg) reduced to one to four segments in the male, and either the normal five or fewer segments in the female; (3) a gradually clubbed antenna, with scales always present (at least near the base of the shaft); (4) a head almost two-thirds the width of the thorax, and bearing short, often shaggy palpi; (5) the cells of the forewings and hindwings being closed by tubular veins; (6) one or more of the principal forewing veins broadened into noticeable swellings toward the base at the junction with the body; (7) predominantly brown or tan wings, with always at least a few ocelli (eyespot) markings; (8) a larva with a forked tail, having two anal projections on the eleventh abdominal segment; (9) a spindle-shaped larva, which is thicker at the middle and tapering to the ends. The adult woodnymphs, browns and satyrs can be easily recognized on the wing by their typical weak, bouncing flight near the ground.

* * * * *

Subfamily Satyrinae Boisduval

45. *Coenonympha californica* Westwood

ADULT BEHAVIOR: The ringlets have a weak flight pattern and bob about over the grassy meadows with little directionality. However, when pursued, they can move quite rapidly for brief spurts. In the early morning hours, they will land on grass blades and spread their wings to sun themselves and warm up.

LIFE HISTORY: The almost spherical egg is yellowish when first laid and changes to ivory with brownish streaks as it matures. The mature larva is olive-green or brown in coloration, and is marked with light and dark longitudinal stripes. It has the typical anal fork of satyrids. The pupa may be green or brown in ground color, with light striping. The entire life cycle can pass in three weeks in the laboratory. The species apparently overwinters as a half-grown larva.

SIMILAR SPECIES: The other common ringlet species in California, *Coenonympha ampelos*, is similar in size but is readily distinguished by the orangish upper sides of the adults.

GEOGRAPHIC AND SEASONAL VARIATION: Populations of the subspecies *californica* are surprisingly similar in facies throughout most of its range. Similarly, the subspecies *eryngii* seems to be fairly uniform within its geographic distribution. Studies of the blend zone between these two subspecies are limited, and the zone has been only roughly defined. Refer to the remarks under Phenology for discussion of seasonal variation.

GENERAL REMARKS: There are two species complexes of *Coenonympha* in North America: *haydeni* (a distinctive primitive *Coenonympha* without any close relatives and living in the Yellowstone area of the Rocky Mountains) and *tullia*, a superspecies name applied to a great number of taxa that have been separated by Emmel (1975) into six species, including the three recorded in our state. Clearly, no simple taxonomic scheme can accurately reflect the complex biological relationships among the entities in this genus. We prefer to treat the species of the *tullia* complex as semispecies *in statu nascendi* (on their way to becoming species). Because there is subspeciation within each of these semispecies, we find it less unwieldy to treat them as distinct species in this book.

SUBSPECIES: This is a small, whitish to cream colored butterfly with rounded forewings and a varying number of eyespots on the undersurface of the hindwing. Typical *C. californica* averages smallest in size of the *Coenonympha*, which is the most demure yet abundant group of satyrines found in the state. Two subspecies have been described.

a) *C. c. californica* Westwood

DIAGNOSIS: A whitish dorsal ground color on the wings of the spring brood is diagnostic, while the summer and fall broods are yellowish above.

ORIGINAL DESCRIPTION: Westwood, in Doubleday, Westwood and Hewitson, *Gen. diur. Lepid.*, 2: 398 (1851).

TYPE LOCALITY: "California," probably vicinity of San Francisco. Holotype in British Museum.

DISTRIBUTION: The subspecies *californica* is found in cismontane southern California, the Coast Ranges, and the west slope of the Sierra Nevada-Cascade Range axis north to the latitude of Redding, California, where it rounds the northern end of the Sacramento Valley and gradually blends with *eryngii* north of Lake Shasta and west in the adjacent Klamath Mountains Assemblage. It is absent from much of the modern-day Great Central Valley floor, and shows some limited contact with *C. ampelos ampelos* to the east through canyons of the Pit and Feather Rivers.

ELEVATION RANGE: This subspecies is found from near sea level up to approximately 5,500' elevation in the mountains, with most populations below 3,000'. Populations are more spotty and scattered as one goes inland from the coast, or up to the higher elevations.

HABITAT AND PLANT COMMUNITIES: The species is typically found in Foothill and Valley Grassland or in grassy areas of Southern and Northern Oak Woodland, as well as Foothill Woodland. As one goes higher in elevation in the mountains, the species tends to be confined to grassy meadows, within such communities as Mixed Chaparral, Southern Mixed Evergreen Forest, or Lower Montane Coniferous Forest. It is often found in populations distributed along the canyons coming down from higher elevations.

PHENOLOGY: There are at least two broods in most populations, and probably three or four generations in populations close to the coast. The earliest adults appear in February in southern California, March in the lowest northern habitats, and April or May at the more northern, mid to higher elevations. Thereafter, adults have been recorded in every month up to October or November. The greatest abundance seems to be in the spring brood, from March through May. The spring-brood specimens have slatey gray shading on the underside, with small ocelli, some of which may be pupiled. Summer and fall broods, which are called form "galactinus," are yellowish above and the underside tends to be tan, with rather well-marked brownish ocelli.

FOODPLANTS: The females have been observed to oviposit near *Melica bulbosa* Geyer ex Porter & Coult. in the San Francisco Bay area by O. E. Sette (personal communication). The larvae will feed readily on *Poa pratensis* L. in the lab. Most of the native grasses used or preferred by this species are still unknown or unconfirmed, and the discovery of the host plants would be an excellent subject of investigation.

b) *C. c. eryngii* Hy. Edwards

- DIAGNOSIS:** In the northern California populations of *california*, the ventral ocelli are lacking in the summer brood and this brood was originally named *eryngii* by Henry Edwards (1877). The northern spring brood, with gray undersides and little ocellation, received the form name "siskiyouensis" from John Adams Comstock (1925).
- ORIGINAL DESCRIPTION:** Henry Edwards, *Pacific Coast Lepidoptera*: (22): 9 (1877).
- TYPE LOCALITY:** "Northern California." Holotype in American Museum of Natural History.
- DISTRIBUTION:** This subspecies is found throughout the northern portion of the state, from the latitude of northern Shasta County to extreme southeastern Oregon in the Modoc Plateau of Siskiyou County, the Northern Cascade Range, the Klamath Assemblage of mountains, Coast Range mountains and the northern coast. A blend-zone with subspecies *california* occurs north of the Lake Shasta region and westward. Areas of contact and blending or hybridization between *eryngii* and *C. ampelos* occur in eastern Siskiyou and Modoc counties and in areas of southwestern Oregon.
- ELEVATION RANGE:** Most populations seem to occur between 2,000' and 5,000' elevation, with some being found at elevations near sea level.
- HABITAT AND PLANT COMMUNITIES:** This subspecies is generally found in grassy areas within Great Basin Sagebrush Scrub, Lower Montane Coniferous Forest, Northern Oak Woodland, Northern Mixed Evergreen Forest, and Serpentine Dwarf Pine Woodland.
- PHENOLOGY:** The spring brood begins flying in late April, to early May or even early June in the northwestern coastal mountains. Summer brood specimens are taken from late June through August, and well into September for northwestern populations. The summer brood lacks ventral ocelli, while the spring brood is lightly marked.
- FOODPLANTS:** Oviposition has been observed near a *Carex* species in Del Norte County, a sedge common in the serpentine uplands there.

46. *Coenonympha ampelos* W. H. Edwards

- ADULT BEHAVIOR:** As with the other *Coenonympha* species, the adults of *ampelos* fly in considerable abundance, with a low bobbing flight that attracts little attention from observers or predators.
- LIFE HISTORY:** These were only partially described by W. H. Edwards (1887). The short, rounded egg is pale yellow-green, turning reddish-brown with maturation. The larva is green with tiny raised bumps and bears a dark green dorsal stripe, with two lighter lateral lines of green. The pupa may be green or brown in basic ground color.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** *Coenonympha ochracea* tends to have more prominent eyespots and a stronger dorsal pattern with a median band. *Coenonympha californica* is paler, with occasionally creamy ground coloration, and has brownish ocelli.

GEOGRAPHIC AND SEASONAL VARIATION: There may be a blend-zone between the subspecies *ampelos* and *mono* just northwest of Reno, Nevada; some specimens from Boca Reservoir in Nevada County appear to be intermediate between *mono* and *ampelos*. As noted above, observations of seasonal phenotypic differences in the two "broods" of *yontocket* on the Fort Dick Sand Dunes led to electrophoretic and other evidence that a new subspecies (and perhaps a new species) was involved. In the nominotypical (and univoltine?) subspecies, there appears to be no obvious seasonal variation between early and late-flying specimens of *C. ampelos ampelos*.

GENERAL REMARKS: This species name includes a complex of orangish-yellow forms that range from a single isolated population in extreme northwestern Del Norte County on the coast and many populations to the east, in the Mono Basin, north along the Great Basin fringe and much of the Modoc Plateau through the Pacific Northwest, and east through Nevada and western Idaho to Utah. It is characterized by its rich yellow to orange coloration, the usual lack of ocelli on all wings (in our area) and a slightly darker basal area (basal patch) on the ventral surfaces of the secondaries, with a pale yellow extradiscal area. This complex is of similar to slightly larger wing size, compared to the *california* group.

a) *C. a. ampelos* W. H. Edwards

DIAGNOSIS: The typical form of this species is characterized by its rich yellowish-orange coloration and the usual lack of ocelli on the wings.

ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Entomological Society*, 3: 213 (1871).

TYPE LOCALITY: "Oregon", restricted to southeastern Oregon by F. M. Brown, *Transactions American Entomological Society*, 90: 342 (1964). Lectotype in Canadian National Collection, designated by F. Martin Brown (1964).

DISTRIBUTION: Within California, the subspecies *ampelos* is found from Plumas and extreme northern Nevada County northward through Lassen and Modoc counties.

ELEVATION RANGE: This subspecies occurs from approximately 3,500' to 6,500', although some specimens stray to higher elevations such as at Donner Pass (A. M. Shapiro, personal communication).

HABITAT AND PLANT COMMUNITIES: This butterfly is typically found in wet sedge meadow habitats within the Great Basin Sagebrush Scrub community. It has penetrated westward into similar meadows within a Lower Montane Coniferous Forest setting along the east slopes of the Cascade and Sierra Nevada ranges in the Great Basin fringe.

PHENOLOGY: Adult captures are recorded from late May through mid-August, indicating that there are probably two broods, at least at the lower-elevation localities. There does not seem to be the seasonal variation between the early and late-flying specimens that exists in the *Coenonymphas californica* complex subspecies within the state.

FOODPLANTS: Unrecorded; possibly *Carex* species rather than grasses, on the basis of the species' preferred wet meadow habitat.

b) *C. a. mono* Burdick

Contrary to Miller and Brown (1981), the subspecies *mono* belongs to the *Coenonympha ampelos* complex rather than to *Coenonympha ochracea*. This conclusion is based on electrophoresis data (Adam Porter, unpublished) and a number of biological differences that show its association with *ampelos*. Also, notable phenotypic similarities occur in the adults.

- DIAGNOSIS: This subspecies is larger in size and a deeper orange in ground color than nominotypical *C. a. ampelos*.
- ORIGINAL DESCRIPTION: Burdick, *Canadian Entomologist*, 74: 2-3 (1942).
- TYPE LOCALITY: Bridgeport, Mono County, California. Holotype in Canadian National Collection.
- DISTRIBUTION: This subspecies is found in the valleys, canyons, and high meadows just east of the Sierra Nevada Crest in Mono County and Alpine County, and extreme western Nevada.
- ELEVATION RANGE: From approximately 6,000' elevation to 8,500' for most populations, with occasional specimens being taken as high as 10,000' near Tioga Pass.
- HABITAT AND PLANT COMMUNITIES: The species is typically found in wet sedge meadow habitats within the Great Basin Sagebrush Scrub community and the lower edge of the Lower Montane Coniferous Forest community on the east slope and base of the Sierra Nevada, including the Sweetwater Mountains of California and adjacent Nevada.
- PHENOLOGY: Our populations all seem to be single-brooded, with adult flight occurring from early June through late July and the peak flight being in late June.
- FOODPLANTS: Undetermined.

c) *C. a. yontocket* Porter and Mattoon

- DIAGNOSIS: This subspecies, recently described as a new subspecies under the Holarctic superspecies name *Coenonympha tullia*, flies in the coastal sand dunes of Del Norte County. It is most similar in phenotype to *C. a. eunomia* Dornfeld from Oregon. It has a dull ochre ground color, with the dorsal surfaces of both wings strongly melanized subbasally. The ventral ground color is a deep ochre, almost orange on the forewing and brownish or greenish on the hindwing. The median band is whitish and well marked. Eyespots are absent in almost all individuals. The spring brood averages slightly larger (males, 16.3 mm) than the fall brood (males, 14.7 mm). This race is immediately separable from surrounding populations of the whitish *C. californica eryngii* by its ochraceous ground color. It differs from *C. ampelos eunomia* ventrally by its stronger expression of the medial markings, and dorsally by gray scaling along the veins and outer wing edges.
- Dornfeld (1967) used the subspecific name, *C. ampelos eunomia*, for populations characterized by brown ventral surfaces except for a slight gray-green margin, and no ocellation. This name was applied to the populations of the valleys of western Oregon, west of the Cascadian Crest area. The nearest known population of *eunomia* is 250 km away in the Umpqua River drainage in southwestern Oregon (Porter and Geiger, 1988).
- ORIGINAL DESCRIPTION: Porter and Mattoon, *Journal of the Lepidopterists' Society*, 33: (1989).

TYPE LOCALITY: 4 km W. Fort Dick, Del Norte County, California. Holotype in

DISTRIBUTION: This unique subspecies of *C. ampelos* is known only from Del Norte County, among the coastal sand dunes north of Crescent City, beginning at the north shore of Lake Earl and extending north 7.5 km to the south bank of the Smith River, in the vicinity of the Yontocket Archeological site. Seemingly suitable habitat between Lake Earl and Point St. George may also be populated by *yontocket*. It is not present in abutting disturbed habitats to the east (mostly cow pastures), or at the Arcata dunes in Humboldt County. It is replaced by white *C. californica eryngii* just 10 km to the east on exposed serpentine hilltops. These two populations show no signs of reciprocal introgression in wing characters (Porter and Mattoon, 1989). This new subspecies flies in the fog belt, and shows the characteristic heavy melanization of the wings and body characteristic of butterflies from this type of environment (Hovanitz, 1941; McCorkle and Hammond, 1988).

ELEVATION RANGE: For our California population, the elevation is from 1' to 25' above sea level, immediately on the coast.

HABITAT AND PLANT COMMUNITIES: This subspecies inhabits coastal sand dunes where combined elements of Coastal Dune Sand Plant, Coastal Salt Marsh, and Closed Cone Pine Forest are juxtaposed. The usual habitat is about 6' above sea level, in grassy areas among dunes with coniferous lee slopes and grassy exposed slopes, and among dunes on slightly elevated ground around seasonally marshy sphagnum bogs which fill during the rainy season. Two females oviposited on dry grass stems approximately 1-2 inches above the soil, in areas which do not flood from rains.

PHENOLOGY: This population is bivoltine, with individuals flying from May through the end of June, and then again from September to October. Adults of the two broods differ phenotypically.

FOODPLANTS: Undetermined.

47. *Coenonympha ochracea* subspecies near *furcae* Barnes & Benjamin

DIAGNOSIS: This is a primarily a Rocky Mountain species that extends west to the eastern edge of California. As far as is known, throughout its range this species is single-brooded.

ORIGINAL DESCRIPTION: *Coenonympha ochracea furcae* was described by Barnes and Benjamin, *Bulletin of the Southern California Academy of Sciences*, 25: 90 (1926).

TYPE LOCALITY: Grand Canyon, Arizona. Holotype in U.S. National Museum.

DISTRIBUTION: A single specimen of *Coenonympha ochracea*, which approaches *furcae* in phenotype, has been taken in California, by Douglas Mullins. This specimen was collected in upper Wildrose Canyon near the Charcoal Kilns, in the Panamint Range, Inyo County.

ELEVATION RANGE: The specimen that was collected was taken at an elevation of approximately 7,200'.

HABITAT AND PLANT COMMUNITIES:	The area in upper Wild Rose Canyon is typical Pinyon-Juniper Woodland, with some elements of Great Basin Sagebrush Scrub.
PHENOLOGY:	The single, somewhat worn male specimen was taken in late June. Most other <i>ochracea</i> populations in the Great Basin fly from mid-June to mid-July. At the Grand Canyon, the type locality of the subspecies <i>furcae</i> , populations fly from mid-May to mid-June.
ADULT BEHAVIOR:	Throughout its range, <i>C. ochracea</i> exhibits behavior similar to that of the other <i>Coenonympha</i> species in flight habits, courtship and mating.
LIFE HISTORY:	These are unknown, despite the wide distribution of this frequently-abundant <i>Coenonympha</i> outside our state.
FOODPLANTS:	Presumed to be grasses and/or sedges.
CHROMOSOME NUMBER:	Unknown.
SIMILAR SPECIES:	See discussion under <i>C. ampelos</i> .
GENERAL REMARKS:	The single specimen of <i>Coenonympha ochracea</i> from the Panamint Range most closely resembles the subspecies <i>furcae</i> from the Grand Canyon and is illustrated in the color plate section. It may represent a stray individual that found its way into the Panamint Range or it may represent an established population or set of populations there. This remains to be investigated. Because the Panamint Range is very extensive and has been poorly collected, we feel that it is possible that relict populations of <i>Coenonympha ochracea</i> from a moister period could exist there, and for that reason we are including this specimen as indicative of an established population within the state. The alternative likelihood of a present-day stray in this area across hundreds of miles of inhospitable desert terrain seems remote. The nearest <i>ochracea</i> populations to the Panamints are found in the Spring Range in Clark County, Nevada; however, the phenotype of these populations is noticeably different from the phenotype of the single specimen taken in the Panamints.

48. *Cercyonis pegala* (Fabricus)

ADULT BEHAVIOR:	This large, prominently spotted (on the forewings) <i>Cercyonis</i> species has a deep bobbing flight as it makes its way through the grasses across the flats and meadows of its favored habitats. Males emerge at least a week before females and normally are somewhat smaller in size. The males avidly pursue passing virgin females and force them to alight on the ground, where mating takes place. Copulation lasts about 60 minutes. This species seems to do little nectaring, in contrast with <i>Cercyonis oetus</i> , <i>C. meadi</i> , <i>C. or sthenele</i> , the other species in its genus. They are well camouflaged when their wings are closed, and they often land on tree trunks or on plant litter.
LIFE HISTORY:	The egg is larger than those of the other <i>Cercyonis</i> species, and is barrel-shaped with about thirty heavy vertical ribs and fine horizontal connecting ribs. It is cream in color, changing to rose with the fertility change and to dark gray within 24 hours of hatching. The mature larva (6th instar) is a dull light green, marked with a dark median line on the dorsum, a lemon yellow lateral band and a white lateral band. The pupa is a more-or-less uniform green in color. The species diapauses as a first-instar larva.

The larva are readily reared on *Poa pratensis* L. in the laboratory; native grasses (or sedges?) used by this species in California remain undetermined.

CHROMOSOME NUMBER: $n = 27$ (T. C. Emmel, unpublished); $n = 27$ in western and central Colorado material (Maeki and Remington, 1961a; T. C. Emmel, P. J. Eliazar, and L. N. Harris, unpublished).

SIMILAR SPECIES: *Cercyonis pegala* is uniformly larger than any of the other *Cercyonis* occurring in California. See Similar Species section under *Cercyonis sthenele* for additional comments.

GEOGRAPHIC AND SEASONAL VARIATION: Very complex geographic variation occurs throughout the range of *pegala*, as reflected by the multiplicity of names proposed for various populations and groups of populations. No seasonal variation occurs because this species is univoltine everywhere.

GENERAL REMARKS: The extinction of *Cercyonis pegala wheeleri* in the Owens Valley around Owens Lake in Inyo County is probably related to the diversion of water sources for Owens Lake, first for farming and ranching and later for a water supply for the city of Los Angeles. The lake bed is now dry in most years and wet meadow habitats are at a minimum at the edges of this lake. The species as a whole shows great variation between localities, and it deserves intensive study of the factors contributing to this ecological and evolutionary diversity (Emmel, 1967a, 1969b).

This is the largest satyrid species in our fauna and the largest in the genus *Cercyonis*. It is remarkably variable in our state, as throughout its geographic range, which extends to the east coast of the United States. In our treatment of the forms and subspecies occurring within our state, we have adopted a "conservative" approach of recognizing eight⁶ subspecies, primarily for the utility of reference to particular phenotypes. We do not mean to imply that these are geographic subspecies with mutually exclusive range. Indeed, there is considerable overlap and variation within single populations.

a) *C. p. ariane* (Boisduval)

DIAGNOSIS: *Cercyonis pegala ariane* has a strongly striated pattern on the underside, with a diffusely-edged yellow forewing flush. Males are well ocellated ventrally, while females have minimal ocellation. It normally occurs in marshy meadows.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 307 (1852).

TYPE LOCALITY: "Californie," restricted to Tuolumne County, California, by F. M. Brown, *Journal of Research on the Lepidoptera*, 4: 139-141 (1966). Re-restricted to Spanish Ranch, Plumas County, California, by Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, : (1998). Lectotype in U.S. National Museum, designated by F. M. Brown (1966).

DISTRIBUTION: Within California, populations referable to the subspecies *ariane* are found along the east side of the Sierra Nevada from Sierra and Plumas counties to the southeastern Mount Shasta region. Eastward, the phenotype tends to blend towards subspecies *stephensi* or *gabbii*. To the west, there is a probable blend-zone with subspecies *boopis* or *baroni* populations.

ELEVATION RANGE: From 3,400' to approximately 7,000'. Most populations seem to be in the 4,000-6,500' range.

HABITAT AND PLANT COMMUNITIES: This satyrid is typically found in Montane Wet Meadow habitats within the Great Basin Sagebrush Scrub community or Lower Montane Coniferous Forest.

PHENOLOGY: The species appears to be strictly univoltine, with first-instar larvae being the overwintering stage. Adults appear in early July and fly through late August or early September.

FOODPLANTS: Unknown.

b) *C. p. boopis* (Behr)

DIAGNOSIS: A series of coastal populations of *pegala* with the characteristics of being large in size, generally with mottled secondaries, and few or no marginal ocelli ventrally. The forewings are dark in color, with no yellow flush in the males.

ORIGINAL DESCRIPTION: Behr, *Proceedings California Academy Natural Sciences*, 3: 164 (1864).

TYPE LOCALITY: Contra Costa County, California. Type destroyed in the 1906 San Francisco earthquake and fire. Neotype designated by Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, : (1998).

DISTRIBUTION: Populations referable to this subspecies are found in the Coast Ranges, from the San Francisco Bay region in extreme northern Monterey County north to the Klamath Mountains Assemblage and the Mount Shasta region.

ELEVATION RANGE: Most populations occur below 3,500' elevation, with many coastal populations close to sea level. Some isolated populations in the eastern Klamath Mountain Assemblage are known from boggy meadows at higher elevations.

HABITAT AND PLANT COMMUNITIES: In contrast to the *ariane* subspecies complex, populations of *boopis* seem to be more often associated with open grassy fields and dry meadows. Plant communities that the butterfly is associated with include North Coastal Prairie, North Coastal Sage Scrub, Redwood Forest, and Northern Mixed Evergreen Forest.

PHENOLOGY: This subspecies is also strictly single-brooded, overwintering as diapausing first-instar larvae. Adults begin flying in early June and captures are recorded as late as early August, with the peak of the flight in late June and early July.

FOODPLANTS: Unknown.

c) *C. p. baroni* (W. H. Edwards)

DIAGNOSIS: A smaller, darker form found in northern California in scattered populations, located geographically between populations of *boopis* and *ariane*.

ORIGINAL DESCRIPTION: W. H. Edwards, *Canadian Entomologist*, 12: 91 (1880).

TYPE LOCALITY: Mendocino County, California. Lectotype in the Carnegie Museum, designated by F. M. Brown, *Transactions American Entomological Society*, 90: 379 (1964).

DISTRIBUTION: *Cercyonis pegala baroni* is a smaller, darker form that occurs in northern California, mainly in the Inner Coast Range.

<MATTOON: Please fill in.>

ELEVATION RANGE:

HABITAT AND PLANT
COMMUNITIES:

PHENOLOGY:

FOODPLANTS: Unknown.

d) *C. p. gabbii*

DIAGNOSIS: A subspecies of southeastern Oregon which is characterized by relatively large size, and well-developed ocelli ventrally in both sexes. In contrast to subspecies *stephensi*, which also has well-developed ocelli, the ventral ground color is darker.

ORIGINAL DESCRIPTION:

TYPE LOCALITY:

DISTRIBUTION: This subspecies is found in a rather limited area of southeastern Oregon, west of the Warner Mountains; it barely enters California in western Modoc County.

ELEVATION RANGE: 5,000' to 6,000' elevation.

HABITAT AND PLANT
COMMUNITIES: *C. p. gabbii* populations are found in wet meadows within Alkali Sink Scrub or Great Basin Sagebrush Scrub plant communities.

PHENOLOGY: Univoltine, with adults flying from early July to late August. Males predominate at the beginning of the flight period, while females predominate in August.

FOODPLANTS: Unknown.

e) *C. p. stephensi* (W. G. Wright)

DIAGNOSIS: A subspecies with whitish undersides and well-developed ocelli, inhabiting alkali flats and meadows in the sagebrush areas of northeastern California.

ORIGINAL DESCRIPTION: W. G. Wright, *Butterflies of the West Coast*: 184 (1905).

TYPE LOCALITY: "NE California", probably Modoc County, California. Lectotype in California Academy of Sciences, designated by Tilden, *Occasional Papers of the California Academy of Sciences* (118): 26 (1975).

DISTRIBUTION: This subspecies is found in the sagebrush areas of extreme northeastern California, eastward to central northern Nevada and northward into extreme southeastern Oregon.

ELEVATION RANGE: From 4,500 to 6,000' elevation.

HABITAT AND PLANT
COMMUNITIES: Populations with this phenotype are found in wet meadow habitats within Great Basin Sagebrush Scrub or Alkali Sink Scrub areas, often with extensive whitish alkaline salt deposits on the surface of the soil.

PHENOLOGY: Univoltine, with adults appearing in early July and flying through late August, and the peak flight in mid-July.

FOODPLANTS: [Mattoon: Please fill in names of grasses that "*blanca*" was associated with in Nevada, and cite the Emmel & Mattoon paper here.]

f) *C. p. wheeleri* (W. H. Edwards)

DIAGNOSIS: A whitish, heavily ocellated subspecies from the Owens Lake area in Owens Valley, now extinct.

ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Entomological Society*, 4: 343 (1873).

TYPE LOCALITY: "Arizona," restricted to near Owens Lake, Inyo County, California, by F. M. Brown, *Transactions American Entomological Society*, 90: 387 (1964). Lectotype in Carnegie Museum, designated by F. M. Brown (1964). A synonym of this name is *hoffmani* (Strecker), which was described later (in 1873) from Owens Lake material.

DISTRIBUTION: Known historically only from the type series collected at Owens Lake in Inyo County, California, by the Wheeler Expedition of the U.S. Army.

ELEVATION RANGE: 3,600' elevation.

HABITAT AND PLANT COMMUNITIES: The environment where *wheeleri* once occurred is presumed to be marshy or wet meadow areas along the edge of Owens Lake, in an Alkalai Sink Scrub or Alkali Meadow situation.

PHENOLOGY: The type series was apparently taken in July, although no specific dates are available.

FOODPLANTS: Unknown.

g. *C. p.* _____ Austin

DIAGNOSIS: A well-ocellated subspecies of the Carson Valley in western Nevada, similar to *wheeleri* but smaller.

ORIGINAL DESCRIPTION: Austin,

TYPE LOCALITY:

DISTRIBUTION: This subspecies is apparently confined to the Carson Valley, just barely entering California in eastern Alpine County in the Carson River drainage.

ELEVATION RANGE:

HABITAT AND PLANT COMMUNITIES:

PHENOLOGY:

FOODPLANTS: Unknown

h. *C. p.* _____ **Austin**

- DIAGNOSIS: A darker, less-ocellated subspecies of the east base of the Sierra Nevada in Mono County, California, and extreme western Nevada.
- ORIGINAL DESCRIPTION: Austin,
- TYPE LOCALITY:
- DISTRIBUTION:
- ELEVATION RANGE:
- HABITAT AND PLANT COMMUNITIES: Populations of this subspecies are found in wet meadows within the Great Basin Sagebrush Scrub plant community.
- PHENOLOGY: Univoltine, with adults first appearing in early July and flying into late August.
- FOODPLANTS: Unknown. Reared in the laboratory on *Poa pratensis* L. (J. F. Emmel, unpublished data).

49. *Cercyonis sthenele* (Boisduval)

- ADULT BEHAVIOR: The adults are very rapid fliers. They are generally most active in mid-morning and by noon they have often settled in the shade of trees in their favorite canyon habitats. This species will visit strongly scented flowers such as *Melilotus* (sweet clover) or alfalfa. The most difficult subspecies to capture are desert adults, which fly much more rapidly than the coastal mountain *behrii* or western Sierran *silvestris*. Like the other *Cercyonis*, the females lay their eggs singly at a rate of approximately 10 to 12 a day. Copulation lasts about an hour.
- LIFE HISTORY: The egg is almost spherical, with a flattened top and bottom, and has approximately 26 pronounced vertical ribs with fine horizontal connecting ribs. It is cream-colored. The mature larva is a dull light green, marked with a dark median line on the dorsum, a thin white line latero-dorsally, and a broad white line laterally. In *silvestris* larvae, these latter four lines are yellow instead of white. The ventral surface is dark green. The head is the same color as the body and the entire surface is covered with a fine pubescence. The bifid (forked) tail above the anus is reddish. The pupa is green (or sometimes light tan) with light striations or light markings.
- The larvae can be reared in the laboratory on *Poa pratensis* L.; native grasses used by this species remain to be determined.
- CHROMOSOME NUMBER: $n = 27$ (T. C. Emmel, unpublished).
- SIMILAR SPECIES: *Cercyonis sthenele* complex members can be distinguished from *Cercyonis oetus* adults by the alignment of the two forewing ocelli. In *oetus* the posterior ocellus is displaced towards the margin, whereas in *sthenele* the two forewing ocelli are equidistant from the wing margin. In *Cercyonis pegala*, the posterior forewing

ocellus is larger than the anterior ocellus or is equal in size, whereas in *sthenele* the posterior ocellus tends to be smaller than the anterior ocellus.

GEOGRAPHIC AND
SEASONAL VARIATION:

There is considerable geographic variation in *Cercyonis sthenele*, as exemplified by the fact that there are seven subspecies represented in the state of California. Generally, the pattern of variation is more straightforward in this species than in the preceding one (see *C. pegala*), primarily because populations tend to be more widespread and are not highly isolated by being confined like *pegala* to discrete boggy meadows or other limited habitats. There is no seasonal variation because the species is univoltine and has a relatively short emergence period throughout its range in California.

GENERAL REMARKS:

As with the other *Cercyonis*, considerable field work remains to be done on the ecological and evolutionary factors that control and contribute to the remarkable variation in ocellation and other wing characters in the adults. The native grass species used by *C. sthenele* and the other *Cercyonis* species remain to be determined.

This *Cercyonis* is one of our most successful satyrid butterflies and occupies a variety of habitats across California. It is characteristically a lowland species, flying in oak grassland or hot semi-desert areas. Considerable geographic variation occurs. It also has the distinction of having been the first California butterfly (in the form of the nominotypical subspecies) to be driven to extinction by direct human action.

a) *C. s. sthenele* (Boisduval)

DIAGNOSIS:

The nominotypical subspecies was characterized by a heavily marked median band on the underside of the ventral hindwings, with extensive white scaling on the distal half of the wing.

ORIGINAL DESCRIPTION:

Boisduval, *Ann. Soc. Ent. France*, (2)10: 308 (1852).

TYPE LOCALITY:

San Francisco, California. Lectotype in U.S. National Museum, designated by F. M. Brown, *Journal of Research on the Lepidoptera*, 4: 141 (1966).

DISTRIBUTION:

The nominotypical subspecies was found only in the area now occupied by the city of San Francisco and has been extinct since approximately 1880. There are very few specimens surviving in collections, most having been in the California Academy of Sciences collection and thus destroyed in the fire that followed the San Francisco earthquake of 1906.

ELEVATION RANGE:

Sea level to perhaps 50' elevation.

HABITAT AND PLANT
COMMUNITIES:

Unknown, but likely grassy slopes within Northern Oak Woodland.

PHENOLOGY:

The only details of *C. s. sthenele*'s biology that were ever recorded were that it flew in the month of June, had only one generation and preferred to "settle on the ground" rather than "on the underside of oak branches" like *silvestris*. It is apparent that *sthenele* passed into oblivion due to man's destruction of its restricted habitat on the San Francisco peninsula.

FOODPLANTS:

Unknown.

b) *C. s. silvestris* (W. H. Edwards)

- DIAGNOSIS: This taxon is represented by a series of western slope Sierran populations that share a general light brown ground color and small number of ocelli on the ventral surfaces of the wings. A marked median band is lacking.
- ORIGINAL DESCRIPTION: W. H. Edwards, *Proc. Acad. Nat. Sci. Philadelphia*, 13: 162 (1861). This subspecies was misplaced by Miller and Brown (1981) under *Cercyonis oetus*.
- TYPE LOCALITY: "California." Lectotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Entomological Society*, 90: 362 (1964). Type locality specifically fixed by Emmel, Emmel and Mattoon, *Systematics of Western North American Butterflies*, : (1998) to lower Feather River Canyon, Plumas County, California. The types were collected by Lorquin, given to Behr, and transmitted to Edwards, who described it.
- DISTRIBUTION: This subspecies is found on the west slope of the Sierra Nevada from northern Kern County north to the Mount Lassen region. To the south, it blends with subspecies *behrii*; to the north, it blends with subspecies *sineocellata*.
- ELEVATION RANGE: From approximately 1,500 to 5,000' elevation, mostly below 4,000'.
- HABITAT AND PLANT COMMUNITIES: This subspecies is typically found in grassy areas within Foothill Woodland, Mixed Chaparral, or lower edges of the Lower Montane Coniferous Forest.
- PHENOLOGY: Univoltine, with diapause in the newly hatched first-instar larvae. The adults begin emerging in early June and the flight continues through mid-August, with a peak in early July.
- FOODPLANTS: Presumably grasses, as yet undetermined.

c) *C. s. behrii* (F. Grinnell)

- DIAGNOSIS: The status of the subspecies *behrii* has been unclear for many years because of the destruction of the original type series and lack of topotypical material until recently. Emmel, Emmel, and Mattoon (1989) have designated a neotype of *behrii* and have shown that this is the name which refers to populations of *sthenele* in the California Coast Ranges. There are characterized by a dark basal half of the ventral hindwing, with a contrastingly lighter distal half of the hindwing, and a lack of ocelli.
- ORIGINAL DESCRIPTION: F. Grinnell, *Entomological News*, 16: 33 (1905).
- TYPE LOCALITY: Mount Tamalpais, Marin County, California. The original type was lost in the 1906 San Francisco earthquake and fire. Neotype designated from the type locality by Emmel and Emmel, *Systematics of Western North American Butterflies*, : (1998) and deposited in the Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is found in the California Coast Ranges from San Diego County northward to approximately Humboldt County. North of Humboldt County, it blends into the subspecies *sineocellata*. To the east in the southern portion of its range (e.g., the Tehachapi Mountains), it blends with the west-slope Sierran subspecies *silvestris*.

- ELEVATION RANGE: From nearly sea level to approximately 5,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The typical habitat is wooded slopes or canyon bottoms within the Northern or Southern Oak Woodland community, near edges of Mixed Chaparral, and open areas near Northern and Southern Mixed Evergreen Forest.
- PHENOLOGY: The flight period is from early to mid-June into early August, with a peak in early July.
- FOODPLANTS: Unknown.

d) *C. s. paulus* (W. H. Edwards)

- DIAGNOSIS: A well-ocellated subspecies with silvery gray mottling on the underside of the wings. It occurs in the western Great Basin areas just inside California.
- ORIGINAL DESCRIPTION: W. H. Edwards, *Canadian Entomologist*, 11: 50 (1879).
- TYPE LOCALITY: "Nevada", restricted to Virginia City, Storey County, Nevada by F. M. Brown, *Transactions American Entomological Society*, 90: 365 (1964). Neotype in Carnegie Museum, designated by F. M. Brown (1964).
- DISTRIBUTION: In California, the subspecies *paulus* is restricted to an area east of the Sierra Nevada crest, from Mono County south into the northern half of Inyo County, mostly along the east slopes of the Sierra Nevada but with populations extending into the White Mountains as well. The exact eastern and northern limits of its range are unclear at the present time. Populations from areas east and southeast of *paulus*' range show some blending towards the facies of the typical western Colorado subspecies *masoni* (Cross).
- ELEVATION RANGE: From 4,500 to 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This species is typically found in the Great Basin Sagebrush Scrub or Pinyon-Juniper Woodland plant communities. Its favored habitat seems to be small dry canyons and washes, particularly where nectar sources such as *Melilotus* (sweet clover) occur.
- PHENOLOGY: Records extend from late June into early August, with a peak flight in mid-July. The species overwinters as a first-instar larva.
- FOODPLANTS: Unknown.

e) *C. s. masoni* (Cross)

- DIAGNOSIS: A subspecies of *sthenele* with a striated, umber-brown underside bearing a strong median band and prominent ocelli. Freshly caught males often have a flush of rusty color on the underside of the forewing at the apex. This reddish tint soon fades after death.
- ORIGINAL DESCRIPTION: Cross, *Proceedings Colorado Museum Natural History*, 16(1): 9-10 (1937).
- TYPE LOCALITY: Black Ridge Breaks, Mesa County, Colorado. Holotype in Denver Museum of Natural History.

- DISTRIBUTION:** This widely distributed subspecies is found from the canyon country of extreme western Colorado westward through Utah and southern Nevada to southeastern California and also into northern Arizona and extreme northwestern New Mexico. Within California, it is found in the higher mountains of the eastern Mojave Desert, such as the Granite Mountains north of Amboy, the Providence Mountains, the New York Mountains, the Clark Mountains, and the Kingston Range. It is also present, at least in a blend-zone, with subspecies *paulus* in the Inyo Mountains, Last Chance Range, and Grapevine Mountains of Inyo County.
- ELEVATION RANGE:** From approximately 4,000' to 8,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** This subspecies is typically found within the Pinyon-Juniper Woodland of the desert mountains, both on open slopes and in canyon bottoms.
- PHENOLOGY:** Our records extend from mid-June to early August, with a peak in early July.
- FOODPLANTS:** Unknown.

f) *C. s. sineocellata* Austin and Emmel

- DIAGNOSIS:** A subspecies of extreme northern California in the northwestern Great Basin, characterized by a whitish to light grayish underside that generally lacks ocelli.
- ORIGINAL DESCRIPTION:** Austin and Emmel, *Systematics of Western North American Butterflies*, : (1998).
- TYPE LOCALITY:** West side of Crump Lake, 8.2 mi. N. Adel, Lake County, Oregon. Holotype in Nevada State Museum.
- DISTRIBUTION:** This subspecies is rather widely distributed in the Great Basin areas of northwestern Nevada and northeastern California, northward into southeastern Oregon and westward to the Klamath Mountains assemblage and the southern Cascade Range of Oregon.
- ELEVATION RANGE:** From 2,500' to 6,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** Within the Great Basin area, most populations are found within the Great Basin Sagebrush Scrub or Pinyon-Juniper Woodland communities. Westward in the Klamath Mountains and southwestern Oregon populations, the habitat is typically Northern Oak Woodland or open areas within Northern Mixed Evergreen Forest.
- PHENOLOGY:** Adult captures are recorded from mid-June to early August, with a peak in early to mid-July.
- FOODPLANTS:** Unknown.

g) *C. s. hypoleuca* Hawks and Remington

- DIAGNOSIS:** A maritime subspecies of Santa Cruz Island off the coast of California, superficially resembling the extinct nominotypical subspecies *sthenele* with a strongly accentuated ventral median band; specimens average larger than nominotypical *sthenele*.

- ORIGINAL DESCRIPTION: Hawks and Remington, *Systematics of Western North American Butterflies*, : (1998).
- TYPE LOCALITY: , Santa Cruz Island, Santa Barbara County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies appears to be confined to Santa Cruz Island, although the possibility of a population on Santa Rosa Island remains to be investigated.
- ELEVATION RANGE: From sea level to approximately 2,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The subspecies is found within Southern Oak Woodland, on slopes and in canyon bottoms.
- PHENOLOGY: Captures are recorded from early June to early July, with an apparent peak flight in late June.
- FOODPLANTS: Unknown.

50. *Cercyonis oetus* (Boisduval)

- ADULT BEHAVIOR: This small species flies with a weakly bobbing flight, frequently stopping at yellow composite flowers such as *Senecio* and rabbitbrush (*Chrysothamnus*) in the grassy sagebrush areas. Adults mate for approximately one hour and the females lay their eggs singly, depositing about 10 to 12 eggs a day during their lifetime of as much as four weeks. This species frequently settles on bare gravelly slopes, where its mottled gray underside camouflages the butterfly nicely.
- LIFE HISTORY: The cream-colored egg is barrel shaped, with about 28 pronounced vertical ribs and very fine horizontal connecting ribs. The mature larva is similar to that of *Cercyonis sthenele*, except that the dark green mid-dorsal line is bordered by a thin white line on each side. The pupa is similar to those of the other *Cercyonis* species in California, and shows variation in color ranging from light green with no striations to dark brown with heavy linear markings.
- CHROMOSOME NUMBER: $n = 27$ (T. C. Emmel, unpublished).
- SIMILAR SPECIES: See *Cercyonis pegala* and *C. sthenele* for discussion.
- GEOGRAPHIC AND SEASONAL VARIATION: Most of the subspecies of *Cercyonis oetus* are generally weakly differentiated and intergrade. However, *pallascens* is quite distinctive from most *oetus*, *charon* (W. H. Edwards) (Rocky Mountains), and *phocus* (W. H. Edwards) (British Columbia and the extreme northwestern U.S.). Our single subspecies on the West Coast in the Sierra Nevada, *Cercyonis oetus oetus*, grades towards *pallascens* in Modoc County, as discussed in the distribution section above. There is no seasonal variation in this univoltine species.
- GENERAL REMARKS: Extensive mark-recapture studies have been done by T. C. Emmel (unpublished) in Colorado populations, which show that the butterfly can persist in even very small populations from year to year (sometimes fewer than 50 individuals represent a stable population). These local populations may exhibit considerable variation over short distances in the spotting pattern on the underside of the wing. Some larger populations may number tens of thousands of individuals and spread out over many square miles. These studies have also shown that females and males may live as three to four weeks in the wild, though the usual lifespan is

probably shorter. Similar studies need to be done in California populations by interested individuals. Studies of natural predation on the Colorado *oetus* adults suggests that birds and other predators may have their attacks deflected by the spotting pattern on the hindwing. These spots apparently offer a tempting target for birds to grab at and thus allow the butterfly to escape, leaving behind only a small triangle of broken wing section in the bird's beak.

This small western *Cercyonis* species is occasionally confused with *Cercyonis sthenele*, but it can be immediately distinguished by the fact that the posterior ocellus on the underside of the forewing is closer to the wing margin than the anterior eyespot (in *C. sthenele*, the two ventral forewing ocelli are equally distant from the wing margin). Also, on the underside of the hindwing, the inner margin of the median band of *oetus* is strongly lobate.

a) *C. o. oetus* (Boisduval)

- DIAGNOSIS: The underside of *oetus* is gray to gray-brown, and the mesial band is well marked by dark borders that are sharply indented in a zig-zag pattern throughout their lengths.
- ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. Belgique*, 12: 63 (1869).
- TYPE LOCALITY: "California." Lectotype in the United States National Museum, designated by F. M. Brown, *Journal of Research on the Lepidoptera*, 4: 142-143 (1966). Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, : (1998) designated the type locality as Hwy. 70 at Betterton Creek, 6.5 road miles W. of Portola, 5000' elevation, Plumas County, California.
- DISTRIBUTION: In California, the species tends to be found east of the Sierran-Cascade axis, from approximately Mono County north to the Oregon border, although some populations are known from the Sierran crest proper, such as at Donner Pass or above the west side of Lake Tahoe. It is also present in the higher elevations of the White Mountains.
- ELEVATION RANGE: From 5,000 to 10,000' elevation. Most populations occur between 7,000 and 9,000'.
- HABITAT AND PLANT COMMUNITIES: The species is typically found in Great Basin Sagebrush Scrub habitats on the east slope of the Sierra Nevada. In the White Mountains, it is predominately associated with Mountain Sagebrush Scrub.
- PHENOLOGY: This species is strictly univoltine. The adults fly from late June through mid-August, with the majority of records in mid to late July. It overwinters as a first-instar larva.
- FOODPLANTS: Native grasses used by this species remain to be determined. In the laboratory, larvae can be readily reared on *Poa pratensis* L.

b) *C. o. near pallescens* Emmel & Emmel

- DIAGNOSIS: *Cercyonis oetus pallescens* was described by Emmel & Emmel (1971) from the Reese River Valley area of Lander County, Nevada, and is characterized by heavy white scaling across the ventral surface. In fresh specimens, the dorsal surface is also noticeably lighter than the coloration in all other subspecies, presumably

helping to protect them in the bright white alkaline flats, their characteristic habitat in Nevada.

- ORIGINAL DESCRIPTION: Emmel and Emmel, 1971, *Pan-Pacific Entomologist*, 47 (2): 155-157.
- TYPE LOCALITY: Reese River Valley, 4 road miles northeast of Reese River Crossing on Nevada Highway 2, 5,700' elevation, west southwest of Austin, southwest corner of T.19 north, R.43 east, Lander County, Nevada.
- DISTRIBUTION: Within California, populations referable to this subspecies or similar to it are found in the Surprise Valley region of Modoc County, just east of the Warner Mountains.
- ELEVATION RANGE: The Surprise Valley populations are found at approximately 5,000' elevation.
- HABITAT AND PLANT COMMUNITIES: These populations are found in an Alkali Sink Scrub valley bottom, with Great Basin Sagebrush Scrub and Alkali Meadow habitats in close proximity.
- PHENOLOGY: These populations fly primarily in July and early August.
- FOODPLANTS: Unknown.

51. *Neominois ridingsii* (W. H. Edwards)

- ADULT BEHAVIOR: This butterfly is remarkably like a gray grasshopper, flying rapidly from its resting position in one spot to another location some 20 or 30 yards away and settling quickly on the substrate, where its gray mottling helps it blend well into the gravel or grass background. Scott (1973b) studied the population biology and behavior of *Neominois* in Colorado and found that it is a sedentary species, rarely moving more than 200 meters and having an expected life span of about one week. Adults perched and hilltopped, mating on low (3 meters high) hills. Mating was observed in the morning between 0750 and 1040. Similar mate-locating behavior was noted in Mono County, California (Scott, 1975).
- LIFE HISTORY: The egg is barrel-shaped, with about 15 raised vertical ribs. They are laid singly on the host or on nearby plants and shrubs. The larva has the typical satyrid globular head, cylindrical tapering body, and two anal "tail" projections. It is reddish-tan in color, with short white hairs, and whitish lines lying between six stripes which are black, tan or greenish-brown in color. The pupa is red-brown with green wing cases and abdominal joints. Pupation is in a hole in the soil, dug by the larva. Hibernation in Colorado is in the third or fourth larval instar. In Tuolumne County, California, high in the Hudsonion Zone, the species is known to fly in even-numbered years, apparently hibernating as young larvae the first winter and as old larvae the second winter (Scott, 1986). At other Sierra Nevada locations (e.g., Carson Pass), the species flies in abundance during odd-numbered years (Austin, 1986). Probably all California populations are biennial.
- CHROMOSOME NUMBER: Unknown.
- SIMILAR SPECIES: No similar species occur in North America.
- GEOGRAPHICAL AND SEASONAL VARIATION: As pointed out by Austin (1986), this species exhibits considerable geographic variation throughout its range and also shows substantial variation within a population. While this species is believed to be

single-brooded, some data suggest a possible second brood in several areas outside California.

GENERAL REMARKS: The adult *Neominois* have a flight behavior very much like that of the arctics in the genus *Oeneis*. They usually do not fly until disturbed; then they travel only a short distance, at a relatively low height above the ground. When the butterfly alights, it leans to one side, showing its cryptically marked underside. In the Old World, the closely-related genus *Karanasa* shows tremendous geographic change and speciation in the various mountain ranges of the Near East, the great Asian mountains, and high interior desert areas.

This butterfly represents a monotypic Nearctic genus which is closely related to a number of Eurasian genera, especially *Karanasa* in Afghanistan, the northern Himalayas and western China. Its distribution is restricted to portions of the western United States and adjacent southern Canada. An excellent modern review of geographic variation in the genus has been published (Austin, 1986).

a) *N. r. near stretchii* (W. H. Edwards)

DIAGNOSIS: *Neominois ridingsii stretchii* occurs across Nevada, Utah, northern Arizona and western Colorado and western Wyoming. It is characterized by a yellow-brown color on the dorsal surface and a deep serration of the sub-marginal band on the secondaries.

ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Entomological Society*, 3: 192-193 (1870).

TYPE LOCALITY: "Nevada." Restricted to Mount Jefferson, Nye County, Nevada, by F. M. Brown, *Transactions American Entomological Society*, 90: 357-359 (1964). Neotype in Carnegie Museum, designated by F. M. Brown (1964).

DISTRIBUTION: The distribution of *stretchii* is from the west slope of the Rocky Mountains, western Wyoming and eastern Idaho through Utah and northern Arizona to central Nevada, north to extreme northeastern California, adjacent to extreme southern Oregon and northern Nevada (Austin, 1986). In California, we have records from the Warner Mountains.

ELEVATION RANGE: **[MATTOON: PLEASE FILL IN.]**

HABITAT AND PLANT COMMUNITIES: The butterfly is found in an open Sagebrush Scrub community on montane slopes or flats in the Warner Mountains.

PHENOLOGY: The records from the Warner Mountains range from **[MATTOON: PLEASE FILL IN.]**

FOODPLANTS: Unknown.

b) *N. r. pallidus* Austin

DIAGNOSIS: This subspecies is characterized by a gray-brown dorsal and ventral surface, with a moderate degree of serration of the sub-marginal band on the secondaries. Additionally, the color of the submarginal bands dorsally is white, whereas on *stretchii* it is yellowish.

ORIGINAL DESCRIPTION: Austin, *Bulletin of the Allyn Museum*, 107: 1-27 (1986).

- TYPE LOCALITY: Alkali Valley, Larkin Dry Lake Road, 4.8 miles north of Nevada Highway 359, Mineral County, Nevada. Holotype deposited at the Nevada State Museum.
- DISTRIBUTION: This western Great Basin taxon has a rather narrow distribution, from the central Sierra Nevada (Carson Pass to the Bishop Creek drainage) on the west to the White Mountains and on into Nevada on the east. It also occurs in the Adobe Hills, in Mono County.
- ELEVATION RANGE: 6,700' to above 10,000'.
- HABITAT AND PLANT COMMUNITIES: This butterfly's habitat ranges from sandy flat valleys and sagebrush hillsides to high rocky ridges, within the following plant communities: Mountain Sagebrush Scrub, Great Basin Sagebrush Scrub, and sparse Pinyon-Juniper Woodland. Populations tend to be local, but the butterfly is often common where found.
- PHENOLOGY: One brood occurs, with adults present from early June at low elevations to early August at high elevations.
- FOODPLANTS: In the populations in the Adobe Hills of Mono County, the species is closely associated with the grass *Stipa nevadensis* B. L. Jones and this is the probable host. In the more alpine areas of the Sierra Nevada and the White Mountains, the grass species utilized are unknown. In the laboratory, larvae can be reared on *Poa pratensis* L. Scott (198) found that the host for at least one Colorado population was *Bouteloua gracilis* (Willd. ex HBK) Lag. (Poaceae).

52. *Oeneis nevadensis* (C. & R. Felder)

- ADULT BEHAVIOR: Scott (1986) states that males exhibit perching behavior, waiting on fallen trees in glades, valley bottoms and on hilltops for passing females.
- LIFE HISTORY: The egg is the usual subconical shape for the genus, and is gray-white in color. There are 18-19 vertical ribs. The stage lasts about 15-18 days. The larva is yellowish-buff, with a black dorsal stripe and six stripes of white alternating with darker brownish or greenish tan. The species is biennial, the first winter being passed as a first- or second-instar larva (Edwards, 1897) and the second winter being passed as the mature larva. The pupa is [TCE: DESCRIBE FROM SLIDES.]
- CHROMOSOME NUMBER: Unknown.
- SIMILAR SPECIES: No similar species occur within the state.
- GEOGRAPHIC AND SEASONAL VARIATION: This rather rarely collected species probably exhibits a blend-zone in the northern Coast Range between the two known subspecies, and further collecting is clearly needed to determine the total range of the species in California.
- GENERAL REMARKS: The similar species *Oeneis macounii* (W. H. Edwards), which occurs from British Columbia east to northern Minnesota and Michigan around Lake Superior, is probably a subspecies of the western *nevadensis* and needs to be studied critically. This large arctic occurs in forest habitats rather than the typical arctic-alpine habitat of its congeneric relatives.

a) *O. n. nevadensis* (C. & R. Felder)

- DIAGNOSIS: This large arctic is characterized by its wood-brown dorsal surface and almost-unmarked ventral surface.
- ORIGINAL DESCRIPTION: C. & R. Felder, *Reise...Freg. Novara*, 3: 489 (1866).
- TYPE LOCALITY: Sierra Nevada, California. Restricted by Emmel, Emmel & Mattoon, *Systematics of Western North American Butterflies Contributions in Science*, : (1998) to Meadow Valley, Plumas County, California. Holotype in the British Museum and illustrated in the preceding reference.
- DISTRIBUTION: This subspecies is found in the mountainous areas of the northern third of the state, from Plumas County north to the Warner Mountains, westward through the Mount Shasta district to the Klamath Mountains Assemblage. A single record is known from El Dorado County, which probably represents a temporary population establishment.
- ELEVATION RANGE: [MATTOON: PLEASE FILL IN.]
- HABITAT AND PLANT COMMUNITIES: The species is typically found in open pine woods, flying in sunny glades within the Lower or Upper Montane Coniferous Forest plant community.
- PHENOLOGY: The species is univoltine and is apparently biennial in virtually all populations. In some localities it flies only in even years and in other localities it flies only in odd years. Then there are some localities where it apparently has regular emergences of both odd-year and even-year populations. Records range from early June to late July or early August, with a peak in early to mid-July.
- FOODPLANTS: Unknown. In the laboratory, it can be reared on *Poa pratensis* L.

b) *O. n. iduna* (W. H. Edwards)

- DIAGNOSIS: This subspecies is lighter than typical *nevadensis*, with pale yellowish-brown on the outer half of the wings. The distal band is less scalloped and the wings are larger than in the typical subspecies.
- ORIGINAL DESCRIPTION: W. H. Edwards, *Butterflies of North America*, 2: [275-277] (1874).
- TYPE LOCALITY: Mendocino County, California. Lectotype in the Carnegie Museum, designated by F. M. Brown, *Transactions American Entomological Society*, 90: 390-392 (1964).
- DISTRIBUTION: This subspecies is found in the outer Coast Ranges from Sonoma County north to Del Norte County.
- ELEVATION RANGE: From sea level to approximately 2,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This arctic is typically found in wooded areas within Northern Mixed Evergreen Forest, North Coastal Coniferous Forest, or near the edges of Redwood Forest habitats.
- PHENOLOGY: Captures range from mid-May to late June, mostly in even-numbered years but there are some odd-numbered year records, also. Some of these odd- and even-

numbered records are for the same locality, indicating that two populations which are allochronic exist sympatrically.

FOODPLANTS: Unknown.

53. *Oeneis chryxus* (Doubleday and Hewitson)

ADULT BEHAVIOR: The males of *Oeneis chryxus* tend to be avid hilltoppers, while the females are found in somewhat lower elevations seeking oviposition sites. The extraordinary cryptic coloration on the underside renders these butterflies nearly invisible when they settle into the tundra vegetation following a short rapid flight. On a rock slide they are nearly impossible to capture, being extraordinarily alert and taking flight on the collector's approach.

LIFE HISTORY: The egg and first-instar larva of California *ivallda* were described and illustrated by Edwards, and the egg is also figured in Comstock (1927b); the larva has been reared to maturity by J. F. Emmel. The subconic egg is white, with 19 vertical ribs, and is laid singly on grasses and sedges. It hatches in 14-15 days. The young larva is greenish-white in ground color, with reddish hairs, a reddish mid-dorsal stripe, and five lateral stripes of reddish-brown coloration. The mature larva

[TCE: DESCRIBE FROM SLIDES.]

The pupa of typical *chryxus* (from Colorado) is brown, with the thorax being yellow-brown and the abdomen a lighter yellow-brown covered with black dots. The species is biennial, with the larvae hibernating in the first or second instar during the first winter, and in the third, fourth, or fifth instar during the second winter (Scott, 1986, from Colorado material).

CHROMOSOME NUMBER: $n = 32$ in Colorado *O. chryxus chryxus* material (Emmel and Eliazar, unpublished).

SIMILAR SPECIES: None in California.

GEOGRAPHIC AND SEASONAL VARIATION: The subspecies *stanislaus* and *ivallda* intergrade between Carson Pass and Ebbetts Pass at the north end of *stanislaus*' range, and again there is a zone of intergradation between the two subspecies in the northern part of Yosemite National Park, in the vicinity of Virginia Creek. Virtually every color intermediate can be found in these two areas, and for this reason the two subspecies are considered conspecific.

In the southern Sierra Nevada, most specimens have ocelli larger than those of the more northern *ivallda* populations.

Since the species is univoltine, there is no seasonal variation.

GENERAL REMARKS: William Hovanitz (1940) has analyzed the remarkable match of the distribution of these color forms to the background coloration of rocks in the central Sierra Nevada. From his observations, he concluded that the two are probably races of the same species, contrary to the then-existing treatment of the two as separate species in the literature (e.g., Comstock, 1927b).

It is possible that *ivallda* represents an earlier segregate of *O. chryxus* in the predominately granitic Sierra Nevada, and that *stanislaus* is a more recent invader from the Great Basin ranges (via the Sweetwater Mountains). With the gradual drying of the Great Basin since the last glacial period, *O. chryxus* populations in

the intervening mountain ranges (between the Sweetwater Mountains and the eastern Nevada ranges where *chryxus* still survives) would have become extinct. In the portions of the central Sierra Nevada where dark rock substrate is present, the more closely matching *stanislaus* phenotype would have displaced *ivallda* populations in those areas.

For many years, it was believed that two species of *Oeneis* occurred in the Sierra Nevada of California: *Oeneis ivallda* (Mead) and *O. chryxus stanislaus* Hovanitz. However, recent evidence has shown in California that this smaller *Oeneis* species is highly variable, ranging from pale tan to yellowish-brown to cream, and that the distribution of each color form generally follows the distribution of light-colored granitic rock and of dark volcanic rock in the Sierra; large blend zones are found between the two taxa.

a) *O. c. ivallda* (Mead)

- DIAGNOSIS: This *Oeneis* is pale tan, with whitish or yellowish areas around the forewing spots.
- ORIGINAL DESCRIPTION: Theodore Mead, *Canadian Entomologist*, 10: 196 (1878).
- TYPE LOCALITY: Summit and Freel Peaks and Tallac Mountain, Lake Tahoe, Placer County, California. Syntypes in Carnegie Museum.
- DISTRIBUTION: In the Sierra Nevada, the distribution of *ivallda* is disjunct, with two separated sets of populations. In the Lake Tahoe region, populations are found from Castle Peak in Nevada County south to approximately Carson Pass, and they are found on the peaks on both sides of Lake Tahoe as well. In the southern half of the Sierra Nevada, populations are found from the northern area of Yosemite National Park southward to the highest mountains of Tulare County, approximately at the latitude of Olancha Peak.
- ELEVATION RANGE: 7,000' at Donner Pass to 12,000' on some of the higher Sierran Peaks.
- HABITAT AND PLANT COMMUNITIES: This butterfly is typically found on open alpine fellfields, rock gardens, and open slopes, within the following plant communities: Arctic-Alpine Cushion Plant, Subalpine Forest, and Montane Dry Meadow..
- PHENOLOGY: Records range from mid-June at the lower elevations to mid-August at the highest elevations, with the majority of records recorded for the month of July. Most records for the Sierra Nevada are for odd-numbered years, although a number of even-numbered year populations are known as well. The species is inferred to be biennial, from these peaks of abundance every other year in a given locality.
- FOODPLANTS: The subspecies *ivallda* seems closely associated with the sedge *Carex spectabilis* Dewey in a number of localities in the Sierra Nevada. A satyrid larva, which unfortunately was not reared to adulthood, was found on this *Carex* above Tioga Pass by Oakley Shields (personal communication). In view of the high elevation, it was likely a larva of this particular satyrid, so this *Carex* species is strongly suspected as the foodplant. Undoubtedly, several grass or sedge species may serve as hosts. In the laboratory, larvae can be reared on *Poa pratensis* L.

b) *O. c. stanislaus* Hovanitz

- DIAGNOSIS: This subspecies is quite dark-brown in color and occurs in the central Sierra Nevada and Sweetwater Mountains.

- ORIGINAL DESCRIPTION: Hovanitz, *Entomological News*, 48: 228 (1937).
- TYPE LOCALITY: Sonora Pass, 9,400', Alpine County, California. Holotype in California Academy of Sciences.
- DISTRIBUTION: The subspecies *stanislaus* is found in the central Sierra Nevada, from Sonora Pass to Ebbetts Pass in a rather limited area. It is also found just to the east in the Sweetwater Mountains, along the California-Nevada border.
- ELEVATION RANGE: From 8,400' to 11,000' elevation.
- HABITAT AND PLANT COMMUNITIES: Similar to *ivallda*. This subspecies is usually found on open gravelly or rocky slopes and peaks within the Arctic-Alpine Cushion Plant community.
- PHENOLOGY: Records range from late June to early August, with virtually all records known to us occurring in odd-numbered years. There is a single record for an even-numbered year, in 1936.
- FOODPLANTS: Unknown.

NYMPHALIDAE

The true Nymphalids comprise this large butterfly family. As defined here, this family includes the subfamilies Apaturinae (the hackberry butterflies), subfamily Limenitidinae (the admirals and their relatives), the subfamily Nymphalinae (the true nymphs), the subfamily Melitaeinae (the checkerspots, crescent spots, and their relatives), the subfamily Argynniinae (the fritillaries), and the subfamily Heliconiinae (the long wings or Heliconiines). Approximately 4,500 species of butterflies worldwide belong to these groups. There are other tropical and Old World subfamilies that do not reach our fauna, including the subfamily Brassoliniinae (the owl butterflies and their relatives, comprising approximately 80 species in the Neotropics), the Amathusiinae (the pale owl butterflies or Amathusiines, comprising about 80 species restricted to the Indo-Australian tropics), the subfamily Morphinae (the morpho butterflies, comprising approximately 70 species in the Neotropics), the Calinaginae (a single genus found in the Himalayan and western China region), subfamily Charaxinae (the leafwing butterflies and their relatives comprising approximately 400 species, mostly in the tropics of the world), the Acraeinae (the acraeines, with about 250 species, mostly in Africa with a few in Asia and the Neotropics), and the subfamily Ithomiinae (the clear-wing or ithomiine butterflies, with approximately 400 species almost entirely in the Neotropics and one genus in the New Guinea subregion).

The Nymphalids are characterized by having (1) greatly reduced forelegs, brush-like in appearance, with the remaining two pairs of legs serving as four walking legs; (2) feet composed of one long elongate segment in the male butterfly and five segments in the female, and lacking any true claws at all on their tips; (3) clubbed antennae that are always scaled along their shafts; (4) a head that is almost as wide as the thorax, with short palpi; (5) a cell on the hindwing that is never closed by a tubular vein; (6) a forewing cell that is also usually open and not closed by a tubular vein; (7) a pupa which is usually suspended from a cremaster at the abdominal tip, and not fastened by a silken girdle; (8) larvae which usually bear many branched spines in rows over the entire body, in the species of our fauna.

* * * * *

Subfamily **Apaturinae** Boisduval

54. *Asterocampa celtis* (Boisduval and Leconte)

See **Appendix** for this apparently erroneously recorded species.

Subfamily **Limnitiinae** Behr

55. *Limnitis archippus* (Cramer)

- ADULT BEHAVIOR:** The adults fly in a typical *Limnitis* fashion, that is, with a gliding or soaring flight. This is in contrast to the Queen, which it mimics; the Queen flies with a more constant flapping flight. The adults tend to be found in close proximity to willow or young cottonwood thickets, with the males perching on prominent twigs or branches of the willows or cottonwoods and females flying from plant to plant in obvious oviposition behavior.
- LIFE HISTORY:** The mature larva is grayish-white on the thorax, yellowish-brown back to the mid-abdominal region, white in the middle of the abdomen, and brownish posteriorly to the anal segment. Small nodules and spots occur over the body except in the central light patch. The larval pattern is undoubtedly protective, imparting a resemblance to a bird dropping. Two plume-like scoli, which are larger than those of *Limnitis lorquini*, extend forward from the thorax. Like other *Limnitis*, the larva frequently holds a resting posture with both its anterior end and posterior end elevated above the substrate. The pupa is equally unusual, with a highly raised hump on both the thorax and the forward portion of the abdomen. The thorax and wing covers are brownish; the abdominal segments are whitish. The larva overwinters in the third instar in a structure called a hibernaculum, consisting of a rolled-over willow leaf. These are frequently found on willows growing in standing water, during the winter months.
- FOODPLANTS:** This species uses both *Populus fremontii* Wats., and *Salix* species (willows) (Salicaceae). The particular *Salix* species used are currently unknown.
- CHROMOSOME NUMBER:** $n = 30$ for the eastern *L. a. archippus* (Maeki and Remington, 1961b).
- SIMILAR SPECIES:** In southern California, the adults are excellent mimics of the Queens, *Danaus gilippus strigosus*, which are abundant in the same areas. It is possible from recently obtained evidence that both the Queens and the Viceroys are distasteful. Thus although it has been long assumed that the Arizona Viceroy is a harmless Batesian mimic of the distasteful Queen, recent experiments by David B. Ritland and others are showing that in some cases, the Queen populations may be edible and *Limnitis* butterflies may be distasteful, or both may be distasteful in a Mullerian mimicry complex.
- GEOGRAPHIC AND SEASONAL VARIATION:** There is no apparent seasonal variation among the different broods. All southern California populations of this butterfly are the same geographic subspecies, *obsoleta*, which extends eastward into southern Arizona.
- GENERAL REMARKS:** The human activities on the lower Colorado River of dam building, water diversion, real estate development, and water recreational development have all apparently altered the habitat of this butterfly and greatly reduced its numbers, as the species is decidedly less common today than it was 50 years ago. Whether

the subspecies will make a comeback with stabilization of the river border areas and wildlife game refuges on the lower Colorado River remains to be seen.

A second subspecies of *Limenitis archippus* may possibly occur in northern California in Lassen County. This is the western Great Basin subspecies, *L. a. lahontani* Herlan. This was described from the moist bottomlands of Lyon County, Nevada, by Peter Herlan in 1971. There is a possible sight record for this butterfly in eastern Lassen County at Secret Creek along Highway 395 (Opler, personal communication). This area needs to be explored further by lepidopterists for possible documented records of this subspecies in Lassen County.

SUBSPECIES: This is a medium to large-sized reddish-brown butterfly with black margins and black veining which superficially resembles the Monarch or the Queen. One subspecies is regularly found within our state; a second subspecies (see Appendix) may be encountered along the border with northern Nevada.

a. *L. a. obsoleta* W. H. Edwards

DIAGNOSIS: This is a small subspecies with a more tan ground color and lighter wing markings than the typical subspecies. It is an apparent mimic of *Danaus gilippus*.

ORIGINAL DESCRIPTION: W. H. Edwards, *Papilio*, 2: 22 (1882).

TYPE LOCALITY: "Southern Arizona". Type specimens lost (F. M. Brown, *Transactions American Entomological Society*, 93: 365-366, 1967).

DISTRIBUTION: In California, this subspecies is found primarily along the Colorado River in the Colorado River Valley. Sporadic occurrence has been noted in the Imperial Valley and in the well watered desert canyons of eastern San Diego County. There are apparently no permanently established colonies in these latter areas.

ELEVATION RANGE: This butterfly is found from below sea level in the lower Imperial Valley to approximately 1,000' elevation in the eastern San Diego County area.

HABITAT AND PLANT COMMUNITIES: This subspecies is found in the Desert Riparian Woodland community of the Colorado Desert. It is typically found in situations along watercourses or at the edges of man-made lakes where there are numerous willows or cottonwoods, particularly younger plants.

PHENOLOGY: This species is multivoltine, with records ranging from early March to October; the majority of our records seem to be for the months of September and October, when it reaches its peak abundance.

56. *Limenitis weidemeyerii latifascia* E. & S. Perkins

DIAGNOSIS: This rather large butterfly is black with broad white bands extending across the forewing to the anal margin of the hindwing, and is the westernmost representative of the species that occurs predominantly in the Rocky Mountain region and Great Basin area.

ORIGINAL DESCRIPTION: E. M. and S. F. Perkins, *Journal Lepidopterists' Society*, 21: 221-222 (1967).

TYPE LOCALITY: Mink Creek, 10 miles south of Pocatello, Bannock County, Idaho. Holotype in American Museum of Natural History.

- DISTRIBUTION:** The subspecies *latifascia* is found in California only in the area immediately adjacent to Mono Lake. Eastward, the subspecies extends across the northern half of Nevada to southeastern Idaho, northern Utah, and extreme western Wyoming. The species as a whole ranges through the Rocky Mountains southward into New Mexico and Arizona, and into southern Nevada.
- ELEVATION RANGE:** Populations within California occur in an elevation range of approximately 6,400' to 7,500' elevation.
- HABITAT AND PLANT COMMUNITIES:** The butterfly is typically found in riparian situations within the Great Basin Sagebrush Scrub or Pinyon-Juniper Woodland communities. It is particularly concentrated in small canyons or along watercourses where willow species are especially abundant.
- PHENOLOGY:** All records for adults fall within a period from early July to mid-August, with the majority of records in mid-July to late July. This suggests that the species, at least within our state, is univoltine. Under laboratory conditions, however, this species can be reared through without going into diapause, so it is conceivable that in some years a second brood in September would be possible.
- ADULT BEHAVIOR:** Even more than other *Limenitis*, this large-sized nymphalid has a stately soaring flight among willows as it wends its way along the streams. Males will frequently alight and perch on protruding branches, and will fly out to challenge other butterflies flying through their area. It would be very interesting to do marking studies on the apparent territorial behavior of these males.
- LIFE HISTORY:** The eggs are laid at the tips of the food plant leaves, particularly on new growth. In the case of willow species (the usual host in California populations), plants selected for oviposition are typically younger, smaller plants away from the larger willow thickets. The mature larva is largely dark gray, with a roughly linear white stripe extending along the entire side of the body and a white saddle-shaped marking across the abdominal segments above the prolegs. Two white spots present on the dorsal surface of the first abdominal segment are considerably smaller than similarly placed spots on *Limenitis archippus*. The sides of the thoracic segments and dorsal surface are crossed by whitish vertical and horizontal stripes. The two large scoli coming off of the front of the thorax are black in color. The pupa is largely dark gray on the wing covers and thorax, and whitish-gray across most of the abdomen. The highly raised hump on the thorax and first part of the abdominal segmentation is black to gray in color.
- FOODPLANTS:** In the Mono Lake area, the principal food plant is apparently *Salix exigua* Nutt.; oviposition has also been recorded on *Holodiscus microphyllus* Rydb. in one of the canyons just north of Mono Lake. Outside of the state, the species is known to feed on other *Salix* species, *Populus tremuloides* Michx., *P. angustifolia* James, and various rosaceous plants: *Prunus virginiana* L., *Amelanchier utahensis* Kochne., *Holodiscus boursieri* (Carr.) Rehd. in Bailey, *H. discolor* (Pursh) Maxim, and *H. dumosus*.
- CHROMOSOME NUMBER:** n = 30 from Colorado material (Maeki and Remington, 1961b).
- SIMILAR SPECIES:** None in our area. There is no mimicry complex of other species associated with *Limenitis weidemeyerii*. In fact, the phenotype expressed by *weidemeyerii* and its eastern relative *arthemis* probably represent the ancestral phenotype for the genus. Each of the other species of *Limenitis* mimic either the Pipevine Swallowtail, the Monarch, the Queen, or various *Adelpha* species, all of which are believed to feed on plants with distasteful or repellent compounds.

GEOGRAPHIC AND
SEASONAL VARIATION:

None found within the subspecies populations within our state.

GENERAL REMARKS:

The species hybridizes with *Limenitis lorquini* in our area, producing the form "fridayi" (type locality: Leevining Creek, near Mono Lake, Mono County, California). Specimens of "fridayi" are most commonly encountered within a 15 mile radius of Mono Lake; in this area, *latifascia* and "fridayi" predominate, whereas *lorquini* is rare (Perkins and Perkins, 1967). It is interesting that the gene or genes for the apparent orange-tip mimicry pattern in *lorquini* (which cause it to resemble the oak-feeding California Sister, *Adelpha bredowii*), do not show dominance in the F₁ hybrid, but give intermediate expression of the character in "fridayi." Since *lorquini* very rarely comes in contact with other *Limenitis* species in California, there may have been little selection to make the alleles for "orange-tip" dominant to "non-orange-tip" (the presumed condition in *weidemeyerii*). Ecological interactions in the region around Mono Lake would be a fertile area for further investigation by California lepidopterists.

57. *Limenitis lorquini* (Boisduval)

ADULT BEHAVIOR:

Comstock (1927b) well describes this species' habits: "It frequents watercourses and moist wooded areas, being especially abundant in riverbottom lands that are overgrown with willow. The flight of this boldly marked butterfly is characterized by a series of short twitching motions, with the wings held nearly flat, interspersed with leisurely volplaning. Frequently stops are made on exposed perches, where it delights in basking."

LIFE HISTORY:

The nearly spherical pale green eggs are laid singly at the tip of the foodplant leaf. The mature larva is olive-green, with olive-yellow mottling in the thoracic area and a whitish patch above the mid-abdominal region. A white lateral band runs along the nine abdominal segments. Two plume-like scoli protrude forward from the mesothoracic segment. The pupa has a dorsally raised hump near the front of the abdominal region. It is dull purplish and white on the thorax, mottled white on the abdomen, and translucent dark olive-green on the wing cases.

CHROMOSOME NUMBER:

Unknown.

SIMILAR SPECIES:

The resemblance between *Limenitis lorquini* and the California Sister, *Adelpha bredowii*, has often been noted by authors. This apparent mimicry complex will be discussed under General Remarks. Suffice it to note here that the two species can be readily distinguished by the facts that *lorquini* has a more pointed wing shape, is usually somewhat smaller, and flies around willows in watercourse areas or canyon bottoms, while the *Adelpha* is commonly found in drier hillside areas around oak trees. In the hand, the adults differ noticeably by the shape of the forewing apical patch. The orange *lorquini* forewing tip curves along the margin of the forewing as a continuous orange border, whereas the California Sister has a rounded orange spot set off from the outer margin of the forewing by a dark marginal band of color.

GEOGRAPHIC AND
SEASONAL VARIATION:

There is no apparent variation among the different generations of the lowland populations of *lorquini*. Nominotypical *lorquini* is found in the northern two-thirds of the state, from the southern Sierra Nevada foothills northward along the west slope of the Sierra Nevada and northward through the Coast Ranges to the Klamath Mountain regions, southern Cascade Range, and the Warner Mountains. Along the

northern border of the state, there is apparently the beginning of a blendzone with the subspecies *burrisoni* which has generally darker markings and a reduced orange apex on the tips of the forewings. To the south, nominotypical *lorquini* blends with the southern California subspecies *powelli* in the area of the Transverse Ranges at the south end of the San Joaquin Valley, with no clear zone of demarcation between these two subspecies. From the east slopes of the Sierra Nevada to the Inyo Mountains and White Mountains of Inyo County is found the subspecies *pallida*, which is characterized by a generally paler aspect, wider white bands on the wings and extensive orange apical scaling on the forewing. Populations along the east slope of the Sierra Nevada may form a blendzone with more typical *lorquini* and the subspecies *pallida*.

GENERAL REMARKS: The supposed mimicry between the Lorquin's Admiral and the California Sister is another case in point of where long-standing assumptions may be overturned by more careful examination. In this case, it has been felt that the California Sister was probably protected from bird predation by its larvae feeding on tannin-rich oak foliage, whereas Lorquin's Admiral has been presumed to be edible, its larvae feeding on supposedly palatable willow. Recent evidence accumulated by David A. Ritland and others have shown that the Viceroy, another species in the genus *Limenitis* with *lorquini*, is unpalatable to at least some birds. This suggests that, as in the Viceroy and Queen or Monarch mimicry complex, the California Sister and the Lorquin's Admiral may enjoy a Mullerian mimicry relationship rather than a Batesian status. Careful field tests in laboratory work with captive birds by California lepidopterists could readily resolve this question. In California this interesting butterfly, commonly called Lorquin's Admiral, extends across the state and is present in the form of four subspecies. The species ranges from California and Nevada north to British Columbia and east to Alberta, Idaho, and Montana (Perkins and Perkins, 1960).

a. *L. l. lorquini* (Boisduval)

- DIAGNOSIS:** A medium-sized, dark brownish-black butterfly with broad white postmedial bands on both wings and orange apical areas on the forewings.
- ORIGINAL DESCRIPTION:** Boisduval, *Ann. Soc. Ent. France*, (2)10: 301 (1852).
- TYPE LOCALITY:** "California". Restricted by Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies Contributions in Science*, : (1998) to lower Feather River Canyon, Plumas County, California. Holotype in U. S. National Museum.
- DISTRIBUTION:** Nominotypical *lorquini* is found in the northern two-thirds of California, from the west slope of the Sierra Nevada westward through the southern Klamath Mountains region and southward in the Coast Ranges to approximately the Transverse Ranges in southern California. To the south, it forms a blendzone with the southern California subspecies *powelli* and to the north it blends with subspecies *burrisoni*.
- ELEVATION RANGE:** This subspecies is found from near sea level to approximately 8,000' in the mountains. It does not appear to inhabit the very high montane or Arctic Alpine areas.
- HABITAT AND PLANT COMMUNITIES:** This subspecies is typically found in the Riparian Woodland plant community throughout a wide elevational range, as well as in Montane Wet Meadow habitats in the highest elevations of its range. In these

situations, the willow foodplant species are usually abundant and the butterfly is found in close proximity to these plants, although other foodplants are also used.

PHENOLOGY: The species is multivoltine, particularly in the lower elevation populations. The highest elevation populations may be univoltine, similar to the phenology of the California populations of *L. weidemeyerii*. Adults in the lowland populations fly from March through October, while the preponderance of records for the higher elevation populations is in June and July.

FOODPLANTS: *Salix* species (Salicaceae) are probably the principal and preferred foodplant of this species. *Salix* species which have been documented to be foodplants for this butterfly include *S. lasiolepis* Benth., *S. lasiandra* Benth., *S. lutea* Nutt. Additional salicaceous species recorded include *Populus tremuloides* Michx., *P. trichocarpa* T. & G., *P. fremontii* Wats. Foodplants in the family Rosaceae are also used and these include *Prunus virginiana* L., *P. emarginata* (Dougl.) Walp., *Holodiscus discolor* (Pursh) Maxim, *Spiraea douglasii* Hook, *Malus pumila*. Other records for *Ceanothus* in the family Rhamnaceae and *Quercus* (Fagaceae) probably need further confirmation to be confidently listed as confirmed hosts.

b. *L. l.* near *burrisoni* (Maynard)

DIAGNOSIS: This is a subspecies of the Pacific Northwest which is characterized by greatly reduced orange apical markings; these markings also differ in being a dark red-orange in hue. Additionally, the ventral ground color tends to be darker, becoming very melanic in some individuals.

ORIGINAL DESCRIPTION: Maynard, *Manual of North American Butterflies*, p. 102 (1891).

TYPE LOCALITY: Landsdowne, British Columbia. Location of type not known.

DISTRIBUTION: This subspecies is found in Oregon, Washington, British Columbia, Alberta, Idaho, and Montana (Perkins and Perkins, 1966). Although there are no "pure" populations of *burrisoni* in northern California, individuals from the extreme northern portion of the state tend to show a reduction of the apical orange markings and in many instances are extremely similar to typical *burrisoni* from further north.

ELEVATION RANGE: Records of individuals of the *burrisoni* phenotype range from near sea level to approximately 7,000' elevation within California.

HABITAT AND PLANT COMMUNITIES: Like the nominotypical subspecies *lorquini*, *L. l. burrisoni* is typically found in Riparian Woodland habitats, particularly in heavily forested areas.

PHENOLOGY: Our records for this particular phenotype are concentrated in the months of June and July.

FOODPLANTS: Unrecorded for the California populations referable to this subspecies.

c. *L. l. pallida* Austin and Emmel

DIAGNOSIS: This phenotype is the palest of the species and has extensive orange apex on the forewing, the hue of which is often a very pale orange or even yellowish. Additionally, there are often distinct submarginal white spots on the anterior half

of the forewings of males. Increased white scaling ventrally and broader white bands on the wings give a very pale appearance to the ventral surface.

ORIGINAL DESCRIPTION: Austin and Emmel, *Systematics of Western North American Butterflies Contributions in Science*, : (1998).

TYPE LOCALITY: Trail Canyon, White Mountains, Esmeralda County, Nevada. Holotype deposited in Nevada State Museum, Carson City.

DISTRIBUTION: This subspecies is found in eastern California in the White Mountains and Inyo Mountains of Inyo and Mono counties, and in extreme western Nevada in Esmeralda County. Some individuals from the east slope of the Sierra Nevada in California are close to this subspecies, also.

ELEVATION RANGE: From approximately 6,000' to 8,000' elevation.

HABITAT AND PLANT COMMUNITIES: This admiral is found in canyon bottoms along streams within the Pinyon-Juniper Woodland or Great Basin Sagebrush Scrub plant communities. It typically flies in areas where willows are abundant.

PHENOLOGY: This subspecies is probably univoltine, based on the preponderance of records in late June and July. A sampling of its habitat in September at Hunter Mountain, Inyo County, failed to reveal the presence of a second brood.

FOODPLANTS:

d. *L. l. powelli* (Field)

DIAGNOSIS: William Field (1936) described this phenotype as a transition form from San Bernardino, California. It has since been treated as an aberration in subsequent checklists (dos Passos, 1964; Perkins and Perkins, 1966; Miller and Brown, 1981). The holotype in the U. S. National Museum, however, is not aberrational but is representative of populations in southern California (San Bernardino, Los Angeles, Riverside, Orange and San Diego counties) and northern Baja California, Mexico. Thus it was raised to subspecific status by Austin and Emmel (1989).

This taxon is distinguished at once from nominotypical *L. lorquini* by numerous characters (Austin and Emmel, 1989). Dorsally, the postmedian white bands are broader. The spots are more contiguous and only narrowly separated, appearing as a band narrowly separated by blackened veins. On nominotypical *L. lorquini*, these appear as a series of white spots on a dark field. The apical orange patch is more narrow on *L. l. powelli*, usually not reaching the sub-apical spots on males and not extending beyond those spots on females. On typical *lorquini*, this orange commonly extends proximal to these spots, especially on females.

The key differences are on the ventral surface. The orange-brown color is more extensive at the expense of white. The submarginal series of whitish lunules on both wings are broad on typical *lorquini* but are comparatively very narrow on *powelli*, and the prominent whitish at the base and along the anal margin of the hindwings of *lorquini* is indistinct, nearly obsolescent on *powelli*. The width of the black margins distal to the post-median band on the hindwings is much narrower on *powelli*, and the narrow marginal crescents of bluish-white that are usually present on typical *lorquini* are absent.

- ORIGINAL DESCRIPTION: William Field, *Journal Ent. Zool.*, 28: 24 (1936). Raised to subspecific status from a transition form name or aberration by Austin and Emmel, *Systematics of Western North American Butterflies Contributions in Science*, : (1998).
- TYPE LOCALITY: San Bernardino, California. Holotype in U. S. National Museum.
- DISTRIBUTION: The subspecies *powelli* is found in extreme southwestern San Bernardino County, Los Angeles County, Riverside County, Orange County, and San Diego County, as well as northern Baja California, Mexico. It is found primarily on the coastal side of the crest of the Transverse Ranges and Peninsular Ranges in southern California, although populations do occur on the eastern and northern slopes of these mountains. However, the butterfly does not extend into the desert regions in the latter areas.
- ELEVATION RANGE: Populations are found from approximately sea level to about 8,000' elevation in the mountains.
- HABITAT AND PLANT COMMUNITIES: As with the other *lorquini* subspecies, this one is typically found in Riparian Woodland situations, particularly in wet bottomlands where willow species are abundant.
- PHENOLOGY: Captures are recorded from March through early November, with no particular peak abundance noted through the season. It is multivoltine at the lower elevations, with probably at least three broods in a given season.
- FOODPLANTS:

58. *Adelpha bredowii* Geyer

- ADULT BEHAVIOR: The California Sister in each of its two subspecies flies in the mountains, largely in Transition Zone forest areas and canyons around oak trees. Adults often come to moisture, landing on damp sand or mud around lakes or along streams. Robert Langston (*in litt.*) once observed them swarming on grape squeezings at the San Gabriel River near Whittier. They rarely (if ever) visit flowers, preferring to fly around the larval foodplants where they frequently perch on sunlit oak branches.
- LIFE HISTORY: The pale green ova are deposited on the upper surfaces of the foodplant leaves, usually at the apices but sometimes on one of the dentate projections along the leaf margin. They are larger than *Limenitis* ova, but have a similar morphology.
- The first and second instar larvae construct a perch of frass and silk which projects from the margin of an oak leaf (often at the leaf apex, forming a continuation of the mid-rib); this perch may extend as much as mm. from the leaf margin. By the third instar, the perch is abandoned and the larva rests on a silken mat, usually constructed over the leaf midrib or on the leaf petiole. Larger larvae usually rest on the oak twigs in close proximity to leaves. All instars feed primarily on mature leaves; the enlarged larval head (over that seen in larvae of the closely related *Limenitis*) apparently reflects a greater development of mandibular musculature to allow chewing of the very tough oak leaves. The mature larva is dark green above and lighter below shading into a soft brown. It bears six pairs of long, fleshy tubercles, which are green in color. The larva is superbly camouflaged on the *Quercus* leaves and twigs. The pupa is a soft brown, with darker striations and metallic spots on the dorsal surface.
- Diapause takes place in the third instar larval stage. The larva does not construct a hibernaculum, but instead remains exposed and quiescent on a silken pad,

usually on a leaf petiole or very thin twig of the foodplant. Occasional minimal feeding takes place in this stage from December to February, apparently to maintain hydration. By March, a more regular feeding schedule is resumed, and larvae reach maturity in April and May (unpublished observations by J. F. Emmel).

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: *Limenitis lorquini* is the only species that can be confused with *Adelpha bredowii*; see the account under that species for distinguishing characteristics.

GEOGRAPHIC AND SEASONAL VARIATION: There is no apparent seasonal variation between the earlier and later brood specimens. Geographically, as noted above, the subspecies *eulalia* tends to be large. See above discussion for the distinguishing characteristics of the two California subspecies of this primarily subtropical butterfly.

GENERAL REMARKS: As noted above, the butterfly may be involved in a mimicry complex with *Limenitis lorquini* throughout much of its range. Until detailed experiments are done in the laboratory and in the field, we will not know for certain if the California Sister is distasteful from tannic acids or other chemical compounds sequestered by its larvae while feeding on the oak foodplants. The California Sister resembles Lorquin's Admiral but can be readily distinguished by the lower placement of the orange forewing patch away from the outer edge of the forewing, and the blue lines on the ventral surface of the wings. It is found throughout the state and two subspecies have been credited to our fauna. Elsewhere, the species flies from Oregon and the southern Great Basin through Arizona to Texas and south into Mexico. Scott (1986) places it in the genus *Limenitis*, but there are generic-level adult and larval differences between the Holarctic *Limenitis* and the large neotropical genus *Adelpha*.

a. *A. b. eulalia* (Doubleday and Hewitson)

DIAGNOSIS: This is the largest of the *bredowii* subspecies, with expanded marginal and submarginal lunules, a well-developed broad blue band on the outer white border of the ventral forewing and hindwing, and a wider orange apical patch that is roughly quadrangular. The discal brown area on the ventral hindwing is redder than in *A. b. californica*.

ORIGINAL DESCRIPTION: Doubleday and Hewitson, *Gen. diurn. Lepid.*, 1: pl. 36, fig. 1 [1842].

TYPE LOCALITY: "Mexico". Holotype in British Museum.

DISTRIBUTION: Within California this subspecies is found in several ranges of the eastern Mojave Desert, namely, the New York Mountains, the Mid Hills, the Providence Mountains, and the Granite Mountains north of Amboy. A stray specimen was taken in the Coxcomb Mountains (where no oaks occur) at the northeastern end of Joshua Tree National Monument. From California it ranges eastward through Arizona, New Mexico, and western Texas, southward into central Mexico.

ELEVATION RANGE: Our populations are found in a range from approximately 4,500' elevation to 7,000' elevation, with the majority of individuals taken between 5,500-6,500' elevation.

HABITAT AND PLANT COMMUNITIES: This subspecies is typically found in stands of *Quercus chrysolepis* Liebm. (Golden Oak), an oak which grows on slopes and in canyons of

the desert ranges in the upper portions of the Pinyon-Juniper Woodland plant community.

PHENOLOGY: This subspecies is apparently bivoltine, with a brood in late May, June, and early July, and then another in September and early October.

FOODPLANTS: The foodplant of *eulalia* populations in our area is *Quercus chrysolepis* Liebm. (Fagaceae); *Q. turbinella* Greene, a scrub oak found in the New York Mountains may possibly be used rarely (J. F. Emmel, unpublished data)..

b. *A. b. californica* (Butler)

DIAGNOSIS: A somewhat smaller subspecies which is considered the most widely known and most distinctive race in a review of *Adelpha bredowii* subspecies by Carpenter and Hobby (1944). This subspecies, *californica*, differs from the other subspecies by having a pentagonal orange apical patch on the forewing, and having a white band on the hindwing that is broader than usual and less sinuous in outline. It also has a fainter development of the marginal and submarginal blue lunules; in fact, on the forewing they are replaced by faint linear markings. Carpenter and Hobby (1944) note a further difference on the undersurface of the hindwing where the blue band bordering the white externally is reduced. The white band itself is less strongly edged with black than in any other race, and the whole underside shows less contrast. The brown discal area of the hindwing is much paler than in *eulalia*.

ORIGINAL DESCRIPTION: Butler, *Proc. Zool. Soc. London*, [1865]: 485 (1865).

TYPE LOCALITY: "California". Holotype in British Museum.

DISTRIBUTION: Subspecies *californica* is found from northern Baja California northward to Oregon. It is found primarily west of the Sierran-Cascade axis, although there are records for the east slopes of these ranges. It does not extend into the desert areas. This subspecies is also found on Santa Cruz Island.

ELEVATION RANGE: From sea level to approximately 8,000' elevation in the mountains, with the majority of records below 6,000' elevation.

HABITAT AND PLANT COMMUNITIES: The butterfly is typically found on slopes or in canyon bottoms where the oak foodplant species abound, within the following plant communities: Northern and Southern Mixed Evergreen Forest, Northern and Southern Oak Woodland, Foothill Woodland, Mixed Chaparral, and Riparian Woodland.

PHENOLOGY: Populations in California are apparently at least bivoltine with a spring brood in May and June and then a summer brood, or perhaps two summer broods, with captures recorded from July to early November. The species overwinters as a half-grown larva.

FOODPLANTS: The following species in the family Fagaceae have been recorded for *A. b. californica*: *Quercus chrysolepis* Liebm. (the principal host), *Q. agrifolia* Nee, *Q. vaccinifolia* Kell., *Q. douglasii* H. & A., *Q. wislizenii* A.DC., *Q. kelloggii* Newb., and *Castanopsis chrysophylla* (Dougl.) A.DC. (). Thomas Dimock (personal communication) notes that confined ovipositing females prefer *Quercus dumosa* Nutt. over *Q. chrysolepis*; the larvae will feed on either species without a particular preference.

59. *Myscelia cyananthe* C. & R. Felder

See **Appendix** for the one record of this species in California.

Subfamily *Nymphalinae* Swainson

60. *Anartia jatrophae* (Johansson)

See **Appendix** for the one record of this species from Inyo County in California.

61. *Junonia coenia griseus* Austin and Emmel

DIAGNOSIS: This species, the well-known common Buckeye with its large multi-colored ocelli, occurs throughout the state. Its light brown ground color with large ocelli are unmistakable.

ORIGINAL DESCRIPTION: Austin and J. Emmel, *Systematics of Western North American Butterflies Contributions in Science* : 1998.

TYPE LOCALITY: Los Angeles, California. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This nymphalid is a "weedy species" with widespread distribution throughout most of the state. The only area in which it is scarce are the desert areas; otherwise, it is frequently common in the lower elevations, particularly in areas west of the Sierran-Cascade axis. Whether permanent populations are established in all of these areas remains to be investigated. Because the species is so vagile, virtually all populations in our state may only be transiently established ones. This species has been found also on at least several of the Channel Islands, including Santa Catalina Island. The populations in the western United States differ consistently from those in the East, and were recently named (Austin and Emmel, 1989). This subspecies extends eastward as far as .

ELEVATION RANGE: Most of our records are from below 7,000' elevation, but this species has been recorded at over 9,000' elevation in the Inyo Mountains. The butterfly becomes progressively more abundant as one approaches sea level.

HABITAT AND PLANT COMMUNITIES: This vagile species is found in many habitats and plant communities; however, it tends to concentrate in Riparian situations, canyon bottoms, or in lowland areas such as valley bottoms, vacant lots, etc.

PHENOLOGY: Captures are recorded for virtually every month of the year, with an apparent peak abundance in the summer and early fall months. This species is definitely multivoltine and may breed virtually continuously throughout the year at least in the coastal lowlands of southern California, with a slowdown during the winter months.

ADULT BEHAVIOR: The Buckeye is a pugnacious butterfly, commonly defending a territory around its favorite perching site. It flies with darting aggressive behavior toward any passing butterfly. It may perch most commonly on the ground, but some males will perch preferentially on low vegetation as well. In other areas of the United States (e.g., Florida) and in drier tropical areas, the adults may enter reproductive diapause during the dry season, and stop spermatogenesis and oogenesis until the

resumption of rains. Whether this physiological change in behavior occurs in any California populations is something that should be investigated. The adults are known to live for several months during reproductive diapause in northern Florida.

LIFE HISTORY: The short stout egg is dark green. The mature larva is dark brown to black, with longitudinal stripes of pale yellow spots and rows of black branching spines. At the corners of the head occur two anteriorly pointing spines. The pupa is usually pale wood brown, with various mottlings of other colors.

FOODPLANTS: *Plantago erecta* Morris and *P. lanceolata* L. in the family Plantaginaceae are among the principal hosts in California. Numerous species of Scrophulariaceae are also used. In California, documented foodplants in this latter family include *Mimulus* species, *Antirrhinum* species (garden snapdragon), *Maurandya antirrhiniflora* Humb. & Bonpl. ex Willd., *Orthocarpus* species, and *Cordylanthus* species (J. F. Emmel, unpublished data). Additionally, the following species in the family Verbenaceae have been recorded as hosts within California: *Lippia lanceolata* Michx. and *L. nodiflora* Michx. Additionally, there is at least one documented record of the species using *Epilobium adenocaulon* Hausskn (family Onagraceae). Shapiro (1978) has found it on an introduced Mediterranean weed, fluellin [*Kickxia spuria* (L.) Dumort], growing in large mats in an abandoned roadway at Davis, Yolo County. This prostrate perennial plant is in the family Scrophulariaceae and is closely related to snapdragon. This common Buckeye species is also notable for being relatively easy to rear on an artificial diet composed of augur and various nutrients (Carolina Biological Supply House).

CHROMOSOME NUMBER: $n = 31$ (Emmel and Eliazar, unpublished). This species also has $n = 31$ in Mexican populations (Maeki and Remington, 1961b).

SIMILAR SPECIES: See discussion under the following species.

GEOGRAPHIC AND SEASONAL VARIATION: There is apparent seasonal variation between individuals flying during times of the year when there is a short photoperiod versus times with a long photoperiod. Individuals flying during the spring through early fall months tend to have a tan underside, whereas winter-flying individuals have a reddish cast to the underside which has been called form "rosa". Whether this reddish cast is due to short photoperiod, cooler temperatures, or a combination of both conditions, remains to be worked out. There is no geographic variation of populations within California; however, the *J. coenia* populations of the western states are consistently different in phenotype from populations of the eastern United States, and were recently named (Austin and Emmel, 1989).

GENERAL REMARKS: This is a member of a worldwide genus, with at least several species found in every tropical and sub-tropical area of the world. In the continent of Africa, especially, each species frequently shows remarkable seasonal changes in color form between the wet and dry seasons, even changing from a predominantly brown dorsal ground color to a bright blue and black ground color in the case of several species.

Junonia coenia has been fed to a number of species of birds in feeding experiments as a control carried out in Trinidad by Lincoln P. Brower and associates. In these experiments the Buckeye was totally palatable to several tropical bird species.

62. *Junonia evarete nigrosuffusa* Barnes and McDunnough

- DIAGNOSIS: This is a dark Buckeye species with small ocelli, occasionally found in the fall months in the eastern Mojave Desert or along the Colorado River in our state.
- ORIGINAL DESCRIPTION: Barnes and McDunnough, *Canadian Entomologist*, 48: 222 (1916).
- TYPE LOCALITY: "Palmerlee, Babaquivera Mountains, Huachuca Mountains, Arizona". Syntypes in U. S. National Museum.
- DISTRIBUTION: Subspecies *nigrosuffusa* is found from southern Arizona to Texas, extending south to central Mexico and southern Baja California. It barely enters our area by occurring sporadically either in the Colorado River Valley or in the ranges of the eastern Mojave Desert. There are no permanently established populations in California, and the species apparently only appears here when it experiences years of abundance in its more usual habitat to the southeast.
- ELEVATION RANGE: Within our area, adults have been collected or sighted between 4,000 and 6,000' elevation in the eastern Mojave Desert mountains. In the Colorado River Valley, the elevations of capture sites range between near sea level and approximately 1,000'.
- HABITAT AND PLANT COMMUNITIES: The butterfly is usually encountered in riparian or canyon bottom situations within the desert mountains or along the Colorado River, in the following plant communities: Desert Riparian Woodland, Desert Microphyll Woodland, Creosote Bush Scrub, Mixed Desert Scrub, and Pinyon-Juniper Woodland.
- PHENOLOGY: All records for this species from our area are for the months of August, September, or October, again suggesting introduction into our area during the summer months from expansion of populations to the southeast.
- ADULT BEHAVIOR: Adult behavior is much like that of *J. coenia*, except that adults are even more wary and aggressive, being disturbed very easily and much less readily approached by the collector than is the closely related Buckeye.
- LIFE HISTORY: The early stages are extremely similar to those of *J. coenia*. The larvae are somewhat darker than those of *J. coenia*, whereas the pupae show approximately the same pattern as those of *J. coenia*.
- FOODPLANTS: In our area, the only confirmed foodplant is *Maurandya antirrhiniflora* Humb. & Bonpl. ex Willd. (Scrophulariaceae) (J. F. Emmel, unpublished data). Another possible foodplant in our area is *Stemodia durantifolia* (L.) Sw. (Scrophulariaceae). This plant is found in several canyons in the Palm Springs area and in extreme southwestern San Diego County. It is conceivable that occasional transiently established populations of *nigrosuffusa* could become established in these localities. Another plant which may be utilized by this species also on its transient introductions in the state is several species of *Mimulus*, a genus which grows in moist situations such as seeps in the desert regions. Since these plants are much more abundant than the known host *Maurandya antirrhiniflora*, it could possibly serve as an additional host for the species.
- CHROMOSOME NUMBER: n = 31 from northeastern Mexico populations (Maeki and Remington, 1961b).

SIMILAR SPECIES:	The species is somewhat similar to the Common Buckeye in general markings, but is readily distinguished by the much darker ground color and general black suffusion over the wings.
GEOGRAPHIC AND SEASONAL VARIATION:	None known in the few specimens that have been taken in California.
GENERAL REMARKS:	Under unusual conditions of a very wet summer in the southwestern states, this species and <i>J. coenia</i> may become abundant enough that extensive natural hybridization between the two species would occur. This was apparently the case during the summer of 1984, when a number of individuals intermediate in appearance between <i>J. coenia</i> and <i>J. e. nigrosuffusa</i> were reared from larvae taken in the Providence Mountains on <i>Maurandya</i> along with a number of individuals of typical <i>J. coenia</i> . In the usual haunts of this species and under more normal seasonal conditions, the two species are probably able to maintain genetic separation by use of different hosts and behavioral differences. J. Hafernik studied the relationship between the two species in the southern United States (1983) and the reader is referred to his work for a more detailed explanation of this problem.

63. *Vanessa atalanta rubria* (Fruhstorfer)

DIAGNOSIS:	The Red Admiral is instantly recognized by its black ground color, a horizontal red forewing stripe, and vertical marginal hindwing band, plus several white spots and marks on the forewing. Widespread in California, our butterfly is the North American subspecies of the European <i>Vanessa atalanta</i> .
ORIGINAL DESCRIPTION:	Fruhstorfer, <i>Int. Ent. Zts. (Guben)</i> , 3: 44 (1909).
TYPE LOCALITY:	"Mexico", restricted by W. Field, <i>Smithsonian Contributions Zoology</i> , 84: 16-17 (1971). Lectotype in Museum Nationale de Histoire Naturelle, Paris, France.
DISTRIBUTION:	This species is widespread in California but occurs primarily west of the Sierran-Cascade axis. It seems to be of sporadic occurrence in the desert regions of the state. In North America it is found over much of the continent, from Hudson Bay south to Guatemala. As with other species in this subfamily, it tends to be a vagile butterfly, with possibly no permanently established populations in any given locality.
ELEVATION RANGE:	From sea level to approximately 10,000' elevation; the majority of records seem to be from the lower elevations below 3,000'.
HABITAT AND PLANT COMMUNITIES:	The butterfly is usually found in lowland or riparian situations, particularly in the urban areas or lower parts of the foothills and canyons. However, singleton individuals are frequently sighted or taken in situations away from the usual haunts of the species, such as in the desert mountain ranges. The most commonly associated plant community is Riparian Woodland where nettles (the usual host) are abundant.
PHENOLOGY:	Most records are for the months of March to November. However, occasionally individuals are taken in the winter months; presumably, these are adult hibernants which are in reproductive diapause until the following spring. The species is multiple brooded during the warmer months of the year.

- ADULT BEHAVIOR:** This vanessid commonly exhibits territorial behavior. Even in the suburbs, males frequently set up "territories" on sunlit driveways and similar cleared areas which they visit and perch in every afternoon for several weeks on end. Such areas, if they retain their ecological characteristics of lighting and exposure, may be occupied for many years by successive generations, as shown in Florida by .
[TCE: COMPLETE.]
- LIFE HISTORY:** The barrel-shaped, highly ribbed egg is a delicate pale green. The mature larva is black in ground color and is studded with hundreds of whitish velvety points, along with the usual seven rows of spines (all light colored) found in nymphalids. The larva draws the edges of a leaf together to make a tent. The stout pupa is gray with gilded tubercles.
- FOODPLANTS:** The following species in the family Urticaceae are documented foodplants within California: *Urtica dioica* L. var. *holosericea* (Nutt.) Thorne, *U. urens* L., *Soleirolia soleirolii* (Baby's Tears), and *Parietaria floridana* Nutt. (J. F. Emmel, unpublished data). Records for *Humulus lupulus* L. (Moraceae) need further documentation; an attempt to feed young *V. atalanta* larvae on this plant (J. F. Emmel, unpublished data) resulted in high mortality of larvae. The favorite host in California appears to be *U. dioica holosericea*. In the urban areas it is probable that Baby's Tears (*Soleirolia*) is a commonly used host, thus accounting for the butterfly's frequent presence in urban and suburban situations. In the deserts, *Parietaria* is sometimes locally abundant in the shade of the desert shrubs and rocks after heavy rains, and provides a temporary larval foodplant for the occasional transiently established populations there.
- CHROMOSOME NUMBER:** n = 31 (T. C. Emmel, unpublished data).
- SIMILAR SPECIES:** The wing pattern of this species is unique in our California fauna.
- GEOGRAPHIC AND SEASONAL VARIATION:** No geographic or seasonal variation has been detected.
- GENERAL REMARKS:** Occasionally, this species hybridizes with *Vanessa annabella*, producing intermediate forms. These hybrids, named originally as a form ("edwardsii") of *Vanessa atalanta* by Grinnell, are found in the wild with reasonable regularity. Their parental sources are indicated by information from Christopher Henne (*in litt.*), who reported (in Emmel and Emmel, 1973) that he and Charles Ingham reared a group of larvae collected on *Urtica dioica holosericea* Nutt. in the Palos Verdes Hills, and all but three larvae produced *annabella* and *atalanta* adults. One adult was a perfect intermediate in phenotype ("edwardsii") while the two others displayed slight "edwardsii" tendencies in maculation. No *Vanessa cardui* were reared from this group of larvae (previously, *Vanessa cardui* x *V. atalanta* was thought by Comstock, 1927b, and others to be the parental source of the form "edwardsii"). Thomas Dimock (*in litt.*) has tried repeatedly to cage-pair the two species of *annabella* and *atalanta* without success.

64. *Vanessa cardui* (Linnaeus)

- DIAGNOSIS:** The Painted Lady is perhaps the best known, least variable, and yet most cosmopolitan butterfly in the world. Its migrations into the United States from Mexico, and into Europe from North Africa, are well-documented and frequently observed events. The butterfly itself reaches incredible numbers at times in California. The phenotype is characterized by a general orangish-brown ground color with a variegated pattern of dark brown across both wings, and five white spots occupying the tip of the forewing.

- ORIGINAL DESCRIPTION: Linnaeus, *Syst. Nat.*, ed. 10, 1: 475 (1758).
- TYPE LOCALITY: "Sweden" by implication. Holotype in collection of the Linnaean Society of London.
- DISTRIBUTION: This is probably the most widespread butterfly in California. During periods of mass migration, the butterflies fly into virtually every habitat and, like other members of the genus, are extremely vagile. The greatest concentrations of adults are usually seen in the desert regions in the spring, after winters of above average rainfall in the deserts. These individuals then migrate to the west and north, establishing successive waves of generations of butterflies which continue the northward and westward spread of the species as the season progresses. Thus there are apparently no permanently established populations of the species in any given locality. We have records of this species from virtually every county of the state, and it is also found on the Channel Islands of Santa Catalina and San Clemente.
- ELEVATION RANGE: This species is found over a wide elevation range from sea level to over 10,000' elevation. The majority of records, however, tend to be in the lower elevation areas.
- HABITAT AND PLANT COMMUNITIES: The species has been recorded for virtually every plant community in the state and has been found in virtually every habitat.
- PHENOLOGY: The butterfly has been taken in all months of the year in the deserts. It tends to be found more abundantly in the more coastal and montane sections of the state only in the spring through the fall months. During the winter months, the species apparently breeds in the desert areas, feeding primarily on desert annuals. Then, as noted above, migrating successive generations of these individuals tend to spread the species northward and westward through the state as the season progresses. In the late summer and fall months, there is probably a southward or southeastward migration from the montane and coastal areas back to the deserts. Possibly, these adults move further southeastward into Mexico to form the basis for the next year's "overwintering" generation, which will then give rise to the early spring butterflies that will produce the next year's generations. No mass migrations have been noted in the late summer or fall months in California, but the southward migration at this time of year is inferred from the appearance of relatively fresh individuals in the deserts and lower elevation areas bordering the deserts in August and September, after a hiatus of several months in which no individuals are seen in these areas (see also Emmel and Wobus, 1965 for observations of a major fall migration moving to the south in Colorado). Whether an actual reproductive diapause occurs in adults during the winter months has not yet been established.
- ADULT BEHAVIOR: Non-migratory individuals show the following behavior. Males tend to perch on hilltops. Females search out foodplants in oviposition behavior, generally alighting on and ovipositing on the top surface of the leaves. Adults are also frequent flower visitors. For spring migrating individuals, flight is usually noted to be unidirectional and generally in a direction that ranges from west-northwest to north-northwestern. It is unclear whether this directional orientation is governed by wind direction (many flights are noted to be against the prevailing wind from the west), or whether it is an orientation to the position of the sun.
- LIFE HISTORY: The pale green, barrel-shaped egg bears fourteen to nineteen thin and highly vertical ribs. The eggs are laid singly on the upperside of host leaves. The larvae

live in silken nests on the tops of leaves. The mature larva is a delicate violet color and bears five vertical lines at the junction of each segment: yellow, black, black, white, and yellow (anterior to posterior). Black spots occur over the body. There are seven rows of dark spiny tubercles present. The head is black or reddish-brown and is wider than that of *Vanessa annabella*, with many short hairs. The pupa is normally grayish tan to dark brown (may be metallic greenish to whitish-gold), with raised golden points.

FOODPLANTS: This species is extraordinarily polyphagous. *Malva* species (Malvaceae), *Cirsium* thistles (Asteraceae), *Urtica* species (Urticaceae), *Lupinus* species (Fabaceae), *Cryptantha* and *Amsinckia* species (Boraginaceae) and often many other plant species are used in southern California in years of exceptional abundance and migration (Emmel and Emmel, 1973). In northern California, Shapiro (1975b) has recorded the following host plants: ASTERACEAE: *Silybum marianum* (L.) Gaertn., *Cynamra scolymus* L. (artichoke), *Carduus pycnocephalus* L., *Cirsium vulgare* (Savi) Tenore, *Xanthium strumarium* L. var. *canadense* (Mill.) T. & G., *Centaurea solstitialis* L., *Helianthus annuus* L., *Wyethia glabra* Gray; FABACEAE: *Lupinus bicolor* Lindl.; BORAGINACEAE: *Amsinckia douglasiana* A. DC.; MALVACEAE: *Malva parviflora* L., *M. neglecta* Wallr., *M. nicaeensis* All., *Althaea rosea* L., *Sida hederacea* (Dougl.) Torr.; URTICACEAE: *Urtica urens* L.; PLANTAGINACEAE: *Plantago lanceolata* L.; HYDROPHYLLACEAE: *Eriodictyon californicum* (N. & A.) Torr.

CHROMOSOME NUMBER: n = 31 (T. C. Emmel, unpublished).

SIMILAR SPECIES: The Painted Lady, *Vanessa cardui*, resembles *Vanessa annabella* and *V. virginiensis*. It may be distinguished by the fact that its hindwing has four to five distinct eyespots on the underside of the hindwing in contrast to the large spots on *virginiensis* or several indistinct spots on the underside of *annabella*. Additionally, the Painted Lady is normally larger than the other two species and has different markings on the forewing.

GEOGRAPHIC AND SEASONAL VARIATION: Probably because of the tremendous migratory movements occurring frequently in this species, no geographic or seasonal variation appears in *cardui*. With this constant mixing of the gene pool, as in the Monarch, such variation would not be expected.

GENERAL REMARKS: Extensive discussion of the migratory habits of this butterfly have been published and the reader is referred to this rich body of literature for further information (see Abbott, 1950, 1951, 1959; Essig, 1926; Shields, 1975; Tilden, 1962; Williams, 1930, 1938).

In addition to his observations on migration, Abbott (1959) listed a number of records of the attacks of parasitic wasps and flies on *Vanessa cardui*. The species of flies include *Zenillia blanda*, *Frontina archippivora*, and *Chaetogaedia monticola*. Enormous numbers of chalcid wasps have occasionally been observed in areas where *cardui* larvae are abundant.

65. *Vanessa annabella* (Field)

DIAGNOSIS: A species superficially similar to *Vanessa cardui* but distinguished by its somewhat smaller size, blue dorsal hindwing spotting, obscured ventral hindwing spotting, and its squarely angled forewing tip. Until 1971, this species was known in the literature as *V. carye* Hbn.

ORIGINAL DESCRIPTION: W. Field, *Smithsonian Contributions Zoology*, 84: 56-59 (1971).

- TYPE LOCALITY: First valley west of Arroyo Verde Park, Ventura, Ventura County, California. Holotype in U. S. National Museum.
- DISTRIBUTION: The species is extensively found throughout the western United States, rarely in southwestern Canada and in the Rocky Mountain region. It extends southward into most of Mexico. Like its close relative *V. cardui*, *V. annabella* is very widely distributed in California and is found in virtually every habitat and plant community; it occurs on all the California islands. It seems to be a somewhat less vagile species than *cardui* and possibly has more-or-less permanently established populations in some of the lower-elevation coastal areas.
- ELEVATION RANGE: The species is found from sea level to over 10,000' elevation, with the majority of records in the lower elevations of the coastal regions and valleys.
- HABITAT AND PLANT COMMUNITIES: As noted above, this species is found in many plant communities and habitats, with a probable preference for suburban vacant lots and waste areas where introduced *Malva* species are abundant.
- PHENOLOGY: The butterfly is recorded for every month of the year in the coastal areas, with a clustering of records in the late spring and summer months for the montane areas. In the deserts it is found primarily in the winter and spring months, but records for every month of the year are known for the desert regions. There are multiple broods within a given year.
- ADULT BEHAVIOR: The species does not exhibit mass migration like its close relative *V. cardui*. Although there is one report (Sicher, 1953) in the literature of supposedly this species showing a mass migration in March 1952 in the Santa Rosa Mountains, the identification of these butterflies as *Vanessa carye* is undoubtedly erroneous. First, *Vanessa cardui* is known to have migrated in large numbers that year in the very area where this observation took place. Secondly, the observation was made by an eastern U. S. lepidopterist who was apparently driving through the area. No voucher specimens from this mass movement were collected or are known and we assume that the observation refers to *Vanessa cardui* unless proven otherwise by subsequent data.
- Adult male *annabella* display typical perching behavior, which may be on hilltops or in suburban yards, even in sunlit walkways or driveways. Typically, this behavior occurs only during the afternoon hours. Females are usually seen visiting flowers or flying slowly in oviposition behavior near the foodplants.
- LIFE HISTORY: The barrel-shaped, vertically ribbed egg is pale green and is laid singly on the host leaves. The mature larva is quite variable, but is usually blackish with numerous orange blotches. Fine whitish hairs are scattered over the surface. There are seven rows of finely branched spines which vary in color between larvae. The stout pupa is glistening light brown with raised whitish points.
- FOODPLANTS: Documented foodplants for California populations of this species seem to be confined to the families Malvaceae and Urticaceae. In the suburban areas, particularly in vacant lots and waste places, several introduced *Malva* species are used: namely, *M. parviflora* L., *M. nicaeensis* All., and *M. neglecta* Wallr. Frequently, hollyhocks (*Althaea rosea* [L.] Cav.) in suburban gardens are used. Native malvaceous hosts are *Sphaeralcea*, particularly *S. ambigua* Gray; *Sidalcea* species including *S. malvaeflora* (DC.) Gray ex Benth., *S. glaucescens* Greene, *S. oregana* (Nutt.) Gray ssp. *spicata* (Regel) Greene; *Sida hederacea* (Dougl.) Torr.; *Malacothamnus fasciculatus* (Nutt.) Greene. In the Urticaceae, *Urtica dioica* L.

var. *holosericea* (Nutt.) Thorne is used (C. Henne, *in litt.*; J. F. Emmel, unpublished data).

CHROMOSOME NUMBER: n = 31 (T. C. Emmel, unpublished).

SIMILAR SPECIES: See discussion under *Vanessa cardui*.

GEOGRAPHIC AND SEASONAL VARIATION: There is no geographic or seasonal variation in the California populations of *V. annabella*.

GENERAL REMARKS: The former familiar name of this species was *Vanessa carye* Hubner, but Field (1971) found that that name actually applies to a species found in the Andes of South America. *Vanessa annabella* is found from British Columbia east to Alberta and south through all the Rocky Mountain states, California, and Texas into Mexico and Guatemala. The butterfly has a remarkably broad range across southern California, including the Channel Islands, and has even been taken 178' below sea level at Furnace Creek Ranch in Death Valley.

Occasionally, as in *Vanessa cardui* and *V. virginiensis*, unusually colored aberrations are found. These involve disruptions of the normal wing pigmental patterns and two of the more extreme recurrent forms have been named "muelleri" and "letcheri." It is not known if these are aberrations induced by environmental shock (e.g., cold or warm shocked pupa) or true genetic mutations that can be inherited. Shapiro (1973) postulates that they may be caused by a dominant, recurrent mutation, with a gene frequency of about 5 in 10,000 in *annabella* populations. Breeding experiments should be carried out by lepidopterists fortunate enough to run across these forms.

66. *Vanessa virginiensis* (Drury)

DIAGNOSIS: While not as common as its near relatives, the Virginia Lady is readily differentiated from them by the delicate cobweb-like pattern on the underside and the presence of two large ocelli on the ventral surface of the hindwing.

ORIGINAL DESCRIPTION: Drury, *Ill. exot. Ent.*, 1: Index +10-11 (1773).

TYPE LOCALITY: "Virginia", restricted by Field, *Smithsonian Contributions in Zoology*, 84: 49 (1971). The type has been lost.

DISTRIBUTION: This species has been taken throughout the state of California, but very sparingly in the desert regions. Even in its favorite haunts, it is usually somewhat scarce. It ranges across the entire United States and extreme southern Canada, and extends southward to Venezuela and the Greater Antilles.

ELEVATION RANGE: From sea level to approximately 8,000' in the mountains, with most records in the lower elevations, particularly in the coastal areas.

HABITAT AND PLANT COMMUNITIES: Because the asteraceous foodplants occur in a variety of habitats, the butterfly is also found in a number of ecological situations. Most commonly, it is found in either disturbed areas and vacant urban lots or along watercourses. A number of its foodplants are introduced European weeds, which accounts for the presence of the butterfly in "weedy" situations. It has been encountered in most plant communities in the state.

- PHENOLOGY:** This species is multivoltine and has been taken in every month of the year in southern California. Most records for the northern part of the state or higher elevations tend to be for the summer months.
- ADULT BEHAVIOR:** In contrast to the considerable numbers usually encountered of *Vanessa cardui* or *annabella* in favorite habitats, *Vanessa virginiensis* is usually found as a solitary butterfly. They frequently land on thistles and other nectar sources to feed, and sometimes they hilltop in mountain areas. Rather than holding territories, the males seem to prefer to hilltop to locate mates.
- LIFE HISTORY:** The yellowish-green egg is barrel-shaped and has thirteen to sixteen vertical ribs. The mature larva is a light lilac in ground color, with large black patches as "saddles" around the upper five rows of black branched spines. Around the upper five of the seven rows of black branched spines, there is a pair of subdorsal silvery white spots on abdominal segments 2 to 8. The pupa is usually a grayish-white or silvery color, although this may vary from gold or green to a brownish color. The pupa has brown ventral and lateral stripes and many orange points. The adults are said to be the overwintering stage (Scott, 1986).
- FOODPLANTS:** The favored foodplants are in the tribe Inuleae in the family Asteraceae. Three genera in this tribe that are used by *V. virginiensis* are *Gnaphalium*, *Antennaria*, and *Anaphalis*. The following *Gnaphalium* species have been documented in California as foodplants of *virginiensis*: *Gnaphalium palustre* Nutt. (Shapiro, 1975b);
- This butterfly has also been recorded from *Anaphalis margaritaceae* (L.) Benth. & Hook in the San Francisco Bay area (J. F. Emmel, unpublished data). Other recorded hosts are somewhat poorly documented and bear further investigation to be confirmed.
- CHROMOSOME NUMBER:** $n = 31$ (Emmel and Eliazar, unpublished).
- SIMILAR SPECIES:** See discussion under *Vanessa cardui* and *annabella*.
- GEOGRAPHIC AND SEASONAL VARIATION:** Despite the wide geographic range of this species and its occurrence in every season, no detectable subspeciation or seasonal variation has been described in the species.
- GENERAL REMARKS:** This butterfly occupies a remarkably broad range of habitats, extending from the tropics in northern South America and the Caribbean north to the Canadian border. It even strays rarely across the Pacific to Hawaii in the west and across the Atlantic to southwestern Europe in the east, yet it is rarely common anywhere.

67. *Polygonia satyrus satyrus* (W. H. Edwards)

- DIAGNOSIS:** The only one of our four anglewing species that is characterized by a light ground color of the dorsal surface and a mottled brown underside.
- ORIGINAL DESCRIPTION:** W. H. Edwards, *Transactions American Entomological Society*, 2: 374-375 (1869).
- TYPE LOCALITY:** Empire, Clear Creek, Colorado, restricted by F. M. Brown, *Transactions American Entomological Society*, 93: 330 (1967). Lectotype in Field Museum of Chicago, designated by F. M. Brown, *Transactions American Entomological Society*, 93: 331 (1967).

- DISTRIBUTION:** The butterfly is found primarily in montane or foothill areas west of the main Sierra-Cascade axis, although we have records from the Warner Mountains in the extreme northeastern corner of the state and several locations along the east slope of the Sierra Nevada. There are very few Central Valley records (in riparian forests) and occasional specimens are taken as strays on the valley floor. It is absent from the desert regions, including the area of the White and Inyo Mountains in Inyo and Mono counties.
- ELEVATION RANGE:** Records range from sea level to 9,000' elevation, with the majority of specimens being found at lower elevations.
- HABITAT AND PLANT COMMUNITIES:** This species is usually found in riparian situations within a number of plant communities, primarily woodland or forest communities. Along the northern California coast, it is primarily in the Redwood Forest zone. Further inland, it is found in Northern and Southern Mixed Evergreen Forest and Northern and Southern Oak Woodland. In the higher montane areas, it is found in Lower and Upper Montane Coniferous Forest. *Satyrus* does follow Riparian Woodland into the Central Valley of California, such as along the Sacramento River, although populations in these areas have apparently declined precipitously in recent years, primarily due to human-caused destruction of the favored habitats.
- PHENOLOGY:** The adults overwinter and are usually seen on the wing in March or April at the lower elevations and in May or June at the higher elevations. There is one record at the end of January for an adult in southern California. Eggs from overwintering adults produce progeny that emerge in June, July, and August, and at the lowest elevations there may be still a third brood in the late summer or early fall which then becomes the overwintering brood. At the highest elevations of the species' range, it may be only univoltine.
- ADULT BEHAVIOR:** *Polygonia satyrus* prefers moister areas such as canyon bottoms where nettles grow in abundance. The species is pugnacious, territorial, and aggressive, which is typical of our four *Polygonia* species. When it has been disturbed, it goes through a short flight. Then it tends to land with wings closed and head downward. This species also tends to be a somewhat more sun-loving species than the other *Polygonia*, often frequenting a perching site at the top of tall trees. Males will fly for hours in combat around a forest glade, spiralling up, returning to rest, and then flying again. It will come to flowers for nectar.
- In the late afternoon, Mattoon has observed a *satyrus* adult rest on a tree trunk, wings spread wide to catch the remaining warmth of the sun, and then close its wings and crawl in under a piece of loosely hanging bark. In this observation at Los Molinos, Mattoon removed the bark after many minutes had passed and to his astonishment he found the immobile *satyrus* wedged tightly beneath the bark next to a gaudily colored *Vanessa atalanta rubria*. When he pulled more bark off the tree, he found additional *Polygonia* and even a specimen of *Nymphalis antiopa*. In all, almost a dozen nymphalids were found resting under the bark for the night! Presumably hibernant adults of these species utilize similar resting sites for the winter.
- LIFE HISTORY:** The delicate green eggs have highly elevated vertical ribs. The eggs are often laid in stacks of three or four on the underside of a host plant leaf. The ground color of the mature larva is black, but it is heavily mottled with greenish-white as shown in the figure. There is a broad greenish-white dorsal stripe. The very heavily branched spines occur in seven rows and are greenish-white. The black head is

spiny and bears a short branching tubercle on each of the upper corners. The pupa is a shiny gray-brown with several raised golden spots.

The larvae of this anglewing can be easily located by looking for the characteristic changes they make in the appearance of the nettle leaf. The larvae partially sew the proximal edges of the nettle leaf together *beneath* the leaf axis to produce a "hanging tent," in contrast to *Vanessa atalanta* larvae (also nettle-feeders) which sew the entire edges of the nettle leaf together and often do this *above* the leaf axis.

FOODPLANTS: Nettle, *Urtica dioica* L. var. *holosericea* (Nutt.) Thorne (Urticaceae). A second documented host in northern California is *Humulus lupulus* (L.). This species has also apparently been recorded on *Salix* (Salicaceae) in southern Arizona; further documentation of the use of this unusual host for this species is warranted.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: The brown striated undersides and the U-shape of the comma mark on the underside of the hindwing distinguishes *satyrus* from any of our other *Polygonia* species.

GEOGRAPHIC AND SEASONAL VARIATION: At the time of the original species description of *Polygonius satyrus* by W. H. Edwards (1869), Edwards had before him specimens from each of the three major geographic areas where subsequent subspecies were described. F. M. Brown (1967) lists these specimens in the Edwards collection from southern Colorado, Washington Territory, and Mendocino, California. Edwards treated all of this material as one species in describing *Polygonia satyrus* in 1869. In 1905, William Greenwood Wright (*Butterflies of the West Coast*, p. 172, 1905) described *Polygonia chrysoptera* as a species distinct from *satyrus* in the mountains of central California. The precise localities given with the color illustrations in his book are Lake County, Lake County, and Mendocino County, California in the month of June, 1894. Finally, dos Passos (*Transactions of the American Entomological Society*, 95: 155-158, 1969) described the third taxon, *Polygonia satyrus neomarsayas*, from Brewster in Washington State. In the original description of this last subspecies, Dos Passos (1969) indicates a distribution extending "along the west coast in the mountains in the states of California, Oregon, and Washington, and the Province of British Columbia. Its habitat then extends eastward in southern Canada through the Provinces of Alberta, Saskatchewan, Manitoba, Ontario, Quebec, and the maritime province of New Brunswick as far as Newfoundland. In the northern United States it occurs in Montana, Idaho, and probably in other border states." Thus, it would appear from the above review that there would be three geographic subspecies of *Polygonia satyrus*: *P. s. satyrus* from the Rocky Mountains, *P. s. chrysoptera* from southern and central California, and *P. s. neomarsayas* from northern California and the Pacific Northwest. Unfortunately for this neat picture, all three phenotypes can be found in the same population area, even on the same day, throughout this general range of the species. Hence, we have decided to treat the California material as indistinguishable from nominotypical *satyrus* from Colorado until further study warrants a separation.

GENERAL REMARKS: The distribution of *P. satyrus* includes the Sacramento Valley, giving *satyrus* the widest distribution range of any of our *Polygonia* species, although outside of the

redwood zone, it is never anywhere as common as *P. zephyrus*. Occasionally, the adults are observed flying in situations outside their normal habitat in unidirectional flight, suggesting that at times they may show migratory behavior. Such an event was witnessed by the first two authors in the Jurupa Mountains west of Riverside in southern California on March 28, 1978. Two individuals of this species were observed flying in a west-northwesterly direction in unidirectional flight on open slopes of Inland Sage Scrub, and both were captured while flying this way. No possible foodplants were noted in the immediate area.

68. *Polygonia faunus* (W. H. Edwards)

ADULT BEHAVIOR: Adults display the typical, seemingly aggressive, territorial behavior of all the other *Polygonia* species. After flying about in "combative behavior," they return to the general area they started from and perch again. However, *faunus* in general tends to remain close to its breeding area and does not seem inclined to range widely. During hot mid-summer afternoons, Mattoon has seen adults retire to the shade of the forest floor in the dense chaparral understory and remain there with restricted activity, principally in the shade. If this factor is common to the daily activity of *rusticus*, it could account for the relatively fresh adult wing condition being displayed long after adult emergence begins. *P. f. rusticus* will nectar at flowers such as rabbitbrush, *Chrysothamnus nauseosus* (Pall.) Britton, in the Warner Mountains. Just north of the California state border in Oregon, Mattoon has observed *rusticus* frequenting roadside mud puddles in a Canadian zone forest glade.

LIFE HISTORY: The eggs are green and are laid singly on either the bottom or top of host plant leaves and twigs. Later instar larvae are easily located by looking from beneath the host towards the sky, to spot the singly situated, silhouetted larvae resting on the translucent azalea leaves. The mature larva is black, bearing orange on the dorsum of the thorax and first two abdominal segments. The remaining abdominal segments bear white with black oblique dashes dorsally, with cream and black transverse lines between segments, a wavy orange line containing dark orange spines above the spiracles, and a wavy orange lateral line containing white spines. The head is black, with an orange "W" on the front and two short black horns. The pupa is light brown or dark gray with gold spots, and often it bears an orange flush in the saddle. There are two long head horns and many subdorsal bumps. The shape is more elongate than in other *Polygonia* pupa. This species hibernates in the adult stage.

PARASITES / PREDATORS: *Polygonia faunus* is never common even in a breeding population, and in nearly every location we have for *faunus* in northern California, the habitat is also an overwintering site for large populations of the ladybird beetle, *Hippodamia convergens* (family Coccinellidae), which are on the wing and swarming over and mainly limited to the warmer sunlit portions of the host, at the time of most first-instar larval development. Eileen Mattoon (personal communication) postulates that *rusticus* population size is being controlled in part by predation of the tiny first-instar larvae. This speculation, based on the number of unoccupied but apparently tiny feeding sites for the species, suggests a higher survival rate for larvae situated in the more sheltered area of banks of rocks or shaded areas of the host, until they become protected by increased size.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: This is a darker and more blackish *Polygonia* than our other three species.

GEOGRAPHIC AND SEASONAL VARIATION: No significant seasonal variation has been noted in the two broods. From the standpoint of geographic variation, specimens of *rusticus* from the Warner Mountains average smaller than Sierra Nevada specimens.

GENERAL REMARKS: When our understanding of the ecological requirements of *faunus* becomes clearer, it should be possible to locate additional colonies and more satisfactorily fill in the distribution of *faunus* in northern California. At present, the scattered known localities at higher elevations present no evidence to explain why populations are so restricted and disjunctly distributed in otherwise continuously appropriate-appearing habitat.

The Green Comma occurs from coast to coast across Canada and north into Alaska as well as south through the Pacific Northwest, the Rocky Mountains, and the Appalachians. While the typical subspecies does not occur in our state, two other races of this species are found here.

a. *P. f. rusticus* (W. H. Edwards)

DIAGNOSIS: Edwards named this butterfly because of its rusty black fulvous underside, considering *rusticus* to be an appropriate name (Brown, 1967). It is a medium-large anglewing usually found in riparian situations near stands of *Rhododendron* shrubs in coniferous forests.

ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions of the American Entomological Society*, 5: 107-108 (1874).

TYPE LOCALITY: "--- at Big Trees, California, and on Vancouver's Island." Restricted to Big Trees, California by dos Passos in Brown (1967). Lectotype in American Museum of Natural History, designated by F. M. Brown, *Transactions of the American Entomological Society*, 93: 343-344 (1967).

DISTRIBUTION: Subspecies *rusticus* is found on the west slope of the Sierra Nevada, from Tulare County northward to the Warner Mountains of Modoc County, and westward through the Mount Shasta and Klamath Mountains region. From here it extends northward into the Pacific Northwest.

ELEVATION RANGE: In northern California we have records from 1,800' to 8,000' elevation, but most commonly the species is encountered in the elevation range of 2,200' to 4,500' elevation.

HABITAT AND PLANT COMMUNITIES: This species is typically found in riparian situations inside Lower Montane Coniferous Forest on the west slope of the Sierra Nevada and in the Warner Mountains. In the Sierra Nevada, it is frequently associated with stands of *Rhododendron occidentale*, the most widely used foodplant. Also, *Salix* species are usually present and certain willow species serve as foodplants for this species in other localities.

PHENOLOGY: The adults overwinter in reproductive diapause, becoming sexually mature and active in the early spring months. Adults are first taken on the wing in the months of April and May at the lower elevations, and in May and June at slightly higher elevations. These then give rise to a summer brood which emerges in June, July, or August, depending on elevation and exposure, and this brood (at least at the lower elevations) in turn gives rise to a second generation which emerges in the late summer and becomes the overwintering generation for the next year.

FOODPLANTS: In California, principally Wild Azalea, *Rhododendron occidentale* (T. & G.) Gray (family Ericaceae) (S. Mattoon and J. Emmel, unpublished data). Bauer (personal communication) has found larvae on *Salix scouleriana* Barr. (Salicaceae) at South Lake Tahoe. *Salix* is likely used in the Warner Mountains, where *Rhododendron* is absent.

b. *P. f. fulvescens* Emmel, Emmel, and Mattoon

DIAGNOSIS: The dorsal surface of the wings of this recently described subspecies are golden orange, with submarginal spots being golden yellow and reduced in size from those seen in typical *rusticus*. On the ventral surface, the amount of white scaling over the marbled pattern of tannish-gray scales is greatly reduced from that seen in *rusticus* and the amount of dark scaling is reduced, rendering an overall pattern of less contrast in the light and dark areas of the wing than is seen in typical *rusticus*. The ventral surface of the hindwing is similar to the forewing pattern except for bearing a chalky-white "C" mark in the distal part of the cell.

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 139-140 (1998h).

TYPE LOCALITY: Pescadero Creek, 400' elevation, near Portola State Park, San Mateo County, California. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This subspecies is found in the Coast Ranges from Santa Cruz County northward to at least Napa and Sonoma counties. North of here, there is probably a blendzone with subspecies *rusticus*, which is known to occur in the Klamath Mountains region.

ELEVATION RANGE: From 300 to 1,000' elevation.

HABITAT AND PLANT COMMUNITIES: This butterfly prefers deep moist canyons in the Redwood Forest plant community, where scattered plants of *Rhododendron occidentale* occur along the creeks.

PHENOLOGY: There are two broods. Overwintering adults begin flying in March and April. The progeny of these adults emerge in June and July, and this emergence gives rise to immatures which then develop and emerge as adults in late August and September, to become the overwintering adults for the next season.

FOODPLANTS: *Rhododendron occidentale* (T. & G.) Gray, Western Azalea (family Ericaceae), serves as a host (Emmel, Emmel, and Mattoon, 1990).

69. *Polygonia zephyrus* (W. H. Edwards)

DIAGNOSIS: A medium-sized anglewing with mottled predominantly gray undersides on both wings.

ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Entomological Society*, 3: 16 (1870).

TYPE LOCALITY: Virginia City, Storey County, Nevada, restricted by F. M. Brown, *Transactions American Entomological Society*, 93: 347-349 (1967). Lectotype in Carnegie Museum, designated by F. M. Brown (1967).

DISTRIBUTION: This species is widespread in the higher mountains of the state, from the San Jacinto Mountains and the Transverse Ranges in the southern part of the state,

northward through the Sierra Nevada to the Mount Shasta region, the Klamath Mountain Assemblage, and south in the North Coast Ranges to approximately northern Napa County. It is also found in the Warner Mountains and in the White Mountains of Inyo and Mono counties.

- ELEVATION RANGE: Our records show a range from 700' to over 10,000' elevation. The majority of our records seem to be in the 5,000' to 10,000' range.
- HABITAT AND PLANT COMMUNITIES: It is frequently encountered flying over open slopes, in wooded areas or in riparian situations within forests, primarily within the following plant communities: Lower Montane Coniferous Forest, Upper Montane Coniferous Forest, Subalpine Forest, and Montane Dry Meadow.
- PHENOLOGY: As with other *Polygonia*, the adults overwinter. Adult activity of these hibernants can be noted at the lower elevations as early as February in some years. These adults then mate and lay eggs, producing the next generation which begins emergence in June at the lower elevations, or late July through August at the higher elevations. The adults produced in June or early July at lower elevations may give rise to a second generation in late summer. At the higher elevations the species is probably univoltine.
- ADULT BEHAVIOR: The males of *Polygonia zephyrus* appear territorial, displaying the typical aggressive, pugnacious behavior in *Polygonia* of darting out often to "combat" invaders within the boundaries of a fairly broad territory. They return repeatedly to one of several perching sites. Under these conditions it is a wary insect, somewhat hard to capture. But as an avid nectaring species, especially in open dry meadows, hillsides or forest glades, it is easily captured while preoccupied in its visits to mint flowers (*Monardella* species) or rabbitbrush (*Chrysothamnus nauseosus* [Pall.] Britton).
- Oviposition behavior has been observed on *Rhododendron occidentale* (T. & G.) Gray by Mattoon. The female landed on the host and spent considerable time crawling or hopping around in search of an appropriate egg-deposition site. Flight up and around the area was then resumed for a brief period, followed by a descent and then, seemingly without hesitation or interruption of flight, the female deposited a solitary egg on the margin of an azalea leaf and promptly departed from the area.
- LIFE HISTORY: The eggs are green, laid on the host leaves. The mature larva is basically black, with a whitish-yellow dorsal pattern. The four lateral rows of branching spines are black and the three dorsal rows are partly reddish and partly white. The pupa is shaded with olive and salmon, and has several silver spots in the dorsal region.
- FOODPLANTS: The principal hosts appear to be species of *Ribes* in the family Grossulariaceae (formerly in the Saxifragaceae). Species documented for the butterfly in California include *R. cereum* Dougl., *R. montigenum* McClat., *R. divaricatum* Dougl. var. *inerme* (Rydb.) McMin., and *R. roezlii* Regel. Additionally, the species frequently uses *Rhododendron occidentale* (T. & G.) Gray (family Ericaceae). David Bauer (personal communication) has found larvae on alder (*Alnus* species, family Betulaceae) at Lake Tahoe in the northern Sierra Nevada. The two favored hosts, however, appear to be *Ribes cereum* and *R. montigenum*.
- CHROMOSOME NUMBER: n = 31 from Colorado material (Emmel, Eliazar, and Harris, in press, and Maeki and Remington, 1961b).

- SIMILAR SPECIES:** This butterfly resembles most closely *Polygonia oreas*, but may be differentiated from it by the grayer underside, its largely allopatric range, and its distribution at usually higher elevations.
- GEOGRAPHIC AND SEASONAL VARIATION:** There is relatively little adult phenotypic variation in *zephyrus*, compared to that found in *satyrus*. The more brownish appearance on the ventral underside in populations found in the Klamath Mountains (Shapiro, *in litt.*) is rather subtle and also highly variable, and it is noted also in the phenotype of adjacent North Coast Range mountains. This more brownish appearance tends to be seen more often in overwintered, worn adult specimens.
- Scott (1986) has treated *zephyrus* as a subspecies of *Polygonia gracilis* (Grote and Robinson), a species which occurs across North America from eastern Canada northwest to Alaska but does not penetrate the western U. S. He notes that the two species have the same narrow downward curved gnathos and broad tegumen in the male genitalia, and their allopatric ranges fit nicely together. The entire genus *Polygonia* needs to be carefully revised by someone. In the meantime, we follow the more conservative treatment espoused by all other authors and do not follow Scott in synonymizing the two species.

70. *Polygonia oreas oreas* (W. H. Edwards)

- DIAGNOSIS:** A *Polygonia* with a darker underside, often blackish-gray, with little contrast between the proximal and distal sections of the wing.
- ORIGINAL DESCRIPTION:** W. H. Edwards, *Transactions American Entomological Society*, 2: 273 (1869).
- TYPE LOCALITY:** "California". Neotype in the Carnegie Museum, designated by dos Passos and F. M. Brown, *in* F. M. Brown, *Transactions American Entomological Society*, 93: 354-355 (1967).
- DISTRIBUTION:** The species is found from the west slope of the extreme northern Sierra Nevada northward through the Mount Shasta region into the Klamath Mountain Assemblage, and southward in the North Coast Ranges, thence south in the South Coast Ranges as far as San Luis Obispo. There are unquestionably many more populations of this species than our records would indicate. The paucity of records is undoubtedly due to collecting artifact, the result of collectors not exploring the usual haunts of this species.
- ELEVATION RANGE:** The species ranges from near sea level to as high as 7,500' elevation. However, the majority of records are below 3,500'.
- HABITAT AND PLANT COMMUNITIES:** The usual habitat of this species is along very moist riparian habitats within Redwood Forest, North Coastal Coniferous Forest, Northern Mixed Evergreen Forest, and Riparian Woodland; sometimes the species is taken in a Montane Wet Meadow habitat such as near Quincy (Plumas County).
- PHENOLOGY:** Overwintering adults begin flying in February or March at the lower elevations. By mid to late April, eggs or larvae from these adults can be found on the species' foodplants. These give rise to adults which emerge in June and early July, which in turn produce a second generation in late summer or early fall which then overwinters for the following season.

- ADULT BEHAVIOR:** We have only limited observations of adults. In one instance a male was observed nectaring on *Monardella* species. In the usual riparian habitats, males will set up perching "territories" and fly in partially sunlit glades near the foodplants of this species. Female oviposition behavior has not yet been observed.
- LIFE HISTORY:** Scott (1986) describes the *oreas* larva from California as follows: "Dark brown, yellowish-orange on top of the thorax and abdomen segments 1 and 2, orangish-yellow on top of 3 and 4, then pale yellowish on top of 5-8, with blackish V-marks around the mid-dorsal spines of segments 3-8 (these broader and much more strongly connected into capital U's than those of *P. gracilis*), a larger brown mid-dorsal triangle within each capital "V", black and cream transverse rings between segments, a wavy orange line above the spiracles containing orange spines, and a wavy pale-yellow lateral line containing pale-yellow lines, the dorsal thoracic spines black (orange in *gracilis*) with pale bases; head black, with many tiny orange cones, a large orange "W" on the front, orange surrounding both black eyepatches, and an orange notch between two spiny black horns." The pupa is a mottled brown, with reddish-brown on top of the second and third abdominal segments and gold or silver spots in the saddle; the abdomen is marked with a brown-edged mid-dorsal line and tan-edged lateral and mid-ventral band, the dark band on the wing often being greenish. The adult stage hibernates.
- FOODPLANTS:** For California, the principal foodplant is *Ribes divaricatum* Dougl. (Grossulariaceae) (J. F. Emmel, unpublished data). The species is also strongly suspected to use *R. divaricatum* Dougl. var. *inerme* (Rydb.) McMin., a gooseberry which is found in fair abundance in the extreme northern Sierra Nevada, and the southern Cascade Range region in southwestern Lassen County and eastern Shasta County. Scott (198) found larvae on another *Ribes* (unidentified as to species, but not *divaricatum*) in Sonoma County.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** See discussion under *Polygonia zephyrus*.
- GEOGRAPHIC AND SEASONAL VARIATION:** Along the northern border of California, occasional specimens are taken which closely resemble the Pacific Northwest subspecies *P. o. silenus* W. H. Edwards. Because specimens representing fairly typical *oreas* are also taken in the same general areas, we conclude that this represents a blendzone area between these two subspecies. Possibly further exploration in the extreme northwestern part of California will produce "pure" populations of *silenus*. No significant seasonal variation has been noted in the two broods.
- GENERAL REMARKS:** The species normally occurs in habitats that are generally depauperate for other butterfly species, and most collectors spend little time exploring these areas. Hence, *P. oreas* tends to be very rare in collections and often is taken as singleton specimens.

71. *Nymphalis milberti furcillata* (Say)

- DIAGNOSIS:** A distinctive small nymphalid with broad orange-red outer bands separated from an inner dark brownish-black band by a diffuse yellow stripe. The undersides of the wings are quite blackish and slightly mottled.
- ORIGINAL DESCRIPTION:** Say, *American Entomologist*, 2: pl. 27 (1825).
- TYPE LOCALITY:** Vicinity of Fort William, "North West Territory". Type apparently lost.

- DISTRIBUTION:** The species is found in the higher mountains of the state, from the Klamath Mountain region eastward to the Warner Mountains of Modoc County, and southward through the Sierra Nevada to the Transverse Ranges in southern California. At the southern end of its range, its occurrence seems to be sporadic, sometimes being established for several years in a row in the San Bernardino Mountains but then becoming seemingly absent for a period of years in the same areas. It is also found sparingly in the Panamint Mountains and in the Inyo-White Mountains of Inyo and Mono counties. There is a single record for a worn individual taken on Mount Palomar in San Diego County at the southern end of the state. This undoubtedly represents a transient introduction into the area.
- ELEVATION RANGE:** Our records range from near sea level to 12,500' elevation, with the majority of records above approximately 5,000'.
- HABITAT AND PLANT COMMUNITIES:** The butterfly is found or encountered in a variety of plant communities in the mountains, including Montane Wet and Dry Meadows, Lower and Upper Montane Coniferous Forest, Subalpine Forest, Great Basin Coniferous Woodland, Mountain Sagebrush Scrub, and Arctic-Alpine Cushion Plant communities.
- PHENOLOGY:** Overwintering adults appear in May or June, producing a summer generation which then appears in August or September and finally overwinters for the following year. In some lower elevation localities, a second generation may be produced.
- ADULT BEHAVIOR:** In Colorado, *Nymphalis milberti* has been observed to be a semi-migratory species (Scott, 1986); adults apparently move from lower altitudes, where they breed, to higher altitudes in July and August, and then apparently return to lower mountain areas in September to hibernate. Adults are known to visit flowers readily and sometimes they drink sap. Males may be found perching on low shrubs and wet riverbottom areas, where they await passing females at mid-day.
- LIFE HISTORY:** The conical green egg has a round top and flattened base, with eight or nine vertical ribs. Eggs are laid in clusters of up to 700 eggs on the underside of the host leaves. Ovipositing females have a preference for dense patches of nettle in full sun, usually in dryish meadows. When young, the larvae are gregarious and live in a silk nest near the top of the plant. The older larvae are usually solitary and may form a rolled leaf tied with silk. The mature larva is generally black, covered with white hairy dots, with a greenish-yellow lateral line and a higher, bright orange stripe. Five upper rows of branching spines are black while the lowest row on either side is yellowish. The pupa is highly variable in color, ranging from an off-white to blackish, and is semi-spiny, somewhat like that of *Nymphalis antiopa*.
- FOODPLANTS:** Within California, the only known host is *Urtica dioica* L. var. *holosericea* (Nutt.) Thorne (Urticaceae), common nettle.
- CHROMOSOME NUMBER:** n = 31 in Colorado material (Emmel, Eliazar, and Harris, unpublished).
- SIMILAR SPECIES:** No similar species occur in our area. The larger California Tortoise-shell, *Nymphalis californica*, has much softer orangish-brown coloration extending across the wing, except at the black border.

GEOGRAPHIC AND SEASONAL VARIATION: None has been noted within our populations. This species occurs across the United States in two known subspecies, and ours is found throughout the west.

GENERAL REMARKS: Lepidopterists living in California should watch for seasonal migratory movements of this species, as has been found in Colorado for mountain populations. Such seasonal migratory movements for *Nymphalis californica* may have been found in the Sacramento Valley area by Shapiro (1975b), and should be looked for in other areas as well.

72. *Nymphalis californica californica* (Boisduval)

DIAGNOSIS: A somewhat larger, medium-sized *Nymphalis* that has a broad blackish-brown border with the remainder of the wings orangish-brown to the body.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 366 (1852).

TYPE LOCALITY: "California". Type in the U. S. National Museum.

DISTRIBUTION: The butterfly is widespread through the state due to its migratory habits. We have records from the mountains of southern California northward through both the Coast Ranges and the Sierra Nevada to all the mountain areas of northern California. There are also records for the Inyo-White Mountains region and the Panamint Range in Inyo County, as well as a single record for Clark Mountain in the eastern Mojave Desert. It is still somewhat poorly understood as to which localities represent areas where the species is permanently established within the state, and which localities represent only transient records for migratory individuals. The main centers of distribution for the butterfly, however, seem to be in the northern Sierra Nevada and Mount Shasta region; in these areas it is consistently taken year after year, although not always in the large numbers of migration years.

ELEVATION RANGE: We have records from near sea level to over 10,000' elevation. Most of the breeding populations in the northern part of the state seem to be in an elevation range of about 4,000' to 7,500' elevation.

PHENOLOGY: In central California, Shapiro (1974, *in litt.*) reports that adults overwinter in the Coast Ranges and Sierran foothills through March. These adults produce the first generation of non-overwintering adults flying in late May to early June, which migrates eastward and upslope across the Central Valley (where the butterfly does not breed, there being no *Ceanothus*) to the higher Sierra Nevada. These migrants then produce a second generation flying in July and August, which often produces a third generation flying in late September to October. In early fall, a surviving population composed of second and third generation adults migrates westward and downslope to the Sierran foothills and Coast Ranges, where they hibernate and become active again the next year in February to early April.

ADULT BEHAVIOR: As noted previously, the California Tortoiseshell becomes abundant during the summer throughout much of the West. In years of exceptional numbers in California and the Pacific Northwest, vast migratory movements occur where millions of butterflies may fly for great distances and for days on end. In years of normal population size, these migrations still occur, as noted by Shapiro above, but in less spectacular numbers. In northern California, the flights tend to be towards the north or northeast during the spring, and in the reverse direction towards the south or southwest in the fall. Adults visit flowers to sip nectar and

sometimes visit mud to sip water. Males will hilltop in the late afternoon and perch on foliage, earthen banks, or other objects to await females.

LIFE HISTORY: The eggs are laid in clusters on the host. The mature larva is deep velvety black, with numerous white dots (each bearing a short whitish hair) accentuating each segmental region. There are seven long branching spines on each segment, all being bluish-black except for the yellow dorsal row. The pupa is gray with a bluish sheen; the abdominal region is fawn-colored. The head bears two blackish extensions. The adults hibernate.

FOODPLANTS: A variety of *Ceanothus* species in the family Rhamnaceae are used in California. The species used within this state include *C. velutinus* Dougl. ex Hook, *C. cordulatus* Kell., *C. integerrimus* H. & A., *C. thyrsiflorus* Esch., and *C. cuneatus* (Hook.) Nutt. Of all of these, the favored foodplant seems to be *C. velutinus* (Tobacco Brush); this plant is usually present in the areas where *N. californica* is consistently taken year after year.

CHROMOSOME NUMBER: Unknown, but the European and Japanese species in this genus all have $n = 31$ (summarized in Maeki and Remington, 1961b).

SIMILAR SPECIES: The California Tortoiseshell is readily differentiated from Milbert's Tortoiseshell by the upperside pattern.

GEOGRAPHIC AND SEASONAL VARIATION: Probably because of the wide migratory movements and consequent mixing of the gene pool annually, no geographic variation has been noted in this species. No seasonal variation occurs.

GENERAL REMARKS: With the vast migratory movements that occur at times in this species, the California Tortoiseshell may be expected to turn up in odd places in these years, such as the mountain ranges of the eastern Mojave Desert or perhaps even the Channel Islands. This species has been recorded for Santa Catalina Island as a stray (Miller, 1985).

73. *Nymphalis vau-album j-album* (Boisduval and Leconte)

There is only a single record of this species in California and the reader is referred to the **Appendix** for details.

74. *Nymphalis antiopa antiopa* Linnaeus

DIAGNOSIS: Known familiarly as the Mourning Cloak, this species is characterized by a maroonish black upperside, fringed by off-yellow margins and blue spots interior to the yellow border.

ORIGINAL DESCRIPTION: Linnaeus, *Syst. Nat.*, ed. 10, 1: 476 (1758).

TYPE LOCALITY: "Sweden". Holotype in Uppsala, Sweden.

DISTRIBUTION: The species is widespread in California, occurring throughout the mountains and in all of the lowland areas west of the Sierran-Cascade axis. There are few isolated colonies in the eastern Mojave Desert and in the Death Valley region. Outside of California, the species ranges north to Alaska, eastward throughout southern Canada and most of the United States, and southward to Venezuela. It is also found in the Old World, from Spain and the British Isles east to Siberia.

- ELEVATION RANGE:** This species ranges from near sea level to approximately 10,500' elevation. The majority of records are for localities in the lowland areas.
- HABITAT AND PLANT COMMUNITIES:** In the mountains this species is typically found in riparian situations, usually near willows in all the montane plant communities. In the lowlands, it is found in Riparian Woodland but is more commonly encountered in suburban areas, where introduced foodplants such as Chinese Elm or Weeping Willow serve as hosts.
- PHENOLOGY:** The butterfly overwinters as an adult. Hibernant individuals can sometimes be seen on warm winter days in urban or suburban areas of the state, but the major springtime flight activity seems to take place in March and April. These individuals then give rise to probably several generations of butterflies through the spring and summer months, with possibly only one generation at higher elevations. Scott (1986) even suggests that there may be only one brood in the Central Valley of California, with adults apparently aestivating in the summer. This situation bears additional investigation.
- ADULT BEHAVIOR:** The adult Mourning Cloaks have a strong flight but usually stay near their streamside habitat or willow foodplants. In Europe, H. Roer (1970) marked and released hundreds of Mourning Cloaks and found that adults fly up to 70 kilometers after emergence in June and July. They then apparently aestivate all summer, feed again in the fall and store fat in their abdomen, then hibernate in the winter and mate in the spring. Adults are known to visit flowers and also sip sap, fruit juices, and water at mudflats. Adults are commonly found perching on willow branches along streams from mid-day through late afternoon; usually, these are males awaiting the passage of females. In California, overwintering adults can be seen on warm days in winter months throughout urban and coastal areas. In our cities, the larvae often reach pest proportions on elm trees.
- LIFE HISTORY:** The whitish egg is barrel-shaped with a truncated apex. The eggs are laid in clusters of up to 250 in one layer and usually in rings circling their host twig near its tip. The larvae are gregarious throughout their life, feeding on the leaves of the host. The first instar larva is whitish with a black head. The familiar mature larva bears seven rows of long thin black spines and is basically black with intensive white spotting across the body surface, with orange sub-dorsal spots. The spiny pupa is gray to light brown, with lighter wing cases and many pink-tipped cone-like dorsal bumps. Both the larvae and pupae will twitch in unison when a group of them is disturbed. The adults hibernate.
- FOODPLANTS:** The following plants have been documented as foodplants for this species within California: Salicaceae: *Salix lasiolepis* Benth., *S. exigua* Nutt., *S. babylonica*; *Populus nigra* var. *italica*; Ulmaceae: *Ulmus parvifolia* Jacquin; *Celtis reticulata*. Outside of California, the butterfly is recorded on a variety of hosts, including plants in the families Betulaceae, Aceraceae, Moraceae, Oleaceae, Rosaceae, Tiliceae, Polygonaceae, and Sparganiaceae. Whether any of these families are used within California remains to be ascertained.
- CHROMOSOME NUMBER:** $n = 31$ in European *N. antiopa* (references in Maeki and Remington, 1961b).
- SIMILAR SPECIES:** None in our area.
- GEOGRAPHIC AND SEASONAL VARIATION:** Despite its wide geographic range and occurrence in all four seasons, this butterfly has been able to differentiate into one other subspecies in North America: *hyperborea* (Seitz) occurs in Alaska and the Northwest

Territory area of Canada, where adults are characterized by smaller size, darker borders, and larger blue spots than the typical subspecies.

GENERAL REMARKS: While being one of our most familiar butterflies and being widespread throughout California, the butterfly is usually solitary and rarely occurs in numbers.

Subfamily **Melitaeinae** Grote

75. *Euphydryas chalcedona* (Doubleday)

The genus *Euphydryas* contains a number of species in the Palearctic and Nearctic that have subspeciated abundantly. As a result of this evolutionary divergence, there is often considerable confusion in deciding to which species group a particular subspecies belongs. One extreme reached recently by Scott (1986) was to combine a number of the best known species (which are *chalcedona*, *colon*, and *anicia*) into a single species with some 38 subspecies. In his view, the subspecies seem to form a ring of races in which *colon* races integrate with *chalcedona*, and *chalcedona* races with *anicia*. But Scott himself notes that *colon* races are usually reproductively isolated from *anicia* races, and we have found situations where *colon* and *chalcedona* or *anicia* and *chalcedona* occur in the same locality sympatrically and synchronically and seem to be reproductively isolated in these situations. Therefore, we have kept these three major species, as well as *editha*, as separate species groups and treat them accordingly in this book. Additionally, we have kept the single genus *Euphydryas* for this natural nymphaline group of 14 Nearctic and Palearctic species, rather than elevating the group to the status of a tribe, with four genera in it as split by Higgins (1978) and Miller and Brown (1981).

ADULT BEHAVIOR: All of the subspecies of *chalcedona* share a similar flight behavior of flying low to the ground with a rapid fluttering of the wings. Males are frequently seen, especially early in the flight season, patrolling over the hills in search of females. In the desert areas, males frequently perch on twigs of *Keckiella antirrhinoides* Benth. or other shrubs, or even on rocks or on the banks and floors of sandy washes, waiting for other adults to fly by, which they engage in mid-air flight. Shapiro et al (1981) note that the adults of *E. c. trinitina* are highly territorial, displaying both perching and patrolling behavior. The females lay masses of several hundred eggs at a time on the foodplant, generally on the hosts that occur in sunny locations.

LIFE HISTORY: The eggs in all the subspecies are yellow and are laid in large clusters, principally on undersides of the leaves. They turn reddish-brown and then black before hatching. The newly hatched larvae live gregariously in a silken nest prior to the onset of winter. They feed up to the third or occasionally the fourth instar during the first year. The following winter the post-diapause larvae are solitary, feeding up to maturity by late spring. The mature larva exhibits a number of different color patterns in the various subspecies populations that we have gathered under the name *chalcedona*. Even though the accompanying figures show the typical larval color pattern for most of the subspecies, it should be remembered that there is individual variation in each population which is occasionally as great as that in the adults, and does not necessarily match the geographic picture of subspecific differentiation shown in wing patterns of adults. The mature larva of the typical subspecies *chalcedona* is black with long branching spines and a whitish dorsal and lateral banding pattern which varies considerably in different populations.

The entire body surface bears small white tubercles with short white hairs. The pupa is gray and pearly white, with raised orange spots on the abdomen and black markings, as shown in the figure. Larvae in the populations along the Sierra Nevada range have more strongly marked white stripes laterally and dorsally. Larvae from populations in the Tejon-Tehachapi Transverse Ranges tend to be intermediate in coloration between the uniformly blackish-gray larvae of the coastal populations and the white-striped Sierran larvae. A similar blendzone is not presently known at the northern end of the state above the Central Valley, but should be looked for.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: *Euphydryas chalcedona* may be distinguished from other species of *Euphydryas* in California by a combination of a number of life history and adult characters: (1) it tends to use shrubby hosts in the family Scrophulariaceae; in contrast, *E. colon* uses *Symphoricarpos* (family Caprifoliaceae), *E. anicia* uses herbaceous scrophularaceous hosts, and *E. editha* tends to use small, herbaceous perennial or annual scrophularaceous or plantaginaceous host plants. (2) The pupae of *E. chalcedona* and *E. anicia* are ivory to grayish-white in ground color, in contrast to the pupae of *E. colon*, which have a yellowish ground color. (3) The genitalic similarities and differences among the different *chalcedona* subspecies and *colon* and *anicia* are substantial, and are illustrated and discussed by Gunder (1929). (4) In areas of sympatry, these species continue to behave genetically and ecologically as "good" biological species. Although *chalcedona* and *colon* are said to intergrade (Scott, 1986) and *chalcedona* is said also to intergrade with *anicia* (Scott, 1986), we have yet to see good documentation of this alleged phenomenon. In our experience, when *chalcedona* is sympatric with *colon* or a representative of *anicia*, the two entities seem to largely maintain reproductive isolation and also continue to exhibit biological differences in a given locality. For example, at Adin Pass in Modoc County, *Euphydryas chalcedona* near *chalcedona* flies in the area and uses a *Castilleja* species as a post-diapause foodplant, probably in addition to a shrubby *Keckiella* or *Penstemon* species (all family Scrophulariaceae). Sympatric with this *chalcedona* is *Euphydryas colon* which uses *Symphoricarpos* (family Caprifoliaceae) and has larvae and pupae which are distinguishable in color and pattern from the *chalcedona* larvae and pupae in this locality. (The *colon* pupae have a distinct yellow cast to them, whereas the *chalcedona* pupae are ivory-white in ground color.) David Bauer (personal communication) has studied the two entities in this particular locality and found that *colon* larvae exhibit behavioral differences in the type of silk nests that they spin to protect them during winter diapause, in contrast to the behavior of diapausing *chalcedona* larvae. In another locality, the Trinity Alps, there is a *chalcedona* subspecies (*trinitina*) flying sympatrically with *E. colon*. In this area the *chalcedona* subspecies uses *Penstemon newberryi* Gray as a foodplant, whereas *E. colon* apparently uses *Symphoricarpos*. The phenotypes of the two butterflies in this area are markedly different. In a third locality in California, the Sherwin Summit area of southern Mono County, we have found both *E. c. olancha* and *E. anicia wheeleri* flying sympatrically. In this locality *wheeleri* displays the typical reddish phenotype and is using *Castilleja chromosa* A. Nels. as a larval host, whereas *olancha*, which has a blackish phenotype with large white spots, is using a *Keckiella* species as larval host. We have not detected evidence of interbreeding of these two entities where they occur sympatrically. To the north of this locality there occurs a dark form of *E. a. wheeleri* which resembles *olancha*; however, this entity is biologically nearly identical to *wheeleri* in that it uses *Castilleja* as a foodplant and has similar larval and adult habits and similar larval and pupal patterns to more typical *wheeleri* populations to the east. We do not doubt that some genetic exchange takes place between these different entities

where they are sympatric; however, as in the *Coenonympha "tullia"* superspecies concept, it is unwieldy in both taxonomy and actual field situations to consider them biological entities as all one species. The *Euphydryas* are a dynamic, evolving group and the levels of superspecies, species, semispecies, and subspecies may be applied with almost equal ease to groupings of checkerspot populations. The exhibition of disparate and similar phenotypes is not always related to reproductive isolation or compatibility, or evolutionary distance.

Euphydryas editha, which no one doubts is a distinct species from *E. chalcedona*, has larval color patterns which closely follow those of sympatric *E. chalcedona* and *E. anicia* populations in many areas. For example, in the Coast Ranges, both *editha* and *chalcedona* larvae tend to be dark with little development of any white markings, whereas in the Sierra Nevada, both species' larvae exhibit extensive longitudinal white bands dorsally and laterally. On the east side of the Sierra Nevada, larvae of *E. anicia*, *E. chalcedona*, and *E. editha* all have somewhat less extensive white markings than those in the remainder of the Sierra Nevada and superficially resemble one another. This parallel tracking of color pattern appears to be parallel or convergent evolution to us, rather than evidence of conspecificity. Other workers have cited the similar color patterns of *chalcedona* and *anicia* to support their arguments for the conspecificity of these two species.

GEOGRAPHIC AND
SEASONAL VARIATION:

In the desert populations that are sometimes bivoltine, there is no apparent phenotypic difference between the spring and late summer broods. The extensive geographic variation has been discussed under the individual subspecies names and the reader is referred to the distribution map and the color plates for a better understanding of the complexity of this situation in *chalcedona*.

GENERAL REMARKS:

Some of the ecological factors contributing to the directions of geographic variation in the populations of *chalcedona* were studied by William Hovanitz in the deserts of southern California in the 1940's. Yet, today, despite the great potential interest of the evolutionary and ecological factors that have caused such a burst of divergence in this species, it has been little studied in comparison to its congener *Euphydryas editha*. A detailed study of subspeciation in this species, as well as the other *Euphydryas* in California, would no doubt occupy many lepidopterists for several generations, but it would provide invaluable comparative information.

SUBSPECIES:

Within California there are ten named subspecies of *Euphydryas chalcedona* which we differentiate as follows.

a. *E. c. chalcedona* (Doubleday)

DIAGNOSIS:

The name *chalcedona* was originally applied to populations in the vicinity of San Francisco and we have applied the name to populations with individuals that have mostly black uppersides with cream spots. These include a circle of populations around the Great Central Valley, as will be described in the section on DISTRIBUTION.

ORIGINAL DESCRIPTION:

Doubleday, *Gen. diurn. Lepid.*, 1: 180 [1847].

TYPE LOCALITY:

Type locality not stated in original description, but very likely the vicinity of San Francisco, California. Doubleday described this butterfly in 1847 after obtaining access to specimens collected by the Russian naturalist Johann Friedrich Eschscholtz. Eschscholtz was the outstanding entomological figure during the Russian occupation of California and made two collecting visits, in 1816 and

1824. He collected *Danaus plexippus* and *Euphydryas chalcedona* on the first trip, and his specimens ended up in the Berlin Museum except for those described by Doubleday (Essig, 1972). Holotype in British Museum.

- DISTRIBUTION:** The nominotypical subspecies name *chalcedona* is somewhat loosely applied here to an array of phenotypically fairly similar populations occurring from the lower elevations of the western Klamath Mountains region southward through the Coast Ranges to the Transverse Ranges and coastal foothills of southern California, thence northward through the west slope of the Sierra Nevada, at lower elevations in the foothills, to the extreme western Mt. Lassen region. There are marked differences in larval color pattern between the Sierran foothill populations and the more coastal populations, even though the adults of these populations are fairly similar.
- ELEVATION RANGE:** *E. c. chalcedona* populations range in elevation from approximately sea level to nearly 5,000', with most populations below 4,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** This species is typically found in the following plant communities: North Coastal Sage Scrub, South Coastal Sage Scrub, Inland Sage Scrub, Mixed Chaparral, Serpentine Chaparral, Northern Oak Woodland, Southern Oak Woodland, and the lower edges of Lower Mixed Coniferous Forest. It is less commonly encountered in grassland situations. It rarely occurs in Pinyon-Juniper Woodland, but is found in at least one semi-desert area (north slope of the Ord Mountains southeast of Hesperia in San Bernardino County).
- PHENOLOGY:** These populations are univoltine, with the larvae overwintering as half-grown larvae, feeding through to maturity during the winter and early spring months, and then emerging from as early as March to as late as early June, depending on elevation. The resulting eggs from these spring adults hatch and then feed through as larvae to about the third instar, at which stage they go into diapause and pass the winter.
- FOODPLANTS:** For pre-diapause larvae, the following plants in the family Scrophulariaceae have been documented as foodplants: *Diplacus* species, *Scrophularia californica* Cham. & Schlecht., *Keckiellia* (formerly *Penstemon*) *breviflora* Lindl. Post-diapause larvae are more wide-ranging in their choice of foodplant, often crawling onto other species than the one on which they developed as pre-diapause larvae. In addition to the plants noted above as foodplants for pre-diapause larvae, the following plants have been documented as hosts for the post-diapause larvae: *Collinsia* species, *Castilleja* species (both Scrophulariaceae), *Plantago erecta* Morris, *P. lanceolata* L. (Plantaginaceae); *Lonicera* species (Caprifoliaceae); *Plectritis* species (Valerianaceae); and *Trichostema lanatum* Benth. (Menthaceae). Of the above list of plants, the favored foodplants seem to be *Diplacus* species, *Scrophularia californica* Cham. & Schlecht., and *Keckiellia breviflora* Lindl. In any given locality, there is usually just one favored pre-diapause foodplant.

b. *E. c. macglashanii* (Rivers)

- DIAGNOSIS:** The distinguishing features of this subspecies of *chalcedona* include relatively uniform size of the yellow spots, which are approximately equidistant from each other and give the insect a strongly checkered appearance. It is also smaller in average size than other subspecies of *chalcedona* (Comstock, 1927).
- ORIGINAL DESCRIPTION:** Rivers, *Proceedings California Academy of Sciences*, (2)1: 103 (1888).

- TYPE LOCALITY: Truckee, Nevada County, California. Type is believed to have been destroyed in the 1906 San Francisco earthquake and fire.
- DISTRIBUTION: Populations considered to be this subspecies occur primarily on the east slope of the Sierra Nevada, from the Walker River area in northern Mono County northward to Sierra and Lassen counties. In the Sierra and Lassen counties area, because the Sierran crest is not a particularly high barrier in these areas, some populations are found spilling over onto the west slope.
- ELEVATION RANGE: These populations range from approximately 4,000' to about 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES: *Macglashanii* is typically found on steep, rocky canyon slopes within the Great Basin Sagebrush Scrub or Pinyon-Juniper Woodland communities; on talus slopes in these areas, the *Keckiella* shrub foodplants tend to grow abundantly.
- PHENOLOGY: These populations generally appear in May or early June, and in some areas fly into late June or early July, depending on elevation.
- FOODPLANTS: The principal hosts of *macglashanii* populations are *Keckiella* (formerly *Penstemon*) *breviflora* Lindl. and *K. lemmonii* Gray (family Scrophulariaceae) (J. F. Emmel, unpublished data).

c. *E. c. dwinellei* (Hy. Edwards)

- DIAGNOSIS: This subspecies is characterized by a mostly black upperside, with cream spots and a fairly extensive red coloration in the apex of the dorsal forewing.
- ORIGINAL DESCRIPTION: Henry Edwards, *Papilio*, 1: 51-52 (1881).
- TYPE LOCALITY: McCloud Fishing Station, Shasta County, California. Syntypes in American Museum of Natural History.
- DISTRIBUTION: This appears to be a localized, weakly differentiated subspecies of *chalcedona* found primarily in the region just north and west of Redding in northern California. The types were taken at the McCloud Fishing Station, which was located close to the current site of Lake Shasta Caverns. Unfortunately, the type locality is now under the waters of Shasta Lake, but populations still occur in the immediate vicinity which show the same phenotypic facies as the type series. Populations with this phenotype occur in the vicinity of Shasta Lake and also in the lower elevations of the Salmon Mountains and Trinity Alps area of the Klamath Mountains Assemblage. To the east of the Shasta region, there is an apparent blend zone with *macglashanii* north of Mt. Lassen.
- It might be noted here that this taxon is not identical with a similar *Euphydryas* which flies at Bartle in Siskiyou County. The butterfly at Bartle was named *sperryi* by F. and R. Chermock in 1945. *Sperryi* is a subspecies of *Euphydryas colon* and shows both biological and phenotypic differences in adults, larvae and pupae from the present entity *E. chalcedona dwinellei*. (See further information under *E. c. sperryi*).
- ELEVATION RANGE: Subspecies *dwinellei* colonies occur from approximately 500' elevation to as high as 2,500' elevation, with most populations below 3,500'.

- HABITAT AND PLANT COMMUNITIES: This subspecies is typically found in canyon situations within Foothill Woodland communities.
- PHENOLOGY: Adults of this subspecies appear in May, June and early July, with the peak flight being in early June.
- FOODPLANTS: Larvae have been taken on *Keckiella* (formerly *Penstemon*), probably *K. lemmonii* Gray or *K. breviflora* Lind. (family Scrophulariaceae) (Ken Hansen, personal communication).

d. *E. c. olancha* (W. G. Wright)

- DIAGNOSIS: This eastern Sierran slope race has a strongly white appearance because of the enlargement of the light yellow wing spots.
- ORIGINAL DESCRIPTION: W. G. Wright, *Butterflies of the West Coast*: 150 (1905).
- TYPE LOCALITY: Olancha Peak, Tulare/Inyo counties, California. Lectotype in California Academy of Sciences, designated by J. W. Tilden, *Occasional Papers California Academy of Sciences*, (118): 19 (1975).
- DISTRIBUTION: This subspecies is found from the southern Sierra Nevada in southeastern Tulare County northward along the east slope of the Sierra Nevada to approximately Sherwin Summit in southern Mono County.
- ELEVATION RANGE: Populations of this subspecies tend to occur at higher elevations than the other *chalcedona* subspecies, ranging from approximately 6,000' to nearly 9,000' elevation.
- HABITAT AND PLANT COMMUNITIES: *Olancha* populations are usually found within the Great Basin Sagebrush Scrub community on steep, rocky slopes or talus slopes on the eastern escarpment of the Sierra Nevada, usually in the upper reaches of large canyons.
- PHENOLOGY: Adult captures are recorded from mid May to early August, with the majority of captures being during June and early July.
- FOODPLANTS: *Olancha* populations use at least two *Keckiella* (formerly *Penstemon*) species, namely *K. rothrockii* Gray and *K. breviflora* Lindl. (family Scrophulariaceae) (J. F. Emmel, unpublished data). The principal host seems to be *K. rothrockii*.

e. *E. c. sierra* (W. G. Wright)

- DIAGNOSIS: The subspecies *sierra* is relatively large, with the black areas so reduced that the dominant tone is a rich red across the forewings and hindwings.
- ORIGINAL DESCRIPTION: W. G. Wright, *Butterflies of the West Coast*: 152 (1905).
- TYPE LOCALITY: "Sierra Nevadas, California". Lectotype in California Academy of Sciences, designated by J. W. Tilden, *Occasional Papers California Academy of Sciences*, (118): 20 (1975).
- DISTRIBUTION: The subspecies *sierra* is found in the central Sierra Nevada, from Fresno County northward to the Gold Lake region in Sierra County. Its main stronghold seems to be centered around the west side of Lake Tahoe.

- ELEVATION RANGE: Populations occur from approximately 5000' to 8,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This subspecies is typically found in Lower and Upper Montane Coniferous Forest or Subalpine Forest areas. It prefers areas of extensive granitic outcropping where its foodplant grows abundantly from the granitic rock crevices.
- PHENOLOGY: Most captures are recorded for the month of July, with a species occasionally taken as early as the end of June.
- FOODPLANTS: The principal host of this subspecies is *Penstemon newberryi* Gray (family Scrophulariaceae) (J. F. Emmel, unpublished data); Bauer (in Howe, 1975) also records *P. deustus* Dougl. ex Lindl., which is sometimes abundant along with *P. newberryi* in *sierra* habitats.

f. *E. c. irelandi* (Gunder)

- DIAGNOSIS: A subspecies of the southern Sierra Nevada similar to *sierra* but with even more reduction of the black and greater development of the red areas on the upperside. A rich red suffusion across the wings combined with the presence of a row of yellow spots makes this subspecies even more striking than the *sierra* phenotype. Adults average smaller than *sierra*.
- ORIGINAL DESCRIPTION: Gunder, *Canadian Entomologist*, 61: 44-45 (1929).
- TYPE LOCALITY: Near Alta Peak, Sequoia National Park, California. Holotype in American National Museum of Natural History. This subspecies has been classified under the species *Euphydryas anicia* by Miller and Brown (1981), and has been ignored by Scott's treatment (1986), while Bauer in Howe (1975) lumped it with the subspecies *sierra*. However, it is abundantly distinct.
- DISTRIBUTION: This subspecies is found in the upper Kaweah River drainage in Tulare County. Populations of this phenotype, or of a phenotype intermediate between *irelandi* and *sierra*, may occur in the Kings River drainage in extreme southern Fresno County; records for such populations are currently lacking, though suitable habitats are present there.
- ELEVATION RANGE: Populations range from approximately 6,000 to 8,500' elevation. The types were taken on the trail to Alta Peak, which is over 10,000' elevation. However, it is likely that they were taken on the lower slopes of the peak within the above-noted elevation range..
- HABITAT AND PLANT COMMUNITIES: This subspecies occurs in situations very similar to those for *E. c. sierra*. It prefers areas of extensive granitic outcropping within the Lower and Upper Montane Coniferous Forest communities.
- PHENOLOGY: All records, to our knowledge, are for the first three weeks of July.
- FOODPLANTS: The presumed foodplant of this set of populations is *Penstemon newberryi* Gray (Scrophulariaceae), with which it seems invariably associated (J. F. Emmel, unpublished data).

g. *E. c. trinitina* (Baughman and Murphey)

- DIAGNOSIS: This large subspecies is very similar biologically to *sierra* and *irelandi*, but is blacker and duller in maculation than *sierra*. It has a very dusky, brick red dorsal appearance. It is found in the Trinity Alps of Trinity and Siskiyou counties.
- ORIGINAL DESCRIPTION: Baughman and Murphy, *Systematics of Western North American Butterflies Contributions in Science*, : (1998).
- TYPE LOCALITY: On Sawtooth Ridge in the Trinity Alps, south of Caribou Lake, Trinity Alps, 7300 - 7840 feet, Siskiyou County-Trinity County line, California. Holotype in Los Angeles County Museum.
- DISTRIBUTION: This subspecies, so far as is known, is confined to the Trinity Alps in the Klamath Mountains region of Siskiyou and Trinity counties.
- ELEVATION RANGE: From 6,200' to 7,700' elevation.
- HABITAT AND PLANT COMMUNITIES: As with the subspecies *sierra* and *irelandi*, *trinitina* is typically found on rocky, granitic scree slopes where its *Penstemon* foodplants are concentrated, within Lower and Upper Montane Coniferous Forest.
- PHENOLOGY: The butterfly flies during the month of July, with a peak in mid-July.
- FOODPLANTS: At least one documented foodplant for this subspecies is *Penstemon newberryi* Gray subspecies *berryi* (Eastwood) Keck (Scrophulariaceae) (J. F. Emmel, unpublished data). Possibly one or more other *Penstemon* species are used, as there is at least one locality in the Trinity Alps (Packer's Peak) in which adults have been taken but *Penstemon newberryi* Gray does not seem to occur.

h. *E. c. corralensis* T. C. and J. F. Emmel

- DIAGNOSIS: This is a generally small desert subspecies with a ground color of dull orangish red, even coral red on fresh individuals. The forewings above have yellowish-cream spots extending from the basal to sub-marginal areas, and four wavy vertical rows. The hindwings above are almost uniformly dull orangish red in about half the adults, the remainder having several partial to occasionally nearly complete submarginal and basal rows of cream-colored spots extending forward from the rear margin. This subspecies is named for the type locality rather than the reddish color.
- ORIGINAL DESCRIPTION: T. and J. Emmel, *Journal Research on the Lepidoptera*, 11: 143-144 [1973] ("1972").
- TYPE LOCALITY: Rock Corral, at the south end of Johnson Valley, at the base of the foothills of the northeastern end of the San Bernardino Mountains, in the southwestern Mojave Desert, San Bernardino County, California.
- DISTRIBUTION: Populations with the typical *corralensis* phenotype occur in a number of canyons along the northeastern flank of the desert foothills of the San Bernardino Mountains. From Rattlesnake Canyon as the westernmost locality, populations extend eastward and southward to approximately Little Morongo Canyon. Populations with a phenotype similar to *corralensis* occur in the mountains of Joshua Tree National Monument from the Little San Bernardino Mountains southeastward to the Eagle Mountains. South of the Little Morongo Canyon populations, going southward and then westward along the south base of the San Bernardino Mountains, there are a series of populations which represent a blendzone between *corralensis* and the coastal *E. c. chalcidona*. On the north

slope of the San Bernardino Mountains, just west of the Rattlesnake Canyon locality for *corralensis*, there is an apparent hiatus of *chalcedona* populations until one arrives at the north slope of the Ord Mountains southeast of Hesperia. Here, one encounters a much darker phenotype which is most closely related to the coastal *E. c. chalcedona*.

- ELEVATION RANGE: *Corralensis* populations range from approximately 4,000' to 6,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is typically found in desert canyons within the Pinyon-Juniper Woodland community or at the upper edge of the Mixed Desert Scrub community.
- PHENOLOGY: *Corralensis*, like other desert populations of *E. chalcedona*, is sometimes double-brooded, depending on the presence of summer rainfall. There is a spring brood every year in which adults fly in late March and April, sometimes into mid-May. In years of heavy summer rain in these desert areas, there is sometimes a small late summer or fall brood as well, which usually makes its appearance in September. Because of the spotty nature of summer rainfall in the California deserts, there will frequently be situations where in one locality the butterfly is in full flight in a late-summer emergence, whereas only a few miles away in a similar habitat, the butterfly has failed to produce a fall brood because of lack of rain in that locality.
- FOODPLANTS: The principal pre-diapause and post-diapause foodplant for all the California desert populations of *E. chalcedona* is *Keckiella* (formerly *Penstemon*) *antirrhinoides* Benth. subspecies *microphylla* (Gray) Keck (family Scrophulariaceae). Post-diapause larvae have also been found on the shrub *Bernardia incana* Mort. (Euphorbiaceae!). In this latter situation, several hundred larvae were found nearby on *Keckiella* plants and approximately 20 larvae were found on the *Bernardia*, feeding on the leaves (near Conejo Well, Eagle Mountains, Riverside County). Post-diapause larvae have also been taken on *Castilleja chromosa* A. Nels. (Scrophulariaceae) (J. F. Emmel, unpublished data).

i. *E. c. kingstonensis* T. and J. Emmel

- DIAGNOSIS: This desert subspecies is a small butterfly with a tannish-brown ground color. The forewings above are usually well-marked with black scaling, contrasting sharply with the light tan apical spots. The females are less marked with black on the inner half of the forewings. The hindwings above are light tan in ground color, largely overlaid with a rich, fulvous brown in the medial portions and black along the proximal anal margin.
- ORIGINAL DESCRIPTION: T. C. and J. F. Emmel, *Journal of Research on the Lepidoptera*, 11: 141-143 [1973] ("1972").
- TYPE LOCALITY: T19N, R10E, Section 3, rocky canyon 3/4 mile east Horse Thief Springs, Kingston Range, San Bernardino County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is found in the mountain ranges of the eastern Mojave Desert, with the nominotypical phenotype being found in the Kingston Range. Southeast of here, phenotypically similar populations occur in the New York Mountains, the Piute Range east of Lanfair Valley, Hackberry Mountain, the Providence Mountains, the Granite Mountains north of Amboy, and the Old Woman Mountains. Populations in the Old Woman Mountains tend to be more orange to

orange-red than typical *kingstonensis* and show somewhat of a blending between the subspecies *kingstonensis* and *corralensis*.

- ELEVATION RANGE: Populations are found between the elevations 4,000' and 6,500' elevation.
- HABITAT AND PLANT COMMUNITIES: This subspecies typically occurs in the desert canyons within the Pinyon-Juniper Woodland community, sometimes extending down to the upper edge of the Mixed Desert Scrub community.
- PHENOLOGY: As with *corralensis*, these populations are sometimes bivoltine, depending on summer rainfall patterns. The spring brood, which is regularly encountered, flies from late March to late April with stragglers into the month of May in some years. The late summer brood, when present, usually flies any time from late August to late September, depending on rainfall patterns.
- FOODPLANTS: The principal pre-diapause and post-diapause larval foodplant is *Keckiella antirrhinoides* Benth. subspecies *microphylla* (Gray) Keck. Other Scrophularaceae foodplants used by the post-diapause larvae (usually close to *Keckiella* plants) include several *Penstemon* species (J. F. Emmel, unpublished data).

j. *E. c. hennei* J. Scott

- DIAGNOSIS: This is a southern California subspecies occurring on the west edge of the Colorado Desert in San Diego and Riverside counties and it differs from adjacent *E. c. chalcidona* populations in the increased extent of white dorsal markings and the smaller size.
- ORIGINAL DESCRIPTION: J. A. Scott, *Papilio*, *New Series*, 1: 4 (1981).
- TYPE LOCALITY: Box Canyon, San Diego County, California.
- DISTRIBUTION: This subspecies is found in desert and semi-desert canyons in the foothill areas bordering the western edge of the Colorado Desert in San Diego and Riverside counties. It is also found in similar situations in extreme northern Baja California. Populations along the northeastern edge of the Santa Rosa Mountains and San Jacinto Mountains in western Riverside County tend to show more red on the upper surface and, in fact, represent somewhat of a blendzone between the subspecies *hennei* and *corralensis* to the north.
- ELEVATION RANGE: 2,000' to approximately 4,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This subspecies, much like its close relatives *corralensis* and *kingstonensis*, occurs in rocky desert canyons and on rocky desert slopes within the Pinyon-Juniper Woodland or Mixed Desert Scrub plant communities. In some of the foothill canyons, the surrounding slopes are covered with Desert Transition Chaparral vegetation.
- PHENOLOGY: Again, this desert subspecies may be either univoltine or bivoltine, depending on summer rains. The spring brood flies from March into mid-April with some records for February. The late summer or early fall brood has been recorded for the months of September and October.
- FOODPLANTS: This subspecies is known to feed on *Keckiella antirrhinoides* Benth. subspecies *microphylla* (Gray) Keck, like its two close relatives *E. c. corralensis* and *kingstonensis*. No other foodplants are currently known.

76. *Euphydryas colon* (W. H. Edwards)

- ADULT BEHAVIOR:** *Colon* fly with a rapid wingbeat in more-or-less straight lines across the meadows, males searching for females and females searching for host plants in open gravelly clearings that are at least partly wet meadows. The larger open glades are surrounded by coniferous forest stands, with a dense understory of shrubs and small flower-filled openings including *Symphoricarpos*. Nectaring and patrolling with combative flights by males occurs both in the small glades and out in open meadows, where flowers are especially abundant along the small intermittent watercourses that cross them. Males often perch in sandy areas of the streambed, awaiting passing females.
- LIFE HISTORY:** The early stages of *Euphydryas colon* differ from those of *chalcedona* in both coloration and larval behavior. The eggs are laid in clusters on the foodplant, a cluster including up to several hundred eggs. On Snowberry, the larvae hatch and form small, rather compact webs over the skeletonized leaves and remain in these curled leaves even after winter storms have destroyed the web and knocked the snowberry leaves to the ground. This habit of making these small, compact webs over their leaves in the early instars differs from that of all other American *Euphydryas* larvae. Those larvae using *Penstemon* form the more typical webbing in the base of the perennial host. If webbed, curled-leaf shelters are used here has yet to be determined. The mature larva of *colon* is distinguished by having relatively abundant, rather long white body hairs and also white bristles on the lower half of the tubercles, giving the body a fuzzy white appearance (Bauer, 1975). The head is black and is covered with long black and short white hairs. After the larvae pass the winter hibernation stage, they resume feeding on *Penstemon* or sometimes on *Symphoricarpos* species as post-diapause larvae.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** The subspecies of *Euphydryas colon* have been distinguished above from similar *chalcedona* forms. The most certain characteristics to use are the male genitalia, larval coloration, pupal coloration, and foodplant utilized. Refer to the accompanying text figures for the genitalic differences.
- GEOGRAPHIC AND SEASONAL VARIATION:** As the species is uniformly univoltine throughout its range, there is no seasonal variation. As noted above, there exists a cline between the subspecies *sperryi* in southeastern Siskiyou County and the near *wallacensis* populations in Modoc County. We have not yet detected a similar cline between *E. c. colon* in the northwestern part of the state and *sperryi* or near *wallacensis* populations to the east; however, careful sampling of populations along the northern border of the state may reveal such a cline.
- GENERAL REMARKS:** Because of the remoteness of much of the northern California localities in which these *Euphydryas* fly, most of these populations are still poorly known and inadequately studied. More careful field studies and laboratory studies with these species are needed to more carefully delineate the evolutionary and biological relationships among them.
- The adults of this *Euphydryas* species are similar to *E. chalcedona*, both genitally and in dorsal color pattern, with a predominantly black pattern bearing cream spots. However, the two species differ biologically and in some areas occur sympatrically without intergradation and they remain distinct over

many years of observation. Additionally, on the undersurface of the adults, *colon* differs from *chalcedona* by having a more brick-red surface with tightly defined smaller white spotting in sharply defined crisp rows. Within our state there are three subspecies.

a. *E. c. colon* (W. H. Edwards)

- DIAGNOSIS: Typical *colon* is smaller than *chalcedona* and the wings are of a different shape, with the outer edge of the forewing being somewhat more rounded. The marginal red spots are well-defined in this butterfly and there is a black area internal to the marginal yellow spots on the hindwings which immediately separates *colon* from other *Euphydryas*.
- ORIGINAL DESCRIPTION: W. H. Edwards, *Bulletin Brooklyn Entomological Society*, 3: 80 (1881).
- TYPE LOCALITY: "Mount Hood, Oregon", later corrected by Edwards, then fixed as Kalama, Cowlitz County, Washington, by F. M. Brown, *Transactions American Entomological Society*, 92: 361 (1966). Lectotype in the Carnegie Museum, designated by F. M. Brown (1966).
- DISTRIBUTION: Within California, specimens referable to typical *colon* are found primarily in the extreme northwestern part of the state, namely in Del Norte and western Siskiyou counties. From here, it ranges northward into western British Columbia.
- ELEVATION RANGE: In California, this subspecies is found from approximately 5,000' to 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES: In California the butterfly is usually found in areas of Montane Coniferous Forest, but within this plant community it tends to prefer openings such as cleared areas, meadows, hillsides and roadsides.
- PHENOLOGY: Our records for this particular subspecies are all in either June or July.
- FOODPLANTS: This subspecies uses *Symphoricarpos* species (Caprifoliaceae); the particular species used in our area remains to be determined.

b. *E. c. wallacensis* Gunder

- DIAGNOSIS: Although typical *wallacensis* is of smaller size than typical *colon*, the *wallacensis* populations in the Warner Mountains tend to be of a larger size. A more constant character is the marginal row of red spots, which is almost always present, and the larger pale yellow spots on the upperside, giving the specimen somewhat lighter appearance than typical *colon*.
- ORIGINAL DESCRIPTION: Gunder, *Pan-Pacific Entomologist*, 5: 50 (1928).
- TYPE LOCALITY: Wallace, Shoshone County, Idaho. Holotype in American Museum of Natural History.
- DISTRIBUTION: Within California, specimens referable to this subspecies are taken only in the extreme northeastern part of the state, namely in Modoc County. From there it extends northward through eastern Oregon and Washington, then eastward to western Montana and most of Idaho.

- ELEVATION RANGE: Our specimens occur in an elevation range of 4,500' to approximately 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This butterfly occurs in a much drier habitat than that of *E. c. colon*.
- PHENOLOGY: Our records range from late May to mid-July with an apparent peak in early July for most populations.
- FOODPLANTS: This subspecies is known to use *Symphoricarpos* species at Adin Pass in Modoc County (Bauer, personal communication). Whether other secondary hosts are used is currently not known.

c. *E. c. sperryi* F. and R. Chermock

- DIAGNOSIS: The most reddish of the three *colon* subspecies in California, *sperryi* has a prominent row of marginal red spots on both wings, and on the forewing much of the area of the creamy yellow spots is suffused with red.
- ORIGINAL DESCRIPTION: F. and R. Chermock, *Proceedings Pennsylvania Academy of Sciences*, 19: 39 (1945).
- TYPE LOCALITY: Vicinity of Bartle Lumber Camp, Siskiyou County, California. Holotype probably in the Carnegie Museum.
- DISTRIBUTION: Specimens with this subspecific phenotype have been found only in the vicinity of the type locality; however, very similar specimens are found to the east of here and form a cline with the near *wallacensis* populations just to the east in southwestern Modoc County. The town of Bartle is located in the extreme southeastern corner of Siskiyou County, approximately 22 air miles southeast of Mount Shasta.
- ELEVATION RANGE: From approximately 3,900' to 4,200' elevation.
- HABITAT AND PLANT COMMUNITIES: This butterfly flies in a markedly different habitat than that of *E. c. dwinellei*, with which it has often been confused. At the Bartle location, the typical habitat is an open pine forest flatwoods with extensive dry to wet meadows in which two of the subspecies' foodplants occur abundantly: namely, a mat-like *Penstemon* species and *Symphoricarpos* species.
- PHENOLOGY: The flight period is from approximately mid-June to mid-July, with a peak in early July. Mature larvae formerly were always abundant on the mature *Penstemon* at the type locality of Bartle Meadows at the end of June, with the same feeding activity still occurring when the first male adults started to fly. In the early 1980's, the entire gravelly, flat habitat for the *Penstemon* was bulldozed clean of all plant life; then the construction project was abandoned. If not for the adjacent "reservoir" of *Symphoricarpos* host, this population might be extinct today. It is still surviving, at low population levels.
- FOODPLANTS: Post-diapause larvae have been found on both *Penstemon shastensis* Keck. (Scrophulariaceae) and *Symphoricarpos* species (Caprifoliaceae) (S. Mattoon and K. Hansen, unpublished data). Of these two hosts, *Penstemon shastensis* seems to be the preferred foodplant, at least for post-diapause larvae. In most years, *sperryi* is found only sparingly on *Symphoricarpos* (also known as Snowberry).

77. *Euphydryas anicia* (Doubleday and Hewitson)

- ADULT BEHAVIOR:** The adults are frequently noted nectaring at flowers, including the following species in the Inyo Mountains of California: *Agoseris glauca* (Pursh.) Greene var. *monticola* (Greene) Q. Jones (Compositae), *Cryptantha confertiflora* (Greene) Pays. (Boraginaceae), and a wallflower, *Erysimum capitatum* (Dougl.) Greene (Brassicaceae). The prime nectar source in the Cottonwood Mountains population of *veazieae* is *Peraphyllum ramosissimum* Nutt. (Rosaceae). The males tend to perch in openings along canyon bottoms or in washes; occasionally, hilltopping behavior is noted. Females, when not visiting nectar sources, are usually found in the immediate vicinity of the foodplant species.
- LIFE HISTORY:** Relatively little has been published of the life histories of this group. The yellow eggs are laid in clusters on the underside of the leaves of the host plant. The mature larva vary considerably in color pattern among *anicia* populations. The mature larva of *Euphydryas anicia wheeleri* has with a broad white lateral band and a dorsal band with large expanded orange spots on each segment, in which the dorsal row of spines is centered. The bristly tubercles are black, except for the mid-dorsal row and the lower lateral rows which are orange. The pupa is white in ground color, with black markings on the former tubercle sites and wing cases, as seen in the accompanying figures. Diapause occurs in the third or fourth instar larva, usually under rocks at the base of the foodplant. Metamorphosis is completed the following spring.
- CHROMOSOME NUMBER:** $n = 31$ (from Colorado material, Emmel, Harris, and Eliazar, unpublished).
- SIMILAR SPECIES:** See preceding discussions under *Euphydryas chalcedona* and *E. colon*, as well as the accompanying line drawings of the genitalia.
- GEOGRAPHIC AND SEASONAL VARIATION:** Our populations of *anicia* all seem to be strictly univoltine, so there is no seasonal variation. The populations of *E. a. wheeleri* in the northern Mono County area are much darker than typical *wheeleri* and, in fact, in one area have been given the name "*georgi*" by Gunder (1928, *Entomological News*, 39: 206; type locality: Casa Diablo Hills, Mono County, California; holotype in American Museum of Natural History) as a transition form of *E. chalcedona olancha*. However, the biological characteristics of these populations tie them more closely to *wheeleri*, rather than *olancha*.
- GENERAL REMARKS:** As mentioned previously, *Euphydryas anicia wheeleri* is sympatric with *Euphydryas chalcedona olancha* at Sherwin Summit in southern Mono County. This is a very narrow area of sympatry and the evidence to date cannot enable us to choose between two contrasting pictures of the distribution of *anicia*. First, *Euphydryas anicia* and *Euphydryas chalcedona* could be two ends of a continuously distributed species, replacing each other from central Arizona up along the California-Nevada border. This is the view taken by Brussard *et al.* (1989). Alternatively, these could be two well-distinguished species that are so close in ecological requirements and perhaps host plant requirements that they cannot exist sympatrically except under extremely unusual circumstances because of their competitive interaction. The entire genus of *Euphydrya* offers a number of opportunities such as this one for further investigation in the area of evolutionary and ecological biology. This species, *Euphydryas anicia*, is a large and complex group extending from California to the Rocky Mountains, north into Canada and Alaska, as well as south into northern Mexico. Over this great range it has differentiated into a substantial number of subspecies, and perhaps even several closely related species compose this great complex.

Although we are grouping our two subspecies under the name *anicia*, they may be part of several semispecies groups or even distinct species, such as has been found in the *Euphydryas chalcedona* and *Euphydryas colon* species groups.

a. *E. a. wheeleri* (Hy. Edwards)

- DIAGNOSIS: This is a strongly reddish butterfly with a pale red ground color on the upper surface except for the base of the secondaries which are cream white. There are very light black markings on true *wheeleri*.
- ORIGINAL DESCRIPTION: Henry Edwards, *Papilio*, 1: 52-53 (1881).
- TYPE LOCALITY: "Southern Nevada". Holotype in American Museum of Natural History.
- DISTRIBUTION: Within California, *wheeleri* is found in the Inyo Mountains and White Mountains of Inyo and southern Mono counties. From there, it extends northwestward along the east base of the Sierra Nevada to the Sweetwater Mountains in northern Mono County. It then extends eastward across central Nevada through Utah to southwestern Colorado.
- ELEVATION RANGE: This subspecies occupies a broad elevational range from approximately 5,000' to over 10,000' elevation in the White and Inyo Mountains. The majority of records seem to be from approximately 7,000' to 9,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This subspecies is typically at home in the Sagebrush Scrub and Pinyon-Juniper Woodland communities of the Great Basin. It is found on mountain slopes, in canyon bottoms, and in open dry meadows or sagebrush flats.
- PHENOLOGY: Records range from early May to early August, depending on elevation and exposure. The majority of records seem to be for June or early July.
- FOODPLANTS: The principal foodplant of this butterfly is *Castilleja chromosa* A. Nels. (Scrophulariaceae); additionally, pre-diapause larvae have been found on *Penstemon bridgesii* Gray (Scrophulariaceae) in the Inyo Mountains. In the localities where *P. bridgesii* Gray is used, larvae are also still found on *Castilleja chromosa* A. Nels.

b. *E. a. near veazieae* (Fender and Jewett)

- DIAGNOSIS: Quite different from subspecies *wheeleri*, *E. a. veazieae* has a very whitish appearance, with great expansion of the whitish-cream areas on both forewings and hindwings. The red is restricted to several small areas on the forewing and a reduced marginal row of spots along the edges of both wings.
- ORIGINAL DESCRIPTION: Fender and Jewett, *Wasmann Journal of Biology*, 11: 117 (1953).
- TYPE LOCALITY: Jackass Mountains, Harney County, Oregon. Syntypes in Jewett collection.
- DISTRIBUTION: The subspecies *veazieae* has extensive distribution throughout the sagebrush country east of the Cascade Mountains, from south central Washington southward as far south as Pyramid Lake, Nevada. It extends into California in only a very narrow corridor along the eastern boundary of the state, just east of the Warner Mountains in Modoc and Lassen counties.

- ELEVATION RANGE: In California, from 4,500' to 6,000' elevation.
- HABITAT AND PLANT COMMUNITIES: Subspecies *veaziae* in California and adjacent Nevada is always a resident of lava rubble rock flats, hillsides, and occasionally Basin range summits, where the scrub and desert woodland vegetation types come together. While the habitat is primarily Sagebrush Scrub, these drier areas are usually bordered by elements of the Northern Juniper Woodland plant community.
- FOODPLANTS: Both pre- and post-diapause larvae have been found on *Penstemon*, as yet undetermined as to species.

c. *E. a. variicolor* (Baughman and Murphy)

- DIAGNOSIS: This is a small, dark, high-elevation *anicia* found in the Sonora Pass region of the Sierra Nevada Range. It displays virtually equal proportions of red, yellow and black on the dorsal surfaces. It was described as a subspecies of *E. chalcedona* (under which *E. anicia* had been considered conspecific by the same authors). The original description stated that it differed from its geographically nearest relatives by having more red than nominotypical *chalcedona*, and more of both black and yellow than *sierra*. The upper prong on the male valvae of the genitalia is extremely long, as in *anicia*, much longer than that of the geographically adjacent *E. c. sierra* (Baughman and Murphy, 1989), linking it to the *wheeleri* populations just to the east. These characters help to place it as a subspecies of *E. anicia*. Additionally, it is suspected to use an herbaceous scrophularaceous host, an alpine *Penstemon* or *Castilleja* species, characteristic of *E. anicia* subspecies.
- ORIGINAL DESCRIPTION: Baughman and Murphy, *Systematics of Western North American Butterflies Contributions of Science*, : (1998).
- TYPE LOCALITY: Ridge south of Sonora Pass in the Sierra Nevada, 9,600', Mono County, California.
- DISTRIBUTION: Populations with this phenotypic expression are known only from the Sonora Pass region of the central Sierra Nevada in Tuolumne and Mono counties.
- ELEVATION RANGE: Specimens have been taken in an elevational range of approximately 9,600' to 11,000'.
- HABITAT AND PLANT COMMUNITIES: This subspecies flies over open rocky slopes and on rocky ridge tops, basically in the Arctic Alpine Cushion Plant community.
- PHENOLOGY: All records of this subspecies, to our knowledge, are from late June to late July, with a peak in early to mid-July.
- FOODPLANTS: Larvae have been collected on a *Penstemon* species, which has not been specifically identified.

78. *Euphydryas editha* (Boisduval)

This checkerspot species is the most highly differentiated of the four species residing in California, including some eighteen subspecies within our state. The range of variation in size and in coloration and pattern is considerable, and has probably been substantially the result of the "stay-at-home" tendencies of the butterflies. Ehrlich (1961) first showed via mark-recapture studies that *editha*

normally does not wander considerable distances from its home area and is very much a colonial butterfly. These intrinsic genetic barriers to dispersal have led to a high degree of local adaptation to restricted areas of habitat and, hence, many phenotypically different populations.

ADULT BEHAVIOR:

LIFE HISTORY: *Euphydryas editha* utilize at least five genera of plants for oviposition and pre-diapause larval feeding: *Collinsia*, *Castilleja*, *Pedicularis*, *Orthocarpus* (all Scrophulariaceae), and *Plantago* (Plantaginaceae). White and Singer (1974) have nicely summarized the disjunct distribution of foodplant choice among *editha* populations. Normally, only a single plant species is selected in each population, even though plants that are selected elsewhere may be abundant. Post-diapause larvae may transfer onto secondary foodplants and may even prefer these to primary hosts. The plant species chosen in these populations are correlated with (a) timing of flight season, and (b) type of community inhabited. White and Singer's groupings are as follows:

1. Early-flying, coastal populations: feed on *Plantago*, with some ovipositing on *Orthocarpus* and a few on *Collinsia*.
2. Low elevation, late-flying populations in chaparral belt of the Inner Coast Ranges on serpentine soils: all feed on *Pedicularis densiflora* Benth. ex. Hod.
3. One population on scree at mid (6,900') elevation, Mendocino County: feeds on small and scarce annual *Collinsia greenei* Gray.
4. Mid-elevations, Sierra Nevada and San Bernardino Mountains: feed on small *Collinsia*, including *C. childii* Parry ex Gray, *C. callosa* Parish, and *C. parvifolia* Dougl. ex Lindl. (on both east and west slopes of Sierra).
5. Mid-elevations, southern Sierra Nevada: interspersed with the above *Collinsia*-feeding populations are those using *Pedicularis semibarbata* Gray.
6. Lower elevations (1,000 - 4,000'), western Sierra: feed only on *Collinsia tinctoria* Hartw. ex Benth.
7. High elevation (8,000 - 11,500') populations along crest of the Sierra: utilize *Castilleja nana* Eastw. for oviposition.

As White and Singer (1974) point out, the complexity of this pattern of foodplant relationships emphasizes the importance of evolution at the population level in the strategy of *Euphydryas editha*. Such evolution has allowed rapid exploitation of new food resources, such as the imported *Plantago lanceolata* and *Plantago insularis* Eastw. as they have become available to *editha* populations. The females have a very high reproductive potential (Labine, 1968) and a migrant female, which apparently has increasing oviposition motivation as she searches, is willing to accept a wider range of plants (Singer, 1971). This would explain how a new population utilizing a new host could be found even though that foodplant would not have been exploited in the parental population area, even if present among the original host plants.

CHROMOSOME NUMBER: n = 31 ()

SIMILAR SPECIES: See general discussions under *Euphydryas chalcedona*, *E. anicia*, and *E. colon*, as well as the individual subspecies of *E. editha*.

GEOGRAPHIC AND SEASONAL VARIATION:

GENERAL REMARKS: *Euphydryas editha*, particularly the nominotypical subspecies (formerly appearing as *E. e. bayensis* in the literature), is undoubtedly the most thoroughly studied species of butterfly in the world, due to the work and publications of Paul

R. Ehrlich and generations of graduate students and research assistants at Stanford University.

a. *E. e. editha* (Boisduval)

- DIAGNOSIS: This coastal central California subspecies is characterized by a heavy black pattern with a little red on the upperside of the wings, giving the butterfly a dark appearance.
- ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 304 (1852).
- TYPE LOCALITY: "California", restricted by Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies Contributions in Science*, : (1998), to San Francisco, California. Syntypes in the American Museum of Natural History.
- DISTRIBUTION: Through a misunderstanding of the original types of *Euphydryas editha*, it was originally thought by various authors that the subspecies *editha* was from the foothills of the Sierra Nevada. However, careful examination of the syntypes in the American Museum of Natural History shows that they are very typical San Francisco Bay area *editha*, to which the name *bayensis* Sternitzky has been applied since he proposed the name in 1937.
- Lorquin apparently collected these *editha* types for Boisduval in the immediate San Francisco Bay area, rather than the foothills of the southern edge of the San Joaquin Valley as suggested by Bauer (in Howe, 1975; see also Miller and Brown, 1981). This confounding discovery makes it necessary (Emmel, Emmel and Mattoon 1989) to sink the well-known name *bayensis* in synonymy with *E. editha editha*. Populations with the nominotypical *editha* phenotype are found in the hills along the west and east side of the southern portion of San Francisco Bay southward into Santa Clara County. South of that point populations occur which closely resemble *bayensis* but tend to show some blending towards the southern California subspecies *quino* Behr.
- ELEVATION RANGE: From 500' to approximately 3,500' elevation, with most colonies below 2,500'.
- HABITAT AND PLANT COMMUNITIES: This checkerspot is usually found in abundance on serpentine hills and grassland.
- PHENOLOGY: This subspecies starts flying in late March and reaches its peak throughout the months of April.
- FOODPLANTS: The pre-diapause foodplant is either *Plantago erecta* Morris (Plantaginaceae) or *Orthocarpus* species (Scrophulariaceae), depending on the particular locality. Post-diapause larvae feed primarily on *Plantago erecta* Morris (first discovered by Tilden, 1958a), although other scrophularaceous hosts are sometimes used by the larvae if they are in close proximity to where the pre-diapause larvae went into diapause the previous season. See the text under General Remarks for further discussion of foodplant utilization and foodplant hierarchies in the entire *editha* complex.

b. *E. e. quino* (Behr)

- DIAGNOSIS: This coastal and interior southern California subspecies has a generally redder appearance due to the expansion of the red into the yellowish-cream spots of

typical *editha*. Additionally, the males do not have as rounded wings as the more northern coastal subspecies.

- ORIGINAL DESCRIPTION: Behr, *Proceedings California Academy of Natural Sciences*, 3: 90 (1863).
- TYPE LOCALITY: San Diego, California. Type destroyed in 1906 San Francisco earthquake and fire. Neotype designated by Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies Contributions in Science*, : (1998) and deposited in the Natural History Museum of Los Angeles County.
- DISTRIBUTION: Populations of this subspecies are widely scattered over the cismontane areas of southern California at lower elevations, from the coastal San Diego County area to extreme western Riverside and San Bernardino counties. Populations are known to the north along the coast in the Santa Monica Mountains (now probably extinct) to the Santa Barbara region. Populations in these areas tend to show some intermediacy between subspecies *quino* and *editha*, and it is probable that a broad blendzone exists between southern California and the San Francisco Bay area between these two subspecies.
- ELEVATION RANGE: From sea level to approximately 2,600' elevation, with the majority of populations below 2,000'.
- HABITAT AND PLANT COMMUNITIES: The butterfly is typically found on grassy mesas or rolling grassy hills within the Coastal Sage Scrub plant community.
- PHENOLOGY: Most records are for the month of March, although there are some February records and one record for early December, with some records extending into April or early May. The timing of the flight seems to be variable from year to year, based on rainfall patterns.
- FOODPLANTS: The larvae feed on a *Plantago* species or possibly more than one *Plantago* species: namely, *P. erecta* Morris or *P. hookeriana* F. & M. var. *californica* (Greene) Poe. *Plantago* taxonomy in California has not been clearly resolved and these two species may be the same species of *Plantago* or they may be separate species. Similarly, it is unclear whether the records for larvae being found on this *Plantago* simply represent differences in foodplant identification or whether two separate, closely related *Plantago* species are involved. Unlike the central California populations of *E. e. editha*, *E. e. quino* appears to use exclusively the *Plantago* species as both a pre-diapause and post-diapause larval foodplant.

c. *E. e. insularis* T. and J. Emmel

- DIAGNOSIS: This is a very dusky, blackish subspecies with melanic scaling that greatly reduces the moderate to extensive yellow and red spotting present on other coastal and montane *Euphydryas editha* subspecies in California.
- ORIGINAL DESCRIPTION: T. C. and J. F. Emmel, *Journal of Research on the Lepidoptera*, 13: 131-136 [1975] ("1974").
- TYPE LOCALITY: Santa Rosa Island, Santa Barbara County, California. Holotype in Natural History Museum of Los Angeles County of Western North American Butterflies.
- DISTRIBUTION: So far as known, this subspecies is confined to Santa Rosa Island; it has not been taken on any of the other Channel Islands. Coastal populations of *E. editha* in Santa Barbara and southern San Luis Obispo County approach the phenotype of this subspecies probably more closely than they do that of *E. e. editha* to the north.

- ELEVATION RANGE: The type locality is at approximately 300' elevation; the range of elevation that the subspecies occurs in throughout Santa Rosa Island is not currently determined.
- HABITAT AND PLANT COMMUNITIES: The typical habitat of *insularis* is rolling grassy hills.
- PHENOLOGY: The type series was taken in late March and early April, and presumably this represents a typical flight period.
- FOODPLANTS: Unknown, but presumed to be a *Plantago* species.

d. *E. e. baroni* (W. H. Edwards)

- DIAGNOSIS: This north coastal subspecies, centered in Mendocino County, has a redder and brighter pattern above, while on the underside it has much more red and less black than typical *editha* from the San Francisco Bay area. While paralleling the variation in subspecies *luestherae*, described below, *baroni* tends to be smaller and darker as a rule. Interestingly, this subspecies *baroni* was originally described by William Henry Edwards on the basis of having quite different larvae, perhaps the first butterfly taxon to be described on the attributes of a non-adult stage.
- ORIGINAL DESCRIPTION: W. H. Edwards, *Canadian Entomologist*, 11: 129-131 (1879).
- TYPE LOCALITY: Mendocino County, California. Lectotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Entomological Society*, 92: 374 (1966).
- DISTRIBUTION: This subspecies is found along the immediate coast in Mendocino County, from approximately the area of the town of Mendocino northward to the Mendocino-Humboldt County line.
- ELEVATION RANGE: Populations are located just slightly above sea level.
- HABITAT AND PLANT COMMUNITIES: Typical habitats are on bluffs overlooking the ocean in the North Coastal Prairie plant community.
- PHENOLOGY: This subspecies flies in late May and June, with a peak flight in early June.
- FOODPLANTS: The butterfly is known to use both a Scrophulariaceae species and a Plantaginaceae species. The first is a *Castilleja* species, possibly *C. wightii* Elmer; the other known host is introduced *Plantago lanceolata* L., which grows abundantly in several of the localities for this subspecies.

e. *E. e. luestherae* Murphy and Ehrlich

- DIAGNOSIS: This new subspecies is phenotypically distinguishable from *Euphydryas editha editha* and *E. editha baroni* by the overall whiter appearance of the dorsal aspect of the wings, due to more extensive red and yellow scaling and reduced black areas. Along the outer margin of the upperside of the forewing is a narrow row of red spots bordered on the inside by black and then a row of yellow chevrons, then a wider band of black, then a row of yellow spots followed again by a narrow band of black. The next band is red and is found approximately one-third the distance from the margin to the base of the wing in the postmedian region. Its color and extent is the key character for visually distinguishing this form from other northern California *editha* subspecies (Murphy and Ehrlich, 1980). In *E. e.*

luestherae, this red band is very well-developed, being much wider than those rows surrounding it. On the underside of the forewing, *luestherae* is heavily suffused with brick red across the basal two-thirds of the wing, disrupting the overall checkered appearance of the ventral surface of other *editha* subspecies.

- ORIGINAL DESCRIPTION: Murphy and Ehrlich, *Journal Lepidopterists' Society*, 34: 316-320 (1980).
- TYPE LOCALITY: 22 miles west of Patterson, Del Puerto Canyon, Stanislaus County, California. Holotype in American Museum of Natural History.
- DISTRIBUTION: This subspecies is widely distributed in scattered colonies in the inner Coast Ranges from Mendocino County southward to San Luis Obispo County.
- HABITAT AND PLANT COMMUNITIES: The typical habitat is steep canyon slopes of the inner Coast Range where the *Pedicularis* foodplants grow as hemiparasites in the shade of shrubs. This habitat is primarily in Chaparral and Foothill Woodland plant communities.
- PHENOLOGY: In contrast to the more coastal *Plantago*-feeding populations, *luestherae* tends to have a later flight period, with a peak flight in mid-May to early June. Some specimens are taken in late April.
- FOODPLANTS: The pre-diapause foodplant is *Pedicularis densiflora* Benth. ex Hook (Scrophulariaceae). Post-diapause larvae may also use the *Pedicularis*, but in addition often crawl onto plants of *Castilleja* or *Collinsia* species, also in the family Scrophulariaceae.

f. *E. e. colonia* (W. G. Wright)

- DIAGNOSIS: This is a medium-sized to large subspecies of *editha*, with expansion of the central red band of the forewing. On the hindwing, the submarginal yellow spots are partially or completely replaced by red scaling; this effect is particularly noted in females. We are using this name to apply to several sets of populations in the Klamath Mountains Assemblage and North Coast Ranges in interior Humboldt and Trinity counties. These populations all have a somewhat similar phenotype which seems to most closely resemble that of true *colonia* from Oregon; possibly all of these populations use *Collinsia* as a principal host and it is suspected that at least several *Collinsia* species are involved. Until further extensive and detailed field work is done on these sets of populations, we are unable to characterize them in a more detailed and meaningful manner.
- ORIGINAL DESCRIPTION: W. G. Wright, *Butterflies of the West Coast*: 158 (1905).
- TYPE LOCALITY: Mount Hood, Oregon. Lectotype in California Academy of Sciences, designated by Tilden, *Occasional Papers California Academy of Sciences*, (118): 21 (1975).
- DISTRIBUTION: This subspecies is distributed from central Washington southward to Oregon and along the Cascadian crest into California. In California, populations are scattered through the mid-elevations of the Klamath Mountains Assemblage, southward into interior Humboldt and Trinity counties.
- ELEVATION RANGE: A considerable range of elevation exists for populations included under the subspecies *colonia*, ranging from approximately 2,000' to 7,000' in the Trinity Alps.

- HABITAT AND PLANT COMMUNITIES:** Toward the coast, *colonia* is primarily a resident of Mixed Evergreen Forest. Inland from the Klamath Assemblage of mountains, it occupies more of a coniferous forest setting with Douglas Fir or Yellow Pine present. Within these plant communities, *colonia* is usually associated with rocky ridges, outcroppings, or rubble flats, always involving rich serpentine rock and soil. The proper balance of these floristic elements appears necessary for prolific growth of its larval host plant, and these sites often provide adjacent wetter areas with suitable abundance of sources. Very often, populations are located along the canyonsides adjacent to a watercourse, and are oriented south-to-southwest, receiving maximum benefit of sun exposure during early months of the year.
- PHENOLOGY:** The single brood of this subspecies starts to fly in the first week of May at lower elevations, with the main flight from mid-May through mid-June. The adult flight is completed by the first of July. Egg masses are placed on the underside of lower leaves of the host *Collinsia*, and webbing of the plant occurs as the feeding larvae advance to approximately third instar. They then diapause at the base of plants in the serpentine rubble rock until the following spring, when feeding resumes and the life cycle is completed.
- FOODPLANTS:** Confirmed *colonia* larval hosts include *Collinsia linearis* Gray at Low Divide Road near High Divide in Del Norte County. Other *Collinsia* species, unidentified to date, have been collected as larval hosts in other *colonia* populations.

g. *E. e. karinae* Baughman and Murphy

- DIAGNOSIS:** This is a small subspecies similar to *luestherae* in general color pattern, but somewhat smaller in size.
- ORIGINAL DESCRIPTION:** Baughman and Murphy, *Systematics of Western North American Butterflies Contributions in Science*, : (1998).
- TYPE LOCALITY:** Monkey Rock, 1.5 miles north of Hull Mountain, 6,353 feet, Mendocino County, California.
- DISTRIBUTION:** This subspecies is found in the higher elevations of the North Coast Range, from approximately Hull Mountain (6,800' elevation) northward to the Anthony Peak area along the border of Mendocino and Lake counties in Mendocino National Forest. On Anthony Peak, the butterfly flies near "treeline" in open windswept habitat. On Hull Mountain, the habitat is less open, with red fir growing nearly to the summit and the butterflies and host plants being found among large stands of bracken ferns.
- ELEVATION RANGE:** From approximately 6,000 to 7,400' elevation.
- HABITAT AND PLANT COMMUNITIES:** The butterfly is typically found on open rocky or gravelly scree slopes within the Montane Coniferous Forest community.
- PHENOLOGY:** The species begins flying in April and continues into late May or even June, depending on annual conditions. Baughman and Murphy (1989) note that the adults appear in the earliest spring season, when patches of snow still remain under red and white firs on protected north and east-facing slope exposures.

FOODPLANTS: The foodplant of this species is *Collinsia greenii* Gray (Scrophulariaceae), which occurs on open talus and scarf slopes that have south-facing exposures and support a variety of chaparral species (including *Arctostaphylos*).

h. *E. e. rubicunda* (Hy. Edwards)

DIAGNOSIS: *E. e. rubicunda* is the *editha* subspecies on the western slope of the Sierra Nevada; this is the western counterpart of *E. e. monoensis* on the eastern slope, and it is larger than that subspecies when at lower elevations (2,500') while being smaller at higher elevations. It differs in the heavier black pattern above and the smaller light, creamy spots. The submarginal row of creamy spots is particularly reduced and infused with red -- hence the name "rubicunda."

ORIGINAL DESCRIPTION: Henry Edwards, *Papilio*, 1: 52 (1881).

TYPE LOCALITY: "Sierra Nevada...from 2,500' to 7,000'..." [California]. Restricted to Mariposa County, California, by Gunder, *Pan-Pacific Entomologist*, 6: explanation for Figure 15 (1929). Syntypes in American Museum of Natural History.

DISTRIBUTION: Populations referable to this subspecies are widely distributed along the west slope of the Sierra Nevada at low to mid-elevations, from Butte County in the north, southward to Tulare or northern Kern counties.

ELEVATION RANGE: From approximately 2,000' to 5,000' elevation.

HABITAT AND PLANT COMMUNITIES: The butterfly is typically found on canyon slopes within either Foothill Woodland or the lower edges of the Mixed Coniferous Forest community, as well as in Chaparral areas.

PHENOLOGY: Most records for this species are from mid May to mid June, with some records in mid to late April.

FOODPLANTS: At least one documented pre-diapause foodplant is *Collinsia tinctoria* Hardw. ex Benth. (Scrophulariaceae); probably other *Collinsia* species are used as well. Post-diapause foodplants include *Collinsia sparsiflora* F. & M. var. *bruceae* (Jones) Newsom., *Plectritis ciliosa* (Greene) Jeps. (family Valerianaceae), and *Lonicera interrupta* Benth. (Caprifoliaceae).

i. *E. e. aurilacus* Gunder

DIAGNOSIS: This subspecies is generally similar to *colonia* but differs in having the submarginal row of spots expanded, and these are almost always completely red, not yellow as in *colonia*. It also tends to be a smaller insect than *colonia*.

ORIGINAL DESCRIPTION: Gunder, *Pan-Pacific Entomologist*, 5: 49-50 (1928).

TYPE LOCALITY: Near Gold Lake Camp, Gold Lake, Sierra County, California. Holotype in American Museum of Natural History.

DISTRIBUTION: Populations with this subspecific phenotype are found from the Mount Lassen region southward along the west side of Lake Tahoe to approximately Fresno County. The subspecies seems to be most abundant in the areas just west of Lake Tahoe and in the Gold Lake region of Sierra County.

ELEVATION RANGE: Populations of *aurilacus* range from approximately 6,000 to 9,000' elevation.

HABITAT AND PLANT COMMUNITIES: The butterfly is typically found in open, gravelly or rocky slopes within the Montane Coniferous Forest community.

PHENOLOGY: Virtually all records are for the month of July, with an apparent peak flight during the first two weeks of July.

FOODPLANTS: Currently unknown, although a *Castilleja* species is suspected for the Gold Lake population (Dennis Murphy, personal communication).

j. *E. e. singeri* Emmel, Emmel, and Mattoon

DIAGNOSIS: This is a small *editha* subspecies with marked expansion of the red areas on the upperside, giving the butterfly an overall very red appearance; this phenotype is superficially similar to that of *E. chalcidona irelandi*, which occurs in the same general area.

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies Contributions in Science*, : (1998).

TYPE LOCALITY: Along the General's Highway, Tulare County, California.

DISTRIBUTION: The populations with this specific phenotype occur on the west slope of the Sierra Nevada at relatively high elevations in Tulare and extreme southern Fresno counties.

HABITAT AND PLANT COMMUNITIES:

PHENOLOGY: This butterfly flies in June and early July, with an apparent peak flight in late June.
FOODPLANTS:

k. *E. e. nubigena* (Behr)

DIAGNOSIS: This is a tiny checkerspot with predominantly red-brown to orange-brown uppersides. It is found at very high elevations in the Sierra Nevada range.

ORIGINAL DESCRIPTION: Behr, *Proceedings California Academy of Natural Sciences*, 3: 91 (1863).

TYPE LOCALITY: Headwaters of the Tuolumne River, up to 11,500', [California]. Types destroyed in 1906 San Francisco earthquake and fire.

DISTRIBUTION: This subspecies is found in the highest elevations of the Sierra Nevada, from the Sonora Pass region southward to the Sierra Nevada of Tulare County.

HABITAT AND PLANT COMMUNITIES: The butterfly is typically found on open gravelly slopes and ridgetops within the Arctic Alpine Cushion Plant community.

PHENOLOGY: This butterfly flies in July and August, with one record to our knowledge for late June, and an apparent peak abundance in late July and early August.

FOODPLANTS: In populations studied by Michael Singer near Tioga Pass, California, it was found that adults of this subspecies oviposited on *Castilleja nana* Eastw., which the

larvae used as a pre-diapause foodplant, but that post-diapause larvae were all found on *Penstemon heterodoxus* Gray. The two plants are used because at the later summer time *nubigena* adults are flying, the *Castilleja* plants are in optimal condition for development of young larvae. In the following spring, however, the *Penstemon* species leafs out earlier than the *Castilleja* species, and presents a greater availability of foodplant at the time the larvae are coming out of diapause. Hence, it is apparently more efficient for them to switch over to the *Penstemon* species to feed through to maturity at this early time of the year. It is not known whether all *nubigena* populations require this combination of these two *Scrophulariaceae* species, or whether in some localities they may exist on either plant alone.

l. *E. e. edithana* (Strand)

- DIAGNOSIS:** One of three subspecies of *editha* in the Modoc and Lassen County area, this is the lowest elevation population and it inhabits the open sagebrush areas. It is redder and smaller than subspecies *baroni* described earlier.
- ORIGINAL DESCRIPTION:** Strand, *Arch. f. Naturgesch.*, (A)80 (11): 155 (1914).
- TYPE LOCALITY:** "N. California". Holotype probably in Zoologische Museum der Humboldt Universität, Berlin, East Germany.
- DISTRIBUTION:** In California, populations with this phenotype seem to occur in the lower elevations of Lassen and Modoc counties. From there, according to Bauer (1975), similar populations extend into the northwestern corner of Nevada and northward through the mountains east of the Cascade Range to central Oregon.
- ELEVATION RANGE:** From 4,000 to 5,700' elevation.
- HABITAT AND PLANT COMMUNITIES:** These populations are located typically in the open Sagebrush Scrub plant community. Nectaring on wildflowers in low spots in the *Artemisia* scrub is common, and males have a characteristic habit of congregating around solitary juniper trees where they perch on the tree or nearby ground and engage in combative flights. This may be a mate-locating habit.
- The adults are found in volcanic-type rubble on rocky flats or mountainsides where the small, annual, desert type of *Collinsia* is abundant. Often, the type of available nectar sources and the appearance of the breeding-ground habitat exactly match those requirements of *E. anicia veazieae*, which it appears to replace here. The same niche further out the Great Basin desert is occupied by *veazieae*. There is one location where the two species occur together in the same habitat, and there the *veazieae* are associated with *Penstemon* in slightly drier areas while the *edithana* are associated with *Collinsia* in wetter meadows.
- PHENOLOGY:** Adult emergence of this subspecies starts in the first weeks of May at its lower desert flat locations, and is extended into the first of June at higher locations.
- FOODPLANTS:** *Edithana* is always in close association with a small annual species of *Collinsia*, which is widely distributed in its sagebrush habitat. Other than scattered *Penstemon* plants, this is the only possible recognized host at some locations.

m. *E. e. mattooni* Austin and Murphy

- DIAGNOSIS: This is also a relatively low-elevation Modoc Plateau subspecies which superficially resembles *E. anicia veaziae* but is smaller in size.
- ORIGINAL DESCRIPTION: Austin and Murphy, 1998, *Systematics of Western North American Butterflies Contributions in Science*, : (1998).
- TYPE LOCALITY: Modoc County, Road 1 from Fort Bidwell, California, to Adel, Oregon, at junction of Gravel Pit Road, 9.4 road miles north of junction of County Road 2 at Fort Bidwell.
- DISTRIBUTION: So far as is known, this subspecies is only found along the east base of the Warner Mountains in Modoc County.
- ELEVATION RANGE: 5,250' to 5,600'.
- HABITAT AND PLANT COMMUNITIES: This beautiful little checkerspot inhabits semi-wet grassy meadows along intermittent watercourse adjoined by Northern Juniper Woodland, with abundant *Artemisia* and elements of Sagebrush Scrub plant community interspersed. These areas are flats that form temporary wet meadows from springtime water runoff and vernal basining. This habitat is also occupied at the same flight time by the almost identical and more abundant *E. anicia veaziae*, from which the *editha* subspecies is very difficult to differentiate on the wing, and the *editha* are easily overlooked.
- PHENOLOGY: The single brood flies in the relatively early spring of the Northern Juniper Woodland sagebrush country, and depending on the year, can be found by the first of May or slightly earlier. It mainly flies from mid-May into early June.
- FOODPLANTS: Confirmation of specific hostplant has not yet been made, but the most abundant and available associated plant is an annual springtime blooming *Collinsia* species. Post-diapause larvae have been found on a *Penstemon* species and reared to adults (by Sterling O. Mattoon). The associated host *Collinsia* characteristically grows on the gravelly slopes just above the meadow habitat, under *Artemisia* scrub and scattered juniper.

n. *E. e. warnermontanus* Baughman and Murphy

- DIAGNOSIS: This is a small, dark *editha* subspecies which biologically seems fairly similar to *E. e. nubigena* of the higher elevations of the Sierra Nevada to the south. In a sense, this subspecies is transitional between *E. editha aurilacus* which flies at moderate elevations on the west side of the Sierra Nevada to the south and *E. editha remingtoni* which occurs at high elevations in the central Oregon Cascade Range to the north, yet it is distinct from both. This subspecies is characteristically very dark and predominantly red. The dorsal male forewing has two marginal rows of red spots separated by a black band. These spots are consistently dull red, whereas in more southern subspecies, these spots are often suffused with yellow. A black stripe is located medially to these spots and is broader and more distinct than that of *E. editha aurilacus*.
- ORIGINAL DESCRIPTION: Baughman and Murphy, *Systematics of Western North American Butterflies Contributions in Science*, : (1998).
- TYPE LOCALITY: Crestline Trail in the vicinity of Emerson Peak, 8,200 feet elevation, southern end of Warner Mountains, 3 to 5 air miles north of Patterson Meadows, Modoc County, California.

- DISTRIBUTION:** This subspecies is found along the summit ridges of the Warner Mountains in Modoc County.
- ELEVATION RANGE:** From 7,800' to 8,800' and slightly higher to the highest points along the crest of the Warner Mountains.
- HABITAT AND PLANT COMMUNITIES:** This high-elevation *editha* occupies the sandy, gravelly upper slopes of Mt. Emerson in the Warner Mountains. The lava rubble-rock ridge crests and rim rock outcroppings provide open areas where the upper limits of the Northern Juniper Woodland reach into elements of Subalpine Forest. Here, the larval host, a short yellow-flowered *Castilleja* species near *C. nana* Eastw., is abundant on plants growing in the rimrock or lava rubble. Adults are especially attracted to sandy openings or clearings in the *Artemisia* scrub where their preferred nectar source, an *Eriogonum* species (Pussypaw), grows in blooming carpets at the adult flight season. The habitat is punctuated by an abundance of blooming sunflowers, also used for nectar. Moisture feeds into the sandy habitat from melting snowdrift remnants left from the winter in the shelter of the rimrock crest. This runoff resurfaces in wet grassy and willow-clad springs, and small meadows and seeps, throughout the habitat of this subspecies. It is a beautiful upland habitat where springtime comes in July rather than at the traditional dates.
- PHENOLOGY:** The butterfly has a peak flight period in mid-July.
- FOODPLANTS:** *Castilleja chromosa* A. Nels. (Scrophulariaceae) is the host of this subspecies.

***o. E. e. monoensis* Gunder**

- DIAGNOSIS:** This subspecies has the distinctive character of having "all interior cream spots and lunate marginal cream spots, fuller or broadened" (Gunder, 1928). While the *monoensis* colonies of *editha* along the east slope of the Sierra Nevada are rather variable, most of them show this distinctive pattern character outlined in the original description above.
- ORIGINAL DESCRIPTION:** Gunder, *Pan-Pacific Entomologist*, 5: 49 (1928).
- TYPE LOCALITY:** Rush Creek (below Farmington's Ranch), Mono Lake, Mono County, California. Holotype in American Museum of Natural History.
- DISTRIBUTION:** This subspecies is found along the eastern base of the Sierra Nevada, from extreme northwestern Inyo County northward to extreme northern Mono County.
- ELEVATION RANGE:** From 6,000' to 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** The butterfly is typically found in the Sagebrush Scrub plant community, which is so dominant in this area of the east slope of the Sierra Nevada. Within the areas of sagebrush covered slopes and flats, the butterfly sometimes becomes concentrated around small wet or dry meadows.
- PHENOLOGY:** Dates of capture range from early June to mid-July, depending on elevation, with an apparent peak during the latter half of June.

FOODPLANTS: At least one pre-diapause larval foodplant has been identified as *Collinsia parviflora* Dougl. ex Lindl. (Scrophulariaceae). Possibly an *Orthocarpus* species may also be used (John Masters, personal communication).

p. *E. e. fridayi* Gunder

DIAGNOSIS: While very close to subspecies *monoensis*, *E. e. fridayi* is distinguished by its smaller size and slight enlargement of the yellow markings on the wing in comparison to *monoensis*.

ORIGINAL DESCRIPTION: Gunder, *Bulletin Southern California Academy of Sciences*, 30: 47 (1931).

TYPE LOCALITY: Between June and Silver Lakes, Mono County, California. Holotype in American Museum of Natural History.

DISTRIBUTION: The limits of distribution of this subspecies are currently unclear. It may be confined to the area immediately above Silver Lake and June Lake in Mono County; however, specimens are known from the higher elevations above Bishop Creek in extreme northwestern Inyo County, which may also be referable to this subspecies.

ELEVATION RANGE: From 7,200' to 7,600' elevation.

HABITAT AND PLANT COMMUNITIES: This subspecies, like the preceding, is also apparently found in the Sagebrush Scrub plant community, although at a higher elevation than that occupied by *monoensis*.

PHENOLOGY: The type series was taken in mid-June.

FOODPLANTS: These are presently unknown; perhaps further field work and investigation of hosts will help elucidate the relationship of *fridayi* and *monoensis*.

q. *E. e. augustina* (W. G. Wright)

DIAGNOSIS: Populations in the higher elevations of the San Bernardino Mountains have long been called *augusta* (Edwards) (e.g., Comstock, 1927b; Emmel and Emmel, 1973). However, the type locality of *augusta* is on the small foothills near the town of San Bernardino (*fide* Wright, 1906; Coolidge, 1911) and the lectotype of *augusta* is a typical southern California lowland phenotype of *E. editha*, which would make *augusta* synonymous with *E. e. quino*. Hence, the name *augusta* is not applicable to these phenotypically different, higher elevation populations.

The name *augustina*, although applied to an aberrant specimen (Wright, 1906), was proposed in such a way as to be available to be used to apply to this set of high elevation populations (see also Scott, 1981: p. 4). This re-named subspecies is characterized by smaller size and increase in the extent of red and cream-color markings on the upperside, giving the overall appearance of a very reddish insect.

ORIGINAL DESCRIPTION: W. G. Wright, *Butterflies of the West Coast*: 154 (1905).

TYPE LOCALITY: San Bernardino Mountains, San Bernardino County, California. Holotype in California Academy of Sciences.

DISTRIBUTION: True *augustina* is confined to the higher elevations of the San Bernardino Mountains. Populations with an extremely similar phenotype and biology also

occur in the southern Sierra Nevada in extreme southeastern Tulare County and extreme southwestern Inyo County. The precise relationship of these populations to those in the San Bernardino Mountains remains undetermined; however, they are here lumped with *augustina* until such work can be accomplished. Specific localities in the San Bernardino Mountains include elevations above 8,000' on Sugarloaf Peak, and along forest roads and meadows at about 5,000' near Running Springs, Moonridge, Cedar Pines Park, Wild Horse Creek, Fawnskin, and Onyx Peak.

- ELEVATION RANGE: From 5,000' to 9,600' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is usually found in meadows or clearings within the Montane Coniferous Forest community; some colonies are present on forested slopes such as at Cedar Pines Park.
- PHENOLOGY: Most records are for early and mid-June, but some mid-May records are available.
- FOODPLANTS: A variety of foodplants are used by *augustina* populations. These include *Collinsia childii* Parry ex Gray, *Castilleja miniata* Dougl. ex Hook, and possibly *Pedicularis semibarbata* Gray (all Scrophulariaceae).

r. *E. e. ehrlichi* Baughman and Murphy

- DIAGNOSIS: This is a small to medium-sized subspecies with extensive development of the red and yellow markings on the upperside of the wings. The orange-red is a brighter tone than that found in most other *E. editha* subspecies, giving the butterfly a very orange-red appearance, much like that of *augustina*. Most of the black and cream-colored markings on the upperside of the forewing are reduced. The margin of the hindwing has a full row of orange-red spots which are large and full in comparison to other subspecies. The undersides of both sexes have red and yellow spots but very little black. It is a butterfly that occurs in semi-desert conditions in the Ord Mountains and has a biology differing from that of *augustina*.
- ORIGINAL DESCRIPTION: Baughman and Murphy, *Systematics of Western North American Butterflies Contributions in Science*, : (1998).
- TYPE LOCALITY: Along Bowen Ranch Road, northeast of the Bowen Ranch, Ord Mountains at the northwest end of San Bernardino Mountains southeast of Hesperia and west of Victorville, 4,400-4,520 feet, San Bernardino County, California.
- DISTRIBUTION: This butterfly is found in the desert foothills (the Ord Mountain range) flanking the north base of the San Bernardino Mountains, from approximately Tejon Pass eastward to the Cushenberry Grade.
- ELEVATION RANGE: Populations are found between 3,800 and 5,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The habitat for this subspecies is the high desert within the Juniper Woodland plant community, on the semi-arid desert slopes of the north face of the San Bernardino Mountains. The typical terrain in this area is rolling hills with gravelly soils, with scattered desert shrubs and junipers, including *Yucca brevifolia*, *Salazdria*, *Lycium*, *Salvia*, *Artemisia*, *Eriogonum*, and a number of cactus species.
- PHENOLOGY: The butterfly flies primarily during the month of April, with some records for early May. Post-diapause larvae are active in March.

FOODPLANTS: The apparent only foodplant of this subspecies is *Castilleja plagiotoma* Gray (Scrophulariaceae). It is used by both prediapause and postdiapause larvae. Egg masses and larvae have only been found in sheltered northeast slope exposures (J. F. Emmel, data). This *Castilleja* species is rather locally distributed along the north slope of the San Bernardino Mountains and the San Gabriel Mountains to the Piute Mountains of Kern County, and westward to Caliente Mountain in eastern San Luis Obispo County.

79. *Poladryas arachne monache* (J. A. Comstock)

- DIAGNOSIS:** This unmistakable orange checkerspot has a reticulate black pattern on the dorsal wing surfaces and a broad pearly white banding pattern on the ventral hindwings.
- ORIGINAL DESCRIPTION:** John A. Comstock, *Lepidopterist*, 2: 71 (1918).
- TYPE LOCALITY:** Monache Meadows, Tulare County, California. Holotype in Natural History Museum of Los Angeles County of Western North American Butterflies.
- DISTRIBUTION:** This subspecies represents a California population that is substantially disjunct from the rest of the range of the species. It is confined to the Kern Plateau area of the southern Sierra Nevada, in southeastern Tulare County. The wider distribution of *Poladryas arachne* occurs from Nevada and Arizona to Nebraska, and from Wyoming south to western Mexico, usually in the mountains.
- ELEVATION RANGE:** In California, from approximately 6,500 to 9,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** The butterfly is typically found on open rocky or gravelly slopes and hillsides within the Sagebrush Scrub community or Jeffrey Pine Forest community, in the higher elevations of the southern Sierra Nevada. Adults are frequently taken in dry meadows in this area, but the actual breeding sites of the species are on the gentle slopes surrounding these meadows.
- PHENOLOGY:** The majority of our records are for the month of June and early July; however, the type series was taken by Comstock in August and may represent a partial second brood. Perhaps in years with summer rainfall, some larvae are stimulated to forgo diapause and continue development to adults emerging in August or even early September.
- ADULT BEHAVIOR:** Males exhibit perching behavior, usually landing on open patches of ground, while females tend to remain on the slopes where the foodplants are concentrated. Both sexes are avid flower visitors, particularly being attracted to yellow composites.
- LIFE HISTORY:** The eggs are pale yellow and are laid in clusters of relatively small numbers of eggs (30-40) in comparison to the larger masses laid by *Euphydryas* or *Chlosyne*. The larvae are gregarious in the first two instars, but do not make any kind of webbed nests. The mature larva is blackish-brown ventrally. Above this, laterally, there is a broad lateral white band going through the spiracles and above this is a black band of similar width running the length of the larva. Dorsally, there is a middorsal black band which is flanked on either side by subdorsal white bands. The subdorsal white band has orange splotches which are centered on the subdorsal spines. The head of the larva is dirty orange with small black markings.

- The pupa is ivory-white with black markings, superficially similar to the pupae of our *Euphydryas* species.
- FOODPLANTS: The only foodplant used in our area is *Penstemon speciosus* Dougl. ex Lindl. (Scrophulariaceae).
- CHROMOSOME NUMBER: Unknown in California populations. In Colorado, $n = 31$ (Emmel, Harris, and Eliazar, 1989).
- SIMILAR SPECIES: None in our area.
- GEOGRAPHIC AND SEASONAL VARIATION: The highly restricted distribution of this species in California has led to no geographic differentiation within this area. Elsewhere, outside our state, several subspecies have been named.
- GENERAL REMARKS: The localized distribution of this butterfly is puzzling, as there are seemingly suitable habitats present in such areas as the White Mountains in Inyo and Mono counties, as well as in the Warner Mountains of Modoc and Lassen counties in the northeastern part of the state, in which *Penstemon speciosus* Dougl. ex Lindl., the preferred foodplant of this species, is present in abundance. The factors governing this limited distribution are poorly understood at present but possibly may involve a presence or absence of summer rainfall, as well as other environmental factors. In Texas a second species in this genus, *Poladryas minuta* (W. H. Edwards), is believed to have become extinct now in central Texas, perhaps a victim of overgrazing (Tilden and Smith, 1986: p. 108; Miller and Brown, 1981: p. 152).

80. *Dymasia dymas imperialis* (Bauer)

- DIAGNOSIS: This is a very small checkerspot with yellowish-white or cream-colored wings and a checkered black pattern. On the underside the lighter areas are shiny white, particularly on the hindwings, and the orange-brown areas are reduced.
- ORIGINAL DESCRIPTION: Bauer, *Journal Lepidopterists' Society*, 12: 98-99 [1959] ("1958").
- TYPE LOCALITY: Palm Springs, Riverside County, California. Holotype in Natural History Museum of Los Angeles.
- DISTRIBUTION: Populations of this butterfly are scattered along the western edge of the Colorado Desert in Riverside, San Diego, and Imperial counties. It occurs here from Palm Springs in the northwestern Coachella Valley southeastward to the Mexican border, just east of Mountain Springs Pass at the San Diego/Imperial County line. Populations are also known along the south face of the Cottonwood and Eagle Mountains, just south of Joshua Tree National Monument, and in the Chuckwalla Mountains south of Desert Center in Riverside County. Outside of California, this species ranges from central Arizona southward into northern Mexico.
- ELEVATION RANGE: From approximately sea level to 2,000' elevation.
- HABITAT AND PLANT COMMUNITIES: In California the species is typically found in large desert washes, usually near valley bottoms or at the bases of desert mountains. In these areas the foodplant is sometimes locally abundant and grows with such other desert species as *Ocotillo*, *Dalea* species, *Hyptis emoryi* Torr. (Desert Lavender), *Cercidium floridum* Benth. (Palo Verde), and *Olneya tesota* Gray (Desert Ironwood).

- PHENOLOGY:** The species is usually bivoltine if summer rains are sufficient. The first brood flies any time from late March to late April, depending on winter rainfall patterns, and the second brood, if present, usually flies in September. Comstock's (1929c) rearing studies showed that the pupae from the first brood could either diapause or emerge within a week to yield more adults in the "first" spring brood.
- ADULT BEHAVIOR:** The adult butterflies are frequently seen nectaring at the flowers of *Bebbia juncea* (Benth.) Greene (a yellow *Composite* species). Males exhibit perching behavior in the desert washes, generally landing on the twigs of low shrubs lining the washes.
- LIFE HISTORY:** The life history was first described by Comstock (1929). The egg is a stout globule 0.6 mm wide by 0.7 mm high. Its color is a light lemon-yellow and the upper half of the egg bears 20 to 30 longitudinal ridges, while the lower half is covered with an irregular network of roughly hexagonal cells. The mature larva has a gray body color with white and black mottlings and seven rows of spines. At the base of each of the spines in the median dorsal row, there is a noticeable orange spot having an outer circlet of white. The main trunk of each spine is colorless and the branching subsidiary spines are black. The row of spines next lateral to the above median series is complete on all segments. The next lateral row is placed just above the spiracles on each segment, and the amount of orange coloration at the base of each spine is greatly reduced or absent. A subspiracular row of spines is developed on a wide white band, each spine ringed with a narrow orange circlet at its base. These spines are lighter in color than those on the dorsum. The markings on the gray body are arranged as follows. A narrow black median band is present and a narrow white band occurs in line with the spiracles. Below the spiracles, there is another wide white band, as previously mentioned in connection with the bottom row of spines. The pupa is whitish gray in ground color, with the wing cases and anterior part of the thorax being lighter in color. The abdominal segments are spotted with black. Pupae that do not overwinter hatch in about seven days; the others go into diapause until the following spring.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** None in our area.
- GEOGRAPHIC AND SEASONAL VARIATION:** No geographic variation has been noted in the populations of this species within California. No significant difference between the phenotype of the spring and late-summer specimens has been noted.
- GENERAL REMARKS:** Most recent authors (e.g., Bauer, 1975; Tilden and Smith, 1986) identify two species in the genus *Dymasias*. *D. chara* has two subspecies, in this view, with the typical subspecies *chara* extending from central Arizona east to Texas and south along the west coast of Mexico, and the subspecies *imperialis* occurring in southern California and Baja California. The second species name, *Dymasias dymas* (Edwards), is applied to the Texas material. Miller and Brown (1981) consider *dymas* to be a third subspecies in the *chara* group. Because the oldest name in the group of three names is *dymas*, Miller and Brown (1981) believe there are just three subspecies in one genus: *D. d. dymas* (W. H. Edwards, 1877), *D. d. chara* (W. H. Edwards, 1883), and *D. d. imperialis* (Bauer, 1959). We follow that taxonomic arrangement in providing a name for the California material.

81. *Thessalia leanira* (C. and R. Felder)

This is a highly variable group in the southwestern U.S. and Mexico. In California six subspecies have been identified for our populations, based primarily on

variation in the dorsal color pattern. The underside is rather similar in all subspecies, being whitish to cream-colored or yellow, with black veins and a black median band enclosing a row of light spots.

- ADULT BEHAVIOR:** The adults of all six *leanira* subspecies have a relatively rapid, nearly unidirectional flight when crossing a hillside or flying along a canyon. The males are especially prone to hilltopping in the desert areas, but they will set up territories on hilltops in chaparral areas as well. Both sexes are avid flower visitors, and are particularly attracted to yellow composites.
- LIFE HISTORY:** All subspecies lay clumps of eggs containing up to several hundred ova in a single egg mass. These masses are laid on the foodplant, usually laid near the base of the plant. The newly hatched larvae then crawl up to the top of the plant to begin feeding and will live gregariously in a loose web. The larvae diapause as third instars, usually under rocks or at the base of the foodplant. The mature larva is black, but the extent of orange markings varies among the subspecies. In typical *leanira*, *oregonensis*, and *wrighti*, the orange markings tend to be connected together, forming more of an orange banding effect. Also, the shade of orange tends to be duller in those subspecies, in contrast to the bright orange or orange-red of the spotting on *alma* larvae. The larva of the subspecies on the Oso Flaco Sand Dunes has reduced orange markings and the color of these markings is a very pale orange, sometimes yellow. The pupa is ivory-white in ground color, with black markings on the wing cases, abdomen, and ventral surface, much like those of *Poladryas* and *Euphydryas*. The subspecies *leanira*, *oregonensis*, and *wrighti* tend to have reduced black markings on the pupa, in comparison to the greatly expanded black markings of *alma*. Reference to the accompanying figures will allow differentiation of the *Thessalia* pupae from those of other nymphalid genera.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** None in our area, although other *Thessalia* species occur elsewhere in the Southwest and in Mexico.
- GEOGRAPHIC AND SEASONAL VARIATION:** In the instances where populations have been bivoltine, no significant seasonal variation has been noted. As noted under the individual subspecies accounts, there is considerable geographic variation within California for this species. Between the ranges of the different subspecies, there are frequently blendzone areas where there is a mixing of characters of more than one subspecies. Thus for most of these sets of populations, there are no well-defined absolute boundaries. The accompanying distribution map will help to clarify the principal geographic ranges of these various subspecies. The overall picture of geographic variation in the checkerspot butterflies of the *Thessalia leanira* group, and their relationships with *T. fulvia* and *T. cyneas*, across the southwestern United States and northern Mexico are authoritatively reviewed in a recent treatment by Smith and Brock (1988).
- GENERAL REMARKS:** The overall geographic variation in *Thessalia leanira* parallels the geographic variation found in species of *Euphydryas* in California, particularly *E. chalcedona*. In the cool, moist coastal climates the darker forms predominate, while in the deserts the highly reddish forms are dominant. Intermediate mixtures of yellow, red, and black pattern elements are found in the mountains and foothills lying between these extremes. The pattern of evolutionary development of these

taxa parallels the *Euphydryas* in its complexity and represents a fascinating problem for further study.

a. *T. l. leanira* (C. and R. Felder)

- DIAGNOSIS: This is a blackish subspecies with somewhat reduced cream spots on the upper side and with red scaling confined largely to the apical half of the forewing.
- ORIGINAL DESCRIPTION: C. and R. Felder, *Wiener Ent. Monats.*, 4: 106 (1860).
- TYPE LOCALITY: "California"; type locality restricted to lower Feather River Canyon, Butte County, California by Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, : (1998)..
- DISTRIBUTION: Populations with this phenotype are widely distributed through the Sierra Nevada foothills from Butte County south to Tulare County. They are also found in the inner Coast Ranges from the Mount Diablo area south to Santa Barbara County.
- ELEVATION RANGE: From approximately 1,000 to 4,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This subspecies is typically found in Chaparral areas where its *Castilleja* foodplants species grow as hemiparasites on various chaparral plants.
- PHENOLOGY: Butterflies fly primarily during the months of May and June, with occasional records for late April.
- FOODPLANTS: The following *Castilleja* species have been documented as foodplants of this particular subspecies: *C. foliolosa* H. & A., and *C. affinis* H. & A.

b. *T. l. oregonensis* Bauer

- DIAGNOSIS: This is one of the darkest of the *leanira* subspecies and occurs in southwestern Oregon, with marked reduction of the cream-colored markings on the upper side and reduction of the red scaling in the apical area of the forewing. Blendzone populations just enter California in adjacent Siskiyou County.
- ORIGINAL DESCRIPTION: Bauer, Howe, *Butterflies of North America*: 166-167 (1975).
- TYPE LOCALITY: Jackson County, southwestern Oregon. In Figure 17, Plate 40 of Howe (1975), which by implication represents the holotype female, the locality is given as Mt. Ashland, Loop Road, Jackson County, Oregon. Apparent holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is primarily a resident of southwestern Oregon. Only a few colonies occur into northern California areas (the Cecilville-Crawford Creek population in Siskiyou County and several others), all in the far north and all being somewhat intermediate between this subspecies and typical *leanira*. Not enough is known about the contact between these subspecies, but most populations including those in Del Norte County and just south of Mt. Ashland in the Scott Bar Mountains are the nominotypical subspecies in areas where a normal range extension of *oregonensis* might be expected. There appears to be no evidence or likelihood that any *leanira* of the North Coast Range north of *obsoleta* in Marin County, California, are other than typical *leanira*.

- ELEVATION RANGE: From 3,000' to 5,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This *leanira* subspecies has usually been found in a riparian setting that extends up through combined Douglas Fir and Yellow Pine forests into the Red Fir Forest realm. Usually, a serpentine soil type and rocky outcroppings are associated with the *Castilleja* host for these checkerspot colonies.
- PHENOLOGY: These populations fly primarily in June and early July, with some late May records.
- FOODPLANTS: The particular *Castilleja* species used by these populations has not been determined.

c. *T. l. obsoleta* (Hy. Edwards)

- DIAGNOSIS: This subspecies has as its most unique feature the remarkable obliteration or obsolescence of the usual black banding on the underside in the distal area and post median area of the hindwing, giving the ventral surface a cream- or yellow-washed appearance. On the upper side, however, it tends to have reduced cream-colored spots and reduced red scaling. This reduction of the light dorsal spotting gives the upperside a very dark appearance!
- ORIGINAL DESCRIPTION: Henry Edwards, *Proceedings California Academy of Sciences*, 7: 171 (1877).
- TYPE LOCALITY: San Rafael, Marin County, California. Holotype in American Museum of Natural History.
- DISTRIBUTION: Populations with this striking subspecific phenotype are known only from Marin County and all individuals show this similar phenotype; hence, it is not a form name, as has been assumed by a number of authors (e.g., Comstock, 1927b; Miller and Brown, 1981).
- ELEVATION RANGE: From 1,000 to 2,500' elevation.
- HABITAT AND PLANT COMMUNITIES: This subspecies is found in Chaparral areas on the hills and canyons of Marin County.
- PHENOLOGY: Specimens are recorded from mid May to late June, with an apparent peak in early to mid June.
- FOODPLANTS: The probable foodplant is *Castilleja foliolosa* H. & A. (Scrophulariaceae).

d. *T. l. osafloco*. Priestaf and J. Emmel

- DIAGNOSIS: In this coastal sand dunes subspecies, the ground color tends to be brownish-black rather than black. The cream-colored markings on the upperside are slightly more prominent than in typical *leanira* and it is characterized in particular by the presence of very prominent submarginal red spots on the upperside. In the basal area of the forewing on the upperside, there is reduced red scaling from that seen in the southern California subspecies, *wrighti*. This subspecies is also unique in that it is the only cismontane *leanira* population which is bivoltine.
- ORIGINAL DESCRIPTION: R. Priestaf and J. Emmel, *Systematics of Western North American Butterflies Contributions in Science*, : 1998.

TYPE LOCALITY: Oso Flaco Lake, Santa Barbara County, California.

DISTRIBUTION: This unique subspecies is known only from the Oso Flaco Dunes in western Santa Barbara County. It may possibly extend northward into similar habitats along the immediate coast in San Luis Obispo County.

ELEVATION RANGE: From near sea level to approximately 200' elevation.

HABITAT AND PLANT COMMUNITIES: This subspecies flies on low, sandy ridges in the Coastal Strand plant community.

PHENOLOGY: The spring brood begins emergence in mid-April and continues into early May. A second brood is on the wing in July.

FOODPLANTS: The probable host (by association) of this population is *Castilleja wrightii* Elmer; confirmation of this plant as the foodplant is needed.

e. *T. l. wrightii* (W. H. Edwards)

DIAGNOSIS: This is a southern California coastal foothill and lower mountain subspecies that has an increased extent of the cream-colored dorsal markings as well as very extensive red scaling on the uppersides.

ORIGINAL DESCRIPTION: W. H. Edwards, *Canadian Entomologist*, 18: 64 (1886).

TYPE LOCALITY: San Bernardino, San Bernardino County, California. Lectotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Entomological Society*, 92: 389 (1966). More specifically, the exact locality is Little Mountain, a small hill on the northwestern outskirts of the city of San Bernardino; this was pointed out by Karl Coolidge (1911) who accompanied W. G. Wright to the type locality and was told that this was the locality where Wright had collected the types of *Melitaea* [*Thessalia leanira*] *wrightii*, *Melitaea* [*Euphydryas editha*] *augusta*, and *Melitaea* [*Thessalia leanira*] *cerrita*.

DISTRIBUTION: This subspecies is widely distributed throughout the lower mountain areas and foothills of southern California, from southern San Diego County, northward through western Riverside County and extreme southwestern San Bernardino County, westward through the transverse ranges to Santa Barbara County, where it begins to blend into subspecies *leanira*. Similarly, populations in Kern County on the west slope of the Piute Mountains tend to show blendzone characteristics between the subspecies *wrightii* and *leanira*.

ELEVATION RANGE: From approximately 1,000' to 6,500' elevation, with the majority of records below about 5,000'.

HABITAT AND PLANT COMMUNITIES: Most populations are found in typical Chaparral areas in the southern California mountains. Some specimens have been taken in areas of Coastal Sage Scrub.

PHENOLOGY: Records range from mid-March to late June, with a peak in late April and the month of May. These populations are apparently all univoltine, although the possibility of a late summer emergence might be possible in the years in which there are unusually heavy summer rain in southern California, such as when hurricanes from the Pacific Ocean off the coast of Mexico come northward and result in extraordinary rainfall.

FOODPLANTS: Several *Castilleja* species have been recorded for *wrightii* populations. Probably the most commonly used host is *Castilleja foliolosa* H. & A.. Along the north slopes of the Transverse Ranges, both *Castilleja chromosa* A. Nels. and *C. plagiotoma* Gray have also been recorded.

f. *T. l. alma* (Strecker)

DIAGNOSIS: This is the very orangish desert subspecies of *leanira*. Although some desert populations of this butterfly have been referred to the name *cerrita* (W. G. Wright), this taxon has the same type locality as *T. l. wrightii* (see note above under Diagnosis Section for *T. l. wrightii*) and therefore must be considered a junior synonym of *wrightii*, even though it differs phenotypically. The desert populations which fall under the name *alma* do show some variability and it may be that more than one subspecies is involved here; however, for the sake of simplicity in the present treatment, all desert *leanira* populations in California will be treated as *alma*.

ORIGINAL DESCRIPTION: Strecker, *Lepid. Rhop.-Het.*: 135 (1878).

TYPE LOCALITY: "Arizona [and] S. Utah", restricted by Miller and Brown (1981, *Memoirs Lepidopterist Society* #2: 153) to vicinity of St. George, Washington County, Utah. Holotype in Field Museum of Natural History, Chicago, according to label in Strecker collection (this may be a syntype).

DISTRIBUTION: This subspecies is widely distributed in the deserts of California, occurring along the desert edge from the northeastern flank of the San Bernardino Mountains and extending westward along the north slope of the Transverse Ranges, where it forms a blendzone with subspecies *wrightii*. From here it extends northward through the desert mountains and eastward to the eastern Mojave Desert ranges, thence northward to the mountains of the Death Valley region and along the east slope of the Sierra Nevada as far north as the foothills of the White Mountains and Inyo Mountains. The butterfly again enters our area from Nevada in extreme northern Mono County in the vicinity of Topaz Lake, then again in the lower elevation areas of eastern Lassen County. These more northern populations differ from the southern desert populations in that the orange suffusion on the upperside is not as indistinct as in the southern populations; that is, there is more of a defined pattern on the upperside.

ELEVATION RANGE: From approximately 2,000 to 7,000' elevation, with the majority of populations in the 4,000 to 6,000' range.

HABITAT AND PLANT COMMUNITIES: The butterfly is found in the upper edge of the Creosote Bush Scrub community, in the Sagebrush Scrub community, and in the Pinyon-Juniper Woodland community, as well as Joshua Tree Woodland. The usual habitat consists of open rolling hills, where the adults tend to concentrate in wash bottoms or along roads where males frequently set up perching "territories".

PHENOLOGY: The desert populations are usually univoltine, but the occurrence of an occasional late summer brood has been recorded in several different years of unusually heavy summer rainfall. The spring brood typically flies from mid April to mid May, or to late May in some of the higher elevations; the late summer brood, when present, has been recorded in early September.

FOODPLANTS: By far the most widely used, and perhaps the only, host of *C. l. alma* populations is *Castilleja chromosa* A. Nels. (Scrophulariaceae).

g. *T. l. basinensis* Austin and M. Smith

DIAGNOSIS: This more northern subspecies has a more reddish orange ground color dorsally than the lighter orange coloration of *alma*. It is marked by strong black scaling along all the veins and presents a more striated appearance. It has more strongly darkened basal suffusion. The ventral surface is also more strongly striated and the black-outlined pattern on the ventral hindwing tends to be more strongly marked and not a "washed-out" pattern as in *alma*.

ORIGINAL DESCRIPTION: Austin and M. Smith, Natural History Museum of Los Angeles County Contributions in Science, : (1989).

TYPE LOCALITY:

DISTRIBUTION: This recently described species occurs from north of Mono Lake in Mono County, east to the Toiyabe Range and north to the eastern border of Lassen County.

ELEVATION RANGE: From 4,000' to 6,000' elevation. Hilltopping males may ascend to as high as 6,400'.

PHENOLOGY: This subspecies is univoltine, with records ranging from late April to mid-June, depending on seasonal rainfall patterns.

FOODPLANTS:

82. *Chlosyne lacinia crocale* (W. H. Edwards)

A highly variable butterfly, this species has received many names across its range in the southwestern United States into Mexico. There seems to be almost endless polymorphism of wing color and pattern (Bauer, *in* Howe, 1975). Our populations are placed under the subspecific name *crocale*.

DIAGNOSIS: This is a highly variable nymphalid, but three principal adult forms occur in our California populations. One common form (typical f. "*crocale*") has all white spots and banding on the black forewings, with a narrow white band across black hindwings. Another common form (f. "*rufescens*") has a black ground color on the dorsal surface, with white spots and banding on the apical half of the forewing, two or three russet orange spots on the basal half of the forewing, and a rather broad orange to yellow hindwing band. A less common form (f. "*nigrescens*") has white spots and banding on the forewing, and a narrow, dull reddish to orange hindwing band.

ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Entomological Society*, 5: 17-18 (1874).

TYPE LOCALITY: "White Mtns., Arizona"; [NE Ft. Apache, Navajo Co., Arizona], according to F. M. Brown, *Trans. American Entomological Society*, 92: 407 (1966). Lectotype in Carnegie Museum, designated by F. M. Brown, *Trans. American Entomological Society*, 92: 409 (1966).

DISTRIBUTION: In California, this species occurs principally in cultivated areas in the Imperial and Colorado River valleys, up into surrounding lower desert canyons. Strays are

taken along the western edge of the Colorado Desert, such as on Monument Peak in the Laguna Mountains of San Diego County and at Pinyon Flat above Palm Springs in Riverside County. In the San Jacinto Valley and San Bernardino Valley of southern California, populations may persist for several years in agricultural areas, only to be eliminated by a hard freeze. It became briefly established (apparently on the usual host, *Helianthus annuus* L.) north of the Transverse Ranges for the first time in 1973, when at least two broods occurred in a new population on the American River floodplain at Camp Pollock in the Sacramento Valley (Shapiro, 1975b).

**HABITAT AND PLANT
COMMUNITIES:**

Habitat preferences of this butterfly include the Creosote Bush Scrub on the floors of the deserts and the lower slopes of adjacent foothills or desert mountains. The preferred habitats away from agricultural areas are the lower desert canyons. In the cultivated areas of the Coachella and Imperial Valleys, the species may be found commonly and often in great numbers along roadsides or hedge rows containing sunflower plants.

PHENOLOGY:

The flight period for *crocalle* extends from March through October in a series of broods, with the adults considerably more common in the fall months. This species is extremely abundant around Blythe in the Imperial Valley during September. There are occasional records for late to mid-November. Away from irrigated agricultural areas, this species flies primarily from mid-April to mid-May in a single brood, which may be followed by a second brood in September with summer rains.

ADULT BEHAVIOR:

Butterflies of this species have a weaker flight behavior than those of the other American genera of the tribe Melitaeini, and they frequently stay close to their host plants. They readily visit flowers, especially those of Compositae.

LIFE HISTORY:

Besides the numerous color forms present in the adult stage, the last three larval instars and pupal stage exhibit striking color polymorphisms. The life history of this species has been described in great detail by Drummond, Bush, and Emmel (1970), including laboratory rearing techniques available for genetic studies. A female may deposit up to 500 eggs in several clusters on the underside of a sunflower leaf. The egg is pale greenish-yellow. The mature larvae bear seven rows of branched spines and may be patterned in three basic forms: an almost entirely black form ("*nigra*"), a black form with a prominent mid dorsal light yellow to orange-red stripe ("*bicolor*"), and an all orange to orange-red morph ("*rufa*"). The somewhat complicated genetics of this interesting situation have been worked out thoroughly by Neck, Bush, and Drummond (1971) and Neck (1976); the first paper also illustrates the three morphs in color and the interested reader is referred to this source for details. The pupa itself varies from almost pure white to almost completely black; a number of polymorphic forms are indicated. Under hot field conditions around Blythe in the late summer or fall, a complete generation can pass in about 30 days and the species goes through a number of broods from March to October each year. There appears to be no correlation between the color forms of the larval polymorphism, the pupal polymorphism, and the adult polymorphism. The genetics and adaptive significance of the various morphs in the pupae and adults are completely unknown.

Overwintering is accomplished in the half-grown larval stage (late third instar or early fourth instar). Borders of agricultural fields with sunflowers are the most favored habitat of this species.

FOODPLANTS: Sunflower, *Helianthus annuus* L. ssp. *lenticularis* (Dougl.) Ckll. (family Compositae), is the usual host throughout the species' range in the Southwest. Thorne (1962) reported several *C. lacinia* larvae among a colony of *C. californica* larvae on *Viguiera deltoidea* Gray var. *parishii* (Greene) Vasey & Rose in Sentenac Canyon, 10 miles northeast of Julian, San Diego County, in September 1961. Neck (1973) has presented a complete review of foodplant use by *lacinia* throughout the western United States. His review showed no additional hostplant records from southern California.

PARASITES / PREDATORS: In Texas populations, Drummond, Bush, and Emmel (1970) obtained extensive data on parasitism and predation with this species. They found that parasitism accounts for a considerable proportion of the mortality occurring from the egg to the adult stage in natural populations. A wasp, *Trichogramma fasciatum* (Trichogrammatidae), parasitizes the eggs of *lacinia* and affected 12% of 82 egg masses from three different localities. Selective parasitism on larval morphs was found for one species of Braconidae wasp, *Apanteles lunatus*. Three parasite species were reared from the few *lacinia* pupae collected as larvae or pupae in the field. These included a small pteromalid, ichneumonid, and a chalcid. Two species of tachinid flies are common parasites, ovipositing on fourth and fifth instar larvae (14% of 177 larvae collected at random were parasitized by these flies). Predators take a heavy toll of larvae and adults. A particularly common predator was a metallic blue pentatomid bug, which usually attacked third and fourth instar larvae and often almost completely destroyed a brood. Members of the wasp genus *Polistes* (Vespidae) are also common predators of the later larval instars in Texas. Jumping spiders (Salticidae) were observed to capture and feed on adults, and the butterfly has also been found in the webs of the Orb spiders, *Argiope auranti* and *A. trifasciata* (Argiopidae).

CHROMOSOME NUMBER: n = 31 (from Texas material; Emmel, unpublished).

SIMILAR SPECIES: See discussion under *Chlosyne californica*.

GEOGRAPHIC AND SEASONAL VARIATION: A great many names have been given to the variable phenotypes in the species *Chlosyne lacinia*. Careful breeding studies are needed to determine whether these names represent genetic forms in a balanced polymorphism, or possibly closely related species in the case of forms further to the south in Mexico. It will be particularly interesting to work out the relationships, if any, of the color polymorphism in the larvae, pupae, and adults to variable factors of natural selection in nature. No seasonal variation has been noted, despite the occurrence of multiple broods in our lower desert valleys as mentioned earlier.

GENERAL REMARKS: This butterfly is easily reared in the laboratory and can even be cultured on an artificial diet (Drummond, Bush, and Emmel, 1970). It would be easy for lepidopterists located in the southern California area to do substantial original research on the genetics of this highly polymorphic species.

83. *Chlosyne californica* (W. G. Wright)

DIAGNOSIS: This species is very similar to some of the forms of *Chlosyne lacinia*, but it can always be distinguished by the orange color of the discal cell on the dorsal surface of the forewing, and by the orange marginal series of spots on the dorsal surface of both wings. It is also usually found in a different habitat from *lacinia*, being a typical denizen of desert washes and canyons while *lacinia* is found in river bottoms and agricultural canal areas.

- ORIGINAL DESCRIPTION: W. G. Wright, *Butterflies of the West Coast*: 170 (1905).
- TYPE LOCALITY: Colorado Desert, [California]. Based on our knowledge of Wright's collecting localities, the probable type locality is in the vicinity of Palm Springs. Lectotype in California Academy of Sciences, designated by Tilden, *Occasional Papers California Academy of Sciences*, (118): 24 (1975).
- DISTRIBUTION: This species is widely distributed in our deserts from the foothill and mountain areas of the Colorado Desert in Imperial and eastern San Diego counties, the desert areas bordering the Coachella Valley in Riverside County and the mountain ranges of the Mojave Desert from approximately Lucern Valley on the west, eastward to the Colorado River and thence northward to approximately the Inyo County line in the vicinity of the Kingston Range. From here it ranges eastward into southern Nevada, western Arizona and southward into Sonora and much of Baja California.
- ELEVATION RANGE: From near sea level to approximately 5,500' in the desert mountains, for breeding populations; hilltopping males and stray adults are known from localities as high as 8,000' elevation in the mountains, such as along the north slope of the San Bernardino Mountains.
- HABITAT AND PLANT COMMUNITIES: The favored habitat is canyons in the desert mountains and desert washes within the Creosote Bush Scrub plant community.
- PHENOLOGY: The species is multivoltine, with the size of the second and third broods (or the presence thereof) dependent upon rainfall patterns and elevation. There is a rather regular spring brood flying generally in March and most of April with a peak during the first two weeks in April. We have records for every month of the year except January and August; probably with further collecting in the deserts, records will eventually turn up for these months as well. Appearance and abundance of this species seems to be closely correlated with rainfall, as with most of the other desert butterfly species.
- ADULT BEHAVIOR: The California Patch is generally found in canyons and washes in the Colorado and Mojave Deserts. There, the males perch on hilltops during the later morning hours to await females. The flight pattern of both males and females is rather weak for a nymphalid, as they fly slowly across open slopes or along canyon bottoms.
- LIFE HISTORY: The egg is pale yellowish-green. The eggs are laid in clusters on the underside of the host leaves. The mature larva is usually black with seven rows of black branched spines, and vertical rows of white dots along the entire body. However, the basic "*bicolor*" pattern and "*rufa*" (all orange) morphs present in *C. lacinia* are also found in *C. californica*. The pupa is usually white with variable black streakings across both the wing cases and the abdomen. However, the pupa also occurs in almost all black forms or almost pure white forms. This species hibernates as the third instar larval stage.
- FOODPLANTS: The foodplant across the species' range in California is *Viguiera deltoidea* Gray var. *parishii* (Greene) Vasey & Rose (family Compositae).
- CHROMOSOME NUMBER: Unknown.
- SIMILAR SPECIES: The California Patch differs from *C. lacinia* by having orange in the cell of the ventral side of the forewing, and the fact that the median band and submarginal spots are orange.

GEOGRAPHIC AND SEASONAL VARIATION: from southern Nevada south into Mexico in northern Sonora and Baja California, including some of the off-shore islands in the Pacific Ocean, *Chlosyne californica* has not developed any notable geographic differentiation. Likewise, despite the sequence of multiple broods in canyons surrounding the Colorado Desert, there is no evidence of pronounced seasonal variation in this species.

GENERAL REMARKS: It would be particularly interesting to do a comparative study of the genetics of the larval, pupal and adult color patterns in *Chlosyne lacinia* and *Chlosyne californica*, including laboratory hybridization experiments between them. There is no strongly suggestive evidence from nature of any natural hybridization between these two sympatric and often synchronic species.

84. *Charidryas palla* (Boisduval)

ADULT BEHAVIOR: The flight of the adults of *Charidryas palla* is moderately fast and usually near to the ground. The males and females spend much time feeding at flowers and occasionally land in sunny spots to rest with their wings oriented to the sun. Males will frequently visit puddles and damp ground and may be captured readily.

LIFE HISTORY: The morphology of the egg is undescribed, but they are pale green when first laid in clusters on the underside of host leaves. The young larvae are gregarious for awhile after hatching, but do not build a nest. The mature larva is charcoal black along the dorsal half, speckled with minute whitish spots which outline a black, more mid-dorsal line with a heavier concentration of white dots along each side and eight pairs of orange crescents on either side of the bases of the mid-dorsal spines. Two similar rows of orange spots occur along the sides below the rows of tubercles that are placed just above and below the spiracles. There is also a lateral whitish stripe of larger white marks below which the body is grayish-black. The spines are shiny black and bristly with branches. The pupa may vary considerably, ranging in ground color from pale tan to wood brown and pale gray to mostly black; it is mottled with fine streaks and spots of various shades of gray and brown. This species hibernates as half-grown larvae.

CHROMOSOME NUMBER: $n = 31$ (Emmel, unpublished).

SIMILAR SPECIES: See discussions under *Charidryas whitneyi*, *C. acastus*, *C. gabbii*, and *C. hoffmanni*. There are two other species of *Charidryas* with which *palla* may be sympatric. The first is *C. hoffmanni*, with which *palla* is frequently sympatric in the Klamath Mountains region and the region of eastern Siskiyou County, just east of Mount Shasta. In this latter area, females of *palla* and *hoffmanni* can look extremely similar, and the reader is referred to the color plate figures of these two species to help differentiate them. The second species that *palla* may be sympatric with is *C. acastus* in eastern Lassen County. In this area the two species are probably not intimately sympatric, but there may be certain habitats where strays of one species will wander into the normal habitat of the other. In these instances, *acastus* can usually be separated from *palla* by the more cream-colored spots on the underside, in contrast to the more yellowish cast to these spots in *palla*. Also, the upperside of *palla* tends to be more of a reddish-orange, while *acastus* tends to be a paler orange in these populations.

GEOGRAPHIC AND SEASONAL VARIATION: Because the species is strictly univoltine, there is no seasonal variation. The geographic variation has already been discussed under the various subspecies.

GENERAL REMARKS: Bauer (1975) has suggested that the present variation in the species *Charidryas palla* supports the idea that fragmentation of this species occurred during a cooler glacial period, and the present isolated subspecies, which still maintain their distinctions, have reestablished contact and in some areas apparently interbreed. It would be interesting to extend this approach to look at subspeciation in the other Melitacines from the same perspective, and see how closely the patterns of geographic variation match among these species.

SUBSPECIES: The Northern Checkerspot, *Chlosyne palla*, is distributed from the Rocky Mountains west to British Columbia and into our Pacific states. It reaches its southern limit in the northern mountains of southern California. It is characteristically a foothill canyon and montane species. Three subspecies are present in our state.

a. *C. p. palla* (Boisduval)

DIAGNOSIS: This subspecies is characterized by the red-brown ground color of the males on the dorsal surfaces, with a rather heavy and evenly pigmented black pattern. The Boisduval types show that the female is two-toned in having inner spot rows being yellow and the outer submarginal row reddish, with rather heavy black markings between the spots (see Emmel, Emmel, and Mattoon (1998a) for color illustrations of types).

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 305 (1852).

TYPE LOCALITY: "Dans une grande partie de la Californie", restricted by Miller and Brown (1981, *Memoirs Lepidopterist Society* #2: 156) to vicinity of San Francisco, California. Holotype apparently in U. S. National Museum. Type locality re-restricted by Emmel, Emmel, and Mattoon (1998a) to lower Feather River Canyon, Butte County, California.

DISTRIBUTION: The nominotypical subspecies is found primarily in the foothill areas of the western slope of the Sierra Nevada, from approximately Butte County south to the west slope of the Sierra Nevada in eastern Kern County, southward to the Tahachapi and Tejon Mountains at the south end of the San Joaquin Valley. To the north of the Butte County populations, there is a blendzone with the Coast Range subspecies *eremita*, with varying percentages of dark and light females as one goes from east to west across the north end of the Sacramento Valley.

ELEVATION RANGE: From approximately 2,000 to 5,000' elevation.

HABITAT AND PLANT COMMUNITIES: This subspecies is typically found in well-watered canyons in the foothills with the dominant vegetation being either foothill woodland plant community, or the lower edge of mixed coniferous forests.

PHENOLOGY: We have records from mid-May to mid-July with an apparent peak in mid- to late June.

FOODPLANTS: The Sierran foothill *palla* populations are known to feed on *Aster* (Shapiro, personal communication); these populations also very likely use a *Solidago* species which is known to be used by Coast Range *palla* populations and is locally abundant in many of the localities where the low elevation *palla* occurs. J. A. Comstock (1927b) listed the foodplant of *palla* as *Castillia* [sic] *breviflora*; this foodplant was apparently based on a report by Mead in the Wheeler Survey Report. Undoubtedly, this record is in error as no

subsequent observations have confirmed this foodplant usage; perhaps Mead had found a *palla* pupa on the plant or some other fortuitous association which was not based on a true foodplant choice.

b. *C. p. eremita* (W. G. Wright)

DIAGNOSIS: This is a North and Central Coast Range subspecies characterized by having very dark blackish females, in contrast to the orangish red-brown females which are dominant in the nominotypical *palla* populations. The males of these populations tend to be slightly more darkly marked than nominotypical *palla*. Although the name *eremita* has long been used as a form name for any dark females of any *palla* population, we consider it a distinct subspecific entity. When it was originally named by W. G. Wright, he considered it a distinct species from *palla*. The subspecific distinctness of these Coast Range populations is demonstrated by the consistently high (nearly 100%) percentage of this very dark female phenotype.

ORIGINAL DESCRIPTION: W. G. Wright, *Butterflies of the West Coast*, 157 (1905).

TYPE LOCALITY: "Central California". Lectotype in California Academy of Sciences, designated by Tilden, *Occasional Papers California Academy of Sciences*, (118): 21 (1975). Emmel, Emmel, and Mattoon (1989) fixed the type locality of *eremita* as San Rafael, Marin County, California.

DISTRIBUTION: This subspecies is found in the Coast Ranges of central and northern California. Its southern limits seem to be in the Santa Cruz Mountains and Diablo Range in the Mount Hamilton region. From here it goes northward through both inner and outer Coast Ranges to as far north as the Klamath Mountains Assemblage. In this area there begins a blendzone with the nominotypical *palla*, and the percentage of dark females gradually decreases as one goes eastward and northward from this area. However, in these northern California and southern Oregon populations of *palla*, there tends to be a predominance of the dark female form. Much more field work is necessary to more precisely delineate the varying percentages of dark and light females in these northern lowland *palla* populations.

ELEVATION RANGE: From near sea level to approximately 5,000' elevation, with the majority of populations below 3,000'.

HABITAT AND PLANT COMMUNITIES: The butterfly is usually found in well-watered canyons within the Foothill Woodland and Chaparral plant communities in this area.

PHENOLOGY: Most records for the Coast Range populations are for the month of May, but with some early to mid-June records as well. The butterfly is strictly univoltine.

FOODPLANTS: At least one documented host plant of the Coast Range *palla* populations is *Solidago californica* Nutt.; some California Coast Range populations may also use *Aster* (A. Shapiro, personal communication).

c. *C. p. altasierra* Emmel, Emmel, and Mattoon

DIAGNOSIS: In this high elevation subspecies of the Sierra Nevada there tends to be a lighter orange ground color with reduction of the black markings rendering a paler, more generally orange appearance to the butterfly when viewed dorsally. This subspecies for many years went under the name *whitneyi* Behr, which actually applies to another high-elevation *Charidryas* which has been called *C. damoetas*

malcolmi. Although the type of *whitneyi* was lost in the 1906 San Francisco earthquake and fire, Behr's description and type locality clearly link it to the insect we have been calling *malcolmi*, rather than to this high-elevation subspecies of *palla*.

- ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1989).
- TYPE LOCALITY: Fallen Leaf Lake, 6,400' elevation, El Dorado County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is distributed in the higher elevations of the Sierra Nevada, from approximately the Gold Lake Region in Sierra County south to the Kern Plateau in southern Tulare County.
- ELEVATION RANGE: From 6,400 to approximately 8,500' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is typically found in open areas such as dry meadows or sagebrush flats within the Jeffrey Pine Forest or Yellow Pine Forest communities, as well as the lower edge of the Red Fir Forest community.
- PHENOLOGY: The majority of records are for the month of July, with an apparent peak during the first two weeks of the month. There are some late June records as well.
- FOODPLANTS: David Bauer (personal communication) has found larvae on *Solidago canadensis* L. ssp. *elongata* (Nutt.) Keck. and *Machaeranthera canescens* (Pursch.) Gray. Additionally, he has also found larvae on *Chrysothamnus nauseosus* (Pall.) Britton, and *C. viscidiflorus* (Hook.) Nutt. (all of these plants are in the family Asteraceae).

d. *C. p. australomontana* Emmel, Emmel, and Mattoon

- DIAGNOSIS: This is the most lightly marked subspecies of *palla* in California,
- ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 141-142 (1998h).
- TYPE LOCALITY: Kennedy Meadows Road, 16-20 miles west of Highway 395, Tulare County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is found in the extreme southern Sierra Nevada of Tulare County and the east slope of the Sierra Nevada in Inyo County southward to the western end of the Transverse Ranges. There, it flies in the Tejon Range and Frazier Mountain region.
- ELEVATION RANGE: From approximately 4,000 to 9,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The Southern Mountain Checkerspot is typically found in open dry meadows surrounded by a mixture of Great Basin Sagebrush Scrub and Jeffrey Pine Forest plant communities.
- PHENOLOGY: The single brood of adults flies from early May to mid July, depending on elevation and progression of the season
- FOODPLANTS:

85. *Charidryas whitneyi whitneyi* Behr

DIAGNOSIS: This is the butterfly which for many years has been called *C. damoetas malcolmi*. Behr's types of *whitneyi* were destroyed in the San Francisco earthquake and fire in 1906, and following that loss, the name was applied by various workers to the high-elevation subspecies of *C. palla* in the Sierra Nevada, presumably because the type locality of *whitneyi* was at a high elevation and it was assumed that *C. palla* populations occurred in the type locality. However, *C. palla* does not occur in the type locality of *whitneyi* (which, as originally described by Behr, refers to the area "from the headwaters of the Tuolumne River where it was collected during the stay of the State Geological Survey in the elevated and uninhabited regions"). Because the name *whitneyi* predates the names *malcolmi* (Comstock, 1926) and the name *damoetas* (Skinner, 1902), *malcolmi* falls as a junior synonym of *whitneyi*, and *damoetas* becomes a subspecies name for the Rocky Mountain populations of *whitneyi*. This situation is discussed in more detail in Emmel, Emmel, and Mattoon (1989b), in which the taxa named by Behr are treated.

This species is recognized by the rather dull pale and uniform orangish-brown color of the dorsal surfaces. On the underside the light spots are less pearly than those of *C. gabbii*, but more so than that seen in *palla*, tending to be almost a dirty silvery white.

ORIGINAL DESCRIPTION: Behr, *Proceedings California Academy Natural Sciences*, 3: 88 (1863).

TYPE LOCALITY: "From the headwaters of the Tuolumne River" [Sierra Nevada, California]. Type destroyed in 1906 earthquake and fire in San Francisco.

DISTRIBUTION: This is a high alpine species found along the higher elevations of the Sierra Nevada, from the area of Mineral King in Tulare County northward to approximately Carson Pass in Alpine County. This species is also found in the Sweetwater Mountains of extreme northern Mono County in adjacent Nevada.

ELEVATION RANGE: From approximately 9,500' to 13,500', with most records in the 10,500 to 11,500' range.

HABITAT AND PLANT COMMUNITIES: This butterfly is typically found in the Arctic Alpine Cushion Plant community, where it prefers rockslides or rocky slopes.

PHENOLOGY: This species is univoltine with records recorded for the months of both July and August. The apparent peak of flight is toward late July or early August.

ADULT BEHAVIOR: Males are usually seen flying over the rocky slopes in search of females; they may set up perching sites in open depressions on the rocky slopes. Females are usually seen in close proximity to the foodplants. Both sexes are avid flower visitors, being partial to yellow composites.

LIFE HISTORY: The eggs are pale green when first laid and are deposited in a cluster on the underside of the foodplant leaves. The young larvae are gregarious but do not

make a silken nest. The mature larva is dull charcoal black with many black spines, and is covered with numerous small whitish dots. Ventral to the spiracles, the ground color is dull brown or tan. There is a narrow black mid-dorsal line which has pale orange crescent-shaped markings on either side of the mid-dorsal spines, forming an interrupted pair of pale orange dorsal stripes. A somewhat similar but more obsolescent pale orange line occurs above the spiracles laterally. The spines tend to be slightly shorter than those of either *C. palla* or *C. acastus* larvae. The pupae are variable in color and markings, but tend to be a light grayish-tan with darker brown and brownish-black markings. The larvae diapause as third or fourth instar larvae. In the laboratory, larvae will often break diapause, begin feeding, but then go back into diapause for another season. Thus, the butterfly has the ability to diapause over a two or three year period in nature if conditions are unfavorable for the completed development of the larva in a particular year. This may be particularly advantageous in the Alpine Zone, where the potential growing season is very short, and flexibility in breaking diapause and developing or continuing diapause is a definite advantage.

FOODPLANTS: This species uses two species of Asteraceae in the Sierra Nevada: *Erigeron pygmaeus* (Gray) Greene, and *Solidago multiradiata* Ait.

CHROMOSOME NUMBER: $n = 31$ (from Colorado material; Emmel, Eliazar, and Harris, 1989).

SIMILAR SPECIES: *C. whitneyi* is superficially similar to several other members of the *C. palla* complex, but is readily identified by its association with an Arctic Alpine habitat. Additionally, the quality of orange on the upperside of the wings tends to be very dull and subdued in contrast to the other *C. palla* group species.

GEOGRAPHIC AND SEASONAL VARIATION: As the species is univoltine, there is no seasonal variation. Slight differences exist between populations of this butterfly at the north and south ends of its range. Specimens from the higher elevations of Tulare County tend to be slightly more melanic than their northern counterparts. The Rocky Mountain subspecies, *damoetas*, tends to have a more dusky suffusion at the base of the wings and an even duller ground color; also, the percentage of melanic females in *damoetas* populations tends to be higher than that seen in Sierra Nevada populations of *whitneyi*.

GENERAL REMARKS: The disjunct distribution of this species in the Sierra Nevada and the Rocky Mountains suggests that it is a relic of Pleistocene glaciation advances and retreats.

Although the genitalia and early stages of *C. whitneyi* are extremely similar to those of the *C. acastus* complex and *C. gabbii*, recent unpublished hybridization studies by J. F. Emmel show that these three entities are best treated as three separate species.

86. *Charidryas acastus* (W. H. Edwards)

LIFE HISTORY: The eggs are pale green when first laid and are laid in a cluster on the undersides of leaves or on the stem of the foodplant, usually fairly close to the ground. The young larvae are gregarious on the leaves but do not make an obvious silken nest. The second or third instar larvae of *neumoegeni* will often crawl to the flowers of the foodplant and feed on the ray flowers of the particular composite species that they are using. Third instar larvae go into diapause and in subsequent seasons they may break diapause, feed briefly and then go back into a second diapause as fourth instar larvae. The mature larva is very similar to that described for

whitneyi, except that the orange markings tend to be completely replaced by charcoal-gray. The larval spines in the *acastus* complex tend to be slightly longer than those of *C. gabbii* and *C. whitneyi*. The pupae are variable, tending to be similar to that of *damoetus* for subspecies *acastus*, *vallismortis*, and *waucoba*. The pupa of subspecies *neumoegeni* is usually gray and extensively mottled with brownish-black or black markings.

CHROMOSOME NUMBER: $n = 31$ for *neumoegeni* (Emmel, unpublished).

SIMILAR SPECIES: The only *Charidryas* species with which the *acastus* may be sympatric is *palla* in the northeastern part of the state. See discussion under *C. palla* for the distinguishing characteristics of the populations in this area.

GEOGRAPHIC AND SEASONAL VARIATION: No seasonal variation has been noted between the two broods of *C. neumoegei*. Specimens of *C. acastus* in extreme northeastern California tend to be darker than typical *acastus*, with some females showing melanic tendencies. Presumably, this is the southern end of a long cline going northward which culminates in the extremely dark female subspecies *dorothyi* Bauer. A pair of *acastus* from eastern Lassen County are illustrated on our plates. The subspecies *neumoegeni*, despite its very wide geographic range, is extremely constant in phenotype from one locality to another.

GENERAL REMARKS: Every regional and North American faunal work on butterflies in this century has treated the butterflies included in *Charidryas* differently. The present outline, especially in the *acastus* group, is no different in that regard. This group presents exceptionally interesting ecological and evolutionary problems which will only be solved by further rearing, crossing experiments, and field work during the respective flight seasons of the species and subspecies of this fascinating genus. We feel that the treatment that we have outlined in this book is the most satisfactory, given all the evidence accumulated to date on California material.

This species includes five taxa, several of which have been considered separate species in the past.

a. *C. a. acastus* (W. H. Edwards)

DIAGNOSIS: This subspecies is characterized by various shades of orange as the basic ground color, with a partially obsolescent dark pattern. On the undersurface, the ground color of both sexes varies from glossy white to creamy white.

ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Entomological Society*, 5: 16-17 (1874).

TYPE LOCALITY: "Montana, Nevada, S. Utah", restricted to Provo Canyon, Utah County, Utah, by F. M. Brown, *Transactions American Entomological Society*, 92: 402 (1966). Lectotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Entomological Society*, 92: 404 (1966).

DISTRIBUTION: In California, *acastus* is found along the east slope of the Sierra Nevada in extreme northwestern Inyo County northward through Mono County, and from here eastward to northwestern New Mexico, western Colorado, Wyoming, Nebraska, and southern Alberta and Saskatchewan, and northward to eastern Oregon and southern Idaho.

ELEVATION RANGE: Within California, the nominotypical subspecies occurs from approximately 6,000 to 8,000' elevation.

HABITAT AND PLANT COMMUNITIES: This butterfly is typically found in the Sagebrush Scrub plant community of the Great Basin. Adults are usually found on open sagebrush slopes or in canyon bottoms or gulches, where the males frequently perch.

PHENOLOGY: This subspecies is univoltine, with adults appearing in mid to late May and early June and flying into early August. Although a second brood has never been observed in the California populations of this butterfly, the species is at least bivoltine and possibly trivoltine in New Mexico and southwestern Colorado and southern Utah. In these regions the second and third broods tend to be much smaller and are possibly often overlooked by collectors. In years of unusual summer rain in known *acastus* habitats in California, it would be of interest to specially watch for a late summer brood of adults.

FOODPLANTS: In our experience, the preferred foodplant of *acastus* throughout the major portion of its range is *Machaeranthera canescens* (Pursh) Gray (Asteraceae). In addition, the species is known to use and is commonly associated with *Chrysothamnus viscidiflorus* (Hook.) Nutt. If both *Machaeranthera* and *Chrysothamnus* are present in a given locality, the preferred oviposition substrate is the *Machaeranthera*; however, post-diapause larvae may often crawl onto nearby *Chrysothamnus* plants from their original overwintering site and it may be advantageous to the butterfly to have both plant species present in a given locality for optimal development of larvae. In a number of localities, only *Chrysothamnus viscidiflorus* (Hook.) Nutt is available, and it may represent the primary oviposition substrate as well as the primary foodplant for the larvae.

b. *C. a. vallismortis* (J. W. Johnson)

DIAGNOSIS: This subspecies is characterized by "its large, more regular rows of fulvous spots, the distinct fuscous or black lines between these rows, and particularly the heavy black medial band of the superior surface of the primaries. The undersurfaces are constantly cream, differing thus from *acastus*, which is frequently silvery-white" (Johnson, 1938).

Although originally named as a subspecies of *C. palla*, even in the original description Johnson noted that this subspecies had characters relating it to *C. acastus* as well. Recent life history studies, as well as hybridization studies (J. F. Emmel, unpublished data) indicate that this butterfly is very closely related to *C. acastus* and is best considered a subspecies of that insect.

ORIGINAL DESCRIPTION: Johnson, *Bulletin Southern California Academy of Sciences*, 37: 18-20 (1938).

TYPE LOCALITY: Tuber Canyon, Panamint Range, Death Valley, California. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This butterfly is found only in the Panamint Range in Inyo County, California. Within the Panamints, specific localities for this butterfly are Upper Wildrose Canyon, Tuber Canyon, Upper Surprise Canyon, and Telescope Peak.

ELEVATION RANGE: From approximately 6,500' to 10,000' elevation, with the majority of specimens in the 8,000 to 9,000' range.

HABITAT AND PLANT COMMUNITIES: The butterfly is typically found in steep canyons within the Sagebrush Scrub plant community or at the lower edge of Bristlecone Pine Forest community, or occasionally is found in the upper boundaries of the

Pinyon-Juniper Woodland plant community. Males perch on openings in canyon bottoms or along dirt roads. Females are usually found flying over the open slopes, and both sexes have been observed to visit the flowers of *Hulsea heterochroma* Gray, and *Chaenactis douglasii* (Hook.) H. and A. (Asteraceae) in upper Surprise Canyon.

PHENOLOGY: Records for adults of this univoltine subspecies range from mid June to mid July, with an apparent peak during the latter part of June.

FOODPLANTS: No specific foodplant has yet been determined for this subspecies; however, *Chrysothamnus viscidiflorus* (Hook.) Nutt is abundant in its favored habitats and represents the probable host.

c. *C. a. waucoba* Emmel, Emmel, and Mattoon

DIAGNOSIS: This is a high-elevation subspecies of the Inyo Mountains which combines characters of both subspecies *neumoegeni* and subspecies *vallismortis*. In general, the upperside tends to resemble *neumoegeni*, with reduction of the black markings and a dull orange ground color. On the underside, the ground color tends to be more orange than in *neumoegeni*, and again the black markings are reduced. The cream-colored spots on the underside tend to be paler than those seen in subspecies *acastus*, but darker than the more pearly-white spots seen in subspecies *neumoegeni*. Both careful rearing studies and hybridization studies (J. F. Emmel, unpublished data) indicate that this taxon is a subspecies of *C. acastus*.

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, 1989, *Systematics of Western North American Butterflies*, pp. 142-143 (1998h).

TYPE LOCALITY: One half airmile north of Cerro Gordo (town), Inyo Mountains, 8100' elevation, Inyo County, California.

DISTRIBUTION: This subspecies is apparently confined to the higher elevations of the Inyo Mountains in Inyo County California. A similar insect occurs in the Spring Mountains in Clark County, Nevada, but is phenotypically distinguishable and probably represents a third subspecies of *C. acastus* in the *vallismortis-waucoba* complex.

ELEVATION RANGE: From approximately 7,000' to 10,000' elevation, with most specimens being taken in the 8,000' to 9,000' range.

HABITAT AND PLANT COMMUNITIES: The butterfly is typically found on steep slopes or in ravines within the Sagebrush Scrub and Pinyon Forest plant communities. Males set up perching "territories" in ravine bottoms or in hollow openings on the canyon slopes.

PHENOLOGY: Records for this subspecies range from late May to mid July, depending on elevation and rainfall patterns for the season. Most records are concentrated around the latter part of June. This subspecies is apparently univoltine, as no evidence of a late summer brood has yet come to light.

FOODPLANTS: As with *vallismortis*, the foodplant is unknown for this subspecies but in its favored habitats *Chrysothamnus viscidiflorus* (Hook.) Nutt, a known foodplant of *acastus*, is usually abundant.

d. *C. a. neumoegei* (Skinner)

- DIAGNOSIS:** This subspecies is distinguished from the other subspecies and related species of the *palla* group by its evenly colored orange-red ground color on the dorsal surface of the wings and a strong tendency towards obsolescence of the black network pattern. On the underside of the wing, the light areas are silvery-white and the males have most of the underside of the forewing evenly washed with orange-red.
- ORIGINAL DESCRIPTION:** Skinner, *Entomological News*, 6: 113 (1895).
- TYPE LOCALITY:** "Utah", but type from Virgin River Valley, Washington County, Utah. Holotype in Carnegie Museum.
- DISTRIBUTION:** This subspecies is widely distributed in our deserts. It occurs from the extreme northern end of the Owens Valley in the foothills of the White Mountains and in the area near Benton in southeastern Mono County, southward through the foothills of the Owens Valley and the foothills of the Inyo Mountains to the mountains of the Death Valley region to the mountains of virtually the entire Mojave Desert, southeastward to the mountains of Joshua Tree National Monument and the northeastern slope of the Santa Rosa Mountains. There are several records for eastern San Diego County and the Cargo Muchacho Mountains of Imperial County, but these may represent only transiently established populations. From the California deserts, the butterfly ranges eastward across southern Nevada into extreme southwestern Utah and southward through western Arizona to Baja California.
- ELEVATION RANGE:** From approximately 2,000' to 5,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** The butterfly is typically found in the upper portions of the Creosote Bush Scrub plant community; it is usually encountered in desert washes or canyon bottoms in the desert mountain ranges. Males are usually seen perching in the canyon bottoms or along dirt roads. At times, the adults are abundant in the desert ranges, particularly in years of exceptional winter rainfall.
- PHENOLOGY:** The butterfly is usually univoltine, but in years of unusual summer rainfall there is a late summer brood as well, which tends to be much smaller than the spring brood. Most specimens have been taken from mid-March to late April, with an apparent peak in early April. For the occasional late summer or fall brood, specimens have been taken in the months of September and October.
- FOODPLANTS:** The favored host is *Xylorhiza tortifolia* Greene. Additionally, the butterfly uses *Acamptopappus sphaerocephalus* (Harv. and Gray) Gray var. *hirtellus* Blake, and *A. shockleyi* Gray (Asteraceae) (J. F. Emmel, unpublished; Austin and Austin, 1981).

87. *Charidryas gabbii* (Behr)

- ADULT BEHAVIOR:** This butterfly is a fairly rapid flier and wends its way rapidly across the hillsides in the springtime with other typical California spring butterflies, such as *Anthocharis* and *Glaucopsyche lygdamus australis*.
- LIFE HISTORY:** The eggs are pale green and are laid in masses at the base of the plant. The young larvae are gregarious but do not build nests. They become solitary in behavior as they approach maturity. The mature larva is black with short branching spines. This black ground color is speckled with dull white, and with a velvety black,

mid-dorsal line. The mid-dorsal row of spines has an orange-brown crescent at either side of the base. The ivory ground color of the pupa is nearly obscured by brownish and black blotchings and irrorations. A series of prominent tubercles, each partly colored with light orange, occurs over the dorsal area. This species hibernates as third instar larvae.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: This species is allopatric from other members of the genus. The only species it might be confused with is *C. palla*, in locations where the ranges of the two species approach each other.

GEOGRAPHIC AND SEASONAL VARIATION: In the instances where *gabbii* has had a second summer brood, the specimens of this generation are phenotypically indistinguishable from the earlier spring generation. The phenotype of the populations of *C. gabbii* on the mainland are surprisingly constant, in view of the variety of habitats that the species inhabits. Specimens from the extreme north end of the species' range in Monterey County closely resemble those from San Diego County near the south end of its range. The Channel Island populations are much darker than mainland specimens, presumably a response to the more consistently cool and moist climatic regime there.

GENERAL REMARKS: Although Bauer (1975) states that this species has been found flying with *C. palla* at several localities, we have not been able to confirm this particular observation. All of our field work points to a virtually completely allopatric distribution of these two species.

A small population persists on sand dunes at the west end of the Los Angeles International Airport in the El Segundo Sand Dunes, and represents a remnant of what were once probably very extensive populations of this insect in the coastal Los Angeles basin. Along the Coastal Strand of western Los Angeles County, this population exists in close proximity to populations of an endangered butterfly, the El Segundo Blue (*Euphilotes battoides allyni*), and as a consequence of efforts to preserve this endangered butterfly, this coastal population of *C. gabbii* will probably also be preserved.

This California butterfly, Gabb's Checkerspot, has been divided into two subspecies, one found in the California Coast Ranges and the other along the foothills of the Sierra Nevada Range. Both are identified by the white to pearly underside spots, and the relatively dark dorsal surface patterns. It is sympatric in various localities with *Charidryas palla* and *C. a. neumoegeni* with no apparent crossing, thus showing specific distinctness.

a. *C. g. gabbii* (Behr)

DIAGNOSIS: This species is characterized by the exceptionally pearly-white spots on the underside and increased dark scaling on the upperside in comparison to the other *Charidryas* species; it is lighter, however, than the subspecies from the Channel Islands.

ORIGINAL DESCRIPTION: Behr, *Proceedings California Academy Natural Sciences*, 3: 89 (1863).

TYPE LOCALITY: Mountains near Los Angeles, California. Type destroyed in 1906 San Francisco earthquake and fire. Neotype designated by Emmel, Emmel, and Mattoon,

Natural History Museum of Los Angeles County Contributions in Science, : (1989).

- DISTRIBUTION:** This species is extensively distributed from Monterey County southeastward through the South Coast Ranges to the mountains and foothills of cismontane southern California. It extends southward into northwestern Baja California. The species does not occur in the Sierran foothills at the southeast end of the San Joaquin Valley, contrary to a statement by Bauer (1975); we have no records supporting this assertion, nor have we ever found the species in that area in our extensive field work in our area.
- ELEVATION RANGE:** From sea level to approximately 6,000' in the mountains, with the majority of populations occurring below 3,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** The butterfly usually is found in the Coastal Sage Scrub plant communities or Coastal Strand plant communities, as well as in Chaparral areas. It prefers small ravines, where males frequently perch; in the Coastal Strand habitats, males are often seen simply patrolling over the foodplants in search of females.
- PHENOLOGY:** The butterfly is usually univoltine, but a second summer brood has been noted in some years, with apparently exceptionally high winter or spring rainfall. Spring brood records range from late February to late May, with an apparent peak in early April. For the few summer brood specimens that have been recorded, there are records for late June to mid-July.
- FOODPLANTS:** The most commonly used host of this subspecies is *Corethrogyne filaginifolia* (H. & A.) Nutt.; larvae have also been taken on *Heterotheca grandiflora* Nutt. and *Haplopappus squarrosus* H. & A. (all family Asteraceae).

b. *C. g. nesiotetes* Hawks and Priestaf

- DIAGNOSIS:** Named from the Greek name for "insular" or "islander," this checkerspot occurs only on Anacapa and Santa Cruz Islands off the coast of California. It is characterized by much more extensive dark scaling on both the upperside and underside, giving it a dusky appearance.
- ORIGINAL DESCRIPTION:** Hawks and Priestaf, *Natural History Museum of Los Angeles County Contributions in Science*, : (1989).
- TYPE LOCALITY:** Anacapa Island, Santa Barbara County, California. Holotype in Natural History Museum of Los Angeles County
- DISTRIBUTION:** To date, this subspecies has been found only on Anacapa and Santa Cruz Island off the coast of California in Santa Barbara County.
- ELEVATION RANGE:** Sea level to approximately 300' elevation.
- HABITAT AND PLANT COMMUNITIES:** Coastal Sage Scrub.
- PHENOLOGY:** Apparently univoltine, with adults flying in April and May.
- FOODPLANTS:** Chris Henne (personal communication) found larvae on *Hazardia cana* Greene on Anacapa Island in 1941. *Corethrogyne filaginifolia* (H. & A.) Nutt. is also

found on the Channel Islands and is strongly suspected to serve as a foodplant for this subspecies.

88. *Charidryas hoffmanni* (Behr)

- ADULT BEHAVIOR:** Adults visit flowers and also sip at mud puddles, and may be found commonly along roadsides and openings. Males patrol all day near the host plants, principally in valley bottoms, seeking females. While the flight is rapid, the adult often tends to circle an area and not fly straight away in a linear flight like other members of the genus.
- LIFE HISTORY:** The eggs are light green and are deposited in masses on the leaves of the host plant. During the younger instars, the larvae feed gregariously on the underside of the leaves in silk nests. The mature larva has a black body speckled with white with a cream-colored, scalloped line just above the spiracles. The head is black and covered with hairs. The pupa may be pearly-white to brown, with many irregularly shaped brown to black markings. This species hibernates as half-grown larvae.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** *C. hoffmanni* is often sympatric with *C. palla*; in the portion of their ranges where they overlap in eastern Siskiyou County, the females of the two species can be extremely similar, both being of a rather melanic phenotype. Careful comparison of the underside markings with the color plates will help to differentiate these two species fairly readily.
- GEOGRAPHIC AND SEASONAL VARIATION:** As the species is univoltine, there is no seasonal variation. In the Sierra Nevada populations, specimens at the extreme southern end of the species' range tend to be somewhat lighter and more yellowish in appearance, whereas specimens from the extreme northern end of the Sierra Nevada are darker. A long cline between these two extremes appears to exist throughout the range of the species in the Sierra Nevada. Similarly, the *hoffmanni* populations in the Klamath Mountains Assemblage become gradually darker as one goes north towards the Oregon Cascades, and they blend progressively toward the typical *segregata* phenotype in that region.
- GENERAL REMARKS:** It is probable that *Charidryas hoffmanni* developed as a species earlier than most other members of this genus, in as much as it is distinct from the other members in the structure of the male genitalia and also maintains its specific distinctness in sympatry with members of the *palla* group. Its distribution from the central Sierra Nevada north into British Columbia suggests that this species evolved in the Montane Coniferous forest and is rather tightly adapted to the environment there, compared to the more widely ranging other species in the group.
- This species is distinctive from the other members of the *palla* group in the structure of the male genitalia. Throughout the northwestern part of the ranges of these two species, the appearances are quite similar, but in California, fortunately, the phenotypes usually differ. *Charidryas hoffmanni* differs from *palla* in wing color and pattern, principally in the broad blended postmedian band extending across the dorsal forewing, and by the dark dorsal hindwing basal area. Additionally, the bands of spots on the outer half of the wings tend to be more regular, and the inner band is usually paler, often contrasting markedly with the deeper shade of the outer bands of spots, especially in the Sierran populations. Within our state, there are two recognized subspecies.

a. *C. h. hoffmannii* (Behr)

- DIAGNOSIS: The underside of this subspecies has very regular banding and an extensive creamy yellow area. Dorsally, this species also shows a strong banding effect set off by dark markings.
- ORIGINAL DESCRIPTION: Behr, *Proceedings California Academy Natural Sciences*, 3: 89 (1863).
- TYPE LOCALITY: "Sierra Nevada", California. Type destroyed in 1906 San Francisco earthquake and fire. Neotype designated by Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1989).
- DISTRIBUTION: This subspecies is found on the higher elevations of the western slope of the Sierra Nevada, from Plumas County southward to central Fresno County. Its main stronghold seems to be in the Lake Tahoe region.
- ELEVATION RANGE: From approximately 6,000' to 8,500' elevation.
- HABITAT AND PLANT COMMUNITIES: The species is typically found in moist Mixed Coniferous Forest, particularly the Red Fir Forest community where it is a subset of the greater Mixed Coniferous Forest community. It flies in open meadows, openings in the forest, and across gravelly slopes and in ravine bottoms.
- PHENOLOGY: The species is strictly univoltine, with records ranging from late June to early August, and a peak in early July.
- FOODPLANTS: For typical *hoffmanni*, the principal host is *Chrysopsis breweri* Gray (Asteraceae). Whether other asteraceous hosts are used for these populations is not currently known.

b. *C. h. segregata* (Barnes and McDunnough)

- DIAGNOSIS: This subspecies of *hoffmanni*, found in the North Coast Range area, has a complicated network of dark lines on the outer half of the wings, which is particularly well-developed on the hindwings and greatly encroaches on the center spot band. The inner spot band is generally considerably paler and prominent, although narrower than in typical *hoffmanni*. The underside resembles *palla* more than the Sierran *hoffmanni* populations.
- ORIGINAL DESCRIPTION: Barnes and McDunnough, *Contributions Natural History Lepidoptera North America*, 4: 72-73 (1918).
- TYPE LOCALITY: Crater Lake, Klamath County, Oregon. Holotype in U. S. National Museum.
- DISTRIBUTION: Typical *segregata* is found in the Oregon Cascades, but it is also present in the Siskiyou Mountains of southwestern Oregon and northwestern California. There are also scattered populations throughout the remainder of the Klamath Mountain Assemblage south of the Siskiyou Mountains, and also in the Mount Shasta region. The populations of the Klamath Mountain Assemblage are closest to *segregata* but show some tendencies toward typical *hoffmanni*, so these may be considered a blendzone set of populations. The populations in eastern Siskiyou County just east of Mount Shasta tend to be more typical *segregata*, and are the darkest of our *hoffmanni* populations.

ELEVATION RANGE:	From approximately 4,000' to 7,000' elevation.
HABITAT AND PLANT COMMUNITIES:	This subspecies is typically found in moist Mixed Coniferous Forest areas with habitats similar to those of <i>hoffmani</i> in the Sierra Nevada.
PHENOLOGY:	Our records range from late June to late July, with an apparent peak abundance in mid July.
FOODPLANTS:	The foodplant in the Trinity Alps of Siskiyou County is <i>Aster ledophyllus</i> (Gray) Gray; whether other asters are used in this area remains to be determined. The foodplant of the populations in eastern Siskiyou County has not yet been determined.

89. *Phyciodes mylitta mylitta* (W. H. Edwards)

The Mylitta Crescentspot is found from British Columbia to Baja California in this subspecific form. It is one of our most familiar butterflies from the moister mountain areas.

DIAGNOSIS:	The ground color of this butterfly is suffused with an orangish-brown, more or less concolorless in the male and shading to lighter color towards the wing margins in the female on the upperside. A network of blackish-brown lines occurs across both wings. On the underside, the forewing is largely flushed with light orange, whereas the hindwing pattern is composed of rows of white spots separated by brown ground color.
ORIGINAL DESCRIPTION:	W. H. Edwards, <i>Proceedings Academy Natural Sciences Philadelphia</i> , 13: 160-161 (1861).
TYPE LOCALITY:	"Texas; Kansas; California", restricted to vicinity of San Francisco, California, by F. M. Brown, <i>Transactions American Entomological Society</i> , 92: 439 (1966). Neotype in California Academy of Sciences, designated by F. M. Brown, <i>Transactions American Entomological Society</i> , 92: 442 (1966).
DISTRIBUTION:	This species is widespread in the mountains and foothills of the state, from San Diego County north to the Oregon border. It is also found in the Warner Mountains in the northeastern corner of the state and occasionally in the desert regions. The desert populations, which are probably transiently established, have been noted in the Panamint Range, the Last Chance Range in Inyo County, and in the New York Mountains of the eastern Mojave Desert. One population became established during the summer of 1983 at Ord Mountain southeast of Barstow in the central Mojave Desert. The species is apparently quite vagile, so its distribution in any one year may be influenced by such things as winter rainfall and the subsequent size of populations in that particular season.
ELEVATION RANGE:	From sea level to approximately 8,000' elevation, with the majority of records below about 6,000'.
HABITAT AND PLANT COMMUNITIES:	The butterfly is typically found in moist riparian situations in a variety of plant communities throughout the state, including Montane Coniferous Forests, Foothill Woodland, Chaparral, Coastal Sage Scrub, Northern Coastal Sage Scrub, and Oak Woodland community.
PHENOLOGY:	The species is multivoltine, with the earliest specimens at the lower elevations flying in March and April, and captures then recorded for the subsequent months

through October. In the higher mountain populations, this species may be bivoltine or even univoltine in some seasons.

- ADULT BEHAVIOR:** Males frequently perch throughout the day along ravines or creeks to await females. The butterfly has a fairly rapid wing beat but usually flies in a circle when disturbed off the perch, and will commonly return to the same area again after disturbance. Adults will visit mud readily, as well as flowers, and may occasionally be found visiting animal dung to sip fluids.
- LIFE HISTORY:** The whitish or pale yellowish-green egg is truncated with a flat bottom and top. The eggs are laid in large clusters on the underside of host leaves and the young larvae sometimes live gregariously in a small silken nest. The mature larva is velvety black, with a yellowish or yellow-brown abdomen. There is a pair of yellow dorsal lines, and a pair of similar lines on each side. Pale yellow or cream spots are scattered over the body. Nine rows of branched spines are present; these are black except for those below the spiracles. The head is black with a cream subdorsal stripe. The pupa is wood-brown to ashy gray in color and may have a golden reflective sheen. This species hibernates as half-grown larvae.
- FOODPLANTS:** The primary host plants seem to be various species of *Cirsium* species (thistles). *Cirsium* species recorded for *mylitta* which occur in California include the following: *C. arvense* (L.) Scop., *C. breweri* (Gray) Jeps., *C. californicum* Gray, *C. hydrophilum* (Greene) Jeps., *C. occidentale* (Nutt.) Jeps., and *C. vulgare* (Savi) Ten. Additionally, a closely related thistle-like foodplant is *Silybum marianum* (L.) Gaertn. (Bruce Walsh, *in litt.*). Additionally, eggs and/or larvae have been found on two species of *Mimulus* (Scrophulariaceae): *M. guttatus* Fisch. ex DC. (J. F. Emmel, unpublished data), and *M. cardinalis* Dougl. ex Benth. (D. Hawks, personal communication).
- CHROMOSOME NUMBER:** $n = 31$ (Emmel and Eliazar, unpublished).
- SIMILAR SPECIES:** The other *Phyciodes* with which *P. mylitta* might be confused is *P. orseis*, which tends to have a very similar underside pattern. However, the upperside of *orseis* subspecies in California tend to look more like *P. campestris*. *Orseis* is sometimes sympatric with *mylitta*, as they both use *Cirsium* species for hosts.
- GEOGRAPHIC AND SEASONAL VARIATION:** Specimens from all areas of the state seem uniform in phenotype. There is no apparent seasonal variation between the early and later broods.
- GENERAL REMARKS:** As noted above, this is a vagile species and is sometimes taken in localities away from the usual range of the species, such as some of the desert mountain ranges. In these areas, colonies sometimes become temporarily established, but they do not seem to persist on an indefinite basis.

90. *Phyciodes orseis* W. H. Edwards

- ADULT BEHAVIOR:** As in other *Phyciodes*, males perch throughout the day in canyon bottoms and along creeks to await passing females. Males of *orseis* seek out the canyon bottoms where, along the watercourses, they select a flat broad leaf such as maple to perch on and challenge and investigate passing butterflies. Newly-emerged and unmated females fly to encounters with males here, as the females have a characteristic habit of occasionally dropping down to the watercourse, then returning to hillside breeding areas. Females are wary and most often encountered in the steep chaparral understory on serpentine rubble hillsides where the host thistle grows.

LIFE HISTORY: The eggs are pale yellowish-green and are laid in large single-layered groups on the underside of the foodplant leaves. The larvae are somewhat gregarious in the early instars, but have no silken nests. The third instar larvae diapause, probably in vegetative litter or under rocks near the base of the foodplant. The mature larva is dull brownish-black with a mid-dorsal black mid-dorsal line. On either side of the dorsal black line, there are dull orange-brown longitudinal stripes. There is a rather wide, light dull orange-brown lateral band with numerous small speckled black markings within it. Ventrally, the larva is grayish-brown. The pupa is light brown with darker brown markings, and is somewhat variable in the extent of these dark markings.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: Refer to Introduction to the present species.

GEOGRAPHIC AND SEASONAL VARIATION: As the species is univoltine, there is no seasonal variation. Sierran populations are remarkably consistent in phenotype from north to south. Likewise, populations in the Klamath Mountains and the southwestern Oregon mountains seem fairly consistent. A possible blendzone between the two subspecies could exist southeast of Mount Shasta in the extreme northern Sierra Nevada, such as in eastern Shasta County. This species is generally scarce in collections and its apparent disappearance from the San Francisco Bay region counties is particularly curious.

This butterfly is somewhat larger than *Phyciodes mylitta* and *P. campestris*. Males may be immediately distinguished from the latter two species by the large black block near the center of the hind margin of the dorsal forewing, and by the generally large, more pointed forewing in both sexes. The females are more generally suffused with black scaling than *P. mylitta*. *P. orseis* also generally occurs in higher elevation sites than *mylitta*. There are two subspecies of *orseis* within California.

a. *P. o. orseis* W. H. Edwards

DIAGNOSIS: This subspecies is dark dusky orange on the upperside with an angled forewing, and the underside of the hindwing is mottled as in *mylitta*, unlike the mostly orange underside of the *campestris* underside.

ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Entomological Society*, 3: 206 (1871).

TYPE LOCALITY: Mt. St. Helena, Napa County, California. Lectotype in American Museum of Natural History, designated by F. M. Brown, *Transactions American Entomological Society*, 92: 450-451 (1966).

DISTRIBUTION: Typical *orseis* is found in the mountains of southwest Oregon south through the lower elevations of the Klamath Mountains region and Mount Shasta into the North Coast Ranges. In the past, the species was allegedly taken in Napa, Sonoma, and Marin counties and San Francisco; however, no specimens have been taken in these areas within the last fifty years and whether these represent mislabelling or possibly now-extinct populations has not been determined. Further field work in these geographic areas is needed to shed more light on this enigma.

ELEVATION RANGE: From 2,700' to 6,000' elevation.

HABITAT AND PLANT COMMUNITIES: Nominotypical *orseis* is a riparian species and occurs most abundantly in steep-walled, north-south oriented serpentine rubble rock canyons, where the extent and length of sunlight is somewhat shortened by the narrow steep nature of the terrain. Typically, this habitat is in the Douglas Fir or Mixed Evergreen Forest plant communities, often with atypical floristic elements such as Rabbit-brush and juniper intrusion. This is also true at higher elevations for *orseis*, up into the Red Fir forest nearly to the Subalpine community. Steep-walled streamside situations can be replaced by a more open forest-glade situation at the higher elevations. The known thistle host in northern California is typically found on steep hillsides above a streambed; gullies that extend down these canyons provide habitat for the nectar sources where both males and females meet. An attractive and abundant nectar source appears to be needed for strong populations of *orseis* to develop.

PHENOLOGY: The species is univoltine, with adults flying from as early as mid April to early July, and the majority of specimens being taken in May and June.

FOODPLANTS: The species is associated with *Cirsium cymosum* (Greene) J. T. Howell at Crawford Creek, in the Trinity Alps region of the Klamath Mountains Assemblage. K. Hansen (*in litt.*) has found *P. orseis* eggs on this plant.

b. *P. o. herlani* Bauer

DIAGNOSIS: This is a Sierra Nevadan subspecies that differs from its much rarer Coast Range relative in the reduced black pattern and more extensive and evenly colored orange-brown areas on the dorsal surface. It differs from the sympatric *Phyciodes mylitta* and *P. campestris montana* by having ventral submarginal crescents more equal in size and rarely obscured by brown. Also, the postmedian series of dots are small, brown, and approximately equal sized. In *mylitta* the dot in cell M₃ is generally much larger than the rest of the series, particularly the dots at either end of the row (Bauer, 1975).

ORIGINAL DESCRIPTION: Bauer, *in Howe, Butterflies of North America*: 148 (1975).

TYPE LOCALITY: Glenbrook Creek, Douglas County, Nevada, at an elevation of about 7,000'. Holotype in Bauer collection.

DISTRIBUTION: This subspecies is found in the Sierra Nevada, from Fresno County in the south northward to Placer and Nevada counties. Its distributional pattern within this area seems somewhat disjunct, with several widely separated localities, but this is probably the result of inadequate sampling by collectors as the species is often overlooked.

ELEVATION RANGE: From approximately 6,200' to 9,500' elevation, with the majority of records in the 7,000' to 8,000' range.

HABITAT AND PLANT COMMUNITIES: This subspecies is found in Montane Coniferous forests and typically prefers roadsides or gravelly slopes where its foodplant is concentrated.

PHENOLOGY: The subspecies is univoltine with records from mid June to early August and a peak flight in early to mid July.

FOODPLANTS: Larvae of this subspecies have been collected in several localities on *Cirsium andersonii* (Gray) Petr. (Asteraceae). This may represent the sole host in the Sierra Nevada.

91. *Phyciodes tharos distincta* Bauer

The Pearl Crescent, *Phyciodes tharos*, flies abundantly from Canada through the eastern half of the United States to Mexico. In Colorado it stops abruptly at the Rocky Mountains and is replaced by *Phyciodes campestris* in its favored meadow habitats. But to the south of the main Rocky Mountains, it seems to have moved through New Mexico and Arizona or northern Mexico to our southeastern California area, and established itself in seemingly transient populations in the agricultural areas. In the 1930's, Gunder noted this species as occurring in the Imperial Valley and being phenotypically different from typical *tharos*. Henne also took them at this time (9 October 1935) from a resident population near the Del Rio Club in Brawley, Imperial County. C. M. Dammers (in litt.) found them abundant at Calexico on the weed, Michalmas Daisy (27 September 1939).

In subsequent years, other lepidopterists have found this species in vegetation along irrigation ditches in the Imperial Valley during the late summer and fall months. Before the introduction of irrigation in this arid desert valley, it is doubtful that *P. tharos* could have resided in the natural dry arid habitats of the area. Thus, it is our impression that the butterfly is transient into our area and has only become established in the present century. It is probably not permanently established but becomes periodically reintroduced.

Thus, it is perhaps unfortunate that the particular subspecies residing in the Imperial Valley, *distincta*, which is predominantly a Mexican subspecies and also occurs from southeastern Arizona into Texas, should have its type locality within southeastern California.

ORIGINAL DESCRIPTION: Bauer, in Howe, *Butterflies of North America*: 144 (1975).

TYPE LOCALITY: Calexico, Imperial County, California. Types apparently in Bauer collection.

DISTRIBUTION: Most of our records for this butterfly within California are in the Imperial Valley of Imperial County; the species has also been taken in the vicinity of Blythe in the lower Colorado River Valley.

ELEVATION RANGE: From 200' below sea level to approximately 300' elevation.

HABITAT AND PLANT COMMUNITIES: Within California the species has been taken in agriculturalized irrigated valley bottom areas and is usually taken in close proximity to some sort of permanent water source, such as irrigation canals or the Colorado River.

PHENOLOGY: Our records range from April to October, with the majority of records in October, indicating a probable peak abundance at that time of the year. This butterfly is multivoltine.

ADULT BEHAVIOR: Henne (personal communication) observed adults flying along the edges of irrigation canals, frequently visiting various nectar sources growing on the canal banks.

LIFE HISTORY: The eggs are laid in masses of 20 to 200 on the underside of the leaves of the foodplant. The larvae do not make nests. The mature larva is blackish or dark

brown, with yellow dots and yellow lateral and near dorsal bands. The branched spines are all yellow-brown. The larvae feed communally. Hibernation occurs as partly grown larvae. The pupa is tan to brown in color and is mottled with cream and black, with many small brown dorsal bumps.

FOODPLANTS: C. M. Dammers (unpublished notes) stated that he found larvae on "Michelmas Daisy" in the Imperial Valley. This probably refers to *Bellis perennis* L., the common introduced English lawn daisy. Additionally, two species of "weedy" asters are known to grown along irrigation canal banks in Imperial County. Perhaps one of these species also serves as a foodplant; collectors encountering this species in the future in the Imperial Valley or Colorado River area are urged to make careful observations on the possible foodplant species it may be using.

CHROMOSOME NUMBER: $n = 31$ (Maeki and Remington, 1961b).

SIMILAR SPECIES: The only species with which *Phyciodes tharos* could be sympatric with in California is *P. phaon*, which is much smaller in size.

GEOGRAPHIC AND
SEASONAL VARIATION: None noted in our populations of this species.

GENERAL REMARKS: It will be of interest to continue to monitor the Imperial Valley populations of this butterfly and determine how permanently established it is as a resident of our state.

92. *Phyciodes pascoensis* W. G. Wright

See **Appendix** for the one record of this species from Modoc County.

93. *Phyciodes campestris* (Behr)

ADULT BEHAVIOR: These rather weakly flying small nymphalids may be found most commonly near stream banks and marshy meadows, where they frequently alight on low shrubs and forbs. Males patrol most of the day, flying just above vegetation, in search of females. During courtship, the male pursues the female who will land and keep her wings opened at about a 120 degree angle. Once the male has caused the female to land, the male lands behind her, walks around to the front, and may display his wings, including vibration of the forewings while facing her. He then comes around behind her again, and with his wings slightly open crawls up alongside her hindwings, curves his abdomen around in a "U" shape, and mates. An unreceptive female will either raise her abdomen or flutter her spread wings, which will prevent him from approaching alongside and copulating.

LIFE HISTORY: The early stages were first described by Comstock (1929) for California material. The eggs are pale yellow-green in color and are laid in clusters on the foodplant. Young larvae sometimes live under a loose web. The mature larva is basically black, with numerous branching spines in seven rows. There is a dorsolateral grayish-white band. Beneath the spiracles runs a mottled yellowish-brown band. The abdominal surface of the larva is brown. The pupa is a soft wood-brown color, with a network of darker brown lines and small dorsal bumps. The species hibernates in the third instar larval stage.

CHROMOSOME NUMBER: $n = 31$ (Emmel, unpublished).

SIMILAR SPECIES: *Phyciodes campestris* differs from sympatric or nearly sympatric *Phyciodes mylitta* and *P. orseis* in having a more rounded forewing, usually lighter medium

spots on the dorsal forewing, and the underside of the hindwing being usually more orange with less distinct brown lines and a large brown marginal patch.

GEOGRAPHIC AND
SEASONAL VARIATION:

In some of the lowland multivoltine *campestris* populations, early spring flying individuals seem slightly darker than those flying later in the season. Also, populations close to the coast tend to be slightly darker than those inland. Shapiro (1975c) has described and illustrated minor phenotypic and biological differences in the populations of the Sacramento River delta area. Populations of *campestris* in the Owens Valley and in the valley bottoms east of the Sierran crest in Modoc and Lassen counties have slightly enhanced cream-colored spots on the uppersides which differentiate them slightly from populations to the west. It is of interest to note that the distribution of the high-elevation subspecies *montana* corresponds roughly to that of the high-elevation subspecies of *Phyciodes orseis* (*herlani*), suggesting that similar environmental factors are affecting the selection of this wing characters in both species. The species as a whole is in need of much more field work and biological studies to determine the status of its various components.

GENERAL REMARKS:

This widely distributed western *Phyciodes* species is generally scarce and spotty in the mountains of southern California, perhaps because of the paucity of its favored wet meadow habitats. Formerly, it occurred in wet meadow areas near San Bernardino and the area south of Los Angeles, but today these areas have been drained and are highly urbanized, eliminating the habitat for *campestris*. Today, the sole population south of Kern County is found at Crystal Lake in the San Bernardino Mountains. Yet, suitable habitats are found in a number of areas of the San Bernardino and San Jacinto Mountains, and its absence from these high altitude meadows, which have appropriate *Aster* species as potential hosts, is inexplicable.

This familiar butterfly is found in two subspecies in our state.

a. *P. c. campestris* (Behr)

DIAGNOSIS: With the common name of Field Crescent, this butterfly's most consistent character is the bright orange-yellow ground color of the undersurface of the males. Females show considerably more variation in the ground color and the amount of contrast in the pattern.

ORIGINAL DESCRIPTION: Behr, *Proceedings California Academy of Natural Sciences*, 3: 86 (1863).

TYPE LOCALITY: Vicinity of San Francisco, California, by implication in the Behr paper. Types destroyed in 1906 San Francisco earthquake and fire. Neotypes designated by Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1989).

DISTRIBUTION: Populations of subspecies *campestris* generally occur at low to mid elevations in much of the state, excluding the desert areas and the higher elevations of the Sierra Nevada. Populations are found from Los Angeles and San Bernardino counties northward in widely scattered colonies in the lower Sierra Nevada foothills and Owens Valley region. The butterfly is present in the Central Valley in the region of the lower Sacramento River. It is found in the San Francisco Bay area from northern Monterey County north in scattered colonies through the southern part of the North Coast Ranges. Eastward, it is found in some of the moister valley bottoms east of the Sierran crest in Modoc and Lassen counties. Although all of

these widely separated populations are included here under typical *campestris*, further careful study of the group may reveal that several similarly appearing subspecies can be delineated.

- ELEVATION RANGE: From sea level to 8,300' elevation, with the majority of populations below 6,000'.
- HABITAT AND PLANT COMMUNITIES: The butterfly is usually found in moist meadow or riparian situations except along the immediate coast, where it is usually more typically found on open slopes and dry meadows.
- PHENOLOGY: The species is usually multivoltine, with records ranging from March to October. Some of the highest elevation populations may be univoltine or partially bivoltine.
- FOODPLANTS: For subspecies *campestris*, the following *Aster* species have been documented as foodplants: *A. chilensis* Nees., *A. hesperius* Gray, *A. greatai* Parish, and *A. foliaceus* Lindl. (family Asteraceae).

b. *P. c. montana* (Behr)

- DIAGNOSIS: This subspecies is found in the mountains and higher elevations of the Sierra Nevada Range, and is characterized by being mostly orange on the dorsal surface. It usually lacks a yellow bar found in typical *campestris* just beyond the base in the discal cell.
- ORIGINAL DESCRIPTION: Behr, *Proceedings California Academy Natural Sciences*, 3: 85-86 (1863).
- TYPE LOCALITY: "Vicinity Los Angeles, headwaters of Tuolumne R., Yosemite Valley", California. Types destroyed in 1906 San Francisco earthquake and fire. Neotypes designated by Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1989).
- DISTRIBUTION: This subspecies is found in the higher elevations of the Sierra Nevada, from the area of Mineral King in Tulare County in the southern Sierra Nevada, northward to approximately the Mount Lassen region.
- ELEVATION RANGE: From 4,200' to 8,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This butterfly is typically found in wet meadows within the Montane Coniferous Forest plant community or along streamsides in the same type of habitat.
- PHENOLOGY: The butterfly is apparently univoltine in nature, although laboratory rearings indicate that the species is capable of developing without going through a larval diapause. Our records are mostly for the months of July and early August, with a few mid to late June records.
- FOODPLANTS: For subspecies *montana*, probably several montane aster species are used; however, we have documented records for only one species, namely *A. occidentalis* (Nutt.) T. & G.

94. *Phyciodes phaon* (W. H. Edwards)

- DIAGNOSIS: This butterfly is identified by its distinctive forewing, which has a black, wide median band, a whitish postmedian band, and an orange submarginal band. An

- additional diagnostic feature is the yellowish-cream underside of the hindwing, which bears narrow brown lines in the female.
- ORIGINAL DESCRIPTION: W. H. Edwards, *Proceedings Entomological Society Philadelphia*, 2: 505-506 (1864).
- TYPE LOCALITY: "Saint Simon's Island and Northern Georgia", restricted to Saint Simon's Island, Glynn County, Georgia, by F. M. Brown, *Transactions American Entomological Society*, 92: 434 (1966). Neotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Entomological Society*, 92: 437 (1966).
- DISTRIBUTION: The butterfly is found in scattered populations in the lower Colorado River Valley, the Imperial Valley, lowland areas of San Diego County, and western Riverside and San Bernardino counties.
- ELEVATION RANGE: From near sea level to approximately 2,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is usually found on *Lippia* lawns in suburban or agricultural areas. No populations on native foodplants are known.
- PHENOLOGY: The species is multivoltine, with records ranging from the months of February through early November. The butterfly becomes progressively more abundant towards the end of summer and early fall.
- ADULT BEHAVIOR: The adults remain in close proximity to the *Lippia* lawns, taking nectar at the *Lippia* flowers and exhibiting largely sedentary behavior. Males patrol only a few inches above the foodplant in search of females.
- LIFE HISTORY: The eggs are laid in clusters on the underside of the foodplant leaves. The mature larva is basically olive brown in color, with a longitudinal, dark brown band high on each side and a blackish mid-dorsal line. There is a whitish scalloped lateral band below the spiracles. The whitish head has large brown patches from the top and sides. There are nine rows of highly branched, cream-colored spines along the body. The pupa is tannish-brown, and heavily speckled with white and black marks, along with many tiny brown dorsal bumps. The diapause stage, if any in this southern butterfly, is unknown.
- FOODPLANTS: *Lippia lanceolata* Michx. and *L. nodiflora* Michx. var. *rosea* (D. Don) munz. (family Verbenaceae). The common names of these plants are Fog Fruit and Mat Grass, respectively, or often merely *Lippia*.
- CHROMOSOME NUMBER: $n = 31$ (Macki and Remington, 1961b).
- SIMILAR SPECIES: None.
- GEOGRAPHIC AND SEASONAL VARIATION: Despite its wide range across the southern edge of the United States, no subspecies have been named for this species. Likewise, despite the multiple broods of this species, no distinctive seasonal variation occurs.
- GENERAL REMARKS: Relatively common in the southeastern United States and the states along the Gulf of Mexico, the Phaon Crescent reaches its western limits in the southeastern corner of California. From here it occurs south into Mexico to Guatemala, and from Florida it extends south into the northern Caribbean Islands. During the summer months, it moves north into the central Great Plains states and even into the mountains of Colorado.

95. *Anthanassa texana texana* (W. H. Edwards)

- DIAGNOSIS:** This butterfly belongs to a subgenus of the genus *Phyciodes*, and it is found in the United States from Florida to Arizona, with strays into California. It may be recognized by the orange-brown markings in the basal areas of the dorsal wing surfaces, being obscured by dusky brownish-black scales.
- ORIGINAL DESCRIPTION:** W. H. Edwards, *Proceedings Entomological Society Philadelphia*, 2: 81 (1863).
- TYPE LOCALITY:** "Texas", restricted to New Braunfels, Comal County, Texas, by F. M. Brown, *Transactions American Entomological Society*, 92: 421 (1966). Holotype apparently in Carnegie Museum.
- DISTRIBUTION:** This butterfly has been recorded several times in San Diego County from El Monte Oak Park and Scissors Crossing, once in Orange County at Silverado Canyon near Irvine (June 24, 1964), and also at Bonanza King Mine Canyon (two males on May 18, 1973) in the Providence Mountains in eastern San Bernardino County. One of the San Diego County records and the Providence Mountain record (Priestaf, 1974) were both in the month of May 1973. The San Diego County specimens, as well as one of the two Providence Mountain specimens, were in fairly fresh condition. These records probably indicate that individuals from Arizona populations of this species stray into our area on occasion. As yet, a breeding population has not been discovered.
- ELEVATION RANGE:** Approximately 1,000' elevation in San Diego County, and 4,200' elevation in the Providence Mountains locality.
- HABITAT AND PLANT COMMUNITIES:** In San Diego County in either Chaparral or Desert Scrub, and in the Providence Mountains the upper end of Creosote Scrub in the south fork Bonanza King Mine Canyon.
- PHENOLOGY:** All captures have been in the month of May.
- ADULT BEHAVIOR:** Elsewhere in its range where *texana* has been observed in abundance (e.g., most of Mexico), this is a fairly weak flying butterfly that stays close to the ground. Pyle (1980) notes that males usually perch in canyon bottoms all day to await females, and that in courtship, males fly in loops above the females.
- LIFE HISTORY:** The eggs are laid in clusters on the underside of the host leaves. The larva and pupa has not been described.
- FOODPLANTS:** The reported foodplants are all in the family Acanthaceae: *Dicliptera brachiata*, *Jacobinia carnea*, and *Ruellia carolinensis*.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** None in our area; similar species only in the tropics.
- SEASONAL AND GEOGRAPHIC VARIATION:** This species has been divided into two subspecies across the southern U.S.: *P. t. texana*, occurring from Arizona to Texas and south into Mexico, and *P. t. seminole*, occurring from Louisiana east to central Florida and north to southern Georgia. No seasonal variation has been noted.

GENERAL REMARKS: Pyle (1980) observes that wandering brood individuals may fly up to 600 miles north to other states from their breeding areas, rivaling the long distance flights of *Nathalis iole* and *Brephidium exilis* in the central part of the U.S.

Subfamily **Argynninae** Blanchard

96. *Clossiana epithore* (W. H. Edwards)

ADULT BEHAVIOR: This butterfly has a relatively slow, fluttering flight. Males patrol all day across meadows into the margins of the woods, seeking females.

LIFE HISTORY: The mature larva is gray, with the dorsal surface and the lower portion of each side a darker shade. The intermediate area between these broad bands is streaked with black. There are two gray lines mid-dorsally and a reddish-brown sublateral stripe. The head is black. The spines on the body are reddish, except for the first and last segmental spines which are black. The pupa is pale brown, with the dorsal surface of the head and thorax mottled by white. The wing cases are white at the edge, and the abdomen is whitish, mottled with pale brown and some dark brown lateral patches. The species hibernates in the fourth instar larva. There is only one annual brood.

FOODPLANTS: The known foodplants are all in the family Violaceae: *Viola ocellata* T. & G., *V. glabella* Nutt., and *V. sempervirens* Greene.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: None in California.

GEOGRAPHIC AND SEASONAL VARIATION: The species is univoltine and therefore there is no seasonal variation. Within the state of California, the described subspecies cover the range of geographic variation.

GENERAL REMARKS: The chief information still needed for the three named subspecies of *Boloria epithore* is information on the life history, including the foodplants and comparative aspects of larval and pupal coloration among populations.

This group of three subspecies in California are our only representatives of the Bog Fritillary group. Elsewhere, in the Pacific Northwest and the Rocky Mountains, this genus has diversified more broadly.

a. *C. e. epithore* (W. H. Edwards)

DIAGNOSIS: This race and the following have been well-discussed by Perkins and Perkins (1966), and we follow their treatment here. The typical subspecies, *C. e. epithore*, is characterized by a median row of disconnected black markings on the upper surface of the hindwings. Additionally, its general appearance is larger and lighter than in the other two subspecies. It is restricted to the Santa Cruz Mountains of California.

ORIGINAL DESCRIPTION: W. H. Edwards, *Proceedings Entomological Society Philadelphia*, 2: 503-504 (1864).

TYPE LOCALITY: "California", restricted to Saratoga, Santa Clara County, California by F. M. Brown, *Transactions American Entomological Society*, 91: 334 (1965). Neotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Entomological Society*, 91: 334 (1965). This name is equivalent to the name proposed five years later by Boisduval; hence, the first author (Edwards) receives credit for the name.

DISTRIBUTION: The nominotypical subspecies occurs in the southern half of the Santa Cruz Mountains in San Mateo, Santa Cruz, and Santa Clara counties in the southern San Francisco Bay region. North of here, along the Mendocino County coast, there are some populations which seem referable to this subspecies also, or which may form a blendzone with subspecies *chermocki*, Perkins and Meyer (1973). Williams (1910) also mentions an early record of *epithore* occurring in Golden Gate Park in San Francisco, where it is now extinct. Because colonies of *epithore* tend to be local and not easily discovered, it is probable that there was a series of populations between San Francisco and the southern Santa Cruz Mountains, many of which were probably extirpated by urbanization or other human alteration of the environment.

ELEVATION RANGE: From 500' to 2,000' in the Santa Cruz Mountains.

HABITAT AND PLANT COMMUNITIES: This subspecies is found in Coastal Redwood forests, where it prefers moist forest openings and wet meadows.

PHENOLOGY: Our records range from as early as the end of April to the end of June, with the clear peak of the flight season for this subspecies being in early to mid June.

b. *C. e. chermocki* (E. and S. Perkins)

DIAGNOSIS: This subspecies differs from typical *epithore* in having a yellowish-orange ground color (as opposed to bright orange), and a strong black basal suffusion on the forewing and hindwing, these all being characteristics of the dorsal surface. On the ventral side, *chermocki* differs from typical *epithore* in having chrome yellow coloration of the submedian-median row of spots (as opposed to yellowish-cream), an orange-brown color to the hindwing post-basal area (as opposed to red-brown), and a stronger contrast to the hindwing banding.

ORIGINAL DESCRIPTION: E. and S. Perkins, *Journal Lepidopterists' Society*, 20: 109-112 (1966).

TYPE LOCALITY: 2.9 miles east of Dolph, Yamhill County, Oregon. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This subspecies occurs from southwestern British Columbia south through Washington and Oregon, to north central California. Here, it is limited to the western face of the California coastal ranges immediately adjacent to the coast, such as Mendocino County. A zone of intergradation between *chermocki* and *sierra* (see third subspecies account) occurs in the area of the Modoc Plateau and adjacent volcanic terrains of north central California (Klamath, Lake, Siskiyou, Modoc, Shasta, and Lassen counties).

ELEVATION RANGE: (JOHN: PLEASE FILL IN.)

HABITAT AND PLANT COMMUNITIES: (JOHN: PLEASE FILL IN.)

PHENOLOGY: This species flies in one brood during June and July, with a few records from the end of May.

c. *C. e. sierra* (E. Perkins)

DIAGNOSIS: On the upper surface this subspecies is similar to nominotypical *epithore*, except for a moderate black basal suffusion on the hindwing marginal area, and the relatively small-sized, sub-marginal spots on both wings. On the underside the species is very similar to peninsular *epithore*. The overall characteristic of this subspecies seems to be its smaller size (Perkins and Meyer, 1973).

ORIGINAL DESCRIPTION: E. Perkins, in Meyer, *Bulletin Allyn Museum Entomology*, (11): 10-11 (1973).

TYPE LOCALITY: Sentinel Dome, Yosemite National Park, Mariposa County, California. Holotype in Allyn Museum of Entomology.

DISTRIBUTION: This subspecies occurs from the northeastern corner of California southwestward into the edge of the Coast Range and southeastward along the Sierra Nevada Range down to Kern County. The type locality is in the center of this range, at Yosemite Valley. The southernmost extension of *sierra* was discovered in 1961 by Ray Stanford, who was collecting in the vicinity of Tobias Peak, located in the Greenhorn Mountains south of the Tulare-Kern County line (Perkins and Meyer, 1973: p. 10).

ELEVATION RANGE: (JOHN: PLEASE FILL IN.)

HABITAT AND PLANT COMMUNITIES: This subspecies is found in Montane Coniferous forest, wherever moist forest openings and wet meadows appear.

PHENOLOGY: The peak flight period is during July, with some records from the middle of June to the first part of August.

97. *Speyeria cybele* (Fabricius)

ADULT BEHAVIOR: Adults, though strong fliers, tend to stay within fair proximity of the breeding area. Males are inclined to roam farther than females, departing their patrolling in grassy meadows where *Viola* occurs to visit adjacent nectar sources. It is not uncommon to see males range a half mile or more to thistles in prime condition. Females are more reclusive and are seen primarily at nectar sources or flying to and from the breeding grounds. Because of the more secretive behavioral pattern that they have, females have been mistakenly thought to be less common than males. It is also worth noting that searching males, and *in copulata* pairs with females that are too fresh to fly, will stay in the immediate area where the host violet is most abundant. This apparently indicates that though larvae are rapid crawlers just before they decide on a pupation site, they do not stray outside of the wet meadow situation where the violets are growing, and that pupation occurs within this habitat, where the adults also stay with high fidelity.

LIFE HISTORY: The egg is pale yellow, turning tan with maturity. Eggs are laid singly and seemingly at random near the *Viola* foodplants. The larvae feed on the violet leaves and make no nest. The mature larva is velvety black in this species, with two mid-dorsal lines of gray dots and many black-tipped spines. The base of the spines are colored yellowish to reddish. The head is dark brown, with a reddish-yellow area on the back side. The pupa is a dark mottled brown, although the

abdomen is mostly concolorous. The abdomen has dorsal bumps that are black in front and yellow behind. The larvae hibernate in the first instar before beginning to feed. Females lay eggs on twigs and grasses and other plant material near the *Viola* foodplants, and the larvae presumably estivate or hibernate under this debris during the fall and winter.

Larval feeding usually takes place under a protective grassy canopy where the host *Viola* is most abundant in wet meadow situations.

CHROMOSOME NUMBER: n = 29 in Colorado material (Maeki and Remington, 1961b).

SIMILAR SPECIES: The only other butterfly with a superficial resemblance to our two *cybele* subspecies is another large *Speyeria*, *S. nokomis apacheana*. *Speyeria cybele leto* and *S. n. apacheana* fly together in a number of wet meadow situations along the eastern side of the Sierra Nevada.

GEOGRAPHIC AND SEASONAL VARIATION: The populations of both *S. c. leto* and *eileenae* are remarkably constant from one end of their range to another within the state, and we have detected no significant pattern of differentiation within these segregates.

GENERAL REMARKS: Separation of *S. cybele* and *S. leto* into two different species groups, as has been done by recent authors in other works, appears unwarranted. Laboratory rearing of a number of *cybele* populations by Mattoon from all areas of the United States has shown no habit patterns, biological strategies, superficial morphological characters, or color differences which would warrant the separation.

Much interesting genetic research could be done by rearing the *Speyeria* in this *cybele* group. In the type locality area, Mattoon collected a perfect bilateral gynandromorph and took additional normal-appearing females for eggs. The results of rearing from these "normal" females included the two magnificent sexual mosaics from the same small local colony. In the same year (1965), collecting in another peak bog population near McClellan Mountain near Bridgeville in Humboldt County, produced another outstanding female color mutation. The high frequency of abnormalities in these colonies suggests some interesting genetic phenomena that could be explored with further breeding.

This fritillary species occurs across the breadth of North America, from the east coast of Canada and the northeastern United States to Washington state on the Pacific Coast. In our state of California, there are two subspecies; both are strongly dimorphic and have a bright orange male and a nearly white female, coupled with the usual black markings of the fritillary. They may be found in moist meadows in Transition to Canadian Zone forests in the northeastern half of California, and along the northwestern coastal area.

a. *S. c. leto* (Behr)

DIAGNOSIS: The males are deep orange dorsally, and have reduced black maculation with reduced dark suffusion in the basal area on the dorsal surface. Sexual dimorphism is striking, with the females characterized by a creamy white outer half of the wings, and a deep brown inner half of the wings next to the body. On the underside, a strong discal area contains the silver spots, and is separated from the wing margin by a light tan "band" area.

ORIGINAL DESCRIPTION: Behr, *Proceedings California Academy Sciences*, 2: 173 (1862).

- TYPE LOCALITY: Near Carson City, Ormsby County, Nevada. Neotype in Carnegie Museum, designated by dos Passos and Gray, *American Museum Novitates*, (1370): 7-8 (1947).
- DISTRIBUTION: This subspecies occurs from western Montana into southwestern Wyoming and central Utah westward to Oregon, and southwesterly to the mid- and high-elevation Cascade Range-Sierra Nevada Axis in California. The most westward penetration of *leto* in northern California is limited to the adjacent eastern Trinity Mountains of the Klamath Assemblage near Mount Shasta. Eastward through the Basin Range-Modoc Plateau high country, it has been located only in the Warner Mountains.
- ELEVATION RANGE: From 3,000' in mountain valleys upwards to 10,000' in the higher Sierra Nevada Range. Most populations tend to be below 7,500' elevation.
- HABITAT AND PLANT COMMUNITIES: *S. c. leto* is an inhabitant of permanent wet seeps or wet streamsides, often in boggy meadows, from the upper Transition to particularly the Canadian Forest zone, and into higher elevations. Along the eastern escarpment of the Sierra Nevada and again in the Warner Mountains, such willow-clad and occasionally aspen-dotted habitats occur in the Great Basin *Artemisia*-Juniper Woodland communities.
- PHENOLOGY: The preponderance of records indicates that the usual mid-elevation flight period for this species is July and August, with some higher montane colonies flying through August into September. There are some records for the low-elevation populations showing emergence starting as early as mid June. This species, as in all *Speyeria*, is univoltine.
- FOODPLANTS: In our experience, this butterfly has always been associated with the presence of *Viola nephrophylla* Greene (family Violaceae). At the headwaters of King's Canyon Creek (6,000' elevation), a locality in Nevada approximately 5 miles southwest of Carson City near the California state line, Kenneth Hansen and Mattoon observed a final instar larva of *leto* feeding on a large leaf of this wet meadow violet species. Feeding occurred during the daytime under partially shaded conditions. This larva, found on July 15, eventually was reared to a normal male specimen.

b. *S. c. eileenae* Emmel, Emmel and Mattoon

- DIAGNOSIS: This northwestern coastal set of populations of *cybele* was discovered in the southern half of Humboldt County by Sterling and Eileen Mattoon. Heretofore, *cybele* was not suspected to occur outside of northeastern and north central California. Initially, it was thought that this *Speyeria* represented a southern extension of the subspecies *pugetensis* of the Pacific Northwest. However, careful study has shown that it represents a distinct segregate, and although it is probably most closely related to *pugetensis*, at least in biological characters, the following characters will serve to differentiate it. On the dorsal surface of the male, the ruddy-orange ground color of the wings is distinctively more orange than in *pugetensis*. The subspecies *leto* is whiter than *eileenae*; thus dorsally, the male color pattern appears intermediate between the light *leto* and dark *pugetensis*, both as regards the intensity of the orange ground color and the extent of the dark basal area of the forewings and hindwings. In the female the light discal areas of the wing are suffused with a ruddy scaling, giving the butterfly a darker appearance than *leto*. It is also more orangish-appearing than *pugetensis*. Finally, it should be noted that *eileenae* is smaller than either of the other two subspecies, particularly so in relation to *pugetensis*. On the ventral surface of the wings, the

female of *eileenae* is much more of a chocolate brown, whereas the *pugetensis* female is a deep umber brown. The third subspecies, *leto*, has a dusting or overscaling of yellow scales on top of the dark discal area, giving *leto* a yellowish dusky appearance as compared to the pure chocolate-brown of *eileenae*. The subspecies *eileenae* also has an expansion of the dark markings on the forewing and much more orangish suffusion across the underside of the forewings. The males on the underside show similar characteristics on the hindwing and forewing.

- ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 144-145 (1998h).
- TYPE LOCALITY: Bear River Ridge Road, 0 to 5 roadmiles east of junction with Wildcat Road, 7 airmiles southeast of Ferndale, Humboldt County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: As presently known, this subspecies is limited to Humboldt County. Its southern distribution is in the coastal mountains south of Humboldt Bay, and inland roughly following Highway 36 to the vicinity of the Larabee Valley. Northward from there, several populations have been found along the west-facing flank of the Coast Range mountain fog-break zone. The northernmost location is in the hills east of the town of Orick.
- ELEVATION RANGE: Predominantly between 1,000' and 2,800' elevation, but with occasional strays down to 100' above sea level near the coast.
- HABITAT AND PLANT COMMUNITIES: In Humboldt County, this subspecies utilizes an environmental niche similar to its *leto* counterpart to the east. In this habitat, however, wet meadows have been replaced by the very damp borders of Coastal Redwood Forest that adjoin Coastal Prairie Grassland in the north coastal fog-break zone. Inland in this zone along the Coast Range Mountains, a more traditional boggy or wet streamside meadow is more frequently involved.
- PHENOLOGY: The adult flight period for the single brood of this coastal subspecies is somewhat affected by weather variables, but it has been recorded from mid July to the end of August. The peak of the flight season for both sexes is the last week of July.
- FOODPLANTS: The females are associated with, and make attempts to oviposit around, a single violet species, *Viola nephrophylla* Greene (Violaceae), which is abundant in the habitat of all known populations of this butterfly.

98. *Speyeria nokomis apacheana* (Skinner)

The Apache Fritillary is the westernmost representative of a rare species found across Nevada, Colorado, Arizona, New Mexico, and south into northern Mexico. Always found in small seeps and permanent spring-fed meadows, the colonies have a relative impermanence about them, and many in the Southwest have disappeared with the advent of heavy grazing and draining of the underground water tables for irrigation and domestic water supplies (Savage, 1983). Thus, our California subspecies is of particular interest as a marginal population at the western edge of the range of this endangered butterfly.

- DIAGNOSIS: The Apache fritillary is characterized by its large size, by the orange males and white females, and its lack of a black spot near the base of the forewing cell. The

underside of the hindwing is a strong yellow color in males, and is greenish in females.

ORIGINAL DESCRIPTION: Skinner, *Entomological News*, 29: 67 (1918).

TYPE LOCALITY: "Arizona". Holotype in Carnegie Museum.

DISTRIBUTION: The present-day distribution of *apacheana* in California and areas of Nevada adjacent to the eastern border of California is shown on the distribution map. The most northerly extent of this range occurs along the eastern escarpment of the Sierra Nevada Range just west of Carson City, Nevada. Scattered colonies of this butterfly are then found southward in similar east slope, Great Basin valley floor, or adjacent Basin Range situations. Populations are found more abundantly from the region of the Sweetwater Mountains south to Round Valley, Inyo County. Here is the terminus of the southern extent for the current California distribution of the species. Considerable speculation exists as to the reasons for the loss of any former distribution south of this latitude. A stray taken at Big Pine, California, marks the most southern modern-day record.

ELEVATION RANGE: In the northern part of its range in adjacent Nevada, all populations of *apacheana* range from approximately 4,500' to 5,500' elevation. In the southern end of the butterfly's range, the populations occur from 4,500' to 6,800'. In the intervening area of California where *apacheana* is more abundant, the altitudinal range is broader, extending from 6,500' to 9,500' elevation.

HABITAT AND PLANT COMMUNITIES: The most important factor necessary to support a population of the butterfly is an abundant and constant source of water, such as that provided by a large spring, which can withstand a prolonged drought. The surface water leads to the development of a marshy meadow containing sedges, willow, cottonwood, and especially the bog violet, *Viola nephrophylla* Greene. This violet species is the most important host plant, and along with some species of nectar-producing thistles, from the primary food sources for the larvae and adults. These meadows are found in the upper edges of the Great Basin Sagebrush plant community, at the base of mountain drainages.

PHENOLOGY: The flight period of this subspecies extends from July to mid September, with a peak of abundance in mid to late August.

ADULT BEHAVIOR: Adults of both sexes are avid visitors on thistles and fly across the wet meadow habitat, circling willow thickets and wet boggy places where the *Viola* grows. Males emerge two to three weeks ahead of the females, apparently requiring this period for gonadal maturation.

LIFE HISTORY: The egg is cream-colored and becomes speckled with brown as it matures. The eggs are laid singly and at random near the *Viola* foodplants. The larvae feed on these *Viola* without making nests. The mature larva is a orange-ochre in ground color and is dark ventrally, with six rows of long orange-ochre spines. Black patches occur around the dorsal and sub-dorsal spines, two black transverse stripes occur on the rear of each segment, and the lateral and dorsal stripes are orangish-ochre. The head is black with an orangish suffusion on the top posterior part of the head. The pupa is also an orangish-ochre color, with a serrated black transverse band on the front of each abdominal segment, the thorax, and all but the middle of the wing being black. The top of the thorax has an orangish triangular spot. This species hibernates as a first instar larva immediately after hatching from the egg.

FOODPLANTS:	The sole known foodplant is <i>Viola nephrophylla</i> Greene, in the family Violaceae.
CHROMOSOME NUMBER:	Unknown.
SIMILAR SPECIES:	See discussion under <i>S. c. leto</i> .
GEOGRAPHIC AND SEASONAL VARIATION:	Within California, no significant geographic variation occurs. As the species is univoltine, there is no seasonal variation.
GENERAL REMARKS:	This species has been proposed but not listed yet as an Endangered or Threatened Species for protection under the Federal Endangered Species Act. Its apparent decline in the Owens River Valley and in other areas of the Southwest has been suggested to be linked with the drop of the water table due to man's increasing use and diversion of water from wells and surface sources for human use, both agricultural and urban. The increase of agricultural development in these upper sagebrush habitats, including over-grazing and the spraying of herbicides for the control of thistle and sagebrush where enhanced grass growth is desired, have also been suggested as potential factors affecting the fortunes of this butterfly.

99. *Speyeria mormonia* (Boisduval)

ADULT BEHAVIOR:	<i>S. mormonia</i> adults tend to be restricted to an open, sunny meadow environment. They do not stray far into forest shade, but will join other nectaring butterfly species at flowers within the meadow. Adult nectar sources include <i>Aster</i> species, <i>Monardella</i> , <i>Chrysothamnus</i> , or <i>Cirsium</i> species. The males are more apt to engage strictly in nectaring during morning hours, but as the day progresses, they will combine nectaring with their slow, low, wandering, patrolling flight, as they search for newly emerged females. Mating usually takes place immediately after eclosion of the female, which emerges with fully developed eggs. Her oviposition/foodplant-searching behavior starts soon after mating, in contrast to some of the other <i>Speyeria</i> species in which there is an apparent reproductive diapause in the first few weeks of adult life.
LIFE HISTORY:	The eggs are yellowish, turning purplish-tan at maturation. They are laid singly and at random near the <i>Viola</i> host. The larvae hatch about two weeks after oviposition and eat only a portion of the eggshell before seeking out a location to diapause until the following summer. The mature larva is an ochre-tan in ground color. The larvae make no nests while feeding on the leaves of the violet. and has two dark stripes on either side of the mid-line, along with two dark lateral stripes. The rows of yellowish to tan spines arise from the tan ground color areas on the body. The dark stripes are rather broken by small areas of tan color. The larval head is tan, with scattered black spots. The mid-dorsal tan area has a thin black line running down the exact center of the body.
CHROMOSOME NUMBER:	Unknown in California material. Colorado <i>mormonia</i> have n = 29 (Maeki and Remington, 1961b; Emmel, Eliazar, and Harris, unpublished).
GEOGRAPHIC AND SEASONAL ISOLATION:	All <i>mormonia</i> populations are univoltine, and no seasonal variation has been observed over the extended emergence period of some of the populations. In terms of geographic variation, the four subspecies delineated above cover the major patterns in the state. However, it should be noted that there is considerable variation in the frequency of silvering on the underside, and often in the degree of dark overscaling on the hindwing, within even individual populations. As shown by Shapiro's discoveries in the Mt. Eddy area and Mattoon's discoveries in

the Mt. Lassen area, *mormonia* is often overlooked, and additional populations showing further interesting variation may be discovered in northern California.

GENERAL REMARKS: A rather remarkable parallel ecogeographic trend in coloration occurs in several of these *Speyeria* species in the northeastern part of our state. *Speyeria mormonia*, *S. zerene gunderi*, and *S. callippe* near *nevadensis* all show trends towards lighter greenish suffusion in the Warner Mountains area of this section of the state. Other interesting ecological problems in the distribution of this species, as well as others in the genus *Speyeria*, include the effect of a long, hot, dry summer and fall on the first instar larval diapause, where larval survival and protection from desiccation is probably one of the most critical factors affecting larval survival. The highly variable seasonal weather patterns characteristic of the Warner Mountains, ranging from extremely dry to extremely wet periods of years, probably have an important impact on the relative abundance and distribution of *mormonia* more than any other factor. In studying *Speyeria mormonia* in the Warner Mountains, one of the problems encountered is the abundance of the species *Speyeria egleis*, which is close in size and appearance to *S. mormonia* and causes the *mormonia* adults to be overlooked. This same problem may occur elsewhere in the discovery of *mormonia* populations; that is, they may be easily overlooked if *egleis* is relatively more common in the area.

The small fritillaries in this species are usually denizens of the higher mountain areas in western North America, where they occupy a wide range of habitats. Of the more than a dozen described subspecies, four occur within California. In some populations, silver spotting on the underside has become unsilvered, while in others the populations are entirely silvered on the underside. Males and females are easily distinguished by wing shape and coloration in this species, with the narrow-forewinged males being more deeply fulvous or orangish dorsally and the broad-forewinged females being relatively duller in ground color.

a. *S. m. mormonia* (Boisduval)

DIAGNOSIS: The adults of this subspecies are small and a pale orange dorsally, with fine black maculation. Ventrally, the basal area is rather lightly dusted with medium brown scaling between the silver or unsilvered spots. The overall ventral ground color of the forewing and outer half of the hindwing is a light tan in the males and a dull orangish-tan in the females.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. Belgique*, 12: 58 (1859).

TYPE LOCALITY: "Salt Lake", restricted by Miller and Brown, *Memoirs Lepidopterist Society*, No. 2: 146 (1981) to vicinity of Pyramid Lake, Nevada. Lectotype in U. S. National Museum, designated by dos Passos and Gray, *American Museum Novitates*, (1370): 22 (1947). Type locality re-restricted to Donner Pass, elevation 7,000', Placer County, California by Emmel, Emmel, and Mattoon (1998a).

DISTRIBUTION: This subspecies is found in the higher elevations of the Sierra Nevada, from extreme southern Tulare County in the southern Sierra Nevada, northward to the Donner Pass area, just northwest of Lake Tahoe. It is not known in the typical subspecific form north of Donner Pass.

ELEVATION RANGE: From 4,600' to 12,000' elevation, with the majority of records above 6,300' and below 10,500'.

- HABITAT AND PLANT COMMUNITIES:** This butterfly is essentially restricted to a mesic alpine to sub-alpine, wet, boggy meadow association, and is a sun-loving species, mainly confined to its open meadow realm. While closely tied to this environment, the habitat itself is not restricted to any particular plant community. However, because of the availability of moisture to produce snowmelt-fed meadows, this insect is most commonly encountered through the upper reaches of the Canadian Zone forest of our granitic Sierra Nevada. It also extends upward to near or above treeline, or down into Red Fir or Mixed Coniferous Forest, even Transition Zone Forests, and is capable of invading occasionally into hot, dry Artemisia-Juniper Woodland and the Sagebrush Scrub plant community, should available moisture provide just the right boggy meadow.
- PHENOLOGY:** *S. m. mormonia* males start to fly around the first week of July, depending on the snowpack and weather conditions. Our earliest flight date is June 18th, a very abnormal record. The start of female emergence starts in a week to ten days after the males, and the flight period then extends through August, with a few stragglers in most years making it in early September. Our latest record is for September 14th.
- FOODPLANTS:** This species seems closely associated with the bog meadow violet species, *Viola adunca* Sm., and female oviposition has been noted in areas where this violet is usually abundant. Although actual larval feeding has not been observed on this particular *Viola* species, it is undoubtedly at least one native foodplant for this butterfly. In the laboratory, larvae of *mormonia* will feed on it readily.

b. *S. m. obsidiana* Emmel, Emmel, and Mattoon

- DIAGNOSIS:** This subspecies is found in isolated populations on Glass Mountain, a high volcanic peak just east of the Sierra Nevada in Mono County. It is characterized by a deeper orange ground color and by expansion of the black irregularly placed median spots on the upperside and underside of the forewing and hindwing. On the forewing, these form almost a contiguous but serrated band because of their enlarged size. Ventrally, this subspecies is characterized by an increased amount of reddish-brown scaling in the basal two-thirds of the hindwing, as well as increased orange reddish flush on the underside of the forewing. Silvering of the silver spots tends to be diminished or even absent in some specimens.
- ORIGINAL DESCRIPTION:** Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 145-146 (1998h).
- TYPE LOCALITY:** Sawmill Meadow, 9,200' elevation, Glass Mountain, Mono County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION:** So far as is known, this subspecies is confined to Glass Mountain.
- HABITAT AND PLANT COMMUNITIES:** The habitat of this subspecies is an extensive series of boggy meadows on the east slope of Glass Mountain in a Montane Coniferous community.
- PHENOLOGY:** This subspecies begins flying in mid-July, with a peak abundance during the first week in August. Stragglers probably fly into late August or early September.
- FOODPLANTS:** The particular *Viola* species growing in the boggy meadows at Glass Mountain has not been determined, but is believed to be *V. adunca* Sm.

c. *S. m. olivaria* Emmel, Emmel, and Mattoon

DIAGNOSIS: The Warner Mountains populations of *S. mormonia* are characterized by medium size, a light orange color dorsally on both sexes, fading to very light orange in flown specimens, and a light cast of olive green scaling across the undersurfaces of both wings in many fresh specimens. In both sexes, there is also a tendency towards a reduction of black markings such that often the outer underside margins are virtually devoid of dark markings. The subspecies is generally heavily silvered; however, some individuals in these populations are virtually devoid of silver scaling on the underside hindwing spots, reminiscent somewhat of *artonis* populations adjacent to the east in the Steens Mountains of southeastern Oregon, or perhaps nominotypical *mormona*. These populations of *S. mormonia olivaria* in the Warner Mountains of Modoc County in the extreme northeastern corner of the state seem to be most closely related to populations of the subspecies *S. m. erinna* (Edwards) from the more xerophytic areas of its distribution in Oregon and Washington east of the Cascades. The type locality of *erinna* is Spokane Falls, Spokane County, Washington.

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Holarctic Lepidoptera*, 9(): - (2002).

TYPE LOCALITY:

DISTRIBUTION: This subspecies is apparently limited in distribution to the Warner Mountains in northeastern California and possibly southeastern Oregon.

ELEVATION RANGE: From 7,200' to 8,000'.

HABITAT AND PLANT COMMUNITIES: In the 1980's, a population explosion in the Mount Bidwell-Bidwell Peak areas of the Warner Mountains showed the principal habitat for this subspecies. It is a resident of rather dry subalpine meadows along the crest of the higher Warner Mountains. The host violet grows in profusion in hillside depressions or catch basins which collect the winter rain and snowmelt run-off to form grassy, late-spring meadows in gravelly to sandy decomposed rocky soil. These areas are readily identified during the adult flight period by masses of blooming sunflowers. The habitat tends to be at or just above treeline. But limited breeding also occurs in similar clearings below treeline, where Lodgepole Pine, Limber Pine or Red Fir (in varying combination) form the surrounding forest type. The above-treeline habitat is within an *Artemisia*-dominated Sagebrush Scrub zone, and occurs mostly above the juniper belt of the drier eastern slopes of the Range. Occasional stands of *Potentilla fruticosa* punctuate the prime breeding-ground locations and provide nectar for the adults.

PHENOLOGY: The emergence of this Warner Mountains subspecies is somewhat dependent on the highly variable seasonal weather conditions that can be encountered in the California side of the Warner Mountains. We have seen fresh specimens from mid July to late August, but usually the subspecies starts flying at the end of July.

FOODPLANTS: The foodplant, by strong adult-association and observed oviposition in the base of plants and in adjacent debris, is an unidentified *Viola* species (S. O. Mattoon, unpublished).

d. *S. m. shapiro* Emmel, Emmel and Mattoon

- DIAGNOSIS:** This subspecies from the Mt. Eddy area, southwest of Mt. Shasta in Trinity County, is characterized by the orangest dorsal ground color in fresh specimens of any California subspecies, as well as enlargement of the black markings on the upperside. The black markings in particular form an almost continuous line medially on the hindwing, especially in females. This character is reminiscent of *mormonia* populations in northern Oregon and Washington state. This enhancement of the dark markings on the upperside forms a broad, almost continuous band in males on the outer margin of both forewing and hindwing, and a continuous band in females, giving a serrated edge appearance to the proximal edge of this dark band on which is set a marginal white to orange spot row. On the underside, the hindwing discal area is scaled light to medium brown, darker in females, darkest around the medial spot row, costal and basal areas of the hindwing, leaving the central discal area lighter tannish brown, concolorous with postmedian lightly suffused band. The ventral forewings in males are flushed with light creamish-pink in all but the apical-costal area, becoming a deeper shade of pink in females. All ventral silver spots are very brightly silvered. The overall appearance of the ventral surface of the hindwing is of a band of triangular silver spots at the margins surrounded by dark scaling, a lightly suffused light tannish-brown postmedian band, a central medial row of larger oblong to egg-shaped silver spots, some tapered to points distally, surrounded by dark scaling, and the remaining discal area, except for its central lighter area, of dark scaling around the silver spots there. In older worn specimens, the orange ground color tends to fade much lighter and the contrast between ventral dark and light areas is enhanced. Vague dark spots that project into the postmedian hindwing band distal of each silver spot of the median row take on an almost dull greenish, rather than blackish, cast in older specimens.
- ORIGINAL DESCRIPTION:** Emmel, Emmel, and Mattoon, *Holarctic Lepidoptera*, 9(): - (2002).
- TYPE LOCALITY:** Deadfall Lake, west slope of Mt. Eddy, Trinity County, California.
- DISTRIBUTION:** This subspecies is presently known only from the Dead Fall Lakes area on the west slope of Mt. Eddy, Trinity County, California.
- ELEVATION RANGE:** From 7,500' to 9,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** The specimens to date have been taken in grassy bogs and hillside meadow seeps in the Subalpine Forest plant community. *Potentilla fruticosa*, (Shrubby Cinquefoil) and *Chrysothamnus* (Rabbit-brush) are indicator plants.
- PHENOLOGY:** The specimens to date have been taken from August 15th to September 16th, indicating a fairly late flight period for this subspecies. The first appearance of fresh adults depends on elevation and seasonal conditions that particular year.
- FOODPLANTS:** *Viola adunca* Sm. (Violaceae) occurs in these meadow areas and is believed to be the host plant.

100. *Speyeria adiaeste* (W. H. Edwards)

- ADULT BEHAVIOR:** Starting with the flight behavior of the extinct subspecies *S. a. atossa*, the late Christopher Henne collected an extensive series of females in the month of September, but noted no males or females in late July or throughout the month of August the same year. This behavior suggests the possibility that, at least for this southern California subspecies of *atossa*, the butterfly may have been adapted to

a long dry hot summer by going into reproductive diapause after mating early in the summer. The adults may then have been relatively inactive until September, when with cooler temperatures the eggs could be deposited on vegetation near the dried up violet plants. The newly-hatched young larvae would then be able to go into hibernation until the following spring, without long exposure to desiccating conditions.

In the subspecies *clemencei*, males are strong patrollers of the grassland and oak belt, also flying down canyons along watercourses. They patrol oak grassland-bracken fern associations, seeking emerging females or nectar sources such as thistles. Females, because of their reclusive nature, always seem to be less abundant. Both *clemencei* and typical *adiaste* are avid flower visitors. As in *clemencei*, typical *adiaste* male behavior includes extensive amounts of time spent in patrolling and searching for females.

LIFE HISTORY: The only information we have about the life history of *atossa* is from Comstock and Dammers (1931c). The mature larva was said to be 35 millimeters in length and had "the same general structure and coloration as the larva of [*Speyeria callippe*] *macaria*, but with the following points of variance. A dirty yellow patch occurs along the dorsal end of the head near its juncture with the first thoracic segment. The supra-stigmatal row [above the spiracles] of spines are lighter on their shafts than are the corresponding spines of *macaria*. There is also a greater amount of mottled gray along the sides of the *atossa* larva, below the infra-stigmatal row [below the spiracles] of spines." The pupa, with a length of 20 millimeters, was said to be "very similar to that of *macaria*, the chief difference being in the lighter aspects of the wing covers, with a marked reduction of the black veining and mottling, a narrowing of the veins, and the formation of separate quadrate spots at their outer ends. This feature may be an individual variation of the particular specimen observed." Sims *et al.* (1979) note that mature larvae of both *S. adiate atossa* and *S. egleis* are characterized by an irregular yellowish patch on the dorsum of the head capsule, a trait missing in California *S. callippe* and *S. coronis*.

The larvae of the more northern two subspecies differs somewhat from this description. The last instar larva of *clemencei* is a deep charcoal black and ground color, with all rows of spines being entirely black except for the lateral row just above the spiracles (equals supra-stigmatal row of Comstock and Dammers' description), which is bright orange. Likewise, the mature larva of typical *adiaste* is nearly concolorless black in ground color, with light orange spines only in the lateral row above the spiracles. The only substantive of difference seems to be that in *adiaste* larvae, the orange on that lateral row of spines is confined to the upper half of the spine, whereas in *clemencei* the entire spine is orange.

CHROMOSOME NUMBER: $n = 29$ in *S. adiate clemencei* (Sims, Brittnacher, and Ayala, 1979).

SIMILAR SPECIES: Two other *Speyeria* species fly in the same area as the *adiaste* subspecies. One is *Speyeria callippe* (subspecies *comstocki* and *macaria*), and the other is *Speyeria coronis* (subspecies *coronis* and *hennei*). *S. a. clemencei* can be readily separated from these two other species by its pale orange ground color and its unsilvered underside.

GEOGRAPHIC AND SEASONAL VARIATION: As the species is univoltine, there is no seasonal variation. The geographic variation in visibly discernible characters has been discussed under the three subspecies accounts. No information is available on inter-population or inter-subspecific genetic variation in this *Speyeria* species (Brittnacher, Sims, and Ayala, 1978).

GENERAL REMARKS: The demise of *Speyeria adiaste atossa* remains a subject of much speculation. If *atossa* truly became extinct in 1959 or 1960, this event occurred during an extraordinarily dry period for California (1959-1961). The year 1961 was the driest ever recorded in southern California, and could have provided the fatal blow to already greatly reduced populations. Since the 1920's, overgrazing has probably contributed to the demise of violet foodplants utilized by *atossa*. Additionally, heavy collecting in some of the colonies with restricted distribution and easy access to the public could have eliminated the butterfly, or reduced their numbers so greatly that they could not have survived a period of extreme environmental conditions. It is clear (Orsak, 1974) that this butterfly had already declined in numbers by 1940, almost twenty years before the severe drought in southern California. From reviewing museum and large private collections, we believe that probably relatively few specimens were collected during each of the preceding twenty years between its peak at the time of Comstock's visit (1922) and its virtual disappearance from collecting records. In fact, from the dates of these preserved specimens, we can see that *atossa* underwent a dramatic decline in as little as fifteen years, from approximately 1930 to 1945, after which we have only three records for its existence. It does not seem that either fire damage or encouragement of the growth of foodplant by periodic fires (clearing out grass and thick litter) affected this species, because of the widespread scattering of the original localities for this species. Some of these have remained in their natural states undisturbed by fires, while others have been burned fairly regularly, but the fate of *atossa* in all was the same.

The effect of a general policy of fire suppression on the subspecies *adiaste* and *clemencei* remains to be determined. In recent years, a very extensive fire swept the climax growth forest above Carmel Valley in the Chews Ridge area. The first year after this fire, very low numbers of adults of *S. a. clemencei* were noted in the Chews Ridge locality, but populations have been reported to have recovered in record numbers within the short span of several seasons in the same area. This suggests that regular natural fires in the habitat of *clemencei* are favorable to growth of the foodplant, and provide optimal breeding conditions for the butterfly. In the Santa Cruz Mountains, there has been considerable fire suppression in the last fifty years, and this may account for the apparent gradual decline in numbers of the subspecies *adiaste* in recent years.

Although members of the *S. adiaste* complex were made conspecific with *S. egleis* (Behr) by dos Passos and Gray (1947), this fritillary was subsequently reassigned specific status (Emmel and Emmel, 1973; Howe, 1975) and recent studies of this species both by isoenzyme electrophoresis (Sims, Brittnacher, and Ayala, 1979) and life history comparisons (S. Mattoon and J. Emmel, unpublished data) indicate that *S. adiaste* is best considered a full species. It is a species of the South Coast Ranges, characterized by complete absence of silver scaling on the underside, giving a very uniformly pale and washed-out appearance to the underside. Above, the black maculation tends to be greatly reduced. Also, there is very little dark basal scaling on the uppersides of the three *adiaste* subspecies.

a. *S. a. adiaste* (W. H. Edwards)

DIAGNOSIS: This is the smallest of the three *adiaste* subspecies. It has a rather bright orange ground color, with the greatest extent of dark markings on the upperside of any of the three races. Beneath, it also tends to be darker, with dark overscaling on the discal area of the hindwing in particular.

ORIGINAL DESCRIPTION: W. H. Edwards, *Proceedings Entomological Society Philadelphia*, 3: 436 (1864).

- TYPE LOCALITY: Santa Cruz, Santa Cruz County, California, designated by dos Passos and Gray, *American Museum Novitates*, (1370): 16 (1947). Lectotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Entomological Society*, 91: 291 (1965).
- DISTRIBUTION: This subspecies is confined to the southern two-thirds of the Santa Cruz Mountains in San Mateo, Santa Cruz, and Santa Clara counties.
- ELEVATION RANGE: From 1,700' to 2,800' elevation.
- HABITAT AND PLANT COMMUNITIES: This butterfly has so often been collected as singleton specimens or strays in a bracken fern glade within one of the Redwood Forest remnants that the Redwoods have been assumed to be the breeding area. However, it is strongly suspected that the breeding habitat requirements must include a more open grassland-fern glade setting similar to that utilized by *clemencei*, with floristic elements of the drier Coastal Transition forest, rocky outcroppings and *Monardella* mint species present. This habitat normally borders on the more mesic Redwood Forest setting. Thus the niche for nominotypical *adiaste* probably combines the mesic Redwood environment with adjacent open space and Coastal Transition Forest nectar sources.
- PHENOLOGY: Nominotypical *adiaste* begins flying in early June and extends into early August, with a peak flight period in late June and early July. There are no records of it flying later in the season, as has been reported for the apparently now extinct southern California subspecies *S. a. atossa*.
- FOODPLANTS: Undetermined, but strongly suspected to be *Viola quercetorum* Baker and Clausen (Violaceae), based on the association of females showing pre-oviposition behavior in areas where this violet grows.

b. *S. a. clemencei* (J. A. Comstock)

- DIAGNOSIS: This subspecies is geographically and phenotypically intermediate between the darker northern *S. a. adiate* and the very light southern *S. a. atossa*. The ground color of the male is a light fulvous, whereas *atossa* is a clear, yellow-brown and *adiaste* a rich, dark fulvous. The ventral coloration and spotting is darker than in *atossa*.
- ORIGINAL DESCRIPTION: J. A. Comstock, *Bulletin Southern California Academy Sciences*, 24: 67 (1925).
- TYPE LOCALITY: Atascadero, San Luis Obispo County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: *S. a. clemencei* appears to be restricted to the mountains and canyons of Monterey and San Luis Obispo counties. It is distributed throughout the Santa Lucia Range, from the vicinity of Carmel in the north to the area of Pozo in the south. The southern boundary of its distribution is at the latitude of the city of San Luis Obispo. The species is also found at the north end of Garcia Mountain and in the La Panza Range.
- ELEVATION RANGE: This montane species ranges down canyons to as low as 400' elevation and up ridges and summits to nearly 5,000' elevation in the north and central parts of its range. To the south, *S. a. clemencei* is apparently restricted to the 2,000' to 3,600' elevation level.

- HABITAT AND PLANT COMMUNITIES:** As with nominotypical *adiaste*, this subspecies is adapted to the open, grassy ridgetops, clearings, and hillsides which are characterized by an abundance of ferns and adjacent Mixed Evergreen-Deciduous forests. A distinctive feature of areas inhabited by many *clemencei* populations is the presence of oak woodland next to the grassy breeding areas, with heavy accumulations of oak leaf litter on the ground. The entire distribution of this butterfly appears dependent on the marine influence of the Pacific Ocean to the west.
- PHENOLOGY:** Emergence of the single brood of adults is highly affected by weather conditions each year. Emergence can begin in late May, but the peak of the flight season is the month of June into early July. In some years, *clemencei* has a strong flight extending into the end of July. Females always follow males in emergence by approximately a week to ten days.
- FOODPLANTS:** Although no specific *Violet* species is documented for this subspecies, *Viola quercetorum* Baker & Clausen (Violaceae) is abundant in localities where the females are showing pre-oviposition behavior.

c. *S. a. atossa* (W. H. Edwards)

- DIAGNOSIS:** This subspecies is believed to have been extinct since summer 1960. It was the largest of all the *adiaste* group and was also the most distinctive in appearance, characterized by greatly reduced black maculation on the dorsal surface, and virtually no basal suffusion. Beneath, it has light creamy-buff undersides and pale buff spots in place of the silver spots of the usual fritillary species hindwing. The last known specimens of *atossa* were taken in 1959. One was captured south of the town of Tehachapi by an amateur collector, and the other on June 5th by John S. Garth at McGill Campground in the Mt. Pinos area. A third collector, the late Joe Wilson, took another specimen in the Tehachapi Range on July 1st of that year at an unknown location and an indeterminate locale. The last known report of this species was in 1960, when the late Lloyd Martin reported a sighting on the peak of Mt. Pinos.
- ORIGINAL DESCRIPTION:** W. H. Edwards, *Butterflies of North America*, 3: 125-126 (1890).
- TYPE LOCALITY:** Tehachapi, Kern County, California. Lectotype in Carnegie Museum, designated by dos Passos and Gray, *American Museum Novitates*, (1370): 17 (1947).
- DISTRIBUTION:** The butterfly's former range included the Tehachapi Mountains (type locality), the Tejon Mountains (Ft. Tejon to Bouquet Canyon), and the Mt. Pinos area. An exceptionally large colony evidently existed in the early part of this century near the rest stop called Sandberg's on the Old Ridge Route (Angeles National Forest). On a single day (June 11, 1922), John Adams Comstock took over 500 males and females on the blossoms of the California Buckeye, *Aesculus californicus* (Spach) Nutt., in Liebre Gulch, about 500 feet east of Sandberg's. Other local lepidopterists also captured considerable numbers of *atossa* during the 1920's and early 1930's (Orsak, 1974). The first capture of *atossa* was in 1890 by Burrison in the Tehachapi Range, about 4 miles from the town of Tehachapi, "in a little valley...by a small stream." Orsak (1974) suggests this was probably Antelope Canyon.
- ELEVATION RANGE:** From about 3,000' in the Bouquet Canyon area to the highest known colonies near McGill Campground (7,500'), and on the saddle between Mt. Tehachapi and Double Mountain (7,600').

- HABITAT AND PLANT COMMUNITIES: The exact habitat preferred by this butterfly is rather difficult to define because of the extensive altitudinal gradient of more than 4,000 feet reported for the species. Apparently, *atossa* was frequently found in open canyons with water present, and nectared at flowers of California Buckeye which may occur on open grassy slopes. Yet the highest colonies occurred in areas of substantial coniferous forest, especially Ponderosa Pine.
- PHENOLOGY: The flight period was principally June and July, although females were taken into early September in some years.
- FOODPLANTS: Comstock (1927b) stated that *Viola pinetorum* Green was present in fields where *atossa* was emerging; this suspected foodplant is now called *V. purpurea* Kell. ssp. *purpurea*, and this plant still grows in some of the areas where *atossa* used to fly. Another violet, *Viola quercetorum* Baker & Clausen, is found in the known former *atossa* localities and may have served as a foodplant. Both wild violets are in the family Violaceae.

101. *Speyeria hydaspe* (Boisduval)

- ADULT BEHAVIOR: This taxon has only been encountered in close proximity to its breeding habitat where it has usually been taken at nectar flying with two other *Speyeria* species, *S. cybele* and *S. zereene*. Males tend to patrol the nectar-source areas, searching for females.
- LIFE HISTORY: The eggs are laid singly and on objects near violets. The mature larva is black in ground color, with a faintly lighter and irregularly shaped dorsal stripe. Around the dorsal lateral spines are small areas of dark gray pigmentation. All rows of spines are yellow-orange from their bases out to almost their tips, which are black. This species hibernates as the first instar larva. The pupal coloration tends to be very dark, with virtually the entire surface area suffused with black pigment. Black bands surround the abdomen at each segmental junction and thoracic junction. The eye covers on the head are black, as is the entire ventral portion of the head, thorax, and abdomen to the cremaster.
- CHROMOSOME NUMBER: $n = 29$ in Colorado material (Maeki and Remington, 1961b).
- SIMILAR SPECIES: In the ranges of two of the subspecies of *hydaspe*, other species of *Speyeria* occur sympatrically and may be confused with *hydaspe*. Within the range of *S. h. tehama* occurs *S. atlantis hanseni*. The *atlantis* adults are slightly smaller, the quality of orange (especially in the females) is somewhat lighter and more yellowish, the cream-colored spots on the underside of the hindwing (especially along the margins) tend to be larger and more triangular in shape, and there is more yellow scaling on the *atlantis* subspecies, particularly on the outer half of the wing. Additionally, the ventral-forewing reddish flush is more developed on *hydaspe* than on *atlantis*, and the black markings are more pronounced.

To the north, in the Mt. Shasta and Warner Mountains and Klamath Mountains, *S. hydaspe purpurascens* usually flies with *S. zereene conchyliatus*. The points of difference between the two species in this area are that (1) *conchyliatus*, tends to be larger, (2) the forewings tend to be more angular in *conchyliatus* and more rounded on the apex of the forewing in *purpurascens*, (3) the spots on the ventral hindwing in *conchyliatus* tend to be at least partly silvered and smaller than the unsilvered larger spots of *purpurascens*. The parallel variation in these two species across this region is remarkable.

GEOGRAPHIC AND SEASONAL VARIATION: As the species is univoltine, there is no seasonal variation. The long geographic cline extending from the Mt. Shasta region to the southern Sierra Nevada, from *purpurascens* through typical *hydaspe* to *viridicornis*, has been described above.

GENERAL REMARKS: It is interesting that *hydaspe* tends to be a montane species, even in Oregon in the Pacific Northwest. It has not successfully penetrated coastal mountain ranges.

While *hydaspe* is a species which reaches its greatest development in the Pacific Northwest, there are a series of at least five geographic subspecies of this *Speyeria* in California. All the subspecies are characterized by having a red-brown ground color on the underside and a lavender tint to some degree, especially in the basal two-thirds of the hindwing.

a. *S. h. hydaspe* (Boisduval)

DIAGNOSIS: Nominotypical *hydaspe* is basically a northern Sierra Nevada and southern Cascade Range set of populations which show characters basically intermediate between the subspecies *purpurascens*, found in the southern Cascade Range and adjacent mountain ranges, and *viridicornis* to the south. The ground color of the uppersides is a deep orange, with black markings that are intermediate between the more heavily marked subspecies *purpurascens* and the more lightly marked race, *viridicornis*. On the underside, the ground color of the hindwing tends to be a dull reddish-brown, with very little yellow overscaling as seen in *viridicornis*, but without the deep reddish-brown ground color and purplish to sometimes lavender cast to the band seen in *purpurascens*.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. Belgique*, 12: 60 (1869).

TYPE LOCALITY: Yosemite Valley, Mariposa County, California, designated by dos Passos and Gray, *American Museum Novitates*, (1370): 21 (1947). Lectotype in U. S. National Museum, designated by dos Passos and Gray, *American Museum Novitates*, (1370): 21 (1947). Type locality re-restricted to Upper Feather River Canyon, Plumas County, California, by Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions* (1998a).

DISTRIBUTION: Because this subspecies is involved in a very long geographic cline between *viridicornis* to the south and *purpurascens* to the north, there are no precisely defined limits to its distribution. However, in the typical phenotype it is found on the western slope of the Sierra Nevada from approximately the Lake Tahoe region in the drainages of the Yuba and Feather Rivers northward along the lower to mid elevations of the Cascade Range, extending throughout much of the Klamath Assemblage of mountains, in a much more widespread distribution than has traditionally been applied to this subspecies. In the southern Trinity Mountains, south of Highway 36, a zone of blending begins between nominotypical *hydaspe* and the northern Coast Range subspecies *tehama*. *Hydaspe* is the subspecies in much of northern California, as it is also resident east of the Cascades in parts of the Modoc Plateau, including populations closest to this typical *hydaspe* subspecies in the Warner Mountains and along the Great Basin fringe south to the Mt. Lassen region. There is a very imprecise area of blending into subspecies *purpurascens*, which has a distribution restricted to the mid to high elevation Cascade Range from roughly Mt. Lassen northward through the type locality in the Mount Shasta region, into the adjacent Trinity Mountains, then northward along the higher Cascade Range into Oregon. Blending in southern Oregon

between *hydaspe* or *purpurascens* and *sakuntala* may barely reach the northern edge of California.

- ELEVATION RANGE: From 1,500' in its lower northern distribution to above 7,000' in the southern portion of its range. This subspecies is mostly found from 2,500' to 6,000', however.
- HABITAT AND PLANT COMMUNITIES: Breeding colonies exist from the upper limits of the Foothill Woodland plant community to primarily within the Coniferous Forest, where the subspecies is most often found breeding in the shaded areas of Douglas Fir or Yellow Pine plant communities. The breeding habitat is often characterized by an understory of chaparral species and forbs, such as Manzanita (*Arctostaphylos*), *Potentilla*, and *Ceanothus* species, especially *integerrimus*, with an abundant needle and leaf mat as well as fern-clad glades. Here, the host violet grows out of the needle mat at the edges of the dense coniferous understory. At the higher elevations of its range, nominotypical *hydaspe* seeks out similar settings within the Red Fir forest realm, or in mixtures of the several communities there.
- FOODPLANTS: Although no specific *Viola* species has been documented as a foodplant for *S. hydaspe*, the presence of the species *Viola sheltonii* Torr. (Violaceae) is frequently noted in *hydaspe* habitats.

b. *S. h. viridicornis* (J. A. Comstock)

- DIAGNOSIS: In this southern Sierran subspecies, adults are paler both above and below, and the black maculation is somewhat reduced from that seen in nominotypical *hydaspe*. The most striking differences are on the underside, where the disc is a very pale lavender, the spots are unsilvered, and there is a marked increase of the yellow scaling over the ground color, giving an overall yellowish appearance to the underside of the hindwing.
- ORIGINAL DESCRIPTION: J. A. Comstock, *Bulletin Southern California Academy Sciences*, 24: 64 (1925).
- TYPE LOCALITY: Greenhorn Mountains, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies ranges from the Greenhorn Mountains (the name "*viridicornis*" is a Latinization of "Greenhorn") in northern Kern County northward along the west slope of the Sierra Nevada to the southern Yosemite region. In this latter area, it forms the beginning of a blendzone with nominotypical *hydaspe* to the north.
- ELEVATION RANGE: From 5,400' to above 7,000' elevation but occurring lower in the northern blendzone populations.
- HABITAT AND PLANT COMMUNITIES: This subspecies is found at the upper edge of the Foothill Woodland plant community, extending up into somewhat modified Yellow Pine forest plant community. The breeding habitat is similar in appearance to that described for nominotypical *hydaspe*.
- PHENOLOGY: *Viridicornis* flies from mid-June until the first week or two of August.

FOODPLANTS: The presence of *Viola sheltonii* Torr. (Violaceae) has been noted in the localities in the Greenhorn Mountains where this species has been taken, and is the probable foodplant.

c. *S. h. purpurascens* Hy. Edwards

DIAGNOSIS: In this northern California and southern Oregon subspecies, adults are deep fulvous above and have considerable expansion of the dark markings on the upperside and underside, giving a "melanic" appearance to this subspecies. The ground color on the underside of the hindwings is dull brick red to blackish-purple and the spots are unsilvered.

ORIGINAL DESCRIPTION: Henry Edwards, *Proceedings California Academy of Sciences*, 7: 170 [1877].

TYPE LOCALITY: Soda Springs, Siskiyou County, California. Lectotype in American Museum of Natural History, designated by dos Passos and Gray, *American Museum Novitates*, (1370): 21 (1949).

DISTRIBUTION: Within California, this subspecies has a much more restricted distribution than has previously been applied to it. *Purpurascens* should be sought along the higher slopes and ridges of the southern Cascade Range, from the Mt. Lassen area to Mt. Shasta and west into much of the higher Trinity and Scott Mountains as well as east to the area of Medicine Lake in Siskiyou County. It follows the Cascades north through the Goosenest District of the Klamath National Forest into Oregon. Everywhere flanking this distribution occurs broad blending or grading into populations which are more closely assigned to nominotypical *hydaspe*. However, in more distant areas, especially in scattered, cooler, higher locations, some populations approach *purpurascens* in appearance. Greatly increased sampling will be necessary to fully assess the distribution of *purpurascens* and related populations.

ELEVATION RANGE: From 3,000' in lower sheltered valleys and drainages near Mt. Shasta upwards to 9,000', but mostly from 5,000' to 7,000' elevation.

HABITAT AND PLANT COMMUNITIES: Like all *hydaspe* subspecies, *purpurascens* is a breeding resident of the northern California coniferous forests, being most often found within the upper reaches of the Yellow Pine Forest, then extending up through the Red Fir Forest plant communities. As in *S. hydaspe hydaspe*, the breeding areas are often adorned by a prolific fern and shrub understory with the common denominator of a significant adult nectar source being present, such as large beds of *Monardella* or *Apocynum*.

PHENOLOGY: This subspecies is on the wing starting in late June at lower elevations, but mostly flies from the first of July to late August. There are always a limited number of worn females into September.

FOODPLANTS: Unknown for this set of populations, but believed to be *Viola sheltonii* Torr. (Violaceae).

d. *S. h. tehama* Emmel, Emmel, and Mattoon

DIAGNOSIS: This is the smallest of the five described California *hydaspe* subspecies. It is characterized by a bright, pale yellow-orange ground color on the upperside of both sexes, with reduction in the size of the dark dorsal markings. Beneath, it is paler than *purpurascens*, with a tendency for the cream-colored spots to be much

enlarged over the condition seen in *purpurascens* or typical *hydaspe*. The ground color of the underside of the hindwings varies from chocolate-brown to reddish-purplish-brown or nearly brick-red in some individuals.

- ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 146-147 (1998h).
- TYPE LOCALITY: Covelo Road, 23NO2, at Government Flat, 5900' elevation, Tehama County, California.
- DISTRIBUTION: This subspecies is found in the higher elevations of the North Coast Ranges in Tehama, northeastern Mendocino, western Glenn, western Colusa, and northern Lake counties. Our southernmost record is in the vicinity of Snow Mountain in Colusa County. The northernmost record for pure populations of this subspecies is in the vicinity of North Yolla Bolly Mountain in Tehama County. North of the Cottonwood Creek drainage, which forms a deep east-west canyon barrier at the north base of the Yolla Bolly country, a broad zone of blending with typical subspecies *hydaspe* occurs.
- ELEVATION RANGE: Although *tehama* has been taken in sheltered canyons as low as 1,800', it normally is encountered from 5,000' upwards, the highest record from North Yolla Bolly Mountain summit being 7,863'.
- HABITAT AND PLANT COMMUNITIES: The habitat of *tehama* is less clear-cut than that of the other *hydaspe* subspecies. It is a resident of the coniferous forest realm, as with other subspecies, but the type of habitat varies somewhat from location to location. Usually, breeding occurs within a Yellow Pine Forest or Douglas Fir Forest setting, but along the upper reaches of the butterfly's range, these plant communities are invading the Red or White Fir Forests. Often, elements of Northern Oak Woodland also invade from below, with gravelly, bare flats and ridges off wet seeps and meadows marking the territory in which *tehama* resides at its flight season. The gravelly flats bloom in a profusion of Pussy-paw, a highly attractive nectar source for many of the Lepidoptera and other insects in the area.
- PHENOLOGY: *Tehama* can be expected starting in late June; it becomes abundant in early July, but late stragglers continue into late August.
- FOODPLANTS: The foodplant for this subspecies is unknown but *Viola sheltonii* Torr. (Violaceae), a suspected *hydaspe* foodplant in other portions of this species' range, is present in the North Coast Range localities where this subspecies of *hydaspe* flies.

e. *S. h. davisii* Emmel, Emmel, and Mattoon

- DIAGNOSIS: The overall dark aspect of this unique Humboldt County subspecies resembles *purpurascens*. However, it is readily distinguished from *purpurascens* by the "two-tone" appearance of the dorsal surface of the males, where the medial three-fifths of the wing is extremely dark but the distal two-fifths of the wing is rather light. This pattern contrasts with the more suffused, more uniformly dark aspect of *purpurascens*. The underside of *davisii* (especially in females) is much lighter than *purpurascens*, lacking the heavy purplish-brown scaling which highlights the cream colored spots. *Davisii* differs from the subspecies *rhodope* of the Pacific Northwest by its larger size, much lighter aspect ventrally, and the lack of a uniformly dark dorsal surface as is seen in *rhodope*.

- ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, p. 147 (1998h).
- TYPE LOCALITY: McClellan Mountain peat bog, east of Bridgeville, Humboldt County, California.
- DISTRIBUTION: This subspecies appears to be confined to Humboldt County, where it is found in localities from McClellan Mountain east of Bridgeville northward to the vicinity of Highway 299 between Arcata and Willow Creek. Populations in eastern central Humboldt County occur in the mountains along the western rim of the Mad River drainage adjacent to Highway 36 and the Larabee Valley.
- ELEVATION RANGE: The McClellan Mountain population is at 2,400', the Redwood summit location is at 2,700', while those along Berry Summit and south range from 4,500' to 5,000'.
- HABITAT AND PLANT COMMUNITIES: Habitat-wise, this is unlike any other California *hydaspe* subspecies, finding a home in a typical Mixed Evergreen forest situation. The only conifers present are a few Douglas Fir and an occasional Redwood, although the habitats are at the inland limits of the latter tree's distribution. The McClellan Mountain population can be found sparingly at the edge of the forest, or down a narrow watered draw with wet meadows that adjoin a small natural basin containing a peat bog. Here, the perimeter of the bog is heavily lined with thistles in bloom which act as the nectar source at adult flight time. At present, the privately-owned bog is being mined for peat, and by late 1988, only half of the estimated 40-acre bog remained. For other populations of this taxon, similar habitat should be sought which presents the availability of permanent moisture and nectar sources in the forest understory, where *hydaspe* can breed. The other major habitat factor is sunlight. These north coastal fog break habitats share moderate elevations, cool temperatures, heavy moisture, and relatively frequent sun breaks in the daily fog cycle.
- PHENOLOGY: Based on adult condition when collected, the McClellan Mountain population emerges in early July and flies into late August.
- FOODPLANTS: Unknown.

102. *Speyeria callippe* (Boisduval)

- ADULT BEHAVIOR: This is one of the two *Speyeria* species which are strong hilltoppers (the other being *S. egleis*). Males are also frequently noted patrolling the slopes where the *Viola* foodplant species grow in search of females, and it is unclear what percentage of time is spent hilltopping and how much time they spend patrolling in this manner. This question would be an interesting one to investigate using mark-release techniques. Mating of all *callippe* subspecies takes place soon after females emerge. There is no reproductive diapause in this species and egg laying starts soon after mating. Oviposition takes place in litter and dead leaves at the base of the host violet which will die but produce others close to the diapausing larval location the next year. Larvae at pupation time tend to spin a mesh-like web structure in which leaf and bits of debris are included. This hollow structure in the leaf litter affords excellent camouflage and a place for the larva to suspend itself for pupation. Leaf litter also holds moisture well even in summer, and offers a site where larvae can avoid desiccation.

LIFE HISTORY: The egg has been described and figured by Comstock and Dammers (1931c) and Comstock (1940). It is nearly spherical, and measures 0.75 millimeters in height and width. There is almost no flattening of the base and very little cupping of the micropyle. The vertical ridges are developed much as in the other species of *Speyeria*, but they tend to coalesce in both the upper and lower quarters of the egg. The color when first laid is yellow, changing later to a pinkish-brown.

The mature larva of each of the subspecies differs somewhat in coloration pattern. Comstock (1931a) noted that the *macaria* larva had black spines with black bristles, but that typical *callippe* had orange spines with black bristles, and that only the spines on the first thoracic segment are a solid black. Our observations of the various taxa show that in typical *callippe*, the mature larva has a light gray ground color overlaid with black blotches and a double gray mid-dorsal line is present. The spines are yellowish in color. In subspecies *macaria*, the body is velvety black with an inconspicuous double mid-dorsal line of gray color. The spines are tinged with dull yellowish-gray at their bases and then shade into black at their tips. In subspecies *inornata*, the black ground color is lightly speckled with gray spots, and there is a rather faint orange lateral line. The spines are dull orangish at their base and black along their lengths. In subspecies *juba*, the ground color of the larva is dull black blotched everywhere by faint tannish markings, and there is a broad, double, mid-dorsal line of light tannish-orange. The spines are entirely faint tannish-orange in color.

The pupa is variously marked with black in the different subspecies, but the overall ground color is a dirty ivory, heavily overlaid with black markings as shown in the accompanying figures. The dark veins on the wing covers are fused at their outer ends into a broad black band, which is especially prominent in subspecies *callippe*. The black rings in the anterior half of each abdominal segment are also especially prominent in all the pupae for which we have records. The chrysalis hangs pendantly from a silk button.

Comstock and Dammers (1931c) made some important observations on the feeding habits of the larvae of *Speyeria callippe* and related species. It had been believed that the larvae were nocturnal, but their field study showed that at least a part of their feeding is carried on during the day. They do not, however, rest upon the foodplant, but instead usually have the behavior of concealing themselves in nearby tufts of grass or other vegetation. When they are hungry, they rush out rapidly to the nearest *Violet* plant and proceed to devour an entire leaf, after which they retire to their nearby retreat. Occasionally, they may be found resting at the base of the plant. This behavior is reminiscent of *Papilio indra* subspecies larvae, which exhibit the same feeding behavior pattern.

CHROMOSOME NUMBER: n = .

SIMILAR SPECIES: *Speyeria callippe* subspecies tend to fly earlier in the season than other sympatric *Speyeria* species. Thus, if one captures *Speyeria* early in the flight season one can be reasonably certain that they are *callippe*, and later in the flight season *callippe* will be quite worn while the other species are fresh in wing condition. Distinguishing features in wing maculation have been discussed under the individual subspecies in cases of sympatry, and the reader is referred to the color plates for the important character differences.

GEOGRAPHIC AND SEASONAL VARIATION: As can be readily realized from a review of the large number of subspecies of *callippe* in California, geographic variation and development of subspecies has been pronounced in California. The species has been particularly successful in occupying a variety of

habitats throughout the state and given the extreme climatic and geographic diversity in California, this radiation and adaptation to local conditions would not be unexpected in such a species. The range in underside color variation, including the silvering of the hindwing spots and the greenish to brownish suffusion of the discal area, offers particularly interesting opportunities for microevolutionary studies of variation on local gradient scales, as well as macrogradient scales. No seasonal variation occurs because all races of *callippe* are single brooded.

GENERAL REMARKS: The typical subspecies, *S. c. callippe*, survives in only two populations in the San Francisco Bay area. The continued protection of this remaining bit of biological heritage in the San Francisco Bay region is possible only because of the prevention of development to date of the surviving grassland hillside areas where *callippe* breeds. Due to the population pressure of expanding humanity in the San Francisco Bay region, there will be continued great political pressure exerted by developers and local governments to infringe upon the boundaries of the protected area in the San Bruno Mountains. Loss of that critical habitat would undoubtedly result in the demise of *S. callippe callippe*. The other population in Joaquin Miller Park is very tiny, and is apparently on the verge of extinction. Protection of the Park will probably continue because of its small size, but the population very well may be lost from that site by random chance due to its extreme reduction in size from earlier development encroachments by Man in the surrounding area. Of course, the preservation of the remaining San Bruno Mountain habitat for *callippe* is imperative, not only for its own sake but for the other endemic, rare, and endangered species of butterflies and hundreds of other organisms found in that area, and for the sake of future human generations who need to have some remaining open space in the crush of a giant metropolitan area to retreat to and contemplate the last remnants of the natural environment that once was there.

SUBSPECIES: This species of fritillary occurs from the Rocky Mountains to the West Coast, and north into Canada. Within our state, it reaches its greatest diversity, with thirteen subspecies identified. We trace the ring of subspecies in California north from the typical subspecies at San Francisco Bay to the Oregon border, and then east and south through the Sierra Nevada to southern California, and north again along the coast to central California.

a. *S. c. callippe* (Boisduval)

DIAGNOSIS: This subspecies is characterized by its dark dorsal wing bases, its heavy markings across both the upperside and the underside, and the deeply suffused basal two-thirds of the ventral hindwing, which bears brightly silvered spots.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 302 (1852).

TYPE LOCALITY: San Francisco, San Francisco County, California, designated by dos Passos and Gray, *American Museum Novitates*, (1370): 14 (1947). Lectotype in U. S. National Museum, designated by dos Passos and Gray (1947).

DISTRIBUTION: *S. c. callippe* is found in the San Francisco Bay area, with populations once distributed throughout that region's immediate coastal mountains. Since development of that great metropolitan area, most populations have been destroyed. Only those that have been afforded some degree of protection are still in existence. A strong population exists on the flanks of the San Bruno Mountains in northern San Mateo County, and another population may continue to exist, as it has within the last fifteen years, in Joaquin Miller Park, Alameda County. This

Park is located in the Oakland Hills east of the town of Piedmont. The populations in these two known locations represent, in their entirety, the world's remaining stock of *S. c. callippe*.

- ELEVATION RANGE: From 50' elevation to approximately 1,400' elevation.
- HABITAT AND PLANT COMMUNITIES: The typical habitat of nominotypical *callippe* is north-facing grassy slopes within the Northern Coastal Sage Scrub plant community. On these slopes, bracken ferns (*Pteridium aquilinum* (L.) Kuhn var. *pubescens*) is usually abundant, and in the shade of the ferns, the *Viola* foodplant is abundant.
- PHENOLOGY: Populations of this subspecies appear on the wing in the latter part of May, and continue flying through the month of June. Males emerge first, and are usually flying at least a week prior to the first appearance of most females. Mating takes place almost immediately after female emergence, closely followed by egg-laying, which takes place near the base of the host *Viola* species.
- FOODPLANTS: The sole documented foodplant for these populations of *callippe* is *Viola pedunculata* T. & G. (Violaceae).

b. *S. c. liliana* (Hy. Edwards)

- DIAGNOSIS: This more northerly coastal interior subspecies has adults which are moderately flushed with red-orange above, and are brightly silvered on the ventral surface of the hindwing. The black maculation is variable, but is usually rather heavy. The basal two-thirds of the ventral hindwing is darker brown, and the forewings are flushed with red in the females.
- ORIGINAL DESCRIPTION: Henry Edwards, *Proceedings California Academy of Sciences*, 7: 170 [1877].
- TYPE LOCALITY: Bale Station, near Mt. St. Helena, Napa County, California. Lectotype in American Museum of Natural History, designated by dos Passos and Gray, *American Museum Novitates*, (1370): 14 (1947).
- DISTRIBUTION: This subspecies is found in the North Coast Ranges from just north of San Francisco Bay up through Sonoma, Napa, and Solano counties, where some colonies still exist and others once existed that showed blending with *S. callippe callippe*. Then the range continues northward to northern Lake County and Mendocino County. North of this point, the subspecies begins to form a lengthy blendzone with the subspecies *shasta* of the Mt. Shasta and southern Klamath Mountains region.
- ELEVATION RANGE: From as low as 20' at one time in North San Francisco Bay blend area colonies, but now from 225' upwards to 7,000' elevation, and widely distributed from 3,000' to 6,000' above sea level.
- HABITAT AND PLANT COMMUNITIES: *Liliana* is an inhabitant of the Northern Oak Woodland plant community which, along the North Coast Range mountains, irregularly grades into Foothill Woodland in its lower reaches, and Yellow Pine or Douglas Fir and even Red or White Fir Forests in the higher elevation of the range. Here, *liliana* uses the thick oak leaf mulch and litter under several species of oak (*Quercus*) to lay its eggs near violets that grow from the mulch. Most commonly, breeding areas occur under stands of the low-growing scrub oak of the region.

PHENOLOGY: This subspecies flies relatively early, having been taken in early May at low elevations, but mostly from mid-May extending to late July in higher reaches of its distribution.

FOODPLANTS: *Viola sheltonii* Torr. is known for blend-zone populations with *S. c. shasta*, from observed oviposition records (Sterling O. Mattoon).

c. *S. c. shasta* Emmel, Emmel, and Mattoon

DIAGNOSIS: Starting just southwest of Lake Shasta in Trinity and eastern Humboldt counties, this much darker race extends northward to eventually meet *S. c. elaine* of the Siskiyou Mountains and adjacent area in southwestern Oregon. Adults of *shasta* are deeply reddish-orange above, and are heavily marked in black with a heavy basal suffusion. On the underside they are normally unsilvered or have only a very few silvery scales in the spots. While heavily melanic on the basal area dorsally, the underside disc in the hindwing varies from a leathery tannish-yellow brown to a deep chocolate brown.

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 149-150 (1998h).

TYPE LOCALITY: Forest Route 34N17, 1 mile south of McCloud Arm Bridge, Lake Shasta T35N-R2W-S5, elevation 1,200', near the Southern Cascade Range, Shasta County, California.

DISTRIBUTION: *Speyeria callippe shasta* is the unsilvered *callippe* subspecies of the Mt. Shasta region which formerly went under the name *rupestris*. An investigation of the circumstances surrounding the name *rupestris* was undertaken by Masters, J. Emmel, T. Emmel, and S. Mattoon (1998h), and it was determined that the name *rupestris* actually applies to a set of essentially unsilvered populations on the west slope of the Sierra Nevada in the Yosemite region.

This unsilvered *callippe* subspecies is found in the extreme North Coast Ranges of southern Trinity County, ranging northeastward to the region around Clair Engle Lake and Shasta Lake, to the region immediately south and southeast of Mt. Shasta. To the northwest, this subspecies blends with subspecies *elaine* of the Siskiyou Mountains and adjacent area in southwestern Oregon. To the south it forms a long blendzone with subspecies *liliana* of the North Coast Ranges. Another unsilvered segregate of *callippe* is found just to the southeast of the range of *shasta* in the foothills west and southwest of Mt. Lassen. However, no phenotypically intermediate populations are known between these two subspecies.

More specifically, the distributional stronghold for *Speyeria callippe shasta* is in the Trinity Mountains portion of the Klamath Mountains Assemblage, extending through western Shasta, eastern Trinity, and central Siskiyou counties. Populations are also widespread east of the Shasta-Trinity Divide, extending into the adjacent Cascade Range from central Siskiyou County as far south as southern Shasta County. Populations inhabiting the watershed around Shasta Lake are the purest and most uniform in facies, apparently the result of a lack of contact with the more southerly, low-elevation western Sierra Nevada *inornata* cline. No *shasta* population has yet been recorded south of State Highway Route 44. The most eastward penetration of *shasta* extends along the McCloud River drainages to where it comes into contact with green-brown populations of Great Basin *callippe* in a single area near Bartle, in Siskiyou County. State Highway 89 roughly denotes the limit of eastward distribution south of Bartle, and from there

northwestward, *shasta* is found on the slopes and throughout the region surrounding Mount Shasta.

The northern boundary of distribution is denoted by an extensive contact zone of blending with *S. c. elaine* from the northern slopes of Mount Shasta at the city of Weed, then west-southwestward along the north-facing slopes of the Scott Mountains, into the southern Salmon Mountain and the Trinity Alps of southwestern Siskiyou County. The general blending influence with *elaine* is observed as far south as Clare Engle Lake, Trinity County, and is in part responsible for the high degree of variability present in the Trinity Center area, the mistaken type locality once established for *S. c. rupestris*.

Shasta populations extend both south and west of the southern Trinity Mountains into the North Coast Range in western Tehama in western Trinity County. Occasionally, single atypical specimens are taken more coastward into northeastern Humboldt County, which hint of populations with lighter and possibly larger wings. The Coast Range Mountains from southern Tehama County south to northern Lake and Colusa counties represent an extensive area of blending with the next subspecies to the south, *S. c. liliana*. Throughout this region the percentage of specimens with *shasta* facies varies from population to population and from year to year, but tends to decrease from north to south through this distributional range.

ELEVATION RANGE: From the lowest elevation of 1,100', *shasta* is then widely distributed at all elevations upwards to the highest recorded location at 6,560'. The elevational range for *shasta* recorded in the Klamath Assemblage of mountains is from 2,000' to 6,500'; in the Cascade Range, from 1,100' upwards to 6,000'; and in the North Coast Range, from 2,450' to 7,500'. Most of the higher-elevation records represent specimens engaged in hilltopping activities, with the bulk of the population distributed between 2,000 and 4,500' elevation.

HABITAT AND PLANT COMMUNITIES: In the southwestern part of its range, *shasta* occupies habitats very similar to *liliana* habitat, Northern Oak Woodland blending into Foothill Woodland on lower slopes, or into Yellow Pine or Douglas Fir forests above. To the northeast, Scrub Oak breeding areas are replaced by similar habitat under Black Oak stands in and below the Coniferous Forest belt where Black Oaks often grow in dense stands in the Digger Pine-Chaparral zone. Throughout its range, similar favorable situations extend to Red Fir forests.

Shasta, like others of this species, is most often encountered in congregations around a nectar source. Sources commonly used throughout this insect's range are *Monardella* (Coyote Mint), *Aesculus* (Horse Chestnut or Buckeye), and *Apocynum* (Dogbane). Females are wary, except when preoccupied with nectaring. Males patrol, searching through the oak-forested breeding grounds or roaming across flower patches in search of females. Males also can often be found at wet sand or mud areas. These butterflies are strong, active fliers.

However, *shasta* is primarily an inhabitant of the Mixed Evergreen Deciduous Forest transition zone. Breeding areas are associated with oaks, where accumulated leaf mulch and litter provide the necessary environment for diapausing first-instar larvae and host violet growth. Throughout much of its range, *shasta* is in association with the distribution of Black Oak, *Quercus kelloggii*, and is not normally found below the lower altitudinal distribution of this tree. In much of the Klamath Assemblage, and commonly in the Coast Range and parts of the Trinity Mountains, a low-growing, compact, large-leaved scrub oak

provides the same environmental niche. This *callippe* will follow stands of oak to higher elevations or go there for nectar or hilltopping, but it is primarily a pine-oak dweller. It is often found in association with serpentine-type soils where adjacent rocky outcroppings provide a diversity of plants which are often used as *shasta*'s primary nectar sources.

PHENOLOGY: The single brood of adults appears during the first two weeks of June, although at some low-elevation locations, early males can be taken in late May. The general flight period is primarily over by the end of July, extending sometimes into early August. Males precede females by a week or more, and there are always a few late-emerging females. Mating occurs immediately after emergence and egg-laying proceeds soon after, with oviposition taking place in the accumulated leaf litter and mulch under oaks near the host *Viola* species. Larvae diapause in the first instar and overwinter in the protective environment of the leaf mat.

FOODPLANTS: Unknown. *Viola sheltonii* Torr. grows in the oak leaf mat under the oaks where emerging adults have been taken. Oviposition has been observed once (Mattoon) in oak-leaf litter around *Viola sheltonii* Torr., along the Hirz Mountain lookout tower access road, McCloud arm of Lake Shasta, Shasta County, California, at 2,500' elevation.

d. *S. c. elaine* dos Passos and Gray

DIAGNOSIS: To the north of subspecies *shasta* occurs this heavily marked subspecies, which is usually, but not always, silvered ventrally. The disc is deeply reddish, with some invasion of the outer light band by reddish or russet scaling. The chief distinguishing characteristic of this race is the deep reddish underside combined with the usual heavy silvering of the spots on the ventral surface of the hindwing.

ORIGINAL DESCRIPTION: Dos Passos and Gray, *American Museum Novitates*, (1297): 5 (1945).

TYPE LOCALITY: Butte Falls, Jackson County, Oregon. Holotype in American Museum of Natural History.

DISTRIBUTION: This subspecies, which finds its stronghold in the mountains of southwestern Oregon, penetrates into California in the Siskiyou Mountains area and the area north of Mt. Shasta in Siskiyou County. Along the southern boundary of Siskiyou County, it forms a blendzone with the subspecies *shasta*.

The type locality of *S. c. elaine* at Butte Falls, Oregon is located toward the northeastern extent of the currently known distribution of this subspecies. Specimens northwest of Butte Falls at Tiller Grade, 3,000', in Jackson County, are near *elaine*, but tend to have a more nut-brown ventral hindwing disc. *Elaine* is found throughout the pine-oak belts of the valleys and hills across Jackson County, extending north into extreme southern Douglas County. Westward, *elaine* occupies the Siskiyou Mountains and north of there in scattered locations throughout eastern Josephine County in Oregon. The distribution south into adjacent California includes all of the Siskiyou Mountains, extending to the west just into Del Norte County, and east beyond the Siskiyou Mountains, where it becomes abundant at times through the Klamath River drainage in both California and Oregon (but not east of Highway 97). In this area, *elaine* is well-established, reaching a peak of abundance in the block of the Cascade Range mountains just south of the Klamath River in California. This area is referred to as the Gooseneck District of the Klamath National Forest. Elsewhere, the bulge of southward distribution covers most of central and eastern Siskiyou County, including Shasta

Valley north to the base of Mount Shasta, then along the north-facing slopes of the Scott Mountains westward to the Marble Mountains, and extending down through the Salmon Mountains to the latitude of at least Cecilville, California. Along and southward of this boundary, extensive blending with subspecies *S. c. shasta* is occurring.

- ELEVATION RANGE:** In the Klamath Mountains Assemblage in California, an elevational range from 2,300' to 7,000'. In the California Cascade Range, elevational distribution runs from 2,500' to 6,000'.
- HABITAT AND PLANT COMMUNITIES:** *Speyeria callippe elaine* prefers habitats where oak-chapparral is dominant in the lower dry Transition Forest area, occasionally extending up to the lower edge of the Canadian Forest zone. Many specimens may be attracted from breeding habitat at lower elevations to the abundance of nectar sources here. Extensive beds of *Monardella* mints are highly prized for feeding by *S. c. elaine* and other *Speyeria* species, which are commonly enticed to the upper flanks of these ranges.
- PHENOLOGY:** The single annual brood of *elaine* may start in May, but the bulk of the flight occurs in June through the first weeks of July. Adults become worn and disappear by the end of July. Females emerge mainly after the males, mate, and lay eggs immediately, like *callippe* subspecies. Diapausing first-instar larvae appear to find the necessary protection from desiccation in the thick oak-leaf litter accumulation of a suitable breeding area, and it is here that diapause takes place.
- ADULT BEHAVIOR:** Adults avidly nectar. In the Gooseneck District of the Californian Cascade Range, the most commonly used sources are sunflowers and daisies (Compositae). Elsewhere, throughout its range, coyote mint (*Monardella*) is favored. Males patrol nectar beds and grassy openings in the breeding habitat, looking for unmated females. Larvae of *Speyeria* wander considerably after having completed the feeding cycle. They often pupate some distance from the site of egg-laying. Thus, males tend to search for females in areas often somewhat removed from the actual source of egg-laying. *Elaine* adults, like all *Speyeria*, tend to bask while perched on a nectar source or fly to open ground, such as a roadway, to collect heat by orientation of their wings when the temperature or solar activity is interrupted by clouds or in cool weather.
- FOODPLANTS:** We have no specific documentation of the *Viola* species utilized by *elaine*, but it is probably the same *Viola* as is used by *S. c. shasta*.
- SIMILAR SPECIES:** At the time *S. callippe elaine* flies, the two main species to be confused with it are *S. hydaspe* and *S. zereene*, with the former sometimes the most similar. However, at higher elevations of the Siskiyou Mountains, in some years the end of the *elaine* flight will coincide with the flight of a subspecies of *S. egleis*, and here an extremely close parallel of fashces can occur. Identification of individuals can be very perplexing. *S. coronis* near *simaetha* is sometimes encountered flying with *elaine* and has silver spotting similar to *elaine*, but is much lighter and larger.

e. *S. c. (nr.) semivirida* (McDunnough)

- DIAGNOSIS:** This subspecies was originally named from British Columbia and occurs south in the Cascades to central Oregon. Brownish-green facies reach into northeastern California, in the Warner Mountains area, and extend through much of the sagebrush flats with springtime meadows found in the Modoc Plateau and Great Basin fringe area of Modoc, Lassen and eastern Siskiyou counties. *Semivirida* is

characterized by the basal two-thirds of the underside of the hindwing being brownish-green to brown in color. Ours are similarly marked and have been referred to as *semivirida*, but some confusion exists as to the correct phenotypic expression to be applied to true *semivirida*. There is blending with *S. callippe elane* on the western edge of our distribution (near Bartle), Siskiyou County, and with *Callippe nevadensis* in Lassen County in numerous places north of the latitude of Susanville in Lassen County. Some entirely green individuals show up in the Warner Mountains where the most consistent of our brownish-green populations fly. These individuals look more like *nevadensis* than they do central Oregon "*semivirida*;" thus, we prefer referring to this taxon as (near) *semivirida* until the situation can be further clarified.

- ORIGINAL DESCRIPTION: McDunnough, *Canadian Entomologist*, 56: 42 (1924).
- TYPE LOCALITY: Aspen Grove, British Columbia. Holotype in Canadian National Collection.
- DISTRIBUTION: As stated in the Diagnosis, we use the name *semivirida* to refer to a set of extremely variable populations in the northeastern corner of the state, which show both varying degrees of brown and green scaling on the underside. These populations are found throughout Modoc and northern Lassen County, and extreme eastern Siskiyou County.
- ELEVATION RANGE: This high desert subspecies is found from 4,500' on the flats upwards to 8,780' in the Warner Mountains.
- HABITAT AND PLANT COMMUNITIES: This is a *callippe* of the high basin and open range Sagebrush Scrub plant community. Typical breeding habitat is found in the *Artemisia* scrub along the perimeters of the open grassy meadows and flats that during the spring months. Here, the host violet grows under the are green sagebrush at the edge of the grassy areas, and as with other *callippe*, a source of nectar is adjacent, often in coniferous forest areas on ridges that frequently border these flats or valleys along the Great Basin fringe or in the Warner Mountains. Here the nectar source is commonly *Monardella* or sunflowers, while many of the meadowy areas are damp enough to support heavy stands of yellow composites that bloom during the flight period and often teem with insect life.
- PHENOLOGY: *S. c. (nr.) semivirida* has been taken from late May, but June to early August covers the normal flight, with our latest record in mid-August.
- FOODPLANTS: Unknown, but *Viola beckwithii* T. & G. is strongly suspected to be at least one host of this set of populations.

f. *S. c. nevadensis* (W. H. Edwards)

- DIAGNOSIS: This subspecies of *callippe* has been considered a full species by at least one author (Howe, 1975) because of its range across the Great Basin in several forms, all of which share a greenish underside. We best regard it as a subspecies of *Speyeria callippe*. This subspecies *nevadensis* is characterized by a bright gold-green disc on the underside of the hindwings, with intense silvering of the spots. It is quite constant in phenotype throughout most of its California range.
- ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Ent. Soc.*, 3: 14-15 (1870).
- TYPE LOCALITY: Just north of Virginia City, Nevada. Neotype in Carnegie Museum, designated by dos Passos and Gray, *Transactions American Ent. Soc.*, 91: 355-356 (1965).

- DISTRIBUTION:** Within California, the subspecies *nevadensis* is found in extreme southeastern Lassen County, eastern Plumas County, southward along the east slope of the Sierra Nevada through eastern Sierra and Nevada counties. It is then found east of Lake Tahoe in the vicinity of Carson City and Virginia City, Nevada, and coming southward it again enters California in the Topaz Lake area of extreme northern Mono County, coming south along the east slope of the Sierra Nevada as far south as extreme northwestern Inyo County, just west of Bishop. Areas of blending along the upper eastern escarpment and crest of the Sierra Nevada occurs with subspecies *juba*.
- ELEVATION RANGE:** From 5,300 on the sagebrush flats up the eastern escarpment of the Sierra Nevada to 9,000'.
- HABITAT AND PLANT COMMUNITIES:** This butterfly is typically found in the Great Basin Sagebrush Scrub plant community, and typically flies over low hills, slopes, and flats where *Artemisia tridentata* Nutt. is the dominate plant: it follows such habitat up the dry, rain-shadowed east slopes of the Sierra Nevada. The *Viola* species on which the larvae feed usually grow abundantly in the shelter of these sagebrush plants.
- PHENOLOGY:** As early as late May, but mostly early June to late July.
- FOODPLANTS:** As with the populations of *S. c.* near *semivirida*, at least one suspected foodplant for *nevadensis* is *Viola beckwithii* T. & G., as the butterfly is frequently associated with this particular *Viola* species.

g. *S. c. juba* (Boisduval)

- DIAGNOSIS:** This subspecies inhabits the western slope of the Sierra Nevada. An examination of the Boisduval type (Emmel, Emmel, and Mattoon, 1998a) shows that this is a bright orange subspecies dorsally, with the inner half of the dorsal surface suffused with dark brown. On the underside of the wings, the disc on the hindwing is a uniform brown with a lighter tan marginal area. The dull basal brown is repeated on the forewing with a light tan apical and marginal area beneath. All the spots are silvered (Scott, 1986, is in error on this point). The name *sierra* dos Passos and Gray (1945) is a synonym of *juba*.
- ORIGINAL DESCRIPTION:** Boisduval, *Ann. Soc. Ent. Belgique*, 12: 60 (1869).
- TYPE LOCALITY:** Downieville, Sierra County, California, designated by dos Passos and Gray, *American Museum Novitates*, (1370): 15 (1947). Lectotype in U. S. National Museum, designated by dos Passos and Gray (1947).
- DISTRIBUTION:** This subspecies is found primarily in the higher elevations of the northern Sierra Nevada in areas where there is granitic substrate, from the region just west of Lake Tahoe northward to the region of the north fork of the Feather River. The stronghold of this subspecies is from Downieville to Gold Lake in Sierra County. Some individuals in these populations show some green scaling on the underside, indicating a probable genetic exchange with the *nevadensis* populations just to the east. At the extreme northwestern end of its range, primarily down the Feather River drainage, it begins to blend with the unsilvered subspecies *hagemani* (occurring just to the west).

- ELEVATION RANGE: Although primarily found from 3,000' to 6,000', *juba* follows down the Feather River Canyon bottom to 1,800', and has been reported as high as 7,200' along the higher mountains as pure phenotypic populations.
- HABITAT AND PLANT COMMUNITIES: As with other *callippe*, *juba* is using the oak belts, primarily *Quercus kelloggi* as its breeding habitat which ranges upward from the typical Digger Pine-Oak Foothill Woodland plant community type into Coniferous Yellow Pine Forests and into Red Fir Forests. The actual breeding habitat is suspected to be similar for high-elevation populations but awaits more thorough observations to be conclusive. Buckeye trees, blackberry, dogbane and hemp act as the usual nectar sources for this subspecies. The environmental niche occupied by *juba* seems most often to involve the river bottoms and side canyons of watercourses draining westward down the Sierra Nevada, at least in low to mid-elevations of its distribution. Higher, the habitat seems less restricted to streamside situations, but appears to have other restrictive factors resulting in rather scattered colonies of a fairly uncommon subspecies.
- PHENOLOGY: *Juba* emerges in late June and flies on through the month of July, rarely into early August at highest elevations.
- FOODPLANTS: Unknown.

h. *S. c. hagemani* Emmel, Emmel, and Mattoon

- DIAGNOSIS: This remarkable subspecies looks totally unlike *callippe* in overall appearance, and it is only by tracing through the intermediate populations and careful examination of the wing features that one can place this subspecies in the species *callippe*. On the upperside of both sexes there is a marked reduction of the dark basal suffusion on the wings, as well as the black markings across the dull orange ground color. On the underside, the most unusual feature is the dark chocolate-brown discal ground color of the hindwing with unsilvered spots and a light outer band, which make it look almost like *zerene*. This outer ventral hindwing band is much reduced from that found in the other subspecies. On the ventral surface of the forewing, the females exhibit a marked reddish flush on the lower half and a whitish apical area, because of the enlargement of the cream-colored spots. The males show this ventral forewing coloration to a lesser degree.
- ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 150-151 (1998h).
- TYPE LOCALITY: South side of Highway 44, at 3500' elevation, 2 road miles west of Shingletown, Shasta County, California.
- DISTRIBUTION: This subspecies occurs in a limited area of the foothills and lower coniferous forest slopes of the Southern Cascade Range west and southwest of Mt. Lassen at the extreme northern end of the Sacramento Valley, ranging from the Shingletown area in extreme southern Shasta County southward to the area just northeast of Chico in Butte County. It prefers fern clad glades in chaparral and yellow pine forest, as at the type locality.
- ELEVATION RANGE: From 1,500' to 3,500' but mostly in the 2,000' to 3,000' elevational range.
- HABITAT AND PLANT COMMUNITIES: *S. c. hagemani* is always found in a narrow belt where the Foothill Woodland and lower reaches of Yellow Pine forest intermingle. Most

colonies are found within the lowest distribution of Black Oak, *Quercus kelloggi*, along this belt and the host violet species grows within a sparse understory of chaparral typical to the elevation, *Manzanita* and wild lilac (*Ceanothus integerrimus*). This subspecies is associated with serpentine outcroppings and red-lateritic, clay-loam type soils. As with other *callippe* subspecies, *hagemani* is especially attracted to the bloom of *Aesculus californica* (Buckeye) and *Monardella* (Coyote Mint) which grows equally well in the two mentioned soil types. *Hagemani* nearly always flies with *Speyeria hydaspe* which has abundant adjacent habitat. In the late 1960's, an extensive population of this subspecies was eliminated at Black Butte near Highway 44 in Tehama County, when the soil was stripped of its soil litter of pine and oak leaf mulch. Raising strawberry plants was the intended goal. Although the agricultural enterprise failed to materialize, the simple act of removing the ground cover from under the pines and oaks eliminated the *callippe* population, even though the host violet grew back in profusion thereafter.

PHENOLOGY: *Hagemani* starts flying in early June with a few late May records, and is found until the end of July.

FOODPLANTS: Unknown.

i. *S. c. inornata* (W. H. Edwards)

DIAGNOSIS: This a very rare insect in collections. In former works, such as Howe (1975), it has been confused with other subspecies such as *rupestris* and *juba*. Although the type locality of this taxon was fixed as Downieville, Sierra County, by dos Passos and Gray in F. M. Brown (1965), we have strong reason to believe that it was actually collected just to the west of this area by James Behrens, probably in the vicinity of Camptonville, in northeastern Yuba County. First, it is an unsilvered *callippe* subspecies, and extensive sampling of *callippe* populations in the immediate vicinity of Downieville by Mattoon and Hageman revealed them to be close to, if not 100%, silvered. Secondly, at the time Behrens collected the type of *inornata*, it was common practice to simply refer to the nearest significant town as the locality for collecting a given specimen, and although Behrens may have spent time in Downieville proper, we suspect that he collected the type a few miles west of the town, where unsilvered populations begin showing up. This butterfly is distributed in a narrow band along the west slope of the Sierra Nevada in the foothills, from the Camptonville area southward to Calaveras County. The name *inornata* has been applied also to unsilvered populations south of this region, particularly in the Yosemite area; however, as noted above under the discussion of subspecies *shasta*, these populations fall under the name *rupestris*, and do not have the dark ventral hindwing disc and heavy melanic markings of typical *inornata*.

On the upperside the males tend to be a light tannish-orange, lighter than in *hagemani*, while the extent of the dark markings are bolder, especially in the median zig-zag line and cell-spot markings than seen on subspecies *hagemani*. The females tend to be more yellowish in ground color on the dorsal surface, and have a basal suffusion that has a much greater contrast with ground color than *hagemani*. Females also have greater extent of dark markings. Ventrally, both sexes tend to have a light yellowish cast and are unsilvered except for occasional scattered silver in the female hindwing marginal row. On the forewings, the reddish flush is largely restricted to the basal area of the forewing, with outer spots and ground color a yellowish-cream. On the underside of the hindwing, the outer

band and discal spots are also a yellowish-cream, while the basal disc surrounding the unsilvered spots is a medium brown with less red tones than are seen in *hagemani*.

- ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Ent. Soc.*, 4: 64-65 (1872).
- TYPE LOCALITY: "Supposedly Downieville, Sierra County, California." Neotype in Carnegie Museum, designated by dos Passos and Gray, in F. M. Brown *Transactions American Ent. Soc.*, 91: 275 (1965). Type locality re-restricted by Emmel, Emmel, and Mattoon (1998h, p. 149)), to the vicinity of Camptonville, Yuba County, California.
- DISTRIBUTION: From the vicinity of Camptonville in northeastern Yuba County southward to southern Calaveras County, on the western slope of the Sierra Nevada and the foothills.
- ELEVATION RANGE: This is a subspecies found in a narrow elevational band from 2,000' to 3,000'.
- HABITAT AND PLANT COMMUNITIES: The ecological niche that this subspecies occupies is similar to that of its two closest allies, *hagemani* and *rupestris*. It occupies an oak-dominant habitat, with usually a bracken fern understory, which is at the lower reaches of the Yellow Pine Forest plant community where Foothill Woodland elements invade. *Inornata* appears to have the most restricted habitat of the lower west slopes along the Sierra Nevada-Cascade Range *callippe* cline. In some places, *callippe-juba* facies extend down to lower elevations along drainages and nearly interrupt the continuous *inornata* distribution shown in the map. The habitat of *inornata* is more restricted to *Monardella* as the primary nectar source.
- PHENOLOGY: *Inornata* has been recorded from late June to the first week in August.
- FOODPLANTS: Unknown, but *Viola quercetorum* Baker & Clausen (Family Violaceae) is suspected.

j. *S. c. rupestris* (Behr)

- DIAGNOSIS: This subspecies occurs to the south of *inornata* in the western Sierra Nevada foothills. It is characterized by its relatively large size and by the rich blackish suffusion covering the inner half of the wings in both males and females on the upperside. Occasionally, this melanic suffusion covers three quarters of the wing or more. The ground color is a dull orange on the upperside in both sexes. On the undersurface, the forewing has a reddish-brown ground color up into the apical area, where the cream spots are relatively diffuse and light tan in color compared to other subspecies. The median row of black spots on the ventral forewing forms a jagged black band, but the other black spots are reduced. On the ventral hindwing, there is a dark umber discal band which is expanded to almost cover the light tan outer marginal area. There is considerable variability in the amount of silvering, although most individuals are unsilvered.
- ORIGINAL DESCRIPTION: Behr, *Proceedings California Academy Natural Sciences*, 3: 84 (1863).
- TYPE LOCALITY: Trinity Center, Trinity County, California, designated by dos Passos and Gray, *American Museum Novitates*, (1370): 15 (1947). Lectotype in Field Museum of Natural History, Chicago, designated by dos Passos and Gray (1947). Type locality re-restricted by Emmel, Emmel, and Mattoon (1998h: pp. 147-149) to vicinity of Moore Creek Road at U. S. Forest Service Road 1S29, 1.5 to 2

roadmiles south of Highway 120 at Buck Meadows, elevation 3,200', T1S-R17E-S35, Mariposa County, California.

DISTRIBUTION: This name has been applied in the past to the *S. callippe* populations that we now call *S. c. shasta*. A careful investigation of the itinerary of William Brewer (the collector of the type of *rupestris*) and the probable time of the year that he collected the type has led to the fixation of the type locality of this insect to the area just west of Yosemite National Park (Emmel, Emmel, and Mattoon, 1998h). Thus this subspecies *rupestris* is found in the foothills of the west slope of the Sierra Nevada from approximately El Dorado County and the Yosemite region southward to approximately Mineral King in northern Tulare County. There are probably blendzones between this subspecies and *inornata* to the north and subspecies *laurina* to the south, but these await discovery through further field work.

ELEVATION RANGE: This subspecies has been found from 3,500' to 5,000'.

HABITAT AND PLANT COMMUNITIES: *Rupestris* continues the trend of Sierra Nevada west slopes foothill populations being residents of the lower Yellow Pine Forest plant community from the upper edge of foothill woodland, in oak-dominant situations along flats and ridges, upwards to, but not penetrating significantly, the Red Fir Forest realm except where elements of each intermingle. Here this subspecies finds Coyote Mint beds typically growing in clearings in the mixed pine-oak forest or on open rubble-rock hillsides adjacent to small stream beds. Several violet species occupy the oak leaf mat of litter under shrub and chaparral species in the habitat. At the higher elevations of its distribution, this butterfly can be found along east-west canyon flanks where *Monardella* and thistle grow on rocky outcroppings and side canyons harbor the oaks. They also follow along drier chaparral-dominant ridges that penetrate up into Red Fir and Sequoia groves, which are scattered along the upper reaches in which *Rupestris* flies.

PHENOLOGY: The bulk of records show a mid-June to late July flight but it has been taken from late May on lower slopes, and there are also several mid-August to late August high-elevation records.

FOODPLANTS: Unknown, but *Viola quercetorum* Baker & Clausen is frequently present in the localities where this butterfly is collected.

k. *S. c. laurina* (W. G. Wright)

DIAGNOSIS: *S. c. laurina* is a small subspecies with very light ground color on the upperside with greatly reduced dark markings on the upperside; on the underside the ground color tends to be a very light buff, even in the discal area of the hindwing. Because of the light buff ground color, the unsilvered spots do not tend to be as prominent as in the other unsilvered subspecies.

ORIGINAL DESCRIPTION: W. G. Wright, *Butterflies of the West Coast*: 138 (1905).

TYPE LOCALITY: Greenhorn Mountains, Kern County, California, designated by dos Passos and Gray, *American Museum Novitates*, (1370): 16 (1947). Holotype in California Academy of Sciences.

DISTRIBUTION: This subspecies is found again in the Sierra Nevada foothills of the extreme southern Sierra Nevada, in the region of the Greenhorn Mountains of northern

Kern County and southern Tulare County. To the south it blends with subspecies *macaria*. Within this blendzone, varying numbers of silvered or unsilvered individuals may be found. The geographic transition between these sets of populations was carefully analyzed by Sette (1962), who showed that there was a relatively narrow transitional area between the Greenhorn Mountains, where *laurina* was predominant and areas immediately to the south where *macaria* (silvered form) predominates.

- ELEVATION RANGE: From 2,800 to 7,000' elevation. but primarily between 3,100 and 4,900'.
- HABITAT AND PLANT COMMUNITIES: In general, this Fritillary is found in the upper portion of the Upper Sonoran life zone, or the foothill woodland and Yellow Pine forest communities. The butterfly's habitat is characteristically marked by scattered Blue Oak, Digger Pine, and sparse Chaparral with sagebrush (*Artemisia tridentata* Nutt.) often present. Usually there are broad areas, or at least small patches of grass present, and sometimes these localities occur along streams. Practically all of the known localities today are in grazing land.
- PHENOLOGY: *Laurina* flies from mid-May to late July, but primarily in June to mid-July.
- FOODPLANTS: *Viola quercetorum* Baker & Clausen is abundant in the areas where *laurina* flies, and is suspected to be the major foodplant of this species.

I. *S. c. macaria* (W. H. Edwards)

- DIAGNOSIS: Occurring still further south in the central transverse mountain ranges, this subspecies is characterized by a light orange ground color dorsally, and a very light yellow-buff ventral surface bearing moderately sized, silvered spots. A ventral reddish suffusion occurs towards the base of the forewings. Occasionally, unsilvered individuals are collected in *macaria* populations.
- ORIGINAL DESCRIPTION: W. H. Edwards, *Field and Forest*, 3: 86-87 (1877).
- TYPE LOCALITY: Havilah, Kern County, California. Lectotype in Carnegie Museum, designated by dos Passos and Gray, *American Museum Novitates*, (1370): 15 (1947).
- DISTRIBUTION: This subspecies is found in Kern County in the foothills of the western slope of the Piute Mountains, a southern extension of the Sierra Nevada, southward to the Tehachapi Mountains. There is a blendzone with subspecies *comstocki* in the southern Tehachapi Mountains and in the Tejon Range. At the north end of the range of *macaria* it blends with subspecies *laurina* with varying numbers of silvered or unsilvered individuals in these populations.
- ELEVATION RANGE: Records range from 2,800 to over 7,000' on the slopes of Mt. Pinos. Most populations occur below 5,500'.
- HABITAT AND PLANT COMMUNITIES: This subspecies occurs in a mixture of Oak Woodland, sparse Chaparral, and Sagebrush Scrub plant communities. At the higher elevations, individuals can be taken in Montane Coniferous forests; individuals in these areas are usually hilltopping males, and it may not represent an actual breeding area for the butterfly.
- PHENOLOGY: It flies from late May to late July, emerging earlier than other *Speyeria* species occurring in the same localities.

FOODPLANTS: No specific violet species has been documented for *macaria*, but the presence of *Viola quercetorum* Baker & Clausen is noted in *macaria* habitats.

m. *S. c. comstocki* (Gunder)

DIAGNOSIS: This subspecies, which is found in the mountains and hills along the coast and the southern half of the state, is smaller and less heavily suffused with black, but still heavily silvered beneath. There is somewhat of a clinal effect from southern California northward along the Coast Range to the San Francisco Bay area. However, the differences do not appear enough to warrant subspecific treatment along this cline.

ORIGINAL DESCRIPTION: Gunder, *Entomological News*, 36: 8 (1925).

TYPE LOCALITY: Los Angeles, Los Angeles County, California. Gunder (1930) more precisely noted that the type locality of this subspecies was Griffith Park in Los Angeles (see Emmel and Emmel, 1973).

DISTRIBUTION: This subspecies is widely distributed in the Southern Coast Range and mountains and hills of coastal southern California, from extreme southeastern Alameda County in the north southward to San Diego County. This subspecies has also been taken on Santa Cruz Island, along the ridge south of Chinese Harbor. In the north, it blends with nominotypical *callippe* along the southeastern San Francisco Bay area, at the western end and southern slopes of the Tehachapi Range, similar blending takes place with *Macaria*.

ELEVATION RANGE: From near sea level to approximately 6,300' elevation, with the majority of populations below about 4,000' elevation.

HABITAT AND PLANT COMMUNITIES: This subspecies is usually found on grassy slopes within the following plant communities; Southern Oak Woodland, Chaparral, and Coastal Sage Scrub. In these habitats the *Viola* foodplants grow in the protection of various small shrubs and represent the breeding areas for the butterfly.

PHENOLOGY: In southern low-elevation populations of Ventura and Riverside counties, emergence may commence occasionally in mid-April. However, most populations of this subspecies fly from late May to early July, with a peak flight in early June.

FOODPLANTS: The primary host of this subspecies is *Viola pedunculata* T. & G. (Violaceae). *V. quercetorum* Baker & Clausen may possibly be used in some of the higher elevation habitats of this subspecies.

n. *S. c. adiateoides* Emmel, Emmel, and Mattoon

DIAGNOSIS: This is the westernmost of the unsilvered to minimally silvered *S. callippe* populations. It is distinguished from its geographically closest relative, *S. c. shasta*, by its overall paler aspect, and lighter dark markings both dorsally and ventrally. But it shares with subspecies *shasta* the character of small size in comparison to other *S. callippe* subspecies. The name *adiateoides* is in reference to the superficial resemblance of this *Speyeria* to another Outer Coast Range species, *S. adiate* (W. H. Edwards, 1864).

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 150-151 (1998h).

TYPE LOCALITY: Cahto Peak summit, 4000-4200 feet elevation, Mendocino County, California. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This subspecies is found in the outer North Coast Range of Mendocino County, and is thus far known only from the Cahto Peak area and the vicinity of Laytonville, just to the east of Cahto Peak. It undoubtedly has a much wider distribution than our few records presently indicate, but much of the territory in which it may occur is either roadless or inaccessible because of private ownership.

ELEVATION RANGE: From 4,000 to 4200' elevation, as presently known.

HABITAT AND PLANT
COMMUNITIES:

PHENOLOGY: The types were taken in early July 1993, with reared material (from eggs) emerging late in April the following year. The subspecies probably flies primarily in June, a 1993 was a very wet year with a prolonged cool spring in northern California, causing late emergences and delayed flight periods for summer-flying species.

FOODPLANTS: None documented in the wild

103. *Speyeria hesperis* (W. H. Edwards)

SPECIES SYNOPSIS: The highly diverse western North American species, *Speyeria hesperis* (W. H. Edwards, 1864), with 19 recognized subspecies, was formally given full species status by Scott, Kondla, and Spomer (1998), who summarized the evidence separating it from *Speyeria atlantis* (W. H. Edwards, 1862), a predominantly eastern U.S. and Canadian species that is found as the nominotypical subspecies across this vast area and then three subspecies in the Rocky Mountains. These taxa had been merged under the *atlantis* species name by dos Passos and Grey (1947), who also aggregated numerous other formerly regarded "species" as subspecies of the eastern *atlantis*. Observations of sympatric populations of the two species in South Dakota, Wyoming, Colorado, and New Mexico, as well as the northern Rockies, as well as consistent phenotypic differences, led to this taxonomic decision (previously suggested by a number of authors, but not formally proposed until 1998).

Within California, we have no *S. atlantis* populations as presently recognized, and the three *S. hesperis* subspecies represent a closely related unit. *S. a. irene* (Boisduval), is found in the northern Sierra and is medium in both size and coloration, with dull reddish-brown ventral hindwings and unsilvered spots. *S. a. cottlei* (J. A. Comstock), at times erroneously synonymized under *irene* or *dodgei* by previous authors (see discussion in Emmel et al., 1998h: pp. 151-152), is found in northeastern California from the Klamath Mountains to the Warner Mountains, and is larger and the darkest of the three California subspecies, with very black forewing markings. *S. a. hanseni* occurs in the North Coast Range, and is the lightest and smallest in size of the California races. All the subspecies prefer wet meadows surrounded by coniferous forests.

ADULT BEHAVIOR: *Hesperis* will often remain for long periods within wet meadow habitats to nectar on available thistles or tall yellow blooming composites. Occasionally, they venture out into drier areas to the Pussypaw nectar source so sought by a wide variety of insect life in this habitat. Adults of *S. hesperis hansenii* appear to remain in the vicinity of the breeding habitat, often flying with *hydaspe* which it closely matches in facies, and several other *Speyeria* species.

LIFE HISTORY: The eggs are pale greenish-yellow, turning tan with maturation. They are laid singly and at random near the *Viola* foodplants. In California, we have descriptions of the mature larva and pupae from subspecies *cottlei* only. The mature larva is the darkest in color of all California *Speyeria*. The entire ground color is a dull black with a few scattered dull tan speckles on each segment and a dull faint tan blotch laterally, just below the spiracle on each of the abdominal segments only. The prominent branching spines are entirely dull black in color. The head is entirely dull black. The pupa is the usual *Speyeria* shape, and is one of the more lightly marked pupae in the genus. The wingcases are a dull tan, marked with fine blackish striations over their surfaces. The abdominal segments are more brownish with black spiracles and darker brown intersegmental junctions. The cremaster area, the very top of the thorax, and the shoulders of the wing covers are blackish-brown.

CHROMOSOME NUMBER: Unknown in California material.

SIMILAR SPECIES: In the North Coastal Range, *Speyeria hydaspe tehama* flies in company with *S. hesperis hansenii*. The lighter males of *tehama* resemble the *hansenii* males and females very closely in underside coloration, but the underside of the females of *tehama* is quite distinctive, with reddish flush to the forewings and a purplish overcasting on the hindwings ventrally. A second *hesperis* subspecies, *dodgei*, might be in the Warner Mountains with *Speyeria hydaspe cottlei*, but may be readily distinguished by the larger cream spots on *dodgei* on the underside of the hindwing. The third subspecies of *S. hesperis*, *irene*, in the northern Sierra Nevada range is not sympatric with any species that closely resembles it.

a. *S. h. irene* (Boisduval)

DIAGNOSIS: This is a subspecies found in the northern Sierra Nevada, and it is characterized by its medium size, its dull reddish-brown ventral scaling on the hindwing, the absence of any silvering in the spots, and a medium-orange flush on the lower half of the forewing on the ventral surface.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. Belgique*, 12: 60 (1869).

TYPE LOCALITY: Massack, Plumas County, California, designated by dos Passos and Grey, *American Museum Novitates*, (1370): 20 (1947). Lectotype in U. S. National Museum, designated by dos Passos and Grey (1947). Type locality re-designated as Gold Lake, Sierra County, California, by Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies* (1998h).

DISTRIBUTION: *Irene* is a butterfly of the high Sierra Nevada. Its distribution extends from the juncture of the Cascade Range and the Sierras on the north, such as at Bucks Lake in Plumas County and Gold Lake in Plumas-Sierra counties, south along the upper Sierran reaches to the Yosemite National Park region. It should be noted that the originally designated (dos Passos and Grey, 1947) type locality of Massack is along the floor of the Feather River drainage below the elevation for *hesperis atlantis* probably never even strayed there. Thus to reach *atlantis*, one *hesperis*

either go north or south of Massack into the higher mountains. To the north, one will not find true *irene*. Blending starts in this area with the Basin Range type segregate, which is darker. To the south, one gets into the high country where true *irene* is found, at least in the Gold Lake area adjacent to the east. In considering all the ramifications of re-designating Gold Lake, Sierra County, as the type locality, Emmel *et al.* (1998h) noted that it is an adjacent area, long available to biologists such as Lorquin (who supplied the *irene* types to Boisduval) from both the Yuba and Feather River routes, and is about the most northerly location known at present for *irene*.

ELEVATION RANGE: Rarely found as low as 5,500', *irene* is most common between 6,000' and 7,500', with the highest record being at 8,100'.

HABITAT AND PLANT COMMUNITIES: This butterfly is taken in the upper Transition and Canadian life zones in the Montane Coniferous Forest community, predominantly in Red Fir forests. In the meadows, often dotted with False Hellebore and ringed by Yellow Pines, White Fir, and Red Firs, are found the host plants, and hence this butterfly. Along these meadows, tall composites bloom, and in gravelly glades, *Monardella* grows in profusion, providing nectar at adult flight time.

PHENOLOGY: Adult flight time for *irene* is often quite controlled by climatic conditions at the high elevations of any given year. Thus records show a very broad flight period from mid-June until the last of September, but mostly mid-July through all of August.

FOODPLANTS: None documented, but *Viola purpurea* Kell. is suspected on the basis of adult association with this plant.

b. *S. h. cottlei* (J. A. Comstock)

DIAGNOSIS: This subspecies occurs across the northern end of the state, from the Warner Mountains west to the Klamath Mountains Assemblage. It is the darkest of the three races in our state. Characteristically, the black markings on the upperside of the males and females are slightly more pronounced, and there is a greater expansion of the basal suffusion, giving the specimens a darker appearance. On the underside, the hindwing cream-colored spots are enlarged and often bordered by black, and the discal area expands into this marginal tan area with a purplish scaling. On the forewing, the orange flush extends nearly to the apical region, and the median band of black spots is greatly expanded, forming a very dark irregular marking across the wing. This is a large subspecies in size.

ORIGINAL DESCRIPTION: Comstock, J. A., *Bulletin Southern California Academy of Sciences*, 24: 62-68 (1925).

TYPE LOCALITY: Vicinity of Alturas, Modoc County, California. Holotype illustrated in color in Comstock (1927), *Butterflies of California*, but location is unknown today.

DISTRIBUTION: *Speyeria hesperis cottlei* occurs in northern California in the Warner Mountains of Modoc County, and again south of the Oregon border along the higher Cascade Range, through the Goose Neck District of the Klamath National Forest and Mt. Hebron area to Mt. Shasta. It extends eastward from Mt. Shasta through higher elevations to the Medicine Lake area of eastern Siskiyou County and spreads widely through the lower coniferous forests south and east of Mt. Shasta. It then occurs in scattered Great Basin fringe populations as far south as far as the more arid parts of central and east central Plumas County. West of Mt. Shasta, *cottlei*

penetrates into the northern Trinity Mountains and Trinity Alps, westward through the Scott Mountains into the eastern Salmon Mountains and north into the Marble Mountains. *Cottlei* has been also taken in the western Siskiyou Mountains of southern Oregon within miles of California. While some colonies within this distribution are as dark as typical *S. h. dodgei* which was described by Gunder (1931) from the type locality of Diamond Lake in Douglas County, Oregon. In the Plumas County area, blending takes place with *irene* north of the Gold Lake area.

- ELEVATION RANGE: Except for the area south and east of Mount Shasta where *cottlei* is found as low as 3,300', *cottlei* is usually found from 6,000' to 8,000' but has been taken above 9,000'.
- HABITAT AND PLANT COMMUNITIES: Everywhere that *cottlei* is found in California, there is one unique feature of its upland habitat to be expected. Although found adjacent to or within rather wet meadows or seeps marked by an abundance of Hellibore, the habitat is always at or near the contact of Coniferous False Forest with Sagebrush Scrub. The plant community that predominates may be Red Fir, Limber Pine, Lodge Pole or even Closed Cone Pine. The sagebrush can be *Artemisia* or *Chrysothamnus*, or a mixture. Throughout much of this distribution, sunflowers grow within the Sagebrush Scrub and serve as the preferred nectar source. In the Warner Mountains and places along the Great Basin fringe, Quaking Aspen usually mark the meadow locations, whereas in the Basin fringe valleys such as the Sierra, Genessee and Harvey Valleys of Plumas and Lassen counties, *cottlei* depends on tall yellow flowering composites that prolifically grow within the meadows. The host violet is not found within the wet meadows but around the perimeters; it is more frequent in the drier, more seasonal meadows of the Basin fringe.
- PHENOLOGY: *Cottlei* flies from early July to late August throughout much of its distribution. In the lower elevations and Great Basin fringe, it flies in late June. At highest elevations, it has been recorded in early September.
- FOODPLANTS: As with the other California *hesperis* subspecies, *Viola pupurea* is the suspected host by adult association.

c. *S. h. hanseni* Emmel, Emmel, and Mattoon

- DIAGNOSIS: This subspecies occurs in the North Coast Range, and is the lightest and smallest in size of the three *S. hesperis* subspecies in California. On the underside, the most notable feature is the yellowish cast across both the forewings and the hindwings, giving the butterfly a very light appearance. The cream-colored spots present in other subspecies are yellowish-tan, and the forewing is very lightly marked with orange on the lower portion of the forewing leaving the remaining forewing ground color tannish. This coloration makes *hanseni* extremely difficult to distinguish from the subspecies of *S. hydaspe* with which it flies through much of its distribution. This subspecies is reminiscent of *S. hesperis irene* in adult facies and may represent parallel evolution with its Sierra Nevada counterpart, which occurs at similar elevations and latitudes.
- ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, p. 152 (1998h).
- TYPE LOCALITY: Anthony Peak on Covelo Road, Tehama County, California.

- DISTRIBUTION:** *Hanseni* has a distribution confined to the North Coast Range mountains, from central Glenn County in the general vicinity of Alder Springs north in scattered populations to Highway 299 in the higher mountains south of Berry Summit in Humboldt County.
- ELEVATION RANGE:** From 5,000' to 7,863', but mostly above 6,000'.
- HABITAT AND PLANT COMMUNITIES:** This subspecies is only found along the higher elevations of the Coast Range, usually where the upper extent of Douglas Fir Yellow Pine and Northern Oak Woodland plant communities come in and penetrate into Red and White Fir forests. Within this area, *hanseni* is confined to small wet meadows, usually formed by springs and seeps. The meadows are usually along gravelly ridge crests in open glade areas adjacent to coniferous forest stands, but often not within them. These meadows are characteristically marked by willow and skunk cabbage (False Hellbore), and are usually adjacent to dense ground cover of blooming Pussypaw which grows on the open gravelly ridges in the clearings between the forest elements. At its lower extent of distribution, *hanseni* will breed in wet meadows along ravines and draws that are generated from the seeps and springs above, and these are usually within dense coniferous forests.
- PHENOLOGY:** *Hanseni* flies from early July through mid-August.
- FOODPLANTS:** Unconfirmed, but *Viola purpurea* Kell. is suspected by adult association.

104. *Speyeria egleis* (Behr)

- ADULT BEHAVIOR:** The males of *egleis* are strong hilltoppers, and frequently the presence of the species in a given locality can be determined by collecting on the nearest mountain summit where males will be prone to concentrate. Both sexes are observed flying over open rocky to gravelly slopes, and they are also avid flower visitors, often visiting *Monardella* species. Egg-laying activity of females takes place soon after mating without evidence of any kind of summer reproductive diapause.
- LIFE HISTORY:** The yellow egg is vertically ribbed and stands slightly higher than its width. The mature larva is grey-brown in ground color, being heavily speckled and striped. There are dorsal and sub-dorsal black lines which are edged with dirty white. The branching spines are a dull whitish-yellow color. The pupa is a dark brown and speckled with darker coloration (Comstock, 1927b, p. 93). This material was described from the northern Sierran *egleis* populations.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** There are basically two areas where sympatric species occur with *egleis* that make identification potentially difficult. In the Sierra Nevada, where it is sympatric with *S. mormonia*, the two species very closely resemble each other. *S. mormonia* can be distinguished in the male sex from *egleis* by the sharp, crisp, finely marked veins of the dorsal surface of the forewings. In *egleis*, these tend to have black overscaling that extends slightly out onto the wing membrane next to the vein, most extensively so in the central portion of the vein, so as to give the wings a tapered or slightly swollen appearance. Females are more difficult to separate, probably more so than in any other parallel situation involving a *mormonia* subspecies. Normally, *mormonia* has a row of more whitish or light colored spots seen on the dorsal surface of the forewings in the area formed where the first submarginal band of somewhat triangularly shaped spots touches along its length

the double marginal line. Unfortunately, in the nominate *mormonia* subspecies, the background color that produces these spots is often only slightly than the ground color of the rest of the wing, making it necessary for the inexperienced lepidopterists to collect in series of individuals and learn to see the difference by experience. However, observing the elevation, the species confinement to wet meadows, the size and the county where the butterfly is collected, will all help in distinguishing the two, keeping in mind that *egleis* is a normal inhabitant of rocky hillsides or tailess slopes. It will sometimes wander into the wetter meadows that *mormonia* prefers, but seldom except at the edge of a meadow will *mormonia* fly with *egleis*.

The second area where two species may be confused is in the Siskiyou Mountains, where *S. e. mattooni* flies with *S. atlantis dodgei*. Both species have extremely dark subspecies here. These two subspecies are extraordinarily similar in this area, however, in *dodgei* the medial group of black spots on the ventral surface of the forewing form a broader, more continuous band than in *egleis mattooni*. Second, the spots on *dodgei* are larger and more uniformly cream-colored than those in *mattooni*, which are smaller and usually at least partly silvered, at least near the margins of the hindwings and forewing apices.

GEOGRAPHIC AND SEASONAL VARIATION:

Because this is a univoltine species, there is no seasonal variation. The geographic variation in this species is quite remarkable over its range across the Great Basin states and California. Some subspecies, such as *utahensis*, are extraordinarily variable in underside coloration, thus further characters, such as life history characteristics and perhaps biochemical characters, may shed further light on evolution in this fascinating species complex.

GENERAL REMARKS:

The most recent overall systematic revision of the genus *Speyeria* (dos Passos and Grey, 1947) treated the *Speyeria adiate* complex of three subspecies as simply subspecies of *Speyeria egleis* (Behr). The *adiaste* complex was separated from *egleis* by Emmel and Emmel (1973), followed by Howe (1975), because of basic differences in biology, their complete allopatry in distribution, and other factors. The recent studies by Sims, Brittnacher, and Ayala (1979) show additional evidence of the separation between these groups, including a relatively low degree of genetic similarity in sixteen genetic loci-controlling enzymes. They also record the chromosome number ($N = 29$) of both *adiaste* and *egleis*, which is similar to the majority of the other *Speyeria* species, and does not provide an adequate index of relationship. In fact, Sims, et al (1979) suggests that allozyme characters are better differentiated than chromosome number or immature stage morphology for these two species.

We should also note here that rearing studies would be helpful in clarifying a number of the problems in understanding species' limits in the North American *Speyeria*. Rearing techniques for species of *Speyeria* have been developed by several workers, notably Mattoon, Davis, and Spencer (1971). These authors have used the methods described in that paper to rear more than 4,000 specimens including all of the Nearctic species.

SUBSPECIES: Within California there are six subspecies of this small and highly variable Fritillary.

a. *S. e. egleis* (Behr)

DIAGNOSIS: The adults of this subspecies are rather small, larger than *mormonia* but smaller than *callippe*, *coronis*, or *zerene* with which *egleis* may be sympatric. The upper

side is orangish-brown in both sexes. Veins of the forewing of subspecies *egleis* are margined by black in somewhat of a tapered fashion in males, and can be separated from sympatric *mormonia* males which have fine black veins. The hindwing is usually relatively lightly marked by black in the males and some of the females. On the underside of the wing, the ground color of the forewing is a light orange. The ventral surface of the hindwing has a softly diffuse brown discal area with lightly silvered spots. The discal area brown scaling is not at all concolorless; there are wider areas throughout.

- ORIGINAL DESCRIPTION: Behr, *Proceedings California Academy Natural Sciences*, 2: 174 (1862).
- TYPE LOCALITY: Gold Lake, Sierra County, California, designated by dos Passos and Grey, American Museum Novitates, (1370): 17 (1949). Lectotype in U. S. National Museum, designated by dos Passos and Grey (1947).
- DISTRIBUTION: The nomotypical subspecies of *egleis* is widely distributed in the higher elevations of the Sierra Nevada from approximately the southern boundary of Tulare County northward to the Gold Lake region of Sierra County. North of here we begin to see intermediate populations between the subspecies *egleis* and the subspecies *oweni* of the Mount Shasta region.
- ELEVATION RANGE: From 6,000' to over 11,000' and widely distributed within this range. Some lower populations down to 3,500' at the extreme northern end of distribution. There is one odd record from a 2,200' location.
- HABITAT AND PLANT COMMUNITIES: This is typically a butterfly of open slopes and rocky ridges, or open gravelly slopes or ridges, within the Montane Coniferous Forest community and Sub-Alpine Forest communities. The host violet occurs this open environment. Oviposition on the rocky substrate has been observed at Mt. Ingalls in Plumas County (by Mattoon), and nearly mature post-diapause larvae have been found (Michael Singer).
- PHENOLOGY: [S. O. MATTOON, PLEASE FILL IN.]
- FOODPLANTS: The species is usually associated with *Viola purpurea* Kell. in the usual habitats where it flies. The above-observed oviposition was near *V. purpurea*, the only violet present.

b. *S. e. tehachapina* (J. A. Comstock)

- DIAGNOSIS: This subspecies occurs at the southern end of the Sierra Nevada in the Tehachapi Mountains, and is characterized by a paler orange upperside than in the Sierran *egleis*. They are also less heavily marked with black and have less basal suffusion dorsally. On the ventral surface they are unsilvered except for the outer row of spots which may be silvered on some females. This has long been considered one of the rarest butterflies in North America. Emmel and Emmel (1963a, 1973) give details on the butterfly's ecology and distribution.
- ORIGINAL DESCRIPTION: J. A. Comstock, *Southwest Science Bulletin*: 6 (1920).
- TYPE LOCALITY: Tehachapi Mountains, Kern County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: The Tehachapi Fritillary occurs on the higher peaks of the Tehachapi Mountains, including the ridge running east of the 7,986' northern peak (called Mount Tehachapi) of this range. It also occurs on the summits of the Piute Mountains.

It has not been found on the higher peaks of the Greenhorn Mountains, nor does it occur on the peaks of the extreme southern Sierra Nevada such as Owen's Peak, 8,475', where typical *egleis* is now known to occur.

- ELEVATION RANGE: From 7,000 to 8,300' (at the top of Piute Peak).
- HABITAT AND PLANT COMMUNITIES: In grassy slopes and clearings in the Jeffery Pine region of the Montane Coniferous forest plant community. Males hilltop in erratic, rapid flight along mountain ridges while the females fly about in the grassy slopes in clearings along slopes of such high ridges.
- PHENOLOGY: This lightly marked, almost unsilvered race was long known only from the four type specimens collected in mid-July 1918, in the Tehachapi Mountains. Today we know that the flight period extends from early July to very early August, with a peak in mid-July.
- FOODPLANTS: The host for the larvae is strongly suspected to be *Viola purpurea* Kell. ssp. *xerophyta* Baker & Clausen. This foodplant is locally abundant on the peaks in the Tehachapi Mountains where tehachapina females fly.

c. *S. e. near utahensis* (Skinner)

- DIAGNOSIS: In the Warner Mountains of northeastern California occurs this subspecies complex, with highly variable adults coming closest in appearance to the subspecies *utahensis* from far to the east. The upperside of both sexes is slightly lighter in ground color with more of a dark basal suffusion near the body. On the underside, the disc is more defined than in typical *egleis* on the hindwing, and is a deeper umber brown color with brightly silvered spots.
- ORIGINAL DESCRIPTION: Skinner, *Entomological News*, 30: 216 (1919).
- TYPE LOCALITY: City Creek Canyon, Salt Lake City, Salt Lake County, Utah. Holotype in Carnegie Museum.
- DISTRIBUTION: This subspecies is found only in the Warner Mountains of Modoc and Lassen counties in northeastern California.
- ELEVATION RANGE: This subspecies can be found at elevations as low as 5,500' in sheltered watercourse canyons on the more mesic western slopes of the Warner Mountains. But it normally is not found much below 6,000', and above that elevation it is widely distributed at all elevations up to the crest of the range. Our highest record is 8,762'.
- HABITAT AND PLANT COMMUNITIES: *Utahensis* is found in the Northern Juniper Woodland and Sagebrush Scrub areas that widely invade the Warner Mountains to their crest. The breeding habitat is usually gravelly hillsides or flats at the more mesic edge of coniferous forest stands. Forested areas are more dominant on the western slopes of the range while sagebrush scrub is more dominant on the eastern escarpment. Sagebrush-clad valleys, very often dotted with wet meadows, finger through forested areas throughout the heart of the range, and an admixture of scrub and stands of timber, often including Limber Pine, characterizes the crest of the range. *Egleis* breeds more prolifically along the crest and eastern slopes. Suitable rocky slope-gravelly flat areas are often identified by an increased abundance of sunflowers in the sage scrub, and an altitude sufficient to harbor Quaking Aspen along the wet meadows. *Egleis*

does not breed in the drier sagebrush scrub areas on the lower slopes of the range.

PHENOLOGY: *Utahensis* can be sought throughout July and into late August. It has been taken on lower slopes in late June. The year-to-year variation in weather conditions is great in the Warners' thus, the annual flight period can vary considerably.

FOODPLANTS: *Viola purpurea* Kell. is the suspected host, from adult association.

d. *S. e. mattooni* Emmel and Emmel

DIAGNOSIS: This subspecies resides in the Siskiyou Mountains and is characterized by a much darker dorsal and ventral appearance. On the upperside the basal area is strongly marked over the inner third of the wing by black scaling, and the outer black markings are heavier than in the other subspecies. On the underside, the discal scaling extends essentially to the wing margin on the hindwing, and the inner discal area is strongly umber-brown with cream to lightly silvered spots. On the forewing, ventrally, there is a reddish-orange flush on the lower half, and in the distal portion a light tannish area that is quite yellowish in overall appearance. Additionally, the marginal row of spots is silvered at the tip of the forewing and silvered along the edge of the hindwing, normally.

ORIGINAL DESCRIPTION: Emmel and Emmel, *LACHMNH Contributions in Science*, : (1989).

TYPE LOCALITY: Dry Lake Mountain, along Forest Road 40S01, Siskiyou Mountains, Siskiyou County, California.

DISTRIBUTION: This dark subspecies has been found only in the Siskiyou Mountains to date. In the western portion of the Siskiyou Mountains, which projects southward into Del Norte County, blending with the Coast Range segregate *Yolla bolli* is apparent. Northeastward, *mattooni* extends along the Siskiyous to Mt. Ashland, Jackson County, Oregon.

ELEVATION RANGE: This subspecies is limited to upper areas of the mountains, from 5,000' to 7,500', but mostly 6,000' and up.

HABITAT AND PLANT COMMUNITIES: This *egleis* is a denizen of the Siskiyou Mountain uplands, breeding along the open gravelly ridges that are characterized by a profusion of blooming bush and carpet-type lupine, *Monardella*, *Eriogonum*, and yellow composites that create miles of open natural flower garden at adult flight time. Such areas along the crest of the range are above or within the Red Fir Forest plant community, with Yellow Pine and Douglas Fir forest elements bordering or penetrating from below. The preferred nectar source is *Monardella*.

PHENOLOGY: This insect has been taken from early July until early September. In most seasons, the main flight is from late July on through the month of August. In blendzone areas to the southwest, populations tend to start flying earlier.

FOODPLANTS: Unknown.

e. *S. e. oweni* (W. H. Edwards)

DIAGNOSIS: This subspecies occurs in the Mount Shasta region and the Klamath Mountains Assemblage outside of the Siskiyou Mountains. It is the smallest of all of the

egleis subspecies in California, and is characterized by a deeper orange ground color, as well as a darkly marked interior half of the wings dorsally. There is a marked enhancement of the dark patterned markings on both the forewing and hindwing dorsally. On the underside, the hindwing spots are smaller and more intensely silvered than either typical *egleis* to the southeast in the Sierras or *utahensis* in the Warners. The discal surface of the hindwing ventrally is a flat, dark brown with a narrow light tan marginal area.

SOM Edit 12/5/88

DIAGNOSIS: The type series of 87 males and 6 females of *oweni* were taken at the 7,500' elevation on Mt. Shasta by Professor Edward T. Owen and the description published in the Canadian Entomologist in 1892. Today, specimens from the 7,500' elevation on the southern slopes of the mountain do not quite match the original description, having a more uniform-brown, less-mottled disc than W. H. Edwards saw in the type series. The type series is at the northern extent of a broad area of blending between nominotypical *egleis* and *oweni* along the Cascade Range south from Mt. Shasta to near Mt. Lassen. Possibly, there has been a slight shift of darker facies southward in the 100-year interval since Professor Owen collected the types. The original description clearly shows it was the more heavily-silvered, darker-brown disc facies with bolder black dorsal markings and basal suffusion that applies to the name *oweni*. This subspecies occurs in the Mt. Shasta region, in the Cascades to the north and east, and into the adjacent western Klamath Mountains Assemblage outside of the Siskiyou Mountains. *Oweni* is characterized by a deeper orange ground color, in addition to the more darkly-marked interior half of the wings dorsally than seen in nominotypical *egleis* or in subspecies *moecki*, which has moderate basal suffusion and medium-orange dorsal surfaces with less bold black markings and vein margining. On the underside, the hindwing spots are smaller and more intensely silvered than either typical *egleis* to the southeast in the Sierras, or *utahensis* in the Warners, but are somewhat intermediate to the smaller heavily-silvered spots of *moecki* to the north. The discal surface of the hindwing ventrally is flat dark-brown, especially proximal to the post-median silver spot row. The brown sometimes extends almost uniformly to the base, but mostly with two or more buff internervule patches showing outwards of the discal cell. Occasional specimens have a gray buff disc in varying amounts. The narrow band is also buff, sometimes with a reddish case and heavily invaded by blackish brown margining or projections from the silver spot rows.

ORIGINAL DESCRIPTION: W. H. Edwards, *Canadian Entomologist*, 24: 105-106 (1892).

TYPE LOCALITY: Mount Shasta, Siskiyou County, California. Lectotype in Carnegie Museum, designated by dos Passos and Grey, *American Museum Novitates*, (1370): 17 (1947).

DISTRIBUTION: This subspecies is found in the mountains of the Mount Shasta region and in the Klamath Mountains Assemblage, outside of the Siskiyou Mountains.

SOM Edit 12/5/88

DISTRIBUTION: This subspecies is found in the mid- to high-elevations of the Southern Cascade Range at Mt. Shasta and the Cascade uplands eastward to the Medicine Lake volcanic system. Westward, *oweni* is found in the adjacent Trinity Mountains along the Shasta-Trinity divide north from Castle Lake to Mt. Eddy, extending west along the China-Eddy divide through the Scott Mountains and south through the higher Trinity Alps. From the extensive blend area between Mt. Lassen and Mt. Shasta with *S. e. egleis*, *oweni* extends along the Cascades north into southern Oregon in southern Jackson and Klamath counties, where from Lake of the Woods

to the south edge of Crater Lake, it encounters an area of blending with subspecies *maeckii*.

- ELEVATION RANGE: 3,900' to 9,000', but mostly near 5,000' and above.
- HABITAT AND PLANT COMMUNITIES: *Oweni*, as with all *egleis*, is adapted to gravelly, sandy, ash or pumice open xeric ridges, slopes or flats within the upper limits of Yellow Pine forest into Lodge Pole Pine or Red Fir forest plant communities. The host violet often grows out on such open habitats which are usually adjacent to forested areas with glades containing the nectar source *Monardella odoratissima* (Coyote Mint).
- PHENOLOGY: In the lowest-elevation flats south and east of Mt. Shasta, the butterfly is consistently a late-June flier. Throughout its higher distribution, *oweni* flies from late June to late August but with some extension into early September at highest localities. There is no reproductive diapause in the adults. Females have been observed ovipositing in gravelly substrate, in concealed areas near the base of the host violet.
- FOODPLANTS: Unknown.

f. *S. e. yolaboli* Emmel and Emmel

- DIAGNOSIS: The name of this subspecies means "high snow-covered peak" in the Wintun Indian language. This is a butterfly of the North Coast Ranges. On the dorsal surface, this subspecies differs from *oweni*, its nearest relative, by a lighter orange ground color and much reduced black markings and suffusion. On the ventral surface, it differs from *oweni* in having a less-defined more uniformly colored discal area of brown and a lot of yellow overscaling on both the forewing and the hindwing. This is especially pronounced in the males, but even some females which lack virtually any orange flush on the forewing but have only a pale yellow ground color. It differs substantially from *mattooni*, a second geographically close subspecies, by its dramatically different underside which is much lighter in general ground color and also bears well-silvered spots. An overall feature of this recently described subspecies *yolaboli* is its notably pointed and elongated forewing shape in contrast to the other *egleis* subspecies.
- ORIGINAL DESCRIPTION: Emmel and Emmel, , : (19).
- TYPE LOCALITY: South Yolla Bolly Mountain, Tehama County, California.
- DISTRIBUTION: This subspecies is found in the North Coast Ranges from the Yolla Bolly Mountains south to Snow Mountain. Northward, the populations representing this subspecies extend along the coastal mountains as far as Highway 99 in the vicinity of Berry Summit (Horse Mountain Ski Area), and northeastward the subspecies penetrates the poorly defined boundary separating the Klamath Assemblage from the North Coast Range. Heretofore, the extent of blending and phenetic penetration of this subspecies in the Klamath Mountains has not been recognized. Northeastward in the Klamath Assemblage, blending occurs with *oweni*, at least in the Marble Mountains, and north into the southern extension of the Siskiyou Mountains (at Little Greyback Mountain), *yolaboli* blends into *mattooni*. It appears that the lowlands between mountain ranges of the north part of the state act somewhat as barriers to movement of *egleis*. Thus, distributions appear to follow the fairly contiguous higher ridgelines. The poorly-explored Salmon

Mountains are most likely a corridor of contact between *oweni* and *yollaboli*, and the North Coast Range serves the same function with the western Siskiyou.

ELEVATION RANGE: 5,000' to 7,863'.

HABITAT AND PLANT COMMUNITIES: This subspecies flies on open gravelly slopes within the Montane Coniferous Forest plant community.

PHENOLOGY: This subspecies flies from late June to mid-August, with July representing the peak of flight.

FOODPLANTS: R. Kelson has found larvae of this subspecies feeding on *Viola* (19).

105. *Speyeria zerene* (Boisduval)

ADULT BEHAVIOR: For the coastal populations, the following behavior has been noted. Males are inclined to patrol open fern-clad grasslands in search of newly emerged females. Both sexes are avid visitors to flowers. In the case of myrtleae, the adults will fly on relatively warm days despite dense coastal fogs, one of the few butterfly species known to have the capability of conducting normal activity under completely sunless and relatively cool conditions. The subspecies myrtleae nectars on low-growing plants in the sand dunes, where adults can be fairly easily overlooked.

LIFE HISTORY: The eggs are cream-colored, and are laid singly near the host plants. The mature larva of *S. zerene zerene* from Plumas County and of *S. z. zerene* from Lake County are virtually identical in markings and will be described together. Below the spiracles, the larva is almost a pure ochre-tan, along with the subspiracular row of spines. Above the spiracles is a dark band and another row of light ochre-tan spines. Dark blotchings occur from the spiracles on each segment up to this dark band. Then there is another band of light ochre-yellow and mixed dark blotches continuing up to a double mid-dorsal line of light tan bands. The two rows of dorsal spines are black in color, and are arranged parallel to the outer margins of the double light dorsal band. The head is mostly black. The pupa of typical zerene has light tan wing cases striated with fine black lines and heavy dark suffusion at the thoracic shoulder area, the head, and across the dorsal surface of each segmental junction on the abdomen. The general area around the cremaster is also blackish. In captive rearing, the pupa was formed on the underside of a Violet leaf.

CHROMOSOME NUMBER:

SIMILAR SPECIES: There are only two pairs of subspecies where confusion with other *Speyeria* may exist. First, in northern California in the area of distribution for *S. z. conchyliatus*, it may be sympatric with *S. hydaspe purpurescens*. The distinguishing features between these two butterflies are given under the latter subspecies account. In the other instance, *S. hydaspe hydaspe* may be confused with subspecies zerene in the southern Sierra Nevada, a situation which is discussed under hydaspe.

GEOGRAPHIC AND SEASONAL VARIATION: As all zerene populations are univoltine, there is no seasonal variation. In terms of geographic variation, the cline in the Sierra Nevada from brownish zerene in the south to reddish-purplish zerene in the north has already been described. In the North Coast Ranges, zerene populations tend to resemble the subspecies conchyliatus, but as one goes

southward into Lake County, they become lighter and approach the phenotype of typical *S. z. zerene*.

GENERAL REMARKS: The usual definition of a subspecies includes a geographically separable group of organisms which are the same general phenotype, but which differ from other similar groups enough to warrant a name. The subspecies are then grouped in a larger unit, the species whose components are still able to exchange genetic information if brought into contact again. In the case of the Warner Mountains area of northern California, Grey and Moeck (1962) have pointed out that a light-colored *zerene* (which was called *cynna* in their paper, a name which is synonymized with *gunderi* in this book) and a dark *zerene* (called typical *zerene* in their paper, but identified as *conchyliatus* in this book). These two radically different subspecies overlap in the Warner Mountains, with considerable numbers of intermediate individuals being collected in the same area as the two typical subspecific forms.

The complexity of Warner Mountains *zerene* populations presents a number of interesting biological research opportunities that are unequalled. The contact between *conchyliatus* and *gunderi* appears strongly influenced by environmental conditions of the given year, primarily in the amount of rainfall or snowpack that the area receives. Possibly, this natural selection impacts on diapausing larvae with the genetic make-up most suited to the existing environmental conditions. In a series of wet years, the subspecies *conchyliatus*, and intermediates leaning toward its facies, tend to dominate, and the north-south blend zone area tends to shift to the drier rain-shadowed eastern escarpment of the Warners, with *conchyliatus* facies dominating through the range. In dry years, this situation is reversed and *gunderi* becomes the dominant subspecies form observed throughout the Warner Mountains (S. O. Mattoon, pers. obs.).

All three of our northern coastal *zerene* subspecies are threatened to one degree or another by Man's activity. *Speyeria zerene myrtleae* formally was found in San Mateo County on the north side of San Francisco Bay. Apparently no populations still exist in that county. In fact, the most southerly *myrtleae* population known to still be in existence is along the sand dune area near Point Reyes in Marin County. The North Beach population on Point Reyes would be normally considered as secure inside the National Seashore. However, at Point Reyes and elsewhere along the coast Man's introduction of Ice Plant (*Mesembryanthum* species) to stabilize disturbed sand has resulted in this plant crowding out and replacing the natural floristic elements of such areas. This could become an important factor in Man's inadvertent altering of the biological niche required by *myrtleae* on Point Reyes and elsewhere. In the case of *S. z. behrensii*, the ever-increasing encroachment on the available coastal habitat by Man is of concern, especially the heavy overgrazing of the known habitats by cattle. Probably all of those populations that are currently on privately owned land in both the cases of *myrtleae* and *behrensii*, have the potential for being lost in the future. Those that are preserved in National Seashore or state-owned land are probably protected, aside from the insidious invasion of non-native plants. The third threatened subspecies, *S. z. hippolyta*, is found in only one population within California on the sand dunes near Fort Dick. This butterfly is listed on the federally Endangered Species list. It is found at this location with another uniquely important butterfly, for which the Fort Dick dunes is the only known California location. This area requires careful consideration for permanent preservation and protection.

This species is one of the most variable and vagile of all the *Speyeria*, and includes a number of interesting subspecies which exhibit remarkable responses and adaptations to differing environments. Egg development and oviposition is

environmentally controlled with adult flight period extending into late summer or fall, the female appearing to estivate through the hotter months to then lay eggs. In the Warner Mountains of Modoc County, two radically different subspecies originating in substantially different environments even overlap geographically (Grey & Moeck, 1962) in a remarkable blending of color forms and habitats. On the coast of California, other subspecies are so well adapted to a cooler, moist environment that one is able to fly in the fog. Within our state we have populations representing eight of the subspecies in this group.

DIAGNOSIS: This is a medium to large *Speyeria* species with moderate development of the black markings on the upperside, and is characterized on the underside by having a brownish to reddish-brown or even purplish-brown ground color to the discal area of the hindwings. The spots are usually only partially silvered, giving an overall drab appearance to the underside. Populations falling under nomotypical *zerene* vary somewhat in a north to south cline along the west slope of the Sierra Nevada with typical *zerene* (based on the probable type locality) being somewhat intermediate in phenotype between those of the more southern Sierra Nevada western slope, which tend to be more dull brown on the underside, and the subspecies *conchylatus* to the north, which tends to have a more purplish or reddish-brown ground color to the underside.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 303 (1852).

TYPE LOCALITY: Yosemite Valley, Mariposa County, California, designated by dos Passos and Grey, *American Museum Novitates*, 1371: 12 (1947). Lectotype in U. S. National Museum, designated by dos Passos and Grey (1947). This restriction was not possible since Yosemite Valley was not discovered until 1851. Lorquin could not have collected the types there before 1856 -- four years after the published description of *zerene*. Masters (*Journal Lepidopterist Society*, 33: 137-138, 1979) corrected this type locality and redesignated it as the vicinity of Agua Fria, Mariposa County, California. However, Masters did not examine the phenotype of the lectotype in relation to the phenotype of the population at this new type locality. Therefore, Emmel, Emmel, and Mattoon (*Journal Research Lepidoptera*, : , 1988) re-restricted the type locality to lower Feather River Canyon, Butte County, California, a locality which is consistent with both the phenotype of the lectotype of *zerene* and with what we know about the areas in which Lorquin (the collector of the type) was known to have collected in at the time.

DISTRIBUTION: This is a subspecies with a split geographical distribution. On the east side of the Great Central Valley, it is an occupant of the western slope of the Sierra Nevada from approximately Butte County southward to Tulare County. On the west side of the Sacramento Valley portion of the Great Valley, a highly disjunct set of populations occupies the north Coast Range mountains from Tehama to Lake counties. This *zerene* segregate may be a case of parallel evolution or represent a remaining separate segment of a once much broader distribution of *zerene* facies. Specimens from the Sierra Nevada from generally Yosemite National Park southward are a close match for the Coast Range segregate. Like in the Sierra Nevada, the Coast Range *zerene* are also clinal from south to gradually blend into *conchylatus* northward.

Sierra Nevada *zerene* range from the foothills into the High Mountains in the north end of its range, but to the south, the lower altitudinal limits of distribution become progressively higher. Coast Range populations are generally mid- to-high elevation, primarily associated with the crest or east-facing slopes of the range. As mentioned above, there is a north-south cline in populations of this subspecies

which range from individuals which tend to have a very dull drab brown underside in the southern portions of its range integrating to a phenotype which is somewhat more reddish-purplish brown on the underside at the north end of its range.

- ELEVATION RANGE: From 2,500' to 8,700', with populations most commonly found from 4,500' to 7,000'.
- HABITAT AND PLANT COMMUNITIES: Throughout its distribution, *S. z. zerene* is primarily a resident of the Yellow Pine, Jeffrey Pine, and Douglas Fir Transition-Zone forests of the Sierra Nevada and Northern Coast Range. This distribution also extends into the higher elevation Red Fir or subalpine forests, especially in the southern portions of its range. This species utilizes the open forest floor and glades, where the larval host violet grows well in the leaf mulch accumulation and often a source of nectar is available, such as *monardella* or Dogbane. These slightly moister breeding localities often are marked by typical plant indicators, such as lupine and fern species.
- PHENOLOGY: Emerging *zerene* males regularly appear in late June. The peak of abundance extends through July and August, with mostly females towards the end of the flight period. In all *Speyeria*, emergence of males precedes females, sometimes by as much as two weeks. Many species hatch with females having fully developed egg masses so that mating takes place and oviposition can follow immediately. In others, such as *S. zerene* and *S. coronis*, this is not necessarily so. Research has shown that environmental triggers may be necessary to stimulate egg development in females which eclose with only fatty tissue in place of eggs in their abdomen (Sims,). In subspecies *zerene*, and to a slightly lesser degree in the closely related subspecies *conchyliatus*, there appears to be more variability from individual to individual as to the onset of egg development, and this is somewhat of a departure from *zerene* subspecies found in the more arid distribution within California that we will discuss. Egg laying mostly takes place late in the flight, and as in all *Speyeria*, eggs which are deposited on old violet plants or substrate nearby soon hatch and the tiny first instar larvae overwinter in a state of diapause, beginning feeding and larval development the following spring.
- FOODPLANTS: The species seems regularly associated with *Viola lobata* Benth., a plant which is found in the Transition Zone forests of the west slope of the Sierra Nevada, and the Coast Range Mountains.

b. *S. z. malcolmi* (J. A. Comstock)

- DIAGNOSIS: In contrast to the western slope distribution of typical *zerene*, this subspecies, *malcolmi*, is found on the eastern slope of the Sierra Nevada. The adults are bright ochre dorsally, and the ventral surface of the forewings of the female is very red basally. The adults may have silvered or unsilvered spots on the hindwing. The discal portion on the ventral hindwing surface is rather pale with considerable ochre-yellow suffusion. The outer ventral hindwing band is bright buff-colored and distinct.
- ORIGINAL DESCRIPTION: J. A. Comstock, *Southwest Science Bulletin*: 4 (1920).
- TYPE LOCALITY: Mammoth, Mono County, California. Holotype in Natural History Museum of Los Angeles County.

- DISTRIBUTION:** This is an east slope Sierra Nevada subspecies of *zerene*, occurring from the area west of Big Pine in extreme northwestern Inyo County northward along the east slope to the eastern Lake Tahoe region. Blending influences with *S. z. conchyliatus* continue on northward at least into southern Plumas County near Portola. It is also found in the adjacent Pine Nut Mountains, and in the Carson Range in Nevada.
- ELEVATION RANGE:** 7,000' to 9,700', but to as low as 5,000' in blendzone populations to the north.
- HABITAT AND PLANT COMMUNITIES:** This subspecies is most typically found in the Jeffrey Pine forests and adjacent Great Basin Sagebrush Scrub plant communities of the east slope of the Sierra Nevada.
- PHENOLOGY:** The first appearance of *malcolmi* males can be seen at lower elevations in late June, but the main flight starts in July. The emergence period appears to be quite protracted. *Malcolmi* will then be on the wing into September by which time males will have virtually disappeared and females will have congregated on the blooming artemisia-clad slopes and flats of the habitat. With an abundance of adult food source available, females are in good condition and egg laying has been observed then. The host *Viola* is found in sandy flats and drains near adjacent coniferous stands, and sometimes under the Sagebrush Scrub, but the violets have mostly gone to seed at this time.
- FOODPLANTS:** This subspecies has been observed ovipositing in the vicinity of *Viola purpurea* Kell. plants near Casa Diablo in Mono County (S. O. Mattoon, pers. obs.).

c. *S. z. gunderi* (J. A. Comstock)

- DIAGNOSIS:** This subspecies is found in the Warner Mountains of Modoc County. It differs from all other *Speyeria* in the ground color of the ventral surface, which is a clear lemon-buff of a blonder shade than any other member of this genus. A few greenish scales occasionally are present in close proximity to the silver spots. The hindwing silver spots on the ventral surface are always lustrous and conspicuous. There is no darkening of the disc on the hindwing, and there is little basal suffusion on the upperside.
- ORIGINAL DESCRIPTION:** J. A. Comstock, *Bulletin Southern California Academy of Sciences*, 24: 67 (1925).
- TYPE LOCALITY:** Modoc County, California. Howe (1975) further defines the type locality as the Davis Creek Ranger Station in the Warner Mountains above Alturas in Modoc County. This definition of the *gunderi* type locality places it at the extreme western edge of the blendzone but where pure *gunderi* can be taken.
- DISTRIBUTION:** Within California this subspecies is essentially found only in the Warner Mountains or sagebrush plants to the south in Lassen County. Outside the state, it ranges across northern Nevada to northwestern Utah northward into southeastern Oregon.
- ELEVATION RANGE:** From as low as 3,000' upwards of 8,200', but predominantly 4,500' to 8,000'.
- HABITAT AND PLANT COMMUNITIES:** The *gunderi* subspecies is the race most adapted to a dry, harsh, xerophytic environment. It is an entity of the Great Basin, penetrating California only along the eastern edge of the Modoc Plateau. The high degree of stability in the facies of *gunderi* is probably in part the result of extensive genetic exchange that takes place as a result of this butterfly's strong tendency to disperse, seeking suitable habitat in an

environment that gets its summer supplemental rain in the form of scattered thunderstorms enhancing here and there the long-term quality of a given habitat location. There is need here for field research to verify speculations about female aestivation, dispersal and its timing. *Gunderi* breeds in locations throughout the Artemisia Scrub and Artemisia Juniper Woodland where seeps, springs, watered draws or flats provide for the host violet often growing under the sagebrush scrub. Thus, actual breeding more often is associated with the upland areas of the Basin Ranges where proper habitat is more regularly found. In dry years, these slightly moister areas appear to provide a better quality to the sagebrush bloom, which may be an attracting force to bring in wandering females. Egg development within these females, as in *malcolmi*, does not take place until proper length of photoperiod occurs in later summer or fall (Sims, 19). Eggs that are larger and hatch late in the flight period offer the tiny diapausing first-instar larvae a better chance of protection against desiccation, which all first-instar speyeria larvae are highly vulnerable to.

PHENOLOGY: As in most *zerene* subspecies, low-elevation populations produce a few males by late June while the bulk of the flight occurs in July, extending into late September. At that time, males are not to be found, and the many intact blond females have lost their luster, appearing sun-faded but otherwise in fresh condition. As in *malcolmi*, these females show preference to blooming sagebrush habitat where they congregate. As the summer wanes, careful observation will detect singleton females in unidirectional flight, a behavior which appears to offer a dispersal mechanism of *gunderi* seeking areas of suitable habitat far afield.

FOODPLANTS: Unknown.

d. *S. z. conchyliatus* (J. A. Comstock)

DIAGNOSIS: This subspecies is found across the northern tier of California counties, from the Warner Mountains west to the Klamath Mountains Assemblage and north into Oregon. The adults are deeper orange above than in nominate *zerene*. The black maculation on the dorsal surface is somewhat heavier, with heavy basal dark suffusion. On the ventral surface, the spots are usually silvered and the disc varies from chestnut brown to dark maroon in color. In the Warner Mountains, and southward into the Madeline Plains of Lassen County, this subspecies meets *S. z. gunderi* in a narrow zone of blending with a north-south axis extending into Oregon. The reds of *conchyliatus* meet and combine with the pallid blonds of *gunderi* to produce a magnificent array of intermediate color forms.

ORIGINAL DESCRIPTION: J. A. Comstock, *Bulletin Southern California Academy of Sciences*, 24: 63 (1925).

TYPE LOCALITY: Mount Shasta, Siskiyou County, California. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This subspecies is found through the Mount Shasta region. It extends southward along the Cascade Range to gradually blend into subspecies *zerene* in the lower to mid-elevations, while more completely maintaining its integrity at the higher elevations and along the Great Basin fringe as far south as the Mount Lassen region. Along a narrow zone of the Sierra Nevada eastern escarpment, from Plumas County south to the Lake Tahoe region, blending influences with *malcolmi* can sometimes be noticed, but the eastern fringe south of Mt. Lassen is otherwise an area of *conchyliatus-zerene* intermediacy.

Eastward from the Cascades, especially along the highlands of the Pit River drainage, *conchyliatus* spreads through the Modoc Plateau and blends with *gunderi* in the Warner Mountains. In the Cascades north of Mt. Shasta and throughout the Klamath Assemblage of mountains, *conchyliatus* is common. It extends north into Oregon and also blends with *gloriosa* in the Siskiyou Mountains in the northwest corner of California. South of the Klamath Mountains, an area of gradual blending occurs in the Northern Coast Range. From Highway 36 south to the Yolla Bolly Region is the principal blendzone with the Coast Range *zerene* segregate. From there, it is distributed southward to the highlands south of Clear Lake. Hints of limited contact with *behrensii* and the south North Coastal Prairie Grassland segregates are poorly documented or not understood to date.

ELEVATION RANGE: From rarely as low as 1,300' to upwards of 7,800', but predominantly 3,000' to 6,500'.

HABITAT AND PLANT COMMUNITIES: *Conchyliatus* is essentially a resident of coniferous forests, primarily the Douglas Fir and Ponderosa or Jeffrey Pine belts as seen in subspecies *zerene*. It also establishes itself altitudinally into Red Fir and Subalpine Forests, but appears to be adapted to occupy a slightly drier habitat extending through the Mixed Evergreen Forests of the Klamath Assemblage of mountains and into the Modoc Plateau on extensions of such coniferous forests along the ridges and mountains that invade the Sagebrush Scrub. It is here in the mix of the two distinctive plant associations that blending with *gunderi* occurs. In its forest habitat, *conchyliatus* selects suitable grassy glades with abundant leaf litter, the habitat also utilized by the larval host violet.

PHENOLOGY: *Conchyliatus* begins emerging in mid- to late-June and can become quite common by early July. The emergence is progressively later at higher elevations and the numbers of females that are seen at nectar, extending even into early September, appears proportionately higher in the drier, more xerophytic portion of its distribution. Otherwise, the phenology of *conchyliatus* is much as was reported for subspecies *zerene* and *malcomi*.

FOODPLANTS: Unknown. However, *Viola lobata* Benth. is often found in areas where *conchyliatus* is abundant.

e. *S. z. gloriosa* Moeck

DIAGNOSIS: This beautiful subspecies occurs in the Coast Ranges and Siskiyou Mountains of extreme northwestern California in Del Norte County, northward into Oregon. It is characterized by large size, heavy maculation on the upperside and underside of the forewings, and on the ventral surface it has a more reddish-brown disc than *conchyliatus*. The contrasting buff-colored outer submarginal band has little suffusion in it.

ORIGINAL DESCRIPTION: Moeck, *Geographic Variability in Speyeria*: 21-24 (1957).

TYPE LOCALITY: Illinois River Valley, Josephine County, Oregon. Holotype in American Museum of Natural History.

DISTRIBUTION: This subspecies is found in the extreme northwestern corner of the state, in the lower mountains of Del Norte County, as well as in adjacent extreme southwestern Oregon in Josephine County. There is a subtle cline, from richly marked, heavily silvered *gloriosa* of the type locality (Illinois River Valley)

populations southwestward through southern Curry County of Oregon into the extreme coastal mountains of northern Del Norte County, California. Although Del Norte County specimens average slightly less silvered and richly hued, all within this distribution are referable to the name *gloriosa*. From here, the situation becomes more complex. Hitherto-unstudied out-croppings of identical habitat extend south-southeastward in a narrow zone in places along the coastal mountains to at least Highway 299 in Humboldt County. More field work is needed, but at least the Humboldt County habitat has a population almost identical to Del Norte County *gloriosa* in facies, habits, habitat and host plant. Thus, the distribution of *gloriosa* appears to also extend southward along the fog break zone. For the first time, this is providing insight into the relationship of the fern-clad Coastal populations, which are distributed eastward to the inland fog break zone from Highway 299 to Highway 36, and westward to the coastal mountains above Humboldt Bay, differ in significant ways and do not appear to be included in the Coastal Strand *myrtilae-behrensii-hippolyta* subspecies group. This Coastal Prairie Grassland segregate is very close to the inland and Del Norte County populations of *gloriosa*, especially in females. Blending is taking place between the serpentine and grassland populations in the area of Berry Summit, and it appears likely the Coastal Prairie Grassland segregate which relies on bordering Redwood, Mixed Evergreen Forest, and a differing host violet as elements of its habitat, has probably evolved sufficiently to deserve subspecific ranking in its own right.

- ELEVATION RANGE: In the damp northwestern corner of California and adjacent Oregon, 1,400' to 2,500'. Along the crest of the Coast Range mountains south, 4,500' to 5,500'. Coastal prairie grassland populations, 600' to 4,500'.
- HABITAT AND PLANT COMMUNITIES: *Gloriosa* is primarily associated with rich serpentine soils characterized by the stunted pine barrens of extreme northwestern California and southwestern Oregon. Openness of this habitat provides for a grassy rubbierock understory with occasional wet meadows or seeps with pitcher plant (*Darlingtonia*). Areas where serpentine is less dominant may show intrusion of redwoods, or Mixed Evergreen Forest elements, and everywhere, Bush Chinquapin is dominant. Douglas Fir forests may invade the habitat inland. The entire *gloriosa* habitat is within the area most subject to storms striking the north part of the state, often being raked by those passing to the north. Similar duplications of this habitat and its plant association are to be found in serpentine formations along a narrow band in the Coast Range mountains, from 4,000' to 5,500' southward to at least Highway 299 in central Humboldt County. This band is in the coastal fog break zone, along the flank and crest of the range where the appropriate environmental niche is produced for the fritillary and associated plants.
- PHENOLOGY: *Gloriosa* males are flying some years at the low elevations by the last of June. They become abundant in July, but rarely will females be encountered until late July and August. By late August and early September, primarily females are found visiting the nectar sources in their habitat. Females have developed eggs by then and oviposit in the serpentine rubble rock to which the host violet is restricted.
- FOODPLANTS: The butterfly is associated with *Viola cuneata* Wats., a species typically found on the serpentine slopes in all areas where *gloriosa* flies.

f. *S. z. hippolyta* (W. H. Edwards)

- DIAGNOSIS:** This subspecies, found primarily on the coast side of the Oregon Coast Ranges, is a small, bright orange Fritillary with heavy black medial spots above. These spots usually join in forming an irregularly bent bar or band. Deep basal suffusion occurs on both wings. While the ground color in females is pale, the intensity of darkening of the medial spots gives them an overall dark appearance. On the ventral surface, the disc is deep maroon or rusty red with a distinct outer band, and the spots are bright silver.
- ORIGINAL DESCRIPTION:** W. H. Edwards, *Canadian Entomologist*, 11: 81-82 (1879).
- TYPE LOCALITY:** Oceanside, Tillamook County, Oregon, designated by dos Passos and Grey, *American Museum Novitates*, 1370: 13 (1947). Lectotype in Carnegie Museum, designated by dos Passos and Grey (1947).
- DISTRIBUTION:** In California, found so far only on the Fort Dick Sand Dunes, in Del Norte County in the extreme northwestern corner of California. Northward it is found in several locations on the Oregon coast. There is no blending or contact between *hippolyta* and *gloriosa*, although the distribution of the two comes in very close proximity in Del Norte County.
- ELEVATION RANGE:** Near sea level to 50'.
- HABITAT AND PLANT COMMUNITIES:** In our only known California population, *hippolyta* occupies the grassy sand dune areas north of Lake Earl on the immediate coastal strand of northern Del Norte County. The area is at sea level to no more than 50'. Invading the habitat are both Redwood and Closed-Cone Pine Forest elements. This unique coastal area is noted by local people for its "banana belt" environment, which results from fog breaking away from the dunes area and local environs in the Fort Dick area and to the north in adjacent Curry County, Oregon. This routine occurrence provides the necessary habitat for *hippolyta* and a number of unique sand-dune entities in an area otherwise constantly shrouded in coastal fog for days on end.
- PHENOLOGY:** The adult flight period for *hippolyta* is adapted to the late summer and fall, when the coastal environment is most consistently sunny and warm. Emergence starts in mid-August, depending on the year, and the flight extends on through September. Males patrol over the grassy sand dune areas, searching for hatching females or for those who have gone to nectar on the abundant Tanzy Ragwort, *Senecio*, which has heavily invaded the dunes. Females are able to oviposit soon after emergence, as this subspecies relies more on time of flight than adult reproductive diapause for assuring the best chance for larval survival during winter diapause.
- FOODPLANTS:** *Viola adunca* Sm. is abundant in the habitat of *hippolyta* and almost certainly represents the foodplant.

g. *S. z. behrensii* (W. H. Edwards)

- DIAGNOSIS:** This subspecies is a coastal subspecies occurring from southern Mendocino County southward to extreme northern Sonoma County. It is characterized by having a considerable expansion of the red-brown disc on the ventral hindwing surface into the pale submarginal band, which is virtually absent. As in *hippolyta*, this is a brightly silvered subspecies.
- ORIGINAL DESCRIPTION:** W. H. Edwards, *Transactions American Ent. Soc.*, 2: 370-371 (1869).

- TYPE LOCALITY: Mendocino, Mendocino County, California. Lectotype (?) in Carnegie Museum, designated by dos Passos and Grey, *American Museum Novitates*, 1370: 13 (1947).
- DISTRIBUTION: This subspecies is found along the immediate coast from extreme northern Sonoma County northward to southern Mendocino County. The most southerly population of *behrensii* is found at Stewart's Point, California. The largest and most stable population of *behrensii* is located in the town of Manchester, California.
- ELEVATION RANGE: From near sea level to approximately 1,000' elevation, with most of the populations at or near sea level. But inland, higher elevation specimens are atypically more like coast range *zerene*. This situation is poorly understood, as no intervening populations are yet known.
- HABITAT AND PLANT COMMUNITIES: The favored habitat of *behrensii* is basically North Coast Prairie plant community grassland, which is immediately adjacent to the coastal breakwaters. These grasslands often have abundant fern species, as well as thistles which serve as nectar sources. Presumably the *Viola* foodplants of this subpecies grow underneath the ferns, as is evident for certain other *Speyeria* subspecies such as *S. callippe callippe*.
- PHENOLOGY: This butterfly is on the wing from July to August, with a peak of abundance in mid- to late July, but this is highly dependent on the environmental conditions of a particular season.
- FOODPLANTS: The host of this subspecies, as for its close relatives *hippolyta* to the north and *myrtleae* to the south, is most likely *Viola adunca* Sm. on the basis of close adult association with this plant.

h. *S. z. myrtleae* dos Passos and Grey

- DIAGNOSIS: This generally coastal subspecies cocurs from Sonoma County southward to former population areas adjacent to San Francisco Bay. It is characterized by being bright orange above, with a heavy greenish basal suffusion. There is pronounced hairlike pubescence produced by long scales on the basal wing portions and the body, more accentuated than in any other western *Speyeria* species or subspecies. The disc on the ventral side of the hindwing is reddish-brown with an overscaling of yellowish-green. The submarginal band is bright yellow. The forewings of both sexes show strong reddish development in the basal portion ventrally, which is the greatest red development found on any *zerene* subspecies. The spots on the hindwing are brightly silvered.
- ORIGINAL DESCRIPTION: Dos Passos and Grey, *American Museum Novitates*, 1297: 3 (1945).
- TYPE LOCALITY: San Mateo, San Mateo County, California. Holotype in American Museum of Natural History.
- DISTRIBUTION: Based on old records, this butterfly had a former distribution on the San Francisco Peninsula on both the west and east sides of the Peninsula at extreme northern San Mateo County. These populations have apparently been extinct for some time. There are existing populations now in Marin and Sonoma County along the coast, with the largest populations being found along the coast at Point Reyes in Marin County. North of here, populations exist in the vicinity of Bodega Bay and in the vicinity of Jenner, in Sonoma County. The population at Jenner shows slight

blending between the subspecies *myrtleae* and *behrensii*, but is closest to *myrtleae*.

- ELEVATION RANGE: From sea level to approximately 75' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is found in the Coastal Strand plant community, where it flies over stabilized sand dunes in a very moist coastal marine meadow-type environment.
- PHENOLOGY: Adult emergence occurs in July and the flight period extends into August. This pattern can be highly variable, depending on the environmental conditions encountered and the extent of very dense coastal fog in any given season.
- FOODPLANTS: *Viola adunca* Sm. is abundant in the sand dunes where *myrtleae* flies at Point Reyes, and is strongly suspected to be the foodplant.

106. *Speyeria coronis* (Behr)

- ADULT BEHAVIOR: This is a strong and rapid-flying Fritillary that frequently visits flowers for nectar and occasionally visits mud. Males patrol all day across open areas, often in valleys, seeking females. Females often appear late in the flight season in places where males are rarely seen, suggesting that they delay oviposition and go into reproductive diapause after mating, until late in the flight season when temperatures drop somewhat.
- LIFE HISTORY: The larva and pupa of *S. c. semiramis* have been briefly described by Comstock and Dammers (1931c), and has been reared and photographed by J. F. Emmel. The larva is dull black in ground color, with more intensely black patches on either side of a faint tan double dorsal band. The spines on the dorsal surface are black with black bristles. The two lateral rows of spines above and below the spiracles are orange with black tips. The supraspiracular row of spines also has faint tan patches around their bases. The head is black. The pupa of *semiramis* is extremely dark, with the wing cases entirely black except for the outer edge, the thorax and ventral surfaces being black, and a heavy black band between each segment of the abdomen. The cremaster area and the ventral surface of the abdomen is entirely black.
- CHROMOSOME NUMBER:
- SIMILAR SPECIES: At Stewards Point in Sonoma County, *S. coronis coronis* has been captured flying along the Coastal strand with *S. zerene myrtleae*. This capture, which was a female and which has not been duplicated to our knowledge by additional takes along the immediate coast, is probably a wanderer down from the low coastal hills. Other Sonoma County captures, such as in the area of Occidental, indicate that *coronis* is found along such ridges, and there are enough phenotypic differences between *myrtleae* and *coronis* specimens to separate them as long as the possibility of their being together is understood.
- The area of greatest challenge in separating *zerene* from *coronis* is along the Great Basin Fringe where *gunderi* flies with *snyderi*. Now that the significance of "*cynna*" and *gunderi* is understood, their sympatry resolves much of the difficulty and most students of *speyeria* will be able to sort out the differences.
- GEOGRAPHIC AND SEASONAL VARIATION: There is no seasonal variation, as this is a univoltine species. Each of the subspecies show some geographic variation within the ranges of their populations, particularly those populations that we lump under the

nominate name of *S. coronis coronis*. In southern California, *semiramis* specimens from San Diego County tend to be smaller than those from the San Gabriel Mountains at the northern end of its range.

GENERAL REMARKS: The possible reproductive diapause observed in females of this species in California needs further investigations. (STERLING, DO YOU KNOW OF AN ARTICLE BY SIMS ON THIS, OR ANY OTHER RELATED INFORMATION THAT YOU CAN ADD UNDER THIS CATEGORY?)

Populations of this species in California can be grouped into five subspecies. This is a large Fritillary, with strong orangish dorsal surfaces and silvered spots on the underside.

a. *S. c. coronis* (Behr)

DIAGNOSIS: This subspecies name is applied to a heterogenous set of populations found in the Coast Ranges, from Sonoma County south to San Luis Obispo County. It is a relatively dark subspecies in comparison to the other subspecies, with the basal two-thirds of the underside of the hindwing being light brown and the submarginal band being occasionally suffused with brown scaling. The upperside is pale yellow-brown, becoming somewhat lighter in the middle of the wing where the silver spots show through slightly on the upperside.

ORIGINAL DESCRIPTION: Behr, in William H. Edwards, *Proc. Ent. Soc. Philadelphia*, 3: 435 (1864).

TYPE LOCALITY: Gilroy, Santa Clara County, California, designated by F. M. Brown, *Transactions American Ent. Soc.*, 91: 259 (1965). Neotype in Carnegie Museum, designated by W. H. Edwards (1864), as explained by F. M. Brown (1965).

DISTRIBUTION: Subspecies *coronis* is primarily a resident of the South Coast Ranges. Verified records of specimens close to *S. c. coronis*, not *hennei*, have been taken as far south as the Santa Ynez Mountains in southern Santa Barbara County. Northward, records are scattered and sparse along the coastal mountains, where it becomes more common in coastal south San Francisco Bay counties. Early-day records show a distribution throughout the Bay Area Mountains, extending north into the North Coast Range and along the immediate coast, with the northernmost records at Mt. Vedar in Napa County, and Stewarts Point in northern Sonoma County.

ELEVATION RANGE: From near sea level at 20' elevation along the North Coast, up to 5,000' along the South Coast Range crest.

HABITAT AND PLANT COMMUNITIES: This subspecies is predominantly found within the Mixed Evergreen and Redwood Forest areas of the San Francisco Bay area, and south in the upper reaches of Foothill Woodland plant communities of the Bay area and Coast Ranges on south. It enters the Northern Coastal Scrub rarely north of the Bay. *Coronis* can be found with *S. callippe* often breeding in an area dominated by dense stands of fern in grassy open glades or on open hillsides, with coniferous forest usually adjacent. *Monardella*, Western Wall Flower, and *Aesculus californica* (Buckeye) often act as the nectar sources.

PHENOLOGY: *Coronis* has been taken from late May but mostly from mid-June through July. After July, consistent captures on into mid-September have been recorded for females. All are probably in reproductive diapause, as shown for a few such *coronis* females examined in early summer (Mattoon, unpublished).

FOODPLANTS: Unknown, but *Viola purpurea* Kell. and *V. quercetorum* Baker & Clausen are present in the area where adults fly.

b. *S. c. hennei* (Gunder)

DIAGNOSIS: This larger, lighter brown race of *coronis* has finer black maculation and a greatly reduced basal suffusion on the underside of the forewing. The overall appearance both dorsally and ventrally is of a more ochre-colored butterfly. It occurs in the Tejon-Tehachapi Mountains of southern California.

ORIGINAL DESCRIPTION: Gunder, *Canadian Entomologist*, 66: 126 (1934).

TYPE LOCALITY: Mt. Pinos, Frazier Mountain Park, Ventura County, California. Holotype in American Museum of Natural History.

DISTRIBUTION: This subspecies occurs in the Mt. Pinos region of Ventura County, the Tejon-Tehachapi Mountains, and the Piute Mountains of Kern County. It also occurs in the Greenhorn Mountains and the extreme southern end of the Sierra Nevada Range on the east slope. It is considered a scarce butterfly and difficult to capture. The best known populations are southwest of Frazier Park in Ventura County, the summit area of Mt. Pinos, and on Double Mountain in the Tehachapis. As far as is known at present, there is no blendzone with typical *coronis* to the northwest. However, it meets the subspecies *semiramis* between Tejon Pass and the western end of the San Gabriel Mountains, and in areas variously known as Lebre Mountain and Sawmill Mountain and Sierra Pelona.

ELEVATION RANGE: We have records for *hennei* from 3,600 to 8,900'.

HABITAT AND PLANT COMMUNITIES: This butterfly is found primarily in the Jeffrey Pine forests, but also extends down into Sagebrush and mixed with Pinyon Pine habitats, where it is usually found in open areas flying over the dry slopes and flats.

PHENOLOGY: *Hennei* flies from early June through primarily July. Records extending into late August are mostly females.

FOODPLANTS: The most likely foodplant of this subspecies is *Viola purpurea* Kell., based on the association of this plant with pre-oviposition behavior shown by females. It is the most abundant Violet in the Jeffrey Pine forests where *hennei* flies.

c. *S. c. semiramis* (W. H. Edwards)

DIAGNOSIS: This subspecies inhabits the mountains of southern California from the Transverse Ranges south to San Diego County. It is characterized by a paler ground color dorsally, finer black maculation on the upperside, and greatly reduced basal suffusion on the underside of the forewing. On the underside of the hindwing, the basal two-thirds is light brown. The spots are brightly silvered.

ORIGINAL DESCRIPTION: W. H. Edwards, *Canadian Entomologist*, 18: 61-62 (1886).

TYPE LOCALITY: Vicinity of San Bernardino, California. Lectotype in Carnegie Museum, designated by dos Passos and Grey, *American Museum Novitates*, 1370: 11 (1947).

- DISTRIBUTION:** This subspecies is found in the San Gabriel, San Bernardino, San Jacinto, Santa Rosa, Santa Ana, Palomar, and Laguna Mountains in southern California. Occasionally strays away from its more Montane habitat, particularly in late summer when ovipositing females tend to wander. One female was collected in Box Canyon at Anza-Borrego Desert in San Diego County on August 25th, eastern record (Langston, in litt.). It has not been taken in the Santa Ana Mountains in recent years, and perhaps the records for this species from that Range represented only a transiently established population. In view of the wandering behavior of females in late summer, this would not be unexpected.
- ELEVATION RANGE:** *Semiramis* has been taken from 3,500' to 9,114', but mostly above 5,000'.
- HABITAT AND PLANT COMMUNITIES:** This species is usually found in the Ponderosa Pine-bordered meadows of the Transition Zone in the southern California mountains. The adults are frequently attracted to Thistle species (*Cirsium* sp.) and may be reasonably abundant at times.
- PHENOLOGY:** Adults have been taken from early June to mid-September. It is possible that after mating, females enter a temporary reproductive diapause through the summer months, as ovipositing females are frequently seen in mid-September.
- FOODPLANTS:** At least two *Viola* species are locally common in areas where ovipositing female *semiramis* have been observed. These two species are *Viola douglasii* Steud. and *V. purpurea* Kell.

d. *S. c. snyderi* (Skinner)

- DIAGNOSIS:** This is the Great Basin subspecies of *coronis*, which typically has a green disc below or ventrally on the hindwing. In our area, it is found along the eastern side of the Sierra Nevada and in the Warner Mountains. It is characterized by its very large size, with the basal two-thirds of the ventral hindwing surface being either greenish-brown or varying from greenish-brown to green.
- ORIGINAL DESCRIPTION:** Skinner, *Canadian Entomologist*, 29: 154 (1897).
- TYPE LOCALITY:** City Creek Canyon, Salt Lake City, Salt Lake County, Utah, designated by dos Passos and Grey, *American Museum Novitates*, 1370: 12 (1947). Holotype in Carnegie Museum.
- DISTRIBUTION:** There is some disagreement and uncertainty concerning the distribution between ssp. *snyderi* and ssp. (nr.) *simaetha* in California. Shapiro and Austin would extend *simaetha* down the Great Basin Fringe to at least the Minden/Gardnerville, Nevada area. We conclude it only extends south to the latitude of Mt. Shasta in the Cascades and adjacent Klamath Assemblage. All agree that *S. coronis simaetha* is in the north slopes of Scott Mountains, the Little Shasta Valley, and the Cascade Range Goosenest District of Klamath National Forest. Paul Grey calls all the Sierra Nevada material *snyderi*, as he does the Warner Mountains material. Mattoon has reviewed the data sheets including all of the Paul Grey card records. He finds that green/brown *snyderi* facies consistently show up in Sierra Nevada and Warner Mountains locations. He notes that green/brown shows up in Great Basin Fringe populations even in Lassen County, and thus we call these by the name of *snyderi*.
- ELEVATION RANGE:** *Snyderi* has been reported from 4,300' up to 8,762', but is most commonly found between 5,000 to 7,000'.

- HABITAT AND PLANT COMMUNITIES:** *Snyderi* is always associated with Sagebrush Scrub country. Although most places for which *snyderi* has been reported in California are also associated with coniferous forests, invariably there are mountain valleys with *artemisia* or Rabbit-brush intrusions or these low scrubs are growing nearby. *Snyderi* is also found within the higher forested areas of the Sierra Nevada eastern escarpment, but usually in association with more xerophytic sagebrush intrusion areas. *Snyderi* is, therefore, found throughout the Warner Mountains, and all the other basin ranges within the Modoc Plateau, as a great wanderer, females often turn up at nectar in valleys and plains throughout its general area of distribution.
- PHENOLOGY:** *Snyderi* is often one of the first *Speyeria* to be encountered in a season, occasionally even as early as the end of May. However, the main flight of males and females is June to late July, but because of reproductive diapause, females can be encountered, mainly at nectar, on through the season until late September.
- FOODPLANTS:** Unknown for our populations of this subspecies, but *Viola beckwithii* T. & G. is present in the habitats where *snyderi* flies.

e. *S. c.* near *simaetha* dos Passos and Grey

- DIAGNOSIS:** This weakly differentiated subspecies has its type locality in Washington State, and specimens taken in Siskiyou County resemble that butterfly. Overall, it is rather smaller and paler than *snyderi*. The disc on the hindwing is consistently paler and a uniform olivaceous buff. In males this disc has more ochre coloration. The sub-marginal band and the apical parts of the forewing on the underside are also ochre in color.
- ORIGINAL DESCRIPTION:** Dos Passos and Grey, *American Museum Novitates*, 1297: 2 (1945).
- TYPE LOCALITY:** Black Canyon, near Brewster, Washington. Holotype in American Museum of Natural History.
- DISTRIBUTION:** Using the conservative view expressed under *snyderi*, we limit the California distribution of *simaetha* to Siskiyou County within the Little Shasta and Scott Valleys north and west of Mt. Shasta and the valley-facing slopes of the Trinity and Scott Mountains that form the southern boundaries of these valleys. To the east, *simaetha* is found throughout the Goosenest District of the Cascade Range, to the Meiss Valley, Macdoel, Highway 97 area. Distribution beyond the north-facing slopes of Mt. Hebron to the south and eastward is in question. However, L. Paul Grey gave several determinations in the Warners where he indicated the specimens looked *simaetha*-like. Possibly, the Warner Mountains and south through the Modoc Plateau east of the Cascades may be a *snyderi-simaetha* blend area.
- ELEVATION RANGE:** *Simaetha* has been found from 2,500' to 7,000'.
- HABITAT AND PLANT COMMUNITIES:** Compared with *snyderi*, *simaetha* has an almost identical Sagebrush Scrub habitat around and within the perimeters of Yellow Pine or Mixed Evergreen Forests, with some intrusion of juniper. The most noticeable difference is that the sage scrub is predominantly *Chrysothamnus* (Rabbit Bush) rather than *Artemisia*, in some areas entirely so. In the fall, as this plant blooms, it becomes an important nectar source for *simaetha* females coming out of their reproductive diapause. As elevation records show, *coronis* follows such intruding sagebrush scrub habitats to the crest of adjacent mountains.

PHENOLOGY: This subspecies flies principally from early June to early August, with many females around into late September.

FOODPLANTS: Unknown.

107. *Euptoieta claudia* (Cramer)

This butterfly, commonly known as the Variegated Fritillary, is principally a southern U. S. species that strays northward during the summer into the central and eastern states, as well as the Rocky Mountains area north to Canada.

DIAGNOSIS: The upperside pattern is a tan-brown in the outer half of the wing, and a deeper russet-brown set off by black markings in the basal half of the wings. It cannot be confused with any of our *Speyeria* species.

ORIGINAL DESCRIPTION: Cramer, *Uitl. Kapellen*, 1: 109 [1775].

TYPE LOCALITY: "Jamaica". Location of type not known.

DISTRIBUTION: In years of abundance elsewhere to the south and east, this butterfly strays into the southern California region and may be found in desert and even in interior mountain areas. The records for strays that have come into our area are scattered over the eastern Mojave Desert, the Colorado River Valley, the Imperial Valley, and the lower elevations of Los Angeles, Orange, and San Diego counties. There is one record for the Inyo Mountains in Inyo County and one record from Kern County just off Hwy. 14 near Cinco, in late September 1984 (K. Davenport). In 1988, specimens of this species were encountered in at least three northern California areas between 19 August and 23 October: the Feather River Canyon of Pumas County (S. Mattoon), the C. Davis Campus in Yolo County (A. M. Shapiro), and Jerseydale (3,500') in Mariposa County (O. Shields).

ELEVATION RANGE: From near sea level to approximately 7,000' for the Inyo Mountains record. Most of our records are below 6,000'.

HABITAT AND PLANT COMMUNITIES: As the butterfly in our area is usually a stray, it has been taken in a variety of plant communities or habitats, including agricultural areas, urban areas, Creosote Bush Scrub plant communities, and Desert Riparian Woodland communities. In the New York Mountains, where populations may become at least transiently established, the typical vegetation in the areas where the butterflies are generally taken is Pinyon-Juniper Woodland. The northern California specimens were in foothill woodland and riparian situations.

PHENOLOGY: Our records for this species range from April to early November, with the preponderance of records during the month of September. For one locality in the New York Mountains of the eastern Mojave Desert, where at least two native foodplants of this butterfly occur, we have both a September record for one year and an April record for the following year, indicating a possible successful overwintering of this butterfly in that particular mountain range. The diapause stage of this butterfly, if any, probably involves some sort of reproductive diapause in adults, as the eggs, larvae, and pupae are not known to overwinter.

ADULT BEHAVIOR: This butterfly is a renowned migrant, at least in the sense of a northern movement during each spring and summer. The butterfly probably overwinters only in the south and on into Mexico, but by late summer transient populations are found

more than a thousand miles to the north of that limit. Adults have a fairly rapid flight and frequently visit flowers, especially Star Thistle, for nectar. Scott (1975) has described the courtship, in which the male pursues the female, who lands and holds her wings mostly closed and her abdomen raised slightly. The male then lands behind her and flutters his wings slowly. Then he walks alongside the female and flutters his nearly vertical wings quite rapidly. Then they mate for an hour or so. During mating, the female spreads her wings more than the male and both flutter the wings occasionally, the male more often than the female.

FOODPLANTS: Seemingly transient populations in our area become established at times. For instance, in early September 1936, Lloyd Martin found a rather large population of this butterfly in the New York Mountains of the eastern Mojave Desert. In October, Dammers found immatures on a foodplant in that area. The two tiny foodplants used in that area are *Linum lewisii* Pursh. or Blue Flax, and *Linum puberulum* (Engelm.) Heller, or Yellow Flax. Both of these are in the Flax family, Linaceae. Other genera, such as *Passiflora* (Passifloraceae) and *Viola* (Violaceae), are used by this Fritillary, and other breeding populations in California might use them on occasion.

LIFE HISTORY: The cone-shaped egg is pale green and is laid singly on the leaves and stems of the host plant. The mature larva is a beautiful red-orange in ground color, which has three white dorsal and lateral bands on each side of the orange dorsal surface. There is a black spine on each segment located just above each of the white bands. The position, what would be a mid-dorsal seventh spine, is marked by a white blotch of irregular size on each segment (but no spine). The head is black with a reddish-brown dorsal surface and a small reddish-brown marking on each face. The pupa is pearly white with small black markings as shown in the accompanying figures, and a gold band across each eye cover, gold sheathing of the antennae, a touch of gold around the cremaster, and large gold bumps across the thorax and abdomen in place of the former dorsal tubercles of the larva.

CHROMOSOME NUMBER: $n = 31$ (T. C. Emmel, unpublished).

SIMILAR SPECIES: *Euptoieta hegesia* may be recognized by the relatively unmarked basal area of the dorsal hindwing surface.

GEOGRAPHIC AND SEASONAL VARIATION: No subspecies have been named of this widely ranging species, which occurs from Mexico north into Canada.

GENERAL REMARKS: This is a transient member of our fauna, but its regularity and wide distribution of records indicate that it is a regular stray into our area.

108. *Euptoieta hegesia hoffmanni* W. P. Comstock

DIAGNOSIS: This is a slightly smaller species, which can be immediately recognized by the unmarked basal area of the dorsal hindwing surface.

ORIGINAL DESCRIPTION: W. P. Comstock, *Science Survey Porto Rico & Virgin Islands*, 12: 446 (1944).

TYPE LOCALITY: Escuinapa, Sinaloa, Mexico. Holotype in American Museum of Natural History.

DISTRIBUTION: See **Appendix** for further information.

Subfamily Heliconiinae Swainson

109. *Agraulis vanillae incarnata* (Riley)

This is the butterfly familiarly known as the Gulf Fritillary and its silver-spangled wings are a common sight in the urban areas of southern California, where it breeds throughout the year except perhaps in mid-winter.

DIAGNOSIS: This is the western subspecies of a widely ranging subtropical and tropical species. It is brilliant orange above, with considerably reduced black markings. On the underside of the wing, the forewing is flushed with red and orange basally, and is dotted with silver spots rimmed with black. On the hindwing, large silver spangles are placed across a brown and ochre ground coloration. The spectacular silver spots and beautiful magenta forewing flush on the underside make this bright orange butterfly one of our loveliest species.

ORIGINAL DESCRIPTION: Riley, *Entomologist*, 59: 243-244 (1926).

TYPE LOCALITY: Near Durango, Durango, Mexico. Holotype in British Museum.

DISTRIBUTION: Because it is an introduced species feeding on an introduced foodplant which is used as an ornamental vine, this species is largely confined to urban and suburban areas of lowland California. It is found in the major metropolitan areas in the coastal areas from San Diego north to Sonoma County, and also sparingly throughout the Central Valley of California, becoming progressively scarcer as one moves north. It is absent from the desert regions, although possibly small colonies are established on ornamental *Passiflora* species in towns or cities in those areas.

ELEVATION RANGE: From sea level to approximately 2,000' elevation for most of the breeding colonies. Strays have been taken as high as 5,000' in the mountains of southern California.

HABITAT AND PLANT COMMUNITIES: This species is typically found in gardens in urban and suburban areas of California.

PHENOLOGY: Captures are recorded for every month of the year, with the species being very scarce through the winter months and then becoming progressively more abundant as the spring season progresses, reaching a peak of abundance in late summer and early fall. There is no known diapause stage. Rearing experiments by O. E. Sette in the southern San Francisco Bay area showed that rather than going through any kind of diapause, the larval development and pupal development simply slowed down greatly during the winter months, with concomitant high mortality during this time. It will be of interest to see whether this subtropical and tropical butterfly ultimately evolves a true diapause strategy in our more temperate climate.

ADULT BEHAVIOR: The adults have a rapid, erratic flight and are usually seen in close proximity to their *Passiflora* foodplants. They are avid flower visitors, being particular to the blooms of *Lantana* species which are so commonly used in the gardens of southern California. Courtship behavior has been well studied by Rutowski and Schaefer (1984). During most but not all courtships, the male initially hovers about 15 cm over the female before descending and initiating physical contact. Once he alights, he positions himself with his wings open and his head close to that of the female, with his body at about a 45 degree angle with that of the female. Now he begins a wing clap display, repeatedly clapping his wings together for

about 5 seconds and often catching the female's antennae between his wings during the 30 or so claps. As he ceases clapping, he opens his claspers and curls his abdomen around to copulate. The wing clapping display probably presents chemical signals to the female from the scent-producing androconia, located along the dorsal surface of six of the male's forewing veins.

LIFE HISTORY: The yellow egg has fifteen to twenty longitudinal ribs. The eggs are laid singly on host plant leaves, tendrils, stems, and even buds. The mature larva is slaty grey with burnt orange stripes and black branching spines. The highly convoluted pupa is mottled with whitish-grey, brown and black. The species does not diapause in any stage, but in seasonally cold weather it can slow its larval growth and survive brief periods of near freezing temperatures. Otherwise, populations must be established by new immigrants coming from warmer climates.

FOODPLANTS: *Passiflora incarnata*, *P. caerulea*, and other introduced *Passiflora* species (Family Passifloraceae).

CHROMOSOME NUMBER: $n = 31$ (Emmel and Eliazar, unpublished).

SIMILAR SPECIES: None in our area, although a smaller, related species, *Dione moneta*, has been recorded once in our area.

GEOGRAPHIC AND SEASONAL VARIATION: None in California, although a number of subspecies have been named from the various islands of the Caribbean and south into the mainland neotropics.

GENERAL REMARKS: This butterfly has recently become established in as far north as the San Francisco Bay region, but hard freezes still kill off these northern populations in years with cold winters.

110. *Dione moneta* Hubner

See **Appendix** details.

LIBYTHEIDAE

This tiny family of butterflies, sometimes placed as a subfamily under the Libytheinae in the Nymphalidae, has only ten species worldwide, but the overall distribution is cosmopolitan and very ancient, specimens being known from 37 million years ago in the fossil shales of Florissant, Colorado. The familiar name of snout butterfly is applied to this group because of the great development of the labial palpi. The family is characterized by having: (1) greatly reduced prothoracic (front) legs in the male, while only slightly atrophied prothoracic legs in the female; (2) a tarsus which is brush-like and composed of only one segment without claws in the male, whereas the female has a tarsus with five segments and two normal claws; (3) a clubbed and scaled antenna; (4) a head almost as wide as the thorax, with a very long beak-like palpi stretching forward as a "snout;" (5) the cell in both the forewings and the hindwings being closed by a tubular vening; (6) a larva that is smooth, slender, and has a cylindrical body, looking very much like a pierid larva (totally lacking head capsule ornamentation and the bifid tail found in Satyridae and related tropical groups).

* * * * *

112. *Libytheana carinenta larvata* (Strecker)

This Snout Butterfly is widely distributed in the eastern half of the United States, southern Arizona, and Mexico. In southeastern California, it normally occurs as a stray in the Colorado and southern Mojave Deserts, and occasionally to the coast or to more northern areas.

- DIAGNOSIS: The principal distinguishing characters are the excessive length of the palpi at the front of the head (forming the "snout"), the much reduced forelegs in the male but well-developed forelegs in the female, and the plain elongated larva which resembles those found in the Family Pieridae. The wing colors form an unmistakable pattern of orange flushes on dark brown wings, with several white forewing spots, that is also unmistakable.
- ORIGINAL DESCRIPTION: Strecker, *Lepid. Rhop. Het.*: 130 [1878].
- TYPE LOCALITY: San Antonio, Texas. Syntypes in Field Museum of Natural History, Chicago. This butterfly was originally described as a subspecies of *Libytheana*, but was transferred with good evidence by Scott (1986, The Butterflies of North America: 344-345) to be a subspecies of *L. carinenta* (along with subspecies *bachmanii*) as races of a single species.
- DISTRIBUTION: The strays that have been recorded for our area are from localities widely scattered over our deserts from the Inyo Mountains of Inyo County south to the eastern Mojave Desert and Colorado River Valley westward to the extreme southern San Joaquin Valley and the desert areas of western Riverside and eastern San Diego County. Additionally, strays sometimes penetrate passed the mountain barrier at the west edge of the desert, and are taken in such places as Riverside in Riverside County.
- ELEVATION RANGE: Our records range from near sea level to approximately 6,000' elevation.
- HABITAT AND PLANT COMMUNITIES: Most of our specimens have been taken in either the Creosote Bush Scrub plant community or Joshua Tree woodland plant community of our desert regions.
- PHENOLOGY: Our records are for the months of August to December, with the majority of records for the months of October and November.
- ADULT BEHAVIOR: The adults are rapid, nervous fliers, and males will perch on prominent twigs of shrubs in the desert washes. Adults are sometimes observed to fly into the interior of a very large shrub or small tree and land on the trunk, usually with the head down. Under these circumstances, they become readily concealed and are extremely difficult to discern, particularly if they are resting in mottled shade, as the leaf-like underside markings blend in very well with the bark of the trunks on which they rest.
- Large migrations occur in the adults of this subspecies in Mexico, Texas, and the southwest, sometimes involving thousands of individuals.
- LIFE HISTORY: The conoidal is pale green and longitudinally ribbed. The eggs are laid singly on young terminal leaves of the *Celtis* host plant. The mature larva can be quite variable in color and pattern in different populations. In our general area, larvae raised from a female obtained at Holtville in Imperial County are a velvety bright green, with a light yellow narrow band along the length of the side of the larva just above the spiracles. The rest of the green ground color is covered with fairly widely spaced yellow bumps. There is a very faint, slightly lighter green mid-dorsal line. The head is entirely green. In an Arizona population, the larva is

generally dark green with a lighter yellowish-green subdorsal band on either side and yellowish-green prolegs and thoracic legs. The remainder of the surface is covered with pale green yellow bumps. On the green head are placed two yellow spots around the ocelli. The pupa also varies, but the typical form in California is light green with a yellow stripe along the mid-dorsal abdomen area to the base of the thorax, where it bifurcates and runs diagonally to either side across roughly the front to the wing cases. These two yellow lines then rejoin in a straight line across the bottom of the head on the ventral surface.

FOODPLANTS: This species may become temporarily established on *Celtis douglasii* Planch. (Ulmaceae), which is found in a few scattered canyons in our area (at Clark Mountain, and in the area just north of Banning, Riverside County).

CHROMOSOME NUMBER:

SIMILAR SPECIES: None in our area.

GEOGRAPHIC AND SEASONAL VARIATION: Several subspecies have been named to the south of us in mainland Mexico, and Scott (1986) lumps several of the separately designated Caribbean species as subspecies of this mainland form, *L. carinenta*. No seasonal variation has been noted.

GENERAL REMARKS: The Libytheidae or Snout Butterflies are a small, and in many ways, peculiar family. The group has an ancient history, being represented in the fossil shales of Florissant, Colorado by a species (*Prolibythea vagabunda* Scudder) that flew 34,000,000 years ago, and very probably fed on *Celtis maccoshi* Lesq., the only fossil Hackberry Tree in that location, and representing a plant species in the only host genus utilized by the species today. Another extraordinary eccentricity is the fact that the Snout Butterflies are found on every continent, but there are only ten living species and usually only one species is found in any particular region.

RIODINIDAE

The family Riodinidae, or metalmarks, is one of the most successful and diverse families of butterflies in the Neotropics, with more than a thousand species. There are a few species located on other continents, including the temperate areas such as California, where we have four metalmark species. This family is sometimes placed as the subfamily Riodininae under the great family Lycaenidae. The metalmarks are characterized by having: (1) four walking legs (with the front legs greatly reduced) in males, and six fully functional legs in females; (2) part of the first leg segment (coxa) extends notably beyond the joint of the next segment (trochanter) on the reduced male forelegs, forming a spine-like projection of the foreleg coxa below the articulation of the trochanter; (3) one tarsal segment with a single claw or no claw in the male, and five tarsal segments with normal paired claws in the female; (4) clubbed and scaled antennae; (5) eyes slightly notched around the bases of the antennae; (6) a very narrow head in comparison to the thorax, with quite short palpi; (7) the humeral vein present in the hindwing, in contrast to its absence in the true lycaenids; (8) wings usually held spread after landing, in contrast to lycaenids which normally hold their wings vertically after landing; (9) flattened and slug-like larvae in most species, broadest in the middle and tapering to both ends with a clothing of short to long hairs; (10) a pupa that is relatively thin and elongate, compared to the short, stout pupa of the true lycaenids.

* * * * *

Subfamily Riodininae Grote

The Metalmarks in this family and subfamily are an extremely diverse and well-developed group south of us in the American tropics. The chief diagnostic character between the usual metallic spots and iridescent colors is the notable extension of the first leg segment (the coxa) beyond the joint of the next segment (the trochanter), on the reduced prolegs of the adult male. Our California species share the habit of the tropical species of holding their wings spread horizontally, when landing after a brief flight or when resting. Although the family has its greatest diversity in the New World tropics with more than a thousand species having been described from there, it has a nearly worldwide distribution. The few species found in the Nearctic normally represent northern extensions of widespread neotropical genera or species.

113. *Apodemia mormo* (C. and R. Felder)

The Mormon Metalmark occupies a very broad range throughout the western United States and south into Mexico. It shows great geographic variation and various segregates of populations have received subspecific names. Because of the difficulty in arranging the California *Apodemia mormo* populations into any kind of a meaningful subspecific taxonomic scheme, we have divided our treatment of these populations into the following four groups, based on sure biological characteristics:

GROUP I: SUMMER TO FALL-FLYING, UNIVOLTINE

- a. *A. m. mormo* (North Central Sierra Nevada)
- b. *A. m.* near *mormo* segregates (North and Central California related segregates)
- c. *A. m. langei* and related segregates
- d. *A. m.* subspecies (Western Great Basin populations)
- e. *A. m.* subspecies (Eastern Mojave Desert)
- f. *A. m. cythera* and related segregates
- g. *A. m. tuolumnensis* and related segregates

GROUP II: SPRING THROUGH FALL-FLYING, MULTIVOLTINE, CISMONTANE; DIAPAUSE PROBABLY AS PARTLY TO FULL-GROWN LARVA

- h. *A. m. virgulti*
- i. *A. m.* near *virgulti* (Peninsular Ranges)

GROUP II: SPRING-FLYING, UNIVOLTINE; DIAPAUSE AS PARTLY GROWN TO FULL-GROWN LARVA

- j. *A. m.* subspecies (Kern County, East Slope Piute Mountains, and southern Sierra Nevada)
- k. *A. m.* subspecies (Northern slope San Gabriel-San Bernardino Mountains)
- l. *A. m.* near *dialeuca* (San Bernardino Mountains, high elevations)

GROUP IV: SPRING THROUGH FALL-FLYING, MULTIVOLTINE, LOW-ELEVATION; DIAPAUSE AS MATURE LARVA; FEED ON *E. INFLATUM* AND OTHER ANNUAL OR BIENNIAL *ERIOGONUM* SPECIES

- m. *A. m. deserti*

This outline of geographic differentiation in California represents the picture, as we understand it at present, of this remarkably diverse Metalmark species. In reading the following accounts, repeated reference to the accompanying two maps of the State of California will prove useful.

GROUP I: Summer to Fall-flying Univoltine Populations.

a. *A. m. mormo* (C. and R. Felder)

- DIAGNOSIS:** In nominate *mormo*, the upperside pattern is characterized by a charcoal gray ground color with orangish-brown scaling confined to the forewing, where it is found in the anterior half of the discal two-thirds of the wing; on the hindwing, orange scaling is absent. The submarginal row of white spots is greatly reduced in typical *mormo*. Ventrally, the pattern is characterized by somewhat of a medium contrast on the hindwing, with sufficient white overscaling to give a somewhat pale gray appearance, but not to the degree seen in the desert populations of this species.
- ORIGINAL DESCRIPTION:** C. and R. Felder, *Wiener Ent. Monats.*, 3: 271 (1859).
- TYPE LOCALITY:** "Great Salt Lake", usually attributed to Utah, but restricted by Miller and Brown (Memoirs Lepidopterist Society 2: 131, 1981) to near Pyramid Lake, Washoe County, Nevada. Location of type: British Museum. Type locality re-restricted by Emmel, Emmel, and Mattoon (*Journal Research Lepidoptera*, : , 1988) to Donner Pass, Placer County, California.
- DISTRIBUTION:** Nominate *mormo* is confined in distribution to the north-central Sierra Nevada from the mountains immediately surrounding Lake Tahoe northward to the Donner Pass region and upper Yuba River drainage.
- ELEVATION RANGE:** 4,000 to 8,500' elevation.
- HABITAT AND PLANT COMMUNITIES:** Generally on open rocky or gravelly slopes within the Montane Coniferous Forest plant community.
- PHENOLOGY:** Univoltine, with adults first appearing in mid-August and flying through mid- to late-September.
- FOODPLANTS:** At Donner Pass, the species is closely associated with *Eriogonum wrightii* Torr. ex Benth. (Shapiro, personal communication); at Lang Crossing on the Yuba River, on the west slope of the Sierra Nevada, the butterfly is associated with *Eriogonum umbellatum* Torr. (Shapiro, personal communication).

b. *A. m. near mormo* segregates

1.) Mt. Shasta-Lassen County region segregates

- DIAGNOSIS:** These populations are phenotypically similar to Sierran *A. m. mormo*, but tend to be slightly larger and have slightly greater reduction of the size of the white spots on the upperside wing pattern.
- DISTRIBUTION:** These populations are known from the Trinity Alps eastward through the Klamath River drainage to Lassen County.
- ELEVATION RANGE:** 4,000 to 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** Open gravelly or rocky slopes, within Montane Coniferous forests or Sagebrush Scrub plant communities.

PHENOLOGY: These populations are univoltine with the peak flight period being from late August to late September.

FOODPLANTS: Shapiro *et al* (1981) record *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes ssp. *sulphureum* (Greene) Stokes at Carrville, Trinity County, and in the Klamath River country; additionally, they record *E. umbellatum* Torr. complex (Trinity Alps).

2.) North Coast Range segregates

DIAGNOSIS: These populations are generally similar in phenotype to the Sierran *A. mormo mormo*, but tend to average slightly larger in size.

DISTRIBUTION: Populations are known in the North Coast Ranges, just north of Clear Lake in Lake County and to the east of Clear Lake in Colusa County.

ELEVATION RANGE: From 2,000 to 6,500' elevation.

HABITAT AND PLANT COMMUNITIES: Open, gravelly slopes or flats within the Montane Coniferous Forest or Foothill Woodland plant community.

PHENOLOGY: Univoltine, with captures recorded from mid-August to late September.

FOODPLANTS: In Colusa County, the butterfly is closely associated with *Eriogonum wrightii* Torr. ex Benth. ssp. *trachygonum* (Torr.) S. Stokes (Mattoon and Hageman, unpublished data).

3.) Vallejo segregate

DIAGNOSIS: Adults of this population are similar to *A. m. mormo*, except that the marginal white spots tend to be elongated into thin dashes.

DISTRIBUTION: This population is known from the slopes of Hunter's Hill, 2 miles northeast of Vallejo.

ELEVATION RANGE:

HABITAT AND PLANT COMMUNITIES: Open gravelly and rocky slopes within a grassland community.

PHENOLOGY: Univoltine, with adults flying from mid-August to mid-September.

FOODPLANTS: *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes complex (P. Opler, personal communication).

4.) Southern Santa Cruz Mountains-Marina Dunes segregates

DIAGNOSIS: These populations are phenotypically similar to nominate *mormo*, and there are probably at least two or three sub-segregates within this particular geographic region based on minor differences in habitat and foodplant.

DISTRIBUTION: Populations are scattered at various localities within the southern half of the Santa Cruz Mountains and on the Marina Dunes of Monterey County.

ELEVATION RANGE: From near sea level to 2,000' elevation.

- HABITAT AND PLANT COMMUNITIES:** The Marina Dunes populations are found on stabilized sand dunes of the Coastal Strand plant community, the montane populations are found on rocky to gravelly slopes and flats or areas of sandy soil within the Redwood Forest or Chaparral plant communities.
- PHENOLOGY:** Univoltine, with captures recorded from mid-June to August for the Marina Dunes populations, and early August to late September for the Santa Cruz Mountains populations.
- FOODPLANTS:** *Eriogonum latifolium* Sm. is used by the Marina Dunes populations (J. F. Emmel, unpublished data); the Santa Cruz Mountains populations are associated with *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes ssp. (John Lane, personal communication).

5.) South Coast Range and Kern River segregates

- DIAGNOSIS:** This is another diverse subset of populations which are phenotypically most similar to *A. m. mormo*. Populations on the east slope of the Mt. Hamilton Range have a considerable reduction of the white spotting on the wings, giving a very dark appearance to the butterfly. Populations in southeastern Monterey County and in the northern part of San Luis Obispo County show some specimens with tendencies toward the subspecies *langei*, but for the most part still appear to be fairly typical *A. m. mormo*.
- DISTRIBUTION:** In the South Coast Ranges from the Mt. Hamilton Range in Santa Clara and Stanislaus counties southward to San Luis Obispo County. Additionally, a phenotypically similar population is found along the lower Kern River in Kern County (D. L. Bower, personal communication).
- ELEVATION RANGE:** 1,000 to 3,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** Populations are generally found on rocky slopes or near canyon bottoms within the Chaparral or Foothill Woodland plant communities.
- PHENOLOGY:** Univoltine, with adults flying from mid-August to late September.
- FOODPLANTS:** The Del Puerto Canyon populations are associated with *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes ssp. (G. Pratt, personal communication); presumably most of the other related populations are associated with the same *Eriogonum* species, but further field study of the foodplants of this set of populations is indicated.

6.) Southern California Western Desert and Montane segregates

- DIAGNOSIS:** Again, these populations are phenotypically similar to nominate *mormo*, but tend to be slightly smaller than the other related populations to the north.
- DISTRIBUTION:** Populations are known from the eastern end of the San Bernardino Mountains eastward into the higher elevations of Joshua Tree National Monument.
- ELEVATION RANGE:** 4,000 to 9,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** Sandy washes to granitic slopes and canyon bottoms within Pinion-Juniper Woodland, Sagebrush Scrub, and Montane Coniferous Forests.

- PHENOLOGY: Univoltine, with adults flying from late August to late September.
- FOODPLANTS: These populations are all associated with *Eriogonum wrightii* Torr. ex Benth. (G. Pratt and J. Emmel, unpublished data).

c. *A. m. langei* and related segregates

ORIGINAL DESCRIPTION: J. A. Comstock, *Bulletin Southern California Academy Sciences*, 37: 129-131 (1938).

TYPE LOCALITY: Antioch, Contra Costa County, California. Holotype in Los Angeles Museum of Natural History.

1.) Typical *langei*

DIAGNOSIS: This subspecies is characterized by extensive invasion of orange scaling into the discal spot of the forewing and onto the basal half of the hindwing.

DISTRIBUTION: True *langei* is known only from the Antioch Sand Dunes in Contra Costa County. Because of its restricted distribution, it is currently listed as an endangered species on the Federal Endangered Species List.

ELEVATION RANGE:

HABITAT AND PLANT COMMUNITIES: Open sandy flats where *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes is locally abundant. Further details about the habitat and biology of this butterfly are given by Arnold (1983).

PHENOLOGY: Adults begin emergence in late July or early August, and the flight continues until the middle of September.

FOODPLANTS: The foodplant is *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes ssp. *auriculatum* (Benth.) S. Stokes (Arnold, 1983).

2.) Cholame-Cottonwood Pass populations

DIAGNOSIS: A set of populations in the inner South Coast Ranges which are phenotypically most similar to nominate *langei*, but also show some influence of the more typical *A. m. mormo* phenotype.

DISTRIBUTION: These populations are found in the Pinnacles National Monument area in San Benito County and in the Cholame-Cottonwood Pass area in western Kern and eastern San Luis Obispo counties.

ELEVATION RANGE:

HABITAT AND PLANT COMMUNITIES: Dry, rocky to gravelly or sandy slopes, where *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes ssp. *indictum* is locally common.

PHENOLOGY: Univoltine, with adults flying from mid-August to late September.

FOODPLANTS: *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes ssp. *indictum* (G. Pratt, personal communication).

d. *A. m.* subspecies: Western Great Basin populations

1.) Mono Basin segregate

- DIAGNOSIS:** The phenotype of these populations is again fairly similar to nominate *mormo*, except that the ground color on the upperside tends to be slightly more gray and not blackish in ground color; additionally the white spots are slightly larger than in nominate *mormo*. Phenotypically similar populations occur northward along the east basin of the Sierra Nevada, such as in the Carson City and Reno, Nevada areas.
- DISTRIBUTION:** From the Mono Basin northward to the area around Reno, Nevada; the eastward limit in relation to other populations in the western Great Basin is rather poorly understood at this time.
- ELEVATION RANGE:** 5,000 to 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** Open flats or hillsides within the Sagebrush Scrub plant community.
- PHENOLOGY:** Univoltine, with adults flying from early August to early September.
- FOODPLANTS:** At Mono Lake, the butterfly is associated with *Eriogonum kearneyi* (J. F. Emmel, unpublished data). To the north, it seems associated with both *Eriogonum wrightii* Torr. ex Benth. and *E. umbellatum* Torr. (G. Austin, personal communication).

2.) Inyo-White Mountains region segregate

- DIAGNOSIS:** The phenotype of these populations is somewhat similar to nominate *mormo*, except that there is some gray overscaling dorsally, giving the butterfly a paler appearance, and orange to orange-brown scaling tends to invade the posterior half of the forewing in the discal area. Additionally, the white spotting tends to be more prominent. Adults average larger in size than nominate *mormo* populations.
- DISTRIBUTION:** This butterfly is found in the lower canyons of the Inyo and White Mountains where its foodplant, *Eriogonum heermannii* Dur. & Hilg. is locally abundant. It is phenotypically similar to populations in the western Great Basin mountains, and probably represents the westernmost extension of these populations.
- ELEVATION RANGE:**
- HABITAT AND PLANT COMMUNITIES:** Gravelly canyon slopes within the Shadscale Scrub and Sagebrush Scrub or Pinion-Juniper Woodland plant communities.
- PHENOLOGY:** Univoltine, with adults flying from late June to mid-August.
- FOODPLANTS:** Larvae have been collected on individuals of *Eriogonum heermannii* Dur. & Hilg. ssp. (G. Pratt and J. Emmel, unpublished data).

e. *A. m.* subspecies: Eastern Mojave Desert

- DIAGNOSIS:** The phenotype of these populations is characterized by large size and a grayish ground color with fairly prominent white spotting. Additionally, the orange-brown scaling on the forewing tends to invade the posterior half of the wing and

is also found in small patches in the discal area of the hindwing. Ventrally, there is a fair degree of contrast of the underside markings but with an overall pale appearance.

- DISTRIBUTION:** These populations are known throughout the ranges of the eastern Mojave Desert from the Old Woman Mountains on the south northward to the Kingston Range; from here they extend eastward into extreme southern Nevada.
- ELEVATION RANGE:** 4,000 to 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** Usually in open sandy washes or canyon bottoms within the mountain ranges of the eastern Mojave Desert; these habitats are usually located within the Pinyon-Juniper Woodland or Sagebrush Scrub plant communities.
- PHENOLOGY:** Univoltine, with adults flying from late August to late September.
- FOODPLANTS:** The butterfly is associated with *Eriogonum wrightii* Torr. ex Benth. ssp. *wrightii*, and *Eriogonum heermannii* Dur. & Hilg. ssp. (G. Pratt and J. Emmel, unpublished data). Additionally, the butterfly is closely associated with *Eriogonum microthecum* Nutt. ssp. at Hackberry Mountain in San Bernardino County and may use this *Eriogonum* as a foodplant also (G. Pratt and J. Emmel, unpublished data).

f. *A. m. cythera* (W. H. Edwards) and related segregates

- DIAGNOSIS:** This subspecies "is characterized by a greater extent of orange on both the upper and lower surfaces of the forewing, the orange subterminal band of the hindwing, and the pale, whitish underside of the hindwing" (Opler and Powell, 1961).
- ORIGINAL DESCRIPTION:** W. H. Edwards, *Transactions American Ent. Soc.*, 3: 345-346 (1873).
- TYPE LOCALITY:** "Arizona", restricted and corrected to 9 miles west of Lone Pine, Inyo County, California by F. M. Brown, *Transactions American Ent. Soc.*, 94: 116 (1968). Neotype in California Insect Survey Collection, designated by Opler, *in* F. M. Brown, *Transactions American Ent. Soc.*, 94: 119 (1968).
- DISTRIBUTION:** This subspecies and similar segregates are found along the east slope of the Sierra Nevada from approximately the area of Lake Crowley in Mono County southward along the east slope of the Sierra Nevada to the area west of Owens Lake. To the south, it seems to blend into populations of *A. m. tuolumnensis* of the extreme southern Sierra Nevada. Eastward, it ranges to the Inyo Mountains and the Cottonwood Mountains and Panamint Range, as well as the Coso and Argus Ranges. The populations in the Coso Range and Argus Range tend to be more orange and washed out than the Sierra Nevada populations.
- ELEVATION RANGE:** 5,000 to 7,500' elevation.
- HABITAT AND PLANT COMMUNITIES:** Open, sandy to gravelly to rocky slopes or flats within the Pinion-Juniper Woodland, Sagebrush Scrub, Joshua Tree Woodland, or Shadscale Scrub plant communities.
- PHENOLOGY:** Univoltine, with adults flying from mid-July to late August.
- FOODPLANTS:** Populations on the east slope of the Sierra Nevada are associated with *Eriogonum microthecum* Nutt. ssp. and *Eriogonum umbellatum* Torr. ssp. (J.

Emmel, unpublished data). In the Coso and Argus Ranges, the butterfly is associated with *Eriogonum umbellatum* Torr. ssp. *nevadense*; in the Cottonwood Mountains, it is associated with *E. heermannii* Dur. & Hilg. (J. Emmel, unpublished data). The Panamint Range populations seem to be primarily associated with *Eriogonum microthecum* Nutt. (J. Emmel, unpublished data).

g. *A. m. tuolumnensis* Opler and Powell

- DIAGNOSIS:** The phenotype of populations of this subspecies are characterized by a considerable amount of orange on the upperside combined with a slight reduction in the size of white spots, and a dark underside. The subspecies *tuolumnensis* and *cythera* are superficially similar on the upperside, but are readily distinguished by the marked differences in their underside coloration, with *cythera* being very pale and washed out and *tuolumnensis* being very dark and with a high contrast.
- ORIGINAL DESCRIPTION:** Opler and Powell, *Journal Lepidopterist Society*, 15: 159-160 (1962).
- TYPE LOCALITY:** Grand Canyon of the Tuolumne, Yosemite National Park, Tuolumne County, California. Holotype in California Academy of Sciences.
- DISTRIBUTION:** In the original description (Opler and Powell, 1961), this subspecies was thought to be confined to a geographically small area within the Grand Canyon of the Tuolumne River, in Tuolumne County. However, extensive studies of the populations of *A. mormo* in the mountains of southern California by J. Emmel and G. Pratt indicate that many of the late-summer-flying populations in these areas are referable to subspecies *tuolumnensis*. Phenotypically, they are virtually indistinguishable from topotypical material. *Tuolumnensis* populations are found from extreme southeastern San Luis Obispo County eastward through the Transverse Ranges along the north slope of the San Gabriel and San Bernardino Mountains, and northward into the Piute Mountains region of Kern County. Populations between the Piute Mountains region and the type locality on the west slope of the Sierra Nevada are not currently known, but should be looked for. *Tuolumnensis* populations are known from the east slope of the Sierra Nevada in the area near Ninemile Canyon near the Kern-Tulare County line, and from here they blend northward into subspecies *cythera*.
- ELEVATION RANGE:** 3,000 to 8,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** Populations are typically found on open slopes within the Pinion-Juniper Woodland, Sagebrush Scrub, Chaparral, or Montane Coniferous Forest plant communities.
- PHENOLOGY:** Univoltine, with adults flying from early August to mid-September, depending on elevation.
- FOODPLANTS:** Populations on the north slope of the San Gabriel and San Bernardino Mountains are associated with both *Eriogonum wrightii* Torr. ex Benth. and *E. heermannii* Dur. & Hilg. (J. Emmel and G. Pratt, unpublished data). In the Piute Mountains region, the butterfly is closely associated with *Eriogonum microthecum* Nutt. (G. Pratt, personal communication). In the type locality, the butterfly is closely associated with *Eriogonum wrightii* Torr. ex Benth. ssp. (O. Shields and J. Emmel, unpublished data).

GROUP II: Spring Through Fall-flying Adults, Multivoltine, Cismontane

h. *A. m. virgulti* (Behr) and related segregates

- DIAGNOSIS:** This subspecies is characterized by the distinct orange submarginal band of the hindwing, as well as reduced terminal band spots. Additionally, there is a lack of white scaling in the black ground color of the underside of the hindwing which contrasts sharply with the accompanying white spots. This is a subspecies of cismontane southern California and northern Baja California.
- ORIGINAL DESCRIPTION:** Behr, *Proceedings California Academy Natural Sciences*, 3: 178 (1865).
- TYPE LOCALITY:** Near Los Angeles, California. Type destroyed in San Francisco earthquake and fire 1906. Neotype designated by Emmel, Emmel, and Mattoon, *Journal Research Lepidoptera*, : (1988).
- DISTRIBUTION:** This subspecies is widely distributed in cismontane southern California from the extreme southern Coast Ranges in San Luis Obispo County southeastward through Santa Barbara and Ventura counties to the foothills and lower mountain regions of Los Angeles, western San Bernardino, western Riverside, and Orange and San Diego counties. From here, it extends southward into northern Baja California.
- ELEVATION RANGE:** From sea level to approximately 6,000' in the mountains.
- HABITAT AND PLANT COMMUNITIES:** The butterfly is most commonly found on hillsides, along roads, on broad, open, sandy washes, or stabilized sand dunes near the coast, primarily within the Coastal Sage Scrub and Chaparral plant communities. For the coastal dune populations, the associated plant community is Coastal Strand.
- PHENOLOGY:** This subspecies is multivoltine with a succession of broods ranging from February through November, depending on elevation, exposure, and temperature and precipitation pattern of the particular year. The spring brood is the largest, with the majority of captures recorded in the months of March and April. Populations referable to this subspecies overwinter as partly-grown to nearly full-grown larvae.
- FOODPLANTS:** The principle host for most *virgulti* populations is *Eriogonum fasciculatum* Benth. For this particular *Eriogonum* species, the butterfly has been closely associated with subspecies *fasciculatum* Benth., *foliolosum*, and *polifolium* (Benth.) S. Stokes. This subspecies is also associated with *Eriogonum parvifolium* Sm. in Rees. in the coastal dune populations

i. *A. m. near virgulti* (Peninsular Ranges)

GROUP III: Spring-flying Adults, Univoltine

j. *A. m.* subspecies (Kern County: eastern slope Piute Mountains and southern Sierra Nevada)

- DIAGNOSIS:** A set of populations characterized by univoltism, spring flight period, and increased orange scaling on the forewings dorsally on both sexes, combined with a more whitish underside than is seen in typical *virgulti*. Additionally, the white spots dorsally tend to be more prominent.

- DISTRIBUTION:** Populations with this phenotype are found in the Piute Mountains region of Kern County from approximately the Tulare-Kern county line southward through the Tehachapee Mountains. A possible blendzone with the next subspecies at the extreme western end of the Antelope Valley is postulated.
- HABITAT AND PLANT COMMUNITIES:** Open slopes within Joshua Tree Woodland or Pinion-Juniper Woodland plant communities, where *Eriogonum fasciculatum* Benth. is locally abundant.
- PHENOLOGY:** Univoltine, with adults flying from late March to late May, depending on elevation and temperature and precipitation patterns of the season.
- FOODPLANTS:** This butterfly is intimately associated with *Eriogonum fasciculatum* Benth. ssp. *polifolium* (Benth.) S. Stokes, which is undoubtedly the principal (and perhaps the only) host (J. Emmel and G. Pratt, unpublished data).

k. *A. m.* subspecies (North slope of San Gabriel-San Bernardino Mountains)

- DIAGNOSIS:** The phenotype of these populations is superficially similar to that of nominate *mormo*, except that there is usually a small amount of orange scaling dorsally in the discal area of the hindwing, and a small amount of orange scaling invades the posterior half of the forewing dorsally; the white spotting pattern is enhanced, rendering an appearance not unlike that of the montane Baja California subspecies, *dialeuca*. Ventrally, the phenotype is similar to *virgulti*.
- DISTRIBUTION:** Populations with this phenotype are found along the north slope of the Transverse Ranges from the west end of the San Gabriel Mountains eastward along the north slope of the San Bernardino Mountains and into the north slope of the Little San Bernardino Mountains in Joshua Tree National Monument. To the west, it extends as far as the Cuyama Valley of Santa Barbara and Ventura counties.
- HABITAT AND PLANT COMMUNITIES:** Open desert slopes within the Pinion-Juniper or Joshua Tree Woodland plant communities, where *Eriogonum fasciculatum* Benth. is locally common.
- PHENOLOGY:** Univoltine, with adults flying from mid-March to early May, depending on elevation and progression of the season. Populations of this subspecies overwinter as partly-grown to perhaps fully-grown larvae.
- FOODPLANTS:** The butterfly is closely associated with *Eriogonum fasciculatum* Benth. ssp. *polifolium* (Benth.) S. Stokes, undoubtedly the host.

l. *A. m.* near *dialeuca* Opler and Powell

- DIAGNOSIS:** True *dialeuca* is a subspecies of the high mountains of northern Baja California which is characterized by greatly enlarged white spots and accompanying reduction of orange scaling. In the San Bernardino Mountains, phenotypically extremely similar populations occur at the higher elevations and are here referred to as near *dialeuca*.
- ORIGINAL DESCRIPTION:** Opler and Powell, *Journal Lepidopterist Society*, 15: 167-168 (1962).
- TYPE LOCALITY:** Sierra San Pedro Martir, 5 miles northeast La Encantada, Baja California Norte, Mexico. Holotype in California Academy of Sciences.

- DISTRIBUTION:** Within California, populations with the *dialeuca* phenotype are found in the higher elevations of the San Bernardino Mountains in the vicinity of Sugarloaf Mountain and the upper Barton Flats area.
- ELEVATION RANGE:** 7,000 to 9,500' elevation.
- HABITAT AND PLANT COMMUNITIES:** Typically found on open, gravelly, mountain slopes within sparse Montane Coniferous Forests, where *Eriogonum wrightii* Torr. ex Benth. ssp. *subscaposum* (Wats.) S. Stokes is locally common.
- PHENOLOGY:** Univoltine, with adults flying from mid-May to mid-June. Apparent records for this subspecies from the Barton Flats region in September (Natural History Museum of Los Angeles County) are in fact referable to the *A. mormo* near nominate *mormo* populations which fly the eastern end of the San Bernardino Mountains in late summer and early fall.
- FOODPLANTS:** The butterfly is closely associated with *Eriogonum wrightii* Torr. ex Benth. ssp. *subscaposum* (Wats.) S. Stokes, and this is the presumed foodplant. G. Pratt (personal communication) has found a population near Holcomb Valley which is closely associated with *Eriogonum kennedyi* Porter in Wats.

GROUP IV: Spring Through Fall-flying Adults, Multivoltine, Low-elevation Desert.

m. *A. m. deserti* Barnes and McDunnough

- DIAGNOSIS:** This is a subspecies of the lower elevations in the deserts, characterized by a generally very pale, "washed out" appearance, rendered by an increase in white overscaling dorsally, as well as enlarged white spots. Ventrally, there is extensive white scaling, again giving a very pale gray appearance.
- ORIGINAL DESCRIPTION:** Barnes and McDunnough, *Contributions Natural History Lepidoptera North America*, 4: 75 (1918).
- TYPE LOCALITY:** La Puerta Valley, San Diego County, California. Holotype in U. S. National Museum.
- DISTRIBUTION:** This subspecies is widely distributed through our deserts at low to mid-elevations, from the Death Valley region southward through the Mojave and Colorado Desert into northern Baja California. Although Opler and Powell (1961) restricted true *deserti* to the populations along the western edge of the Colorado Desert, extensive sampling of other desert populations by G. Pratt and J. Emmel indicate that this name is properly applied to the vast majority of these populations in the Colorado and Mojave Deserts.
- ELEVATION RANGE:** From near sea level in the Coachella Valley area to approximately 5,000'.
- HABITAT AND PLANT COMMUNITIES:** Typically found within the Creosote Bush Scrub plant community in washes or on open flats or slopes, commonly in large desert valleys.
- PHENOLOGY:** This subspecies is multivoltine, with captures recorded for every month of the year, but with the spring (and largest) brood appearing primarily in March and April. Captures are then sporadic until September and October when there tends to be another more defined brood, presumably triggered by summer rains. This subspecies diapauses as a partly-grown to fully-grown larva, usually within the inflated stems of the foodplant.

FOODPLANTS: The principal host of this species is *Eriogonum inflatum* Torr. & Frem., which seems to be invariably present in any locality where the butterfly is taken. Additionally, larvae have been taken on *Eriogonum insigne*, and *E. plumatella* Dur. & Hilg. (G. Pratt and J. Emmel, unpublished data). One larva was collected on *Oxytheca perfoliata* T. & G. by G. Pratt (Polygonaceae). Pratt has also reared larvae in the laboratory on *Krameria* (); further investigation may reveal this as a naturally used host in the wild, as it is apparently used in New Mexico (G. Forbes,).

ADULT BEHAVIOR: In all populations of this species, the adult males commonly perch on the foodplant or on low shrubs near the foodplants, particularly along canyon bottoms or small ravines. Females tend to be more sedentary than the males, and spend much of their time landed on the host *Eriogonum* species. Both sexes are avid flower visitors, particularly in the late summer-flying populations. Attraction of the adults to damp sand or mud has not been noted. In many instances, the host *Eriogonum* will bloom at the time the adults fly, and this will serve as the primary nectar resource.

Arnold (1983) describes the courtship of *A. m. langei*. "Males fly out to investigate passing insects, and when a receptive female is encountered, both sexes perch. The male flutters his wings, touching the female and nudging her with his abdomen. If receptive, the female briefly flutters her wings and then assumes a quiescent posture. The male then approaches her and curls his abdomen to effect contact of the copulatory apparatus. Once *in copula*, the butterflies orient themselves on a suitable perch. The female generally is more active than the male during copulation. Copulations observed in the field lasted more than one hour in the mid- to late-afternoon, but none was observed in its entirety."

LIFE HISTORY: All of the segregates identified above in Groups I, II, and III share a common appearance in the egg, larval, and pupal stages. The subspecies in the fourth group, *deserti*, differs considerably. The egg of typical *Apodemia mormo mormo* is a delicate pink. The eggs are laid in small clusters of two to four on the drying lower leaves of the *Eriogonum* foodplants, or sometimes on the inflorescences. The mature *A. m. mormo* larva is a beautiful dark violet in ground color. The four subdorsal rows of pin cushions of spines have black bases and are themselves black along their lengths; each "pin cushion" arises from a semi-circular white spot. The lateral row of pin cushions of long hairy spines (below the spiracles) are yellowish-white in color and arise from a yellowish-white circle. The head is a mottled blackish color. In contrast, the mature larva of *A. m. deserti* is a delicate pink ground color. The pin cushions of spines are all pink and arise from black bases. On the dorsal surface, the whitish semi-circles found in typical *mormo* larvae around the two dorsal rows of spines have enlarged, and are bright yellow, nearly coalescing into a double band of yellow along the mid-dorsal line. Likewise, along the sides of the larvae, the white circles and semi-circles of the other rows have turned bright yellow in *deserti*, and have enlarged to form an almost bandlike appearance. The prolegs and thoracic legs are also pink in color, whereas in typical *mormo* these legs are purplish. The head of the *deserti* larva is a magenta purple, covered with light yellowish spines and hairs. The *deserti* larvae feed both on the epidermis of the stems and leaves, and the purplish-whitish flowers of the *Eriogonum*; thus, this coloration provides remarkable camouflage.

The pupae of the two sets of populations are quite different, also. The typical *mormo* pupa is deep purple in ground color with concolorous purple wing cases and ventral surfaces, and a pattern of black blotches on the dorsal surface, particularly on the abdomen. The *deserti* pupa, on the other hand, is a light

pinkish-purple or magenta in ground color. The wing cases of the *deserti* pupa are the same concolorless magenta, while there is a pattern of yellow blotches on the sides and top (either side of the mid-dorsal line) on the *deserti* pupa. The pupae of both sets of populations are covered with short, translucent hairs.

The larva of *Apodemia mormo deserti* makes a hole in the top of the inflated stem of *Eriogonum inflatum* Torr. & Frem., which is quite noticeable in the field and makes it possible to find the larvae fairly easily. The mature larva pupates inside this inflated stem and then the newly emerged adult crawls out through the hole. Diapause differs in the various subspecies and populations, as indicated in the preceding individual sections.

CHROMOSOME NUMBER:n = (Emmel, Pratt, and Eliazar, 1988).

SIMILAR SPECIES: None in our area.

GEOGRAPHIC AND SEASONAL VARIATION: These topics are discussed under the individual sets of populations above.

GENERAL REMARKS: The *Apodemia mormo* complex is obviously one that is still in a dynamic state of evolution, and it is impossible at the present time to assign rigorous taxonomic classification schemes to the overall pattern of radiation and adaptation. This fact actually makes the group even more interesting to study, and biochemical approaches being utilized by Gordon F. Pratt, life history studies underway by a number of workers, and further biogeographic analyses will prove a fertile ground for research for many years.

114. *Apodemia palmerii* (W. H. Edwards)

DIAGNOSIS: This jaunty and attractive little Metalmark species occurs in the Coachella, Imperial, and Colorado River valleys of southeastern California. It is a desert species that penetrates our area from Arizona and Mexico. This species apparently goes through several broods, depending on rainfall. It is puzzling that this butterfly's distribution in California should be so spotty and limited, considering the wide extent of distribution of its foodplant.

This butterfly can be immediately distinguished from our other Metalmarks by the soft grey ground color with white spots and orange margins on the upperside, and the pale orange underside with white bands. It is almost always associated closely with Mesquite.

ORIGINAL DESCRIPTION:W. H. Edwards, *Transactions American Ent. Soc.*, 3: 195 (1870).

TYPE LOCALITY: "Utah", restricted to St. George, Washington County, Utah, by F. M. Brown, *Transactions American Ent. Soc.*, 94: 121 (1968). Holotype in Carnegie Museum.

DISTRIBUTION: This species is found in several of the well-watered portions of our deserts, including the Colorado River Valley, the Imperial Valley, the Coachella Valley, the desert areas of eastern San Diego County, the Mojave River area from Barstow eastward to Afton Canyon, and the area in the vicinity of the Amargosa River in extreme northeastern San Bernardino County and southeastern Inyo County, where it is found both at Tecopa Springs and in Mesquite Valley east of the Kingston Range.

ELEVATION RANGE: From near sea level to 2,600' elevation.

- HABITAT AND PLANT COMMUNITIES:** This butterfly is typically found in desert riparian woodland vegetation or alkalai sink-salt grass meadow associations within the deserts. Usually, two species of mesquite are present in these localities, at least one of which serves as the primary foodplant of the larvae, although in the laboratory they can be reared on both. These two species are *Prosopis pubescens* Benth. (the principal host) and *P. juliflora* (Sw.) DC.
- PHENOLOGY:** The species is at least bivoltine and possibly trivoltine in most of these desert localities, with the first brood flying in late March through May, and summer and fall captures recorded from July through mid-October.
- ADULT BEHAVIOR:** The adults perch on the Screwbean Mesquite trees (*P. pubescens*) or visit flowers of *Haplopappus acradenius* (Greene) Blake.
- LIFE HISTORY:** The early stages have been described in great detail by Comstock and Dammers (1932). The light green egg is a flattened hemisphere, covered with hexagonal cells formed by raised walls. The mature larva is a pale bluish-green, with a lemon-yellow mid-dorsal line and a subdorsal line of similar color. Six rows of long whitish hair tufts are present. The pupa is a pale bluish-green with lighter, straw-colored wing cases. The larvae of this species spend their entire life, except while feeding, thoroughly concealed in a silk nest formed by the larva drawing two leaflets together on the host. During the winter, the larvae go through a very slow growth period but apparently never go into true hibernation. As soon as the new spring growth of the foodplant begins following spring rains, the larvae rapidly reach maturity and the adults emerge in the first annual brood.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** None in our area.
- GEOGRAPHIC AND SEASONAL VARIATION:** This butterfly occurs from southeastern California southeastward through Arizona, southern New Mexico, and both Baja California and mainland Mexico. A pale form with a conspicuous orange marginal band, called "*marginalis*" (Skinner) was named from California (type locality: Acme, near Tecopa, Inyo County, California). However, this form is not typical of the California populations, and the material that we have seen from this and other areas of California is best considered typical *Apodemia palmerii*.
- GENERAL REMARKS:** This species account concludes our treatment of the only two species of the genus *Apodemia* in California. There are other species of *Apodemia* in Mexico and Arizona, which could potentially reach our area from time to time as strays. The reader is referred to Howe (1975) for color illustrations and discussion of those species, should an unusual *Apodemia*-like Metalmark be taken in southern California.

115. *Calephelis nemesi* (W. H. Edwards)

- ADULT BEHAVIOR:** Males and females fly weakly about the foodplants and stay in close proximity to the shrubs. Adults frequently visit flowers to sip nectar and will also visit mud. The typical resting is with wings outspread and flattened towards the substrate.
- LIFE HISTORY:** The early stages were first described by Comstock and Dammers (1932). The eggs are reddish with white ridges and are deposited on the mid-rib of the host

leaves. The mature larva is dark grey, and is profusely covered with minute silvery nodules and rows of tufts of long, greyish-white and buff or (rarely) brown hairs. The dorsal linear arrangements of tufted hairs are inclined towards the center and thus meet over the larva's back, while the lower series extend horizontally and lie flat on the rather silvery whitish surface of the host plant leaf. The pupa is pale dirty yellow, with a few brown mid-dorsal and lateral dots and dash marks. Clumps of yellowish hairs are arranged over the surface. The pupa is suspended with a supporting thoracic girdle and silken button for attachment of the cremaster hooks, like a papilionid or pierid pupa.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: While superficially similar to the other *Calephelis* species, adults may be distinguished by reference to the Diagnosis sections in the text.

GEOGRAPHIC AND SEASONAL VARIATION: No seasonal variation has been observed in this multiple brooded species. However, considerable variation occurs within populations, with the color ranging from the normal dark brown to red-brown or nearly a rust color.

GENERAL REMARKS: This small reclusive butterfly that stays close to its foodplant may be easily overlooked, and additional populations should be found both in our coastal area and desert region.

Apparently, the last population in the urban area of Los Angeles was found in the Baldwin Hills in western Los Angeles during the 1950's, and may still survive on some of the steep slopes that have not been converted to housing. Its present status is unknown.

This small Metalmark species with drab upper wings but bright orange undersides, occurs along the Pacific Coast in southern California and Baja California Norte, and along the Colorado River at the Arizona border; from there, it extends through central and southern Arizona to southern Texas and most of northern Mexico. An outstandingly complete monographic treatment has been published on the whole genus of these taxonomically difficult butterflies (McAlpine, 1971). There are two subspecies that occur in our area.

a. *C. n. dammersi* McAlpine

DIAGNOSIS: The best known area for the Dammer's Metalmark is from the Colorado River Valley around the city of Blythe. It is notably lighter in color and smaller than *C. n. californica*; genitalic differences between the subspecies exist. The upper surface is a fairly light brown without much reddish tinge crossed by a blackish band. The metallic markings are relatively inconspicuous.

ORIGINAL DESCRIPTION: McAlpine, *Journal Research Lepidoptera*, 10: 31-34 (1971).

TYPE LOCALITY: Blythe, Riverside County, California. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This subspecies is distributed along the lower Colorado River Valley, with populations recorded at Bard, Blythe, and the Parker Dam area.

ELEVATION RANGE: 100 to 400' elevation.

HABITAT AND PLANT

- COMMUNITIES: This species typically occurs in Desert Riparian Woodland.
- PHENOLOGY: This subspecies is known to be multivoltine in the lower Colorado River Valley, with captures recorded from July through November.
- ADULT BEHAVIOR: This Metalmark has a weak, fluttering flight and stays in close proximity. Adults sip flower nectar and mud, and the typical resting position in these activities is with the wings spread flatly.
- FOODPLANTS: *Baccharis glutinosa* Pers. (*Compositae*) is the sole recorded foodplant for this subspecies.

b. *C. n. californica* McAlpine

- DIAGNOSIS: This Metalmark is darker in color (actually a pale chocolate brown) than the preceding form, and both forewings and hindwings are crossed in the middle by a prominent, irregular, darker brown shade in the form of a band. This is primarily a coastal subspecies in southern California.
- ORIGINAL DESCRIPTION: McAlpine, *Journal Research Lepidoptera*, 10: 34-35 (1971).
- TYPE LOCALITY: Riverside, Riverside County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: The Dusky Metalmark is distributed generally in the lower canyons and chaparral areas near the coast in Los Angeles, Orange, western Riverside, and San Diego counties. We also have one record from the Santa Susana Mountains in Ventura County.
- ELEVATION RANGE: From near sea level to 2,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This subspecies is found primarily in either the Coastal Sage Scrub plant community where *Encelia californica* Nutt. grows or in riparian situations in the Cismontane valleys, such as near Riverside along the Santa Ana River where *Baccharis glutinosa* Pers. grows.
- PHENOLOGY: The flight period is recorded from early February to early October, and probably involves three broods near the coast.
- FOODPLANTS: *Baccharis glutinosa* Pers. (*Compositae*) in Riverside County, and *Encelia californica* Nutt. (*Compositae*) in the coastal populations, including the Santa Monica Mountains and Baldwin Hills in Los Angeles County where *B. glutinosa* Pers. does not occur.

116. *Calephelis wrighti* Holland

Wright's Metalmark flies on the Colorado Desert and some parts of Cismontane southern California adjacent to the desert, as well as into southwestern Arizona and northern Mexico. It can be taken in fair abundance in the canyons along the western border of the Colorado Desert from March to October, with the timing of the summer and fall broods depending upon summer rains.

- DIAGNOSIS: This Metalmark species is a rather uniform reddish-brown dorsally, and the entire surface seems to be overlaid with a faint delicate whitish sheen in fresh specimens. The fringes on both forewings and hindwings are conspicuously checkered in

white. This species has a more uniform color on the upperside than in any other *Calephelis*. These diagnostic characters, along with the genitalia (McAlpine, 1971), distinguish this species readily.

ORIGINAL DESCRIPTION: Holland, *Annals Carnegie Museum*, 20: 5-6 (1930).

- TYPE LOCALITY: The species was described on the basis of the figures published by Wright in *The Butterflies of the West Coast* (1906). The types at the California Academy of Sciences bear no locality label. Holland (1930) suggests a type locality near Mendocino, California, but Tilden, *Occasional Papers California Academy Natural Sciences*, (118): 30 (1975) suggests oases in southern California deserts. Our studies of the collecting activities and locations of William Greenwood Wright suggests the type locality was in the northwestern Coachella Valley, in the vicinity of Palm Springs. Holotype in California Academy of Natural Sciences.
- DISTRIBUTION: The species is found in the canyons and washes bordering the lower Colorado River Valley from the Whipple Mountains south to the Yuma area, the canyons and washes bordering the Imperial and Coachella Valleys and the semi-desert canyons of San Diego County, western Riverside County, and extreme southwestern San Bernardino County. Some populations are found along the southern edge of the Mojave Desert such as in the Old Woman Mountains, and occasional captures are recorded for the eastern Mojave Desert, such as in the Providence Mountains and New York Mountains. A very disjunct population is known from Great Falls Canyon in the southern Argus Range in southern Inyo County. The nearest population of *C. wrightii* to the southeast of this locality would be in Morongo Valley, at the east end of the San Bernardino Mountains.
- ELEVATION RANGE: Our captures range from near sea level in the lower desert valleys to as high as 5,500', with most records below about 2,500' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterflies are found only in close association with the foodplant, *Bebbia*, a bush Composite which typically grows along dry washes or rocky slopes in desert or semi-desert situations. Thus, the typical habitat is in washes that lie within the Creosote Bush Scrub or Chaparral plant communities.
- PHENOLOGY: Captures have been recorded in the every month of the year, from January to December, but with peaks in March and April and again in July to September.
- ADULT BEHAVIOR: This weakly flying butterfly stays very close to its foodplant. Adults sip host plant flower nectar, and males frequently perch on the larval host leaves or nearby and may patrol, seeking females.
- LIFE HISTORY: The early stages were described initially by Comstock (1928b?), under the misnomer, *Calephelis australis* Edwards. The egg is about 0.6 mm. in diameter and is echinoid (like a sea urchin skeleton) in shape; it is covered with deep hexagonally shaped cells. The last mature larva is greyish-white, the surface covered with raised white nodules. Rows of other nodules bear long filamentous white hairs. The spiracles are yellow and above each spiracle is a lighter, irregular square-shaped area, margined above with black. The pupa is a light greyish-green, with brownish tinges on the abdomen and on the posterior surface. A series of tubercles bearing short hairs occur over the pupal surface except on the bare wing covers.

FOODPLANTS: The sole known foodplant is *Bebbia juncea* (Benth.) Greene (Compositae). The larva feeds on the greenish epidermis of the stems. Pupation occurs in degree at the base of the plant.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: See Diagnosis sections of the other *Calephelis* in our state.

GEOGRAPHIC AND SEASONAL VARIATION: There are is some variation in ground color, in intensity of the metallic markings and in the smokey or whitish sheen that overlays the wings. No geographic variation within the species has been defined.

GENERAL REMARKS: The curiously scattered distribution of the butterfly is in contrast to the cosmopolitan widespread distribution of the foodplant, which is a common desert shrub across southern California and into the Chaparral on the coastal side of the mountains. Some populations are extraordinarily isolated in the desert areas, as for example the one at Great Falls Canyon in the Argus Range.

LYCAENIDAE

Excluding the metalmarks, the family Lycaenidae is divided into three major subfamilies found in our region. The family comprises some 6,000 species worldwide and is the largest family of butterflies. The subfamily Theclinae, or hairstreaks, is a large diverse group, whose members usually have a hindwing bearing one or two tails. Males commonly have noticeable patches of scent scales or androconia near the leading edge of the forewing dorsal surface. We have 33 species recorded from California. The subfamily Lycaeninae, or coppers, is most diverse in the holarctic, although occurring in limited numbers elsewhere in both the temperate zones and the tropics. We have 12 species in California. Most members of this group are characterized by a bright coppery orange or purplish or yellow color of the wings. The third subfamily, Polyommatae, or Blues, is represented by 26 species in California but a huge number of subspecies due to the sedentary habits of the adults and the highly fragmented distribution of many of the species, allowing local evolutionary adaptation changes and variation to occur.

The hairstreaks, coppers, and blues of the family Lycaenidae are characterized by having the following characteristics: (1) four walking legs (the forelegs somewhat reduced) in the male, with six functional legs in the female; (2) no epiphysis projecting from the tibia in either sex; (3) the feet reduced to one segment and one tarsal claw in the male, but fully developed and functional feet in the female with five segments and two terminal claws; (4) clubbed and scaled antennae; (5) eyes indented or notched around the bases of the antennae, due to the proximity of the antennal bases to the margin of the eye; (6) very narrow head in relation to the width of the thorax, with short palpi; (7) several radius veins lacking in the forewing and no humeral vein in the hindwing; (8) wings held vertically after landing, in contrast to the metalmarks which hold their wings spread after landing; (9) flattened and sluglike in most species, covered with a smooth minute pile of translucent hairs; (10) a stout, naked brown or tan or greenish pupa, covered with a minute pile.

* * * * *

Subfamily Theclinae Swainson

117. *Habrodais grunus* (Boisduval)

ADULT BEHAVIOR: The adults have apparently never been observed feeding on flowers but have been seen to drink at mud. It would be unusual for a hairstreak species not to feed on nectar. Also, because of the relatively long flight season of the species, adults would need an energy and perhaps an amino acid source from nectar, sap, fruit juices, or animal materials. The species is apparently univoltine throughout its

area of distribution. Males will patrol in the early to late afternoon around the canopy of trees, seeking females. In the hottest part of the day, however, large numbers of adults will retreat to shaded dense understory cover, perching there, occasionally interacting, but most butterflies (especially the older, faded, late season adults) remain relatively quiescent.

LIFE HISTORY: The species overwinters in the egg stage (concealed on oak twigs). The larvae then feed on the tender new growth of the oak or other host in the spring months. The slug-shaped mature larva is pale bluish-green in ground color, with many raised tan dots, each supporting a single silvery white hair. There is a sub-dorsal white or pale yellowish line along the body. Immediate behind the flattened head is a cervical shield, below which the head can be withdrawn; the shield area is free of hairs. The pupa is pale bluish-green and is covered with short minute white hairs, as well as brown dots of various sizes. Pupation occurs on the foodplant, using a cremaster and a silken girdle for support. This usually takes place on the underside of leaves where the pupa tends to match the gray to golden undersurface of the oak leaf. The pupal stage lasts fifteen days (Comstock and Dammers, 1935a).

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: This is the only species in this genus and no similar species occur in our fauna.

GEOGRAPHIC AND SEASONAL VARIATION: The two subspecies listed above are the only two in California. Areas of blending between them are broad, and populations are best examined in series. A third subspecies described by William D. Field (1935), *H. g. herri*, is restricted to the Cascades of central Oregon. It is characterized by more orange on the dorsal surface, with the light areas being greatly extended and almost yellow in some specimens. Ventrally, all markings are very faint and almost obliterated. There is a fourth entity in northern Baja California, *H. poodiae*, named as a species but which Scott (1986) considers a subspecies of *H. grunus*. It is very light and mostly ochre-yellow on the dorsal surfaces. *H. grunus* reappears in central Arizona on Mt. Graham and the Mogollon Rim. This curious isolation of the Arizona populations from the coastal and mountain Pacific Coast *grunus* populations needs further investigation.

GENERAL REMARKS: The distribution of the potential foodplants for this species is considerably wider than the presently known distribution of *Habrodais grunus* populations. This is one of two hairstreaks (the other being in the genus *Hypaurotis*, which is found in Colorado, New Mexico, Arizona, and eastern Utah) which has eleven forewing veins and are our North American representatives of a group that is common in Europe and Asia. Most hairstreaks have only ten forewing veins and this group, which is very common in the American tropics, has only a few species occurring in the Old World. *Habrodais grunus* and *Hypaurotis crysahus* also share the behavioral similarity of a tendency to retreat to shade during the heat of the day.

Boisduval's hairstreak occurs throughout the Oak Belt and Transition Zone of the foothills and mountains of California. It ranges from northern Baja California east into a disjunct distribution in Arizona, and north in the Sierra Nevada Range into adjacent Nevada. It continues north through Oregon to the Columbia River and southern Washington. Within our state it occurs in two subspecific forms.

a. *H. g. grunus* (Boisduval)

- DIAGNOSIS: On the dorsal surface of the wing the basal areas are orange-brown, becoming darker towards the margins. On the underside the butterfly is a concolorous light ochre with a faint irregular mesial band of dark brown extending across both wings. This band tends to become more pronounced in old faded flown specimens but when fresh usually contains a few discal white scales. The hindwing bears a faint submarginal row of dark crescents, sprinkled with blue near the anal angle, and a solitary black dot often present in the cell just anterior to the tail.
- ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 289 (1852).
- TYPE LOCALITY: "California". Restricted to Lower Feather River Canyon, Butte County, California, by Emmel, Emmel, and Mattoon, Natural History Museum of Los Angeles County Contributions in Science, : (1989). Neotype designated by Emmel, Emmel, and Mattoon (1989) and placed in the Natural History Museum of Los Angeles County.
- DISTRIBUTION: The distribution of the typical subspecies ranges through the foothills and mountains of southern California, from San Diego County to Santa Barbara County and Kern County, thence northward on the west slope of the Sierra Nevada to the Mt. Shasta region and Klamath Mountains Assemblage. A broad area of blending exists with subspecies *lorquini* south of the Trinity Mountains in the North Coast Range. Scattered populations occur on the east slope of the Sierra Nevada in Inyo County as far north as the latitude of Independence.
- ELEVATION RANGE: From near sea level to 6,500' elevation; rarely taken as a stray to 7,500' elevation in the Lake Tahoe region.
- HABITAT AND PLANT COMMUNITIES: The usual habitat is in open forested areas, particularly along roads, watercourses, and in clearings, wherever its oak foodplants grow, within the following plant communities: Foothill Woodland, Northern Oak Woodland, Northern Mixed Evergreen Forest, and Southern Mixed Evergreen Forest.
- PHENOLOGY: This subspecies is univoltine and flies from mid-June to early October; a peak flight in July is followed by a long adult flight period. Studies of adult longevity are presently lacking but would be of interest to confirm the apparent long adult lifespan of this particular lycaenid.
- FOODPLANTS: *Quercus chrysolepis* Liebm. (Golden Oak) is the apparent preferred foodplant in California. Also used as hosts are *Q. vaccinifolia*, *Castanopsis chrysophylla*, and *Lithocarpus densiflora* (all Fagaceae) (J. F. Emmel and S. O. Mattoon, unpublished data). Mattoon has also observed adults in close association with *Quercus sadleriana* in Del Norte County; this oak species may represent an additional foodplant.

b. *H. g. lorquini* Field

- DIAGNOSIS: This subspecies is darker than nominate *grunus* and has wider dark margins dorsally. On the ventral surface, the ground color is a darker ochre and the sinuous mesial band of dark brown as well as the submarginal row of crescents is more prominent. Females are substantially paler than males.
- ORIGINAL DESCRIPTION: W. D. Field, *Bulletin Southern California Academy Sciences*, 37: 27 (1938).
- TYPE LOCALITY: Mt. Diablo, Contra Costa County, California. Holotype in Allyn Museum of Entomology.

- DISTRIBUTION:** This darker subspecies is found in the South Coast Ranges, from Santa Clara County and Monterey County northward through Alameda, Contra Costa, and Santa Cruz counties to the North Coast Ranges of Marin, Sonoma, Napa, and Mendocino counties. From Mendocino and Lake counties northward to Humboldt and Trinity counties, there are populations intermediate in phenotype between nominotypical *grunus* and *lorquini*.
- ELEVATION RANGE:** From approximately 1,000' to 4,500' elevation.
- HABITAT AND PLANT COMMUNITIES:** This butterfly resides in open forested areas, usually in Foothill Woodland, or Northern Mixed Evergreen Forest.
- PHENOLOGY:** The flight period extends from early July to mid-August, and occasionally into early September. We have one record for early May from Alameda County.
- FOODPLANTS:** *Quercus chrysolepis* Liebm. and *Lithocarpus densiflorus* (H. & A.) Rehd. (Fagaceae) are the principal foodplants of this subspecies (J. F. Emmel and S. O. Mattoon, unpublished data).

118. *Chlorostymon simaethis sarita* (Skinner)

The nominate subspecies of this butterfly is not found in California, but occurs throughout the Caribbean as far north as Cuba. Our subspecies occurs from southern Texas to southern California, as well as south into Baja California and the American tropics on the mainland.

- DIAGNOSIS:** The dorsal surface of the wings are iridescent purple in the male. The darker female largely lacks this iridescence. On the ventral surface the wings of both sexes are a light yellow-green, with a prominent pearly-white post-median line edged with brown scales. There is also a wide brown hoary marginal band which tapers to the outer angle of the hindwing.

ORIGINAL DESCRIPTION: Skinner, *Entomological News*, 6: 112 (1895).

- TYPE LOCALITY:** Comal County, Texas. Holotype in Carnegie Museum.
- DISTRIBUTION:** This exquisite little hairstreak with yellow-green undersides is found as a straggler in San Diego County: it is resident and often abundant in Baja California just across the border. Most of our southern California records are from October in the Mason Valley and Vallecitos Creek area of San Diego County. We have one record from Palm Springs in Riverside County. The presumed foodplant in Mexico does not occur here.
- ELEVATION RANGE:** At about 1,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** This butterfly occurs in the lower chaparral margins.
- PHENOLOGY:** All records to date are in the month of October, from early to late in the month.
- ADULT BEHAVIOR:** In Texas, where the species flies in numbers in November and December, and in Baja California where the species flies in the spring as well as the fall, and is therefore at least double brooded, the adults fly in a quick darting flight among the near desert shrubs.

LIFE HISTORY: Unknown.

FOODPLANTS: In Baja California, the butterfly is found in association with Balloon Vine (*Cardiospermum*), possibly the larval host.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: None in our area.

GEOGRAPHIC AND SEASONAL VARIATION: None in our area. The species is actually rather remarkably stable over a wide distribution from South America to the southern tip of the United States.

GENERAL REMARKS: While this butterfly is probably resident in south Texas, it appears to be a straggler in San Diego County and does not form breeding populations. There are the only two states in which it is regularly found. Surprisingly it does not reach Florida, although it occurs in Cuba.

119. *Harknenus titus occidentalis* Austin and Emmel

This widespread hairstreak occurs in the southern part of Canada and across most of the United States, except for the Gulf Coast and the extreme southwest. In the western United States, it is found in scattered colonies and usually in limited numbers. The subspecies that was formerly believed to have reached California, *immaculosus* (William P. Comstock), ranges from Manitoba south to central New Mexico and west to Vancouver, Washington across the Great Basin.

DIAGNOSIS: This subspecies of *H. titus* occurs in the extreme western Great Basin, and is characterized by a tendency dorsally to have fewer submarginal orange spots on the hindwing of both sexes than that of the geographically nearest subspecies *H. t. immaculosus*. Additionally, the ventral surface of *H. t. occidentalis* is a pale tan with rather bold black post-median spots, in contrast to *H. t. immaculosus* which tends to be darker brown with small and faint spots.

ORIGINAL DESCRIPTION: Austin and Emmel, *Journal Research Lepidopterist*, : (1988).

TYPE LOCALITY: Star Creek Canyon, 5 to 6 miles west of Nevada State Route 400, Humboldt Range, 1890 meters, T31N, R34E, S22 on U.S.G.S. Imlay, Nev., 15", Pershing County, Nevada.

DISTRIBUTION: This subspecies occurs in northwestern Nevada in Pershing County, Humboldt County, and Washoe County. In northeastern California, subspecies *occidentalis* occurs in Modoc County (in the Warner Mountains), Plumas County (Lake Almanor), Lassen County (Hallelujah Junction), and Siskiyou County (Bigelow Meadows near McCloud, California).

ELEVATION RANGE: From approximately 4,500' to 6,500' elevation.

HABITAT AND PLANT COMMUNITIES: Our California populations are usually found in the fringes of the Northern Juniper Woodland plant community with abundant Sagebrush Scrub. But a few locations are within Coniferous Forest settings where these other communities invade. It is a subspecies that is always in association with several species of native *Prunus*, of which only one probably serves as a larval host.

- PHENOLOGY:** This species begins flying in early July and flies at least through mid-August with an apparent peak in late July.
- ADULT BEHAVIOR:** This is an avid nectaring species. In the Warner Mountains, it uses *Apocynum* sp. (Dogbane) and *Trifolium* (White Sweet Clover). The nectar source is usually adjacent to the native *Prunus* host. This close association of adult and larval foodplants is apparently necessary and possibly provides the reason that seemingly suitable areas of larval host plant are not utilized elsewhere in the northeastern state. At all *titus* locations with which we are familiar, there is always an abundant annual nectar source.
- LIFE HISTORY:** The eggs are laid on the twigs of wild *Prunus* species and hatch the following spring. They are pale green in color, turning white. Both in the field and in the laboratory, the larvae tend to feed on the leaves during the night and rest at the plant base during the day. The mature larva is green, with yellowish-green chevrons covering the dorsal surface of each segment, and also a lateral diagonal slash on each segment. On the last three abdominal segments, there is a lateral magenta band of color which unites with a magenta band coming back from the third abdominal prolegs segment and expanding to the anal region. The magenta marking arrangement is present also on the dorsal anterior end of the larva just behind the head, starting as a broad triangle on the first thoracic segment and rapidly tapering to a tiny point by the third thoracic leg segment. The head is green. The pupa is a pale brown covered with small black dots and blotches. It also bears a darker brown blotching around the head but no dorsal or ventral stripe as apparently found in other *titus* subspecies. The above descriptions are from Modoc County material.
- FOODPLANTS:** In our area, the butterfly is associated with *Prunus virginiana* L. var. *demissa* (Nutt.) Sarg. (Family Rosaceae). At the Fort Bidwell (Modoc County) location, Wild Apricot also grows interspersed with *P. virginiana*, but we do not suspect it to be a host. Gordon Pratt showed us the two *Prunus* species at that spot.
- CHROMOSOME NUMBER:** $n =$
- SIMILAR SPECIES:** None in our area. This is a tailless hairstreak species.
- GEOGRAPHIC AND SEASONAL VARIATION:** None within our populations. Elsewhere three subspecies have been identified across the United States, with *mopsis* from Kansas east to the Atlantic Coast, *watsoni* in southern Oklahoma, northeastern New Mexico and Texas; and *immaculosus* in the Rocky Mountains to the Pacific Northwest.
- GENERAL REMARKS:** Because the foodplant is widespread and is used by other butterflies which are virtually cosmopolitan within the state, such as *Papilio multicaudatus*, it is curious that this butterfly has not become more widely distributed. One common factor noted in *titus* colonies is an annually-reliable, stable source of nectar available to *titus* adults right in the breeding area. This subspecies is an avid nectarer and many apparently-suitable habitats do not appear to have reliable annual nectar sources.

120. *Satyrrium californica* (W. H. Edwards)

- ADULT BEHAVIOR:** Emergence begins in June at lower elevations, and in July at the higher elevations. The adults frequently visit flowers and may be quite abundant at times. Males will perch on tree leaves and sometimes around the tops of trees, especially if on hilltops, from mid-afternoon to dusk to await females.

LIFE HISTORY: The mature larva is grey-brown with large subovate grey spots, one to a segment, in the mid-dorsal region. Lateral to these spots are narrow, white chevron markings. Immediately below the level of the spiracles is a white lateral band bordered on either edge by dark brown shading. The head has a greyish-brown ground color. The surface of the larva and head is covered by short tiny hairs. The abdominal surface is greyish-green or soiled ivory. The pupa is red-brown with ivory-green wingcases; the surface is mottled with black spots. The early stages were first described by Comstock (1933).

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: Within some localities *californica* is sympatric with *S. sylvinus*. The former may be distinguished by its darker brown color on the underside. However, in some areas, the coloration of *sylvinus* populations can become confusingly parallel to that of *californica*.

GEOGRAPHIC AND SEASONAL VARIATION: This species is univoltine and so there is no seasonal variation. The populations of *californica* vary somewhat in markings, but most specimens are referable to the two subspecies listed above. In the nominate subspecies, there is a gradual increase in size of adults, slight increase in the dark ground color, and a slight increase in the extent of orange patching from the central Sierra Nevada northward into the Southern Cascades. The increase in orange flush may be accounted for from gene exchange with the Sacramento Valley populations that at one time may have been much more extensive before removal of so much of the Valley or Roble Oak.

There is in northern California a set of populations that still inhabits the native undisturbed stands of *Quercus lobata* (Valley or Roble Oak) on the Sacramento Valley floor. The phenotype which is smaller and slightly darker is sufficiently different to warrant perhaps subspecific differentiation. Here, these appear to be a parallel wing pattern development to the other arid zone subspecies *cygnus* in the amount of both dorsal and ventral orange patch development which is more red-orange and equals or often exceeds the amount on both wings on both sexes. This remnant set of populations probably once existed all over the more arid Sacramento Valley floor in the pristine original state of that region. They are still plentiful in some locations, and this morph extends to the lower edge of the foothills and Lobata. In both the Cascade and Coast Range foothills, there may be some blend into typical *californica*. La Due and others have reported this Valley Oak association as far south as Sacramento County. These, of course, are the first *californica* to fly seasonally in northern California due to the low elevation of their habitat.

GENERAL REMARKS: The coloration of the larva in this species is not cryptic on leaves, but is cryptic on tree bark or mixed litter. This leads us to the supposition that the larvae probably feed principally at night on the leaves, and then retreat during the daytime to areas of hiding on the bark or in the ground litter at the base of the foodplant. This supposition is also supported by the fact that many workers have tried to beat larvae from the leaves of the foodplant, but never found them during diurnal searching, whereas they can be beaten from the same plants at night.

This behavior and dark cryptic coloration is reminiscent of a related species in Michigan, *Satyrium edwardsii*, which is tended by ants. The ants keep the larvae in conical structures of detritus (termed *byers*) which are constructed by the ants. The larvae leave the byers at dusk, feed nocturnally, and are usually surrounded

by a group of attending ants. This symbiotic relationship in *edwardsii* has been recently described by Webster and Nielsen (1984). In Michigan, too, this *Satyrium* species feeds on two species of Oaks in the genus *Quercus*. The fourth instar larvae produce honey-dew on which the ants feed.

It is also of interest that Downey (1966) and Webster and Nielsen (1984) have reported that the pupae of seven *Satyrium* species produce a faint creaking or rattling sound after being disturbed. The stridulatory organs are located between the fifth and sixth abdominal segments and produce the noise when these segments are rapidly moved. In a tropical Metalmark, *Anatole rossi* Clench, these stridulatory organs (in combination with pupal glands on the last thoracic segment) appear to serve as ant-attractant organs (Ross, 1964, 1966).

The very complicated myrmecophilous relationship between *Satyrium edwardsii* and the Michigan ant species, *Formica integra*, is one of the more advanced symbioses known among any of the North American Lycaenidae and ants. It would be very interesting to learn if a similar symbiosis occurs in our California *Satyrium*.

This is a widespread species in the western United States, and it is also often taken on flowers in a variety of habitats. It ranges from southern British Columbia south to California and eastward to the Rocky Mountains. Two subspecies are recognized, both of which occur in California.

a. *S. c. californica* (W. H. Edwards)

DIAGNOSIS: We apply the nomotypical subspecies name to all *S. californica* populations on the west slope of the Sierra Nevada and most of the Cascade Range mountains of southern California, and those populations in the Coast Ranges as well as the Klamath Mountains region. In this subspecies, both sexes tend to be uniform dark brown above with some development of orange scaling on both the forewing and the hindwing in the females, and little or no orange scaling on the hindwing of the male near the anal angle. On the underside, both sexes have a dark grey-brown ground color with a small amount of orange scaling near the anal angle of the hindwing in both sexes, and reduced amount of orange scaling near the posterior margin on the outer part of the forewing on females.

ORIGINAL DESCRIPTION: W. H. Edwards, *Proceedings Academy Natural Sciences Philadelphia*, 14: 223 (1862).

TYPE LOCALITY: "California", restricted to Capell Creek, 9 miles NNE of Napa, Napa County, California, by Opler, in F. M. Brown, *Transactions American Ent. Soc.*, 96: 41-43 (1970). Neotype in Carnegie Museum, designated by Opler in F. M. Brown (1970).

DISTRIBUTION: This subspecies is widespread in the state from the mountains of southern California northward through both the Coast Ranges, and the west slope of the Sierra Nevada, extending north in the Southern Cascade Range to the Mt. Shasta region, and through portions of the Klamath Mountains Assemblage.

ELEVATION RANGE: From 1,500 to about 8,000' elevation.

HABITAT AND PLANT COMMUNITIES: This inhabitant of our mountain forested areas is found in canyons, hillsides, and mountain slopes in several plant communities, including Montane Coniferous forests, Chaparral, Foothill Woodland, Northern Oak Woodland, and Southern Oak Woodland, and Riparian Woodland.

PHENOLOGY: Strictly univoltine, with adults appearing in mid-May to mid-June at the lower elevations, and July to early August at the higher elevations.

FOODPLANTS: Larvae have been found on both *Ceanothus cuneatus* (Hook.) Nutt. (Rhamnaceae), and *Quercus wislizenii* A. DC. (Fagaceae) (G. Pratt and G. Ballmer, personal communication). It is strongly associated with *Quercus kelloggi* and other oaks in the northern mountains.

b. *S. c. cygnus* (W. H. Edwards)

DIAGNOSIS: This subspecies is found on the high east slope of the Sierra Nevada and in adjacent western Nevada. The adults of this subspecies tend to be larger than those of typical *californica*, and are characterized by an increased amount of orange scaling on the upperside and an increased amount of red-orange scaling on the underside, in both sexes. In particular, males of this subspecies, which in subspecies *californica* have little or no orange scaling on the upperside, almost invariably have at least some significant orange scaling on the anal angle of the hindwing.

ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Ent. Soc.*, 3: 207-208 (1871).

TYPE LOCALITY: "Nevada", restricted to 3 miles SW of Virginia City, 6,700', Storey County, Nevada by Opler, in F. M. Brown, *Transactions American Ent. Soc.*, 96: 45-46 (1970). Neotype in Carnegie Museum, designated by Opler, in F. M. Brown (1970).

DISTRIBUTION: This subspecies is found from the high east slope of the Sierra Nevada in extreme northwestern Inyo County northward through the Mammoth Lakes region, and the area above the Walker River Canyon northward into western Nevada in the vicinity of Virginia City, Nevada. It is also found in the White Mountains of Inyo and Mono counties. The precise limits of its distribution in western Nevada are not determined at this time, but it is well established in the Warner Mountains of extreme northeastern California in Modoc and Lassen counties. It ranges in scattered populations westward through the Modoc Plateau, along dry-forested, predominantly oak-clad slopes on the margins of the Sagebrush flats and valleys that penetrate through the Cascade Range to the Shasta Valley of Siskiyou County. *Cygnus* also follows the Klamath River Drainage southward to penetrate into the Scott Valley area in the Klamath Mountain region. While this most western penetration may not be entirely typical *cygnus*, it is much closer in facies to it than to nomotypical *californica*.

ELEVATION RANGE: From approximately 6,500 to 10,000' elevation.

HABITAT AND PLANT COMMUNITIES: This butterfly is typically found on the more arid Sagebrush slopes of the eastern Sierra Nevada, where the Great Basin Sage Scrub and Juniper Woodland plant communities are dominant. Often, it is also found in openings within the extensive Jeffrey Pine Forest in this area where small islands of Sage Scrub exist or similarly in Ponderosa Pine, Douglas Fir, and Oak Forest with Sagebrush Scrub to the north. Typical plants associated with its habitat are *Artemisia tridentata* Nutt., *Purshia tridentata* (Pursh) DC., and *Eriogonum umbellatum* Torr.

PHENOLOGY: As with the nomotypical subspecies, this butterfly is also univoltine, flying from late June into early August, with an apparent peak in mid- to late-July.

FOODPLANTS: At least one host of this butterfly is *Purshia tridentata* (Pursh) DC., on which oviposition has been observed (David Bauer, personal communication).

121. *Satyrium sylvinus* (Boisduval)

ADULT BEHAVIOR: The males habitually perch on low Willows, awaiting females, and both sexes avidly visit flowers. Dogbane (*Apocynum* species) and Milkweed (*Asclepias* species) are strongly attractive nectar sources for these butterflies. An interesting mating behavior was observed by Mattoon along the dry wash of Long Valley Creek near Herlong, Lassen County, where dozens of mating pairs were seen resting on the willow in the wash under strongly windy conditions. The copulating pairs were all on the leeward side of the plants. All copulating pairs were of older flown and chipped individuals, indicating a delayed timing for mating in the flight period or multiple matings for an individual female. The mating time was also interesting, as it was almost 5:00 p.m. in the late afternoon.

LIFE HISTORY: The life history has been previously described by several authors (Comstock and Dammers, 1934; Emmel and Emmel, 1968). The pale greenish-white eggs are laid singly on the willow stems. The mature larva is a pale apple green. There is a subdorsal, thin white band on either side of the center of the dorsal surface, running longitudinally from the front of the first thoracic segment to almost the anal segment. Lateral to this band on each segment are two diagonal white bars, pointing downward and posteriorly. A yellow band then runs longitudinally along the length of the larva below the spiracles. The pupa is pale greenish-brown with a pale olive thorax and wing cases. It is moderately to heavily spotted with dark olive-green and brown. This species hibernates in the egg stage.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: Discussed under individual subspecies above.

GEOGRAPHIC AND SEASONAL VARIATION: As the species is univoltine, there is no seasonal variation. The geographic variation represented in the above five named subspecies is relatively diffuse at the boundaries of these subspecies. Some populations of *S. s. putnami* (e.g., Mono Lake) are remarkably like the coastal *dryope*, in that they are tailless and have markedly pale undersides with reduced black markings, the only difference being that individuals from these populations tend to be larger than typical *dryope*. *S. s. pseudocalifornica*, which are very dark, larger, very *californica*-like individuals, such as those found in Bridgeport Canyon, and are significantly different from *putnami*. These latter populations are in association with *salix*, and adults were taken in an adjacent wet meadow nectaring on exudate from the base of iris flower heads (just below the petals). No oak species was noted in the area.

GENERAL REMARKS: It would be interesting to study the allozyme variation in the enzymatic proteins of these Mono Lake populations and coastal populations to see if they are indeed more closely related genetically than the intervening populations would otherwise suggest.

In the state of California, we distinguish four subspecies of this wide-ranging butterfly which is found throughout much of the western United States west of the Rocky Mountains. While it resembles the preceding species, *Satyrium californica*, it lacks the orange crescent capping the blue spot on the underside of the hindwing and often has a whiter ventral surface with small black spots on the hindwing.

a. *S. s. sylvinus* (Boisduval)

- DIAGNOSIS:** Nomotypical *sylvinus* is the subspecies found on the west slope of the Sierra Nevada and Cascade Range northwestward to the Klamath Mountains Assemblage region. This subspecies tends to have a somewhat darker grey underside than the three subspecies found in southern California, in the western Great Basin low elevation areas, and in the Coast Ranges from Marin County south. It also regularly has tails.
- ORIGINAL DESCRIPTION:** Boisduval, *Ann. Soc. Ent. France*, (2)10: 287 (1852).
- TYPE LOCALITY:** "California", restricted by Emmel, Emmel, and Mattoon, *Journal Research Lepidoptera*, : (1988), to Lower Feather River Canyon, Butte County, California. Lectotype in U. S. National Museum.
- DISTRIBUTION:** From the west slope of the Sierra Nevada from extreme northern Kern County in the north end of the Greenhorn Mountains northward through the west slope of the Sierra Nevada-Cascade Axis to the Klamath Mountains region, from there southward into the North Coast Ranges as far south as Napa and Sonoma counties. A blendzone with the southern California subspecies, *desertorum*, occurs on the west slope of the Greenhorn Mountains in Kern County. As in *Satyrium californica*, the *S. sylvinus* populations inhabiting the Sacramento Valley floor are represented by a phenotype which is larger, with pale whitish undersides and a strong development of orange suffusion and patches on the dorsal surface. With further research, it may be found to be different from nominate *sylvinus*.
- ELEVATION RANGE:** From 1,000' to 10,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** This butterfly is typically found in Riparian situations, where *Salix* species are abundant. Frequently, nectar sources such as *Apocynum* species (Dogbane) or *Asclepias* species (Milkweed) is present. These Riparian habitats extend through several other plant communities, including Montane Coniferous forests, Yellow Pine Forest, Chaparral, and Foothill Woodland.
- PHENOLOGY:** Populations of the nomotypical subspecies, as with all the other *sylvinus* subspecies, are univoltine. Records extend from early June to early September, depending on elevation, with most populations flying at their peak in early July.
- FOODPLANTS:** *Salix* species are used, a conclusion based on our knowledge of foodplants of other subspecies of *sylvinus* and the close association of adults with this particular plant. Additionally, one larva was taken (1985) on willow by Ken Hansen at the Trinity River at Willow Creek, California. No specific *Salix* has yet been identified as a foodplant for the nomotypical subspecies.

b. *S. s. dryope* (W. H. Edwards)

- DIAGNOSIS:** This subspecies is characterized by its lack of tails, the whitish coloration of its underside, and the virtual lack of all black maculation on the ventral surface. It is found from Marin County south through the Coast Ranges to the western end of the San Gabriel Mountains, where it starts to blend with the next subspecies, *desertorum*.
- ORIGINAL DESCRIPTION:** W. H. Edwards, *Transactions American Ent. Soc.*, 3: 19-20 (1870).

- TYPE LOCALITY: "Plain County, Colorado", later corrected to "Placer County, California", restricted to Santa Clara County, California by F. M. Brown, *Transactions American Ent. Soc.*, 96: 49 (1970). Apparent holotype in American Museum of Natural History, *fide* F. M. Brown, *Transactions American Ent. Soc.*, 96: 49-50 (1970).
- DISTRIBUTION: The distribution of this tailless subspecies extends from southern Sonoma County and Marin County on the northwest side of San Francisco Bay, south through Contra Costa, Alameda, and Santa Clara counties to Monterey County, Kern and Ventura counties to Los Angeles County where the southern limit extends to Tujunga Canyon.
- ELEVATION RANGE: From 150' elevation to 5,500' in extreme western Kern County.
- HABITAT AND PLANT COMMUNITIES: Riparian situations within Chaparral and Foothill Woodland plant communities.
- PHENOLOGY: This subspecies flies in one brood from late May to early July.
- FOODPLANTS: A willow species, *Salix lasiolepis* Benth. (family Salicaceae).

c. *S. s. desertorum* (Grinnell)

- DIAGNOSIS: While the type locality of this subspecies is Oak Creek at the eastern end of the Tehachapi Mountains, it occurs from the Tehachapis south to San Diego County through the interior mountains of southern California. It is characterized by having short tails and a very pale ventral surface. The black markings on *desertorum* are a little more pronounced than in *dryope*.
- ORIGINAL DESCRIPTION: Grinnell, *Canadian Entomologist*, 49: 349 (1917).
- TYPE LOCALITY: Oak Creek, Kern County, California. Holotype in American Museum of Natural History.
- DISTRIBUTION: This lighter subspecies occurs in the San Gabriel Mountains southward through the San Bernardino Mountains, the San Jacinto Mountains, and the Santa Ana Mountains to the mountains of San Diego County.
- ELEVATION RANGE: From near sea level to 8,000'.
- HABITAT AND PLANT COMMUNITIES: In Riparian Woodland situations within Coastal Sage Scrub, Chaparral, Foothill Woodland, and Montane Coniferous Forests.
- PHENOLOGY: This subspecies flies from late May to late August (e.g., Barton Flats in the San Bernardino Mountains), depending upon elevation.
- FOODPLANTS: This butterfly is frequently associated with *Salix lasiolepis* Benth. and also closely associated with *Salix* .

d. *S. s. putnami* (Hy. Edwards)

- DIAGNOSIS: This Great Basin subspecies is characterized by its larger size, paler aspect both dorsally and ventrally, its tails (although some individuals can be tailless),

increased yellowish-orange scaling on the upperside, and slight reduction of the ventral black markings seen in typical *sylvinus*.

- ORIGINAL DESCRIPTION: Henry Edwards, *Proceedings California Academy Sciences*, 7: 143 (1877).
- TYPE LOCALITY: Mt. Nebo, Utah. Holotype in American Museum of Natural History.
- DISTRIBUTION: Populations referable to this subspecies occur in the northern Owens Valley, in the canyons of the White Mountains of Inyo and Mono counties, and northward along the western Great Basin where ever the greyish desert wash willow is found in California and western Nevada. It inhabits the eastern Modoc Plateau, being abundant in the canyons of the Warner Mountains and in Lassen County. From here it extends eastward into the Great Basin; the eastern limits of its range are not well understood at present.
- ELEVATION RANGE: 4,000 to 8,000'.
- HABITAT AND PLANT COMMUNITIES: Typically found in Riparian situations, usually within the Sagebrush Scrub plant community or Pinyon-Juniper Woodland community.
- PHENOLOGY: This subspecies flies in July and August, with an apparent peak flight in late July.
- FOODPLANTS: Usually associated with *Salix* species, the presumed foodplant. The particular species used by these Great Basin populations has not been determined, but *putnami* is usually found in close association with the greyish willows of desert streams and washes where roosting, mating, and perching have been observed on the plant.

122. *Satyrrium auretorum* (Boisduval)

This butterfly is a true California native. It was once regarded as one of our rarest butterflies; even today, it is relatively uncommon in collections. It is found typically in Chaparral and Oak Woodland areas where suitable Oak serve as host plants. The butterfly does tend to be cyclic, appearing in large numbers around the host plants in some years, then virtually disappearing for several years. Its normal habitat is in lowland California.

- ADULT BEHAVIOR: Adults are seen perching on the oak foodplants, as well as visiting the flowers of California Horse Chestnut (*Aesculus californica* (Spach.) Nutt.), and *Asclepias* species (Milkweeds), *Eriogonum* species *Rhamnus californica* and *Rhamnus crocea* (Buckthorn).
- LIFE HISTORY: The early stages were first described by Comstock and Dammers (1934). The eggs are deposited singly on the stems of oak and the diapausing eggs overwinter. In the spring the young larvae feed on the tender new shoots of oak leaves. The egg is echinoid (like a sea urchin) with a ground color a light grayish-purple, covered with long green spicules. The micropyle is quite large, and deeply depressed at the top of the egg. When freshly laid, the entire egg is a brilliant green. The mature larva varies in ground color from an apple-green to a pale orange. The apple-green form is covered with off-white dots from which arise short orange-colored hairs. Beneath the spiracles is a fold of skin which is off-white in color, and in some individuals the lower edge is washed with pale magenta. The head is dark brown and the abdomen is slightly paler than the dorsal surface. The abdomen is covered with colorless hairs. The pale orange form varies in having the fold below the spiracles a lemon-white color, as well as

having the overall body color a pale orange. In addition to the above two forms, a pale grayish-green larval morph is known from the mountains of Joshua Tree National Monument (G. Pratt and J. Emmel, unpublished data). The pupa is normally a pinkish-tan with dark brown dots sparingly sprinkled across the head, thorax, and wingcases. The head, thorax and body are covered with short pale buff hairs. The dark-form description given above superficially resembles the early-instar larvae that Mattoon found on *Rhamnus crocea*.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: *Satyrium tetra* has a grey dorsal surface and can sometimes be confused with this hairstreak. The underside of the hindwing, though, has a white suffusion beyond the white median line which helps to distinguish it.

GEOGRAPHIC AND SEASONAL VARIATION: The pattern of subspeciation in this butterfly may be more complex than is currently recognized by lumping all populations under these two names. In particular, a distinctive population in the Santa Monica Mountains of Ventura and Los Angeles counties at Malibu Lake is notably darker on the upperside and underside than typical *spadix* and was recently named a new subspecies, *S. a. fumosum* J. Emmel & Mattoni (_____)

GENERAL REMARKS: The scattered and isolated populations of *Satyrium auretorum* on the floor of the Sacramento Valley are in association with old undisturbed climax plant stands left as remnants of what the valley floor once was probably like. These may be endangered because of the expansion of human urban areas and agricultural activities. Before their extinction (if indeed these populations cannot be saved), work has been started to test the genetic variation present in these populations, and it would be of great interest to test the other northern California and southern California populations with modern investigative techniques such as allozyme and DNA hybridization techniques. It is doubtful that chromosomal counts for the many *Satyrium* species will shed light on evolution in this group because most nearctic hairstreaks that have been investigated to date share the same chromosome number ($n = 24$).

The Sacramento Valley floor taxon found in the Butte County area is almost entirely confined to the mouths of canyons which reach the Valley floor still relatively undisturbed. Few suitable areas remain for this species out in the Valley. This taxon is fairly distinctive in markings, size, and coloration. One fair-sized population is safely within the protective confines of Bidwell Park at Chico.

a. *S. a. auretorum* (Boisduval)

DIAGNOSIS: The underside of this typical or nominate subspecies is a golden brown, and there is a suggestion of one or two yellowish spots near the anal angle of the upperside of the hindwing. On the underside of the wing, which is dull brown, there occurs a submarginal row of spots, inwardly shaded with black. These are small, poorly defined, and fade out as they approach the hindwing margin.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 288 (1852).

TYPE LOCALITY: "Northern California". Restricted to Camptonville, Yuba County, California, by Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies* (1998a). Holotype in U. S. National Museum.

- DISTRIBUTION:** Populations referable to the nomotypical subspecies as consolidated here are scattered throughout the northern half of the state, from the north end of the South Coast Ranges in Alameda and Santa Clara counties, northward through the North Coast Ranges and presumably eastward across the southern edge of the Mt. Shasta region, thence southward in the Cascade Range and Sierra Nevada foothills to approximately Mariposa County. Our records are widely scattered and probably represent inadequate sampling by collectors of this often overlooked species. Several populations are known from the floor of the Sacramento Valley in the vicinity of Davis and Chico, and also show some phenotypic differences.
- ELEVATION RANGE:** From approximately 50' elevation to 3,500' elevation.
- HABITAT AND PLANT COMMUNITIES:** This species is typically found in Oak Woodland, Foothill Woodland, or Chaparral plant communities, as well as in Riparian Woodland on the Sacramento Valley floor, where it is associated with Valley Oak. Foothill and mountain populations are very often associated with *Rhamnus crocea* (Buckthorn) growing in the oak understory. Both *S. auretorum* and *S. californica* use this as a preferred nectar source. Suitable Coast Range mountain locations fail to produce *S. auretorum* even when a favored nectar source, *Aesculus californica* (Buckeye), is present, unless *Rhamnus crocea* is also present. These locations however, do produce *S. californica* in numbers.
- PHENOLOGY:** Captures are recorded from mid-May to early July, with an apparent peak in mid-to late-June.
- FOODPLANTS:** Larvae have been found on *Quercus wislizenii* A. DC. and *Q. douglasii* H. & A.. In 1988, Mattoon found early-instar larvae on *Rhamnus crocea*, a shrub which grows as an understory plant under these oaks in many but not all places where *auretorum* occurs. The larvae, six in number, were found feeding on the flower clusters of *Rhamnus*, and were heavily attended by species of ant. When brought in for rearing, they were not confined, and without the ants in attendance, all larvae left the host and were lost in the rearing room. The cryptic yellow and green larvae were suspected to be *auretorum*. However, *californica* and *saepium* fly at the same location. *S. saepium* here has a green concolorous last instar larvae and feeds on *Ceanothus cuneatus*. The *californica* are associated heavily with *Quercus lobata*, found here also. No hairstreak seems to systematically associate with *Quercus douglasii* here. In *auretorum* habitats in the Coast Range, *Rhamnus crocea* is always present, and always is heavily visited for nectar by adults of both *S. californica* and *auretorum*. Oak association in those sites is predominately with *Q. douglasii*, even when several oak species are present.

b. *S. a. spadix* (Hy. Edwards)

- DIAGNOSIS:** This geographic subspecies occupies the southern half of California from Santa Barbara and Kern counties south to the mountains of San Diego County. It is a lighter colored subspecies which tends to be a mountain butterfly rather than a foothill inhabitant, like the nominate subspecies. There is marked sexual dimorphism in this subspecies, with the male being a uniform dark brown and a lighter shade below. The sub-marginal spots on the underside of the male's hindwings are small and indistinct. The female is a lighter brown, with a yellow-brown area on the upperside of the forewings.
- ORIGINAL DESCRIPTION:** Henry Edwards, *Papilio*, 1: 53 (1881).
- TYPE LOCALITY:** Tehachapi Pass, California. Holotype in American Museum of Natural History.

- DISTRIBUTION:** This subspecies is found at mid-elevations in the inland mountains of southern California, from the Tehachapi, Tejon, and Sierra Madre Range southward to the mountains of San Diego County. It has also recently been discovered in the higher mountains of Joshua Tree National Monument.
- ELEVATION RANGE:** From 1,900' to 5,500'.
- HABITAT AND PLANT COMMUNITIES:** This subspecies is typically found in open sparse Chaparral areas with scattered Oaks.
- PHENOLOGY:** Adults fly from mid-May to mid-July, with an apparent peak during the latter part of June.
- FOODPLANTS:** The butterfly is regularly associated with *Quercus dumosa* Nutt. in southern California. Larvae have been taken on *Quercus wislizenii* A. DC. (G. Pratt and G. Balmer, unpublished data), and on *Q. cornelius-muelleri* Nixon and Steele (G. Pratt and J. Emmel, unpublished data). Scott (1965) has also reported larvae on *Quercus chrysolepis* at Yosemite Village on Highway 41 (near tunnel) opposite Cascade Fall on the south side of the Merced River (July 8, 1964); however, he notes (*in litt.*) that this may have been another oak species. Tilden (1954) reported it feeding on *Q. douglasii* (Blue Oak), and Powell (1969) reported rearing it from *Q. wislizenii* in Shasta County.

c. *S. a. fumosum* J. Emmel and Mattoni

- DIAGNOSIS:**
- ORIGINAL DESCRIPTION:** Emmel, J. F., and R. Mattoni,
- TYPE LOCALITY:**
- DISTRIBUTION:** The Santa Monica Mountains Hairstreak (*S. a. fumosum*) is known only from a few localities in the western Santa Monica Mountains of Los Angeles County, California.
- ELEVATION RANGE:**
- HABITAT AND PLANT COMMUNITIES:**
- This hairstreak's habitat is threatened by urban development which completely surrounds the Santa Monica Mountains and also fragments the range in places. Tremendous economic pressures (with land values in excess of one million dollars per hectare) are pitted against environmentalists in the battle to save the range and the area of about 25,000 hectares that this hairstreak still occupies (Mattoni, 1993).
- PHENOLOGY:**
- FOODPLANTS:**

123. *Satyrrium saepium* (Boisduval)

- ADULT BEHAVIOR:** The adults are fond of perching on various Chaparral shrubs, and frequently males will perch in an open space within the Chaparral. The adults are frequently seen

on flowers, with the apparent favorite being *Eriogonum fasciculatum* Benth., in the cismontane populations of southern California and *Rhamnus californica* in the northern part of the state. MacNeill (1967) first reported down-valley movement of adult Theclini for *Satyrium saepium*. In a small, dry ravine, about 5-15 individuals per minute flew down a valley about a meter above the ground, between 11:30 a.m. and noon; very few individuals flew up-valley. Scott (1973) suggested this behavior might be fairly widespread even at lower population densities, but is seldom noticed in hairstreaks except at high density. He suggested that individuals fly from hillsides to the valley bottom, then downstream to a feeding site. Having fed, they depart to ascend the hillsides again. Flowers and water tend to concentrate in the central portion of small canyons in arid areas of the western United States, and such down-valley flight behavior may be limited to arid areas for that reason.

LIFE HISTORY: The early stages of this species were first described by Comstock and Dammers (1933c). The egg is echinoid in shape, like a small cushion, and is a delicate grey-green of such a light shade as to appear almost white. The surface is covered by a fine reticulation of raised walls, and from the junctures of these walls arise pointed spicules which gives the egg a frosted appearance. The female deposits her eggs singly on the stems of the foodplant. These eggs overwinter and hatch the following spring. The mature larva is a leaf-green, blending well with the leaves of the foodplant. Dorsal-laterally there are faint, light greenish-yellow chevron markings on each segment. These are white in Butte County final-instar larvae (feeding on *C. cuneatus*). The body is completely covered with short stout hairs; the majority of these are frosted white in color and lay down as to lie flat along the body surface. The head is brown, shading to black on the outer margin. Pupation usually occurs on a leaf of the foodplant, the chrysalis being suspended by means of a delicate girdle and cremasteric button. The pupa, about 10 millimeters in length, is at first a uniform green, changing in about six hours to a wood brown, with a profuse sprinkling of black, particularly on the wingcases. The surface is covered with short clubbed hairs, except on the wingcases and facial portions. These hairs are light brown in color.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: This is a distinctive species and there are no similar species in our area.

GEOGRAPHIC AND SEASONAL VARIATION: As noted above, the tremendous geographic variation in this butterfly has been little studied, and it remains for a future worker to do a careful study of this variability.

GENERAL REMARKS: One of the interesting biogeographic islands in California with a native population of *Ceanothus greggii* Gray is the New York Mountains in the eastern Mojave Desert, where *Satyrium saepium* has not yet been recorded.

This hairstreak is characterized by its uniformly metallic reddish-brown dorsal surface, and the species occurs from the Rocky Mountains to the Pacific Coast of California, north into Canada. In our state occur five subspecies, each occurring in a longitudinal band from north to south.

a. *S. s. saepium* (Boisduval)

DIAGNOSIS: This species occurs in the foothills on the western slope of the southern Cascade Range from the northern part of the state to the southern end of the Sierra Nevada Mountains. It is characterized by the bright reddish-brown, metallic shining dorsal surface. The male has a blackish sex patch at the leading edge of the

forewing and has very short tails, while the female is concolorous dorsally and has slightly longer tails. This subspecies is characterized ventrally by a well-defined band of dark scaling in the post-median area which is edged distally by white scaling, rendering a well-defined separation between the proximal and distal halves of the wing. Additionally, the ventral ground color of these populations tends to be a lighter more grayish-tan than that seen in the more coastal populations to the west.

- ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 288 (1852).
- TYPE LOCALITY: "California", restricted to Tuolumne County, California by F. M. Brown, *Transactions American Ent. Soc.*, 96: 33 (1970). Re-restricted by Emmel, Emmel, and Mattoon, *Journal Research Lepidoptera*, : (1988) to Lower Feather River Canyon, Butte County, California. Holotype in U. S. National Museum.
- DISTRIBUTION: The nomotypical subspecies is found on the west slope of the Sierra Nevada Cascade Range Axis from extreme northern Kern County northward to the Mt. Shasta region. There is a blend zone with subspecies *chalcis* at the northwest end of the range of typical *saepium* in the eastern Klamath Mountains region. At the southern end of the range of nomotypical *saepium*, there is a blend zone with subspecies *fulvescens* in the mountains of Kern County. There is an apparently disjunct population in the Warner Mountains of Modoc County.
- ELEVATION RANGE: From 3,500 to 7,700' elevation.
- HABITAT AND PLANT COMMUNITIES: *S. saepium* is typically a butterfly of the California Chaparral plant community. Above the Chaparral zone, there are *Ceanothus* species which occur within the Montane Coniferous forest community and serve as hosts for the butterfly in that particular habitat.
- PHENOLOGY: The species is univoltine, with captures ranging from early June to early September, depending on elevation. The peak of flight is in July.
- FOODPLANTS: Various *Ceanothus* species are used, including the following: *C. cuneatus* (Hook) Nutt., *megacarpus* Nutt., *velutinus* Dougl. ex Hook, *sanguineus* Pursh., and *integerrimus* H. & A.. *C. cuneatus* (Hook) Nutt. is the most widely used host plant in northern California.

b. *S. s. fulvescens* (Hy. Edwards)

- DIAGNOSIS: This is a pale subspecies of the extreme southern Sierra Nevada and the mountains of Kern County. It is characterized by a more fulvous color above, being more of a yellowish-brown rather than the reddish or purplish-brown seen in typical *S. s. saepium* or the more coastal *S. s. chalcis*. On the underside, the ground color is slightly lighter than that seen in typical *saepium*, and the dark markings are reduced in size and are slightly lighter, and the post-median macular band is edged with very little or no white, rendering a more uniform aspect to the underside.
- ORIGINAL DESCRIPTION: Henry Edwards, *Proceedings California Academy Sciences*, 7: 172 (1877).
- TYPE LOCALITY: In the original description, the types were said to be from Lake Tahoe and Tehachapi Pass (Kern County), but the two syntypes in the American Museum of Natural History are labelled as being from Tehachapi Pass and Havilah in the Piute Mountains region, and no syntypes are present in that museum which are labelled as being from Lake Tahoe. Hence, the selection of one of these two syntypes as the lectotype will result in the type locality being fixed at either

Havilah or Tehachapi Pass in Kern County. Lake Tahoe material, in our opinion, is essentially indistinguishable from typical *saepium* from the west slope of the Sierra Nevada. We conclude that Edwards possibly based his inclusion of a Lake Tahoe specimen in the type series of *fulvescens* on the basis of a very worn Tahoe specimen which would have appeared somewhat paler than typical *saepium*.

- DISTRIBUTION:** This subspecies is found in the Tehachapi and Piute Mountains of Kern County and blends northward along the west slope of the Sierra Nevada with typical *saepium*, and northward along the east slope of the Sierra Nevada with the more boldly marked east slope phenotype of *saepium* which also occurs in the western Death Valley region.
- ELEVATION RANGE:** From 3,000 to approximately 6,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** The habitats of *fulvescens* tend to be drier than those of nomotypical *saepium*; in the Tehachapi and Piute Mountains region, it is usually found flying in the Chaparral or Foothill Woodland plant communities, sometimes within Pinion-Juniper Woodland. It occurs on open slopes or along canyon bottoms, frequently perching on small shrubs or being found at nectar sources.
- PHENOLOGY:** This subspecies flies from early June to mid-July, depending on elevation, with an apparent peak in early July.
- FOODPLANTS:** Undoubtedly *Ceanothus* species, but the particular ones for this set of populations have not been determined.

c. *S. s. chlorophora* (Watson and W. P. Comstock)

- DIAGNOSIS:** This is a subspecies of the immediate coast in southern California, from San Luis Obispo County southward to San Diego County. It is characterized by a rather dark brown scaling in the basal half of the undersurface of the hindwing, with a fairly distinct post-median macular band on both forewing and hindwing ventrally. This gives the underside a contrasting, "two-tone" aspect.
- ORIGINAL DESCRIPTION:** Watson and W. P. Comstock, *Bulletin American Museum Natural History*, 42: 452 (1920).
- TYPE LOCALITY:** San Diego, California. Holotype in American Museum of Natural History.
- DISTRIBUTION:** This subspecies is found in scattered rather disjunct populations along the immediate coast from San Luis Obispo County in the Baywood Park area southward to the type locality in San Diego. Populations on Santa Cruz Island appear to be referable to this subspecies also, although they show somewhat greater contrast ventrally than do the San Diego specimens.
- ELEVATION RANGE:** From near sea level to approximately 500' elevation.
- HABITAT AND PLANT COMMUNITIES:** This subspecies is found within the Chaparral plant community along the immediate coast, where it is found on either open slopes or in canyon bottoms.
- PHENOLOGY:** This species flies from late April (Santa Cruz Island records) to late June, depending on seasonal temperature and precipitation patterns.

FOODPLANTS: The suspected host both at the type locality in San Diego and at Baywood Park in San Luis Obispo County is *Ceanothus cuneatus* (Hook.) Nutt. (J. Emmel and J. Brock, unpublished data).

d. *S. s. chalcis* (W. H. Edwards)

DIAGNOSIS: This is the most widespread subspecies in the state. It ranges from San Diego County northward through cismontane southern California to the Klamath Mountains region. It is characterized by a rather dull underside, with little or no contrast between the proximal and distal halves of the wings, and somewhat indistinct dark markings in contrast to typical *saepium* and to the coastal subspecies, *chlorophora*. Within the concept of *chalcis*, there is considerable variation with some specimens approaching typical *saepium* and others approaching the coastal *chlorophora* in any given population. Generally, most specimens of populations referable to *chalcis* all show slightly darker ground color, as well as more distinct markings ventrally as opposed to the very pale, washed-out *fulvescens* subspecies of the Kern County mountains.

ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Entomological Society*, 3:276 (1869).

TYPE LOCALITY: "California," restricted to Isabel Creek, Santa Clara County, California by F. M. Brown, *Transactions American Entomological Society*, 96:30-33 (1970). Neotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Entomological Society*, 96:33 (1970).

DISTRIBUTION: This subspecies is widely distributed in the Chaparral areas of California, from the southern California mountains northward through the Coast Ranges to the Klamath Mountains region. In the Klamath Mountains region, there is a broad blendzone with nomotypical *saepium* of the west slope of the Southern Cascade Range. Southward, in the western Tehachapi Mountains region, there is again a very indistinct blendzone with subspecies *fulvescens*. As populations approach the immediate coast, there appear greater percentages of individuals showing the contrasting *chlorophora* pattern ventrally, until one gets "pure" *chlorophora* populations on the immediate coast.

ELEVATION RANGE: From approximately 300' to 7,000' elevation.

HABITAT AND PLANT COMMUNITIES: This subspecies is typically a butterfly of the California Chaparral plant community in the foothills and mountains of cismontane northern and southern California. The butterfly is found on slopes, in canyon bottoms, and along ridges, and is frequently numerous on nectar sources such as *Eriogonum fasciculatum*.

PHENOLOGY: Captures range from late April to early July, depending on elevation. In most areas, the peak flight period appears to be during the month of June.

FOODPLANTS: Several *Ceanothus* species are used by this set of populations, including the following: *C. cuneatus* (Hook.) Nutt., *C. leucodermis* Greene, and *C. sorediatus* H. & A.

e. *S. s. subaridum* Emmel, Emmel and Mattoon

DIAGNOSIS: In this set of populations, the phenotype is distinguished by a slightly larger size than nominotypical *saepium* and a more boldly marked pattern on the underside, characterized by increased white scaling in the distal half of the wings ventrally,

with enlarged dark spots and markings in these areas. This contrasts with the basal half of the wings ventrally, which is of a dark grayish-tan, giving a "two-tone" or bicolor appearance to the ventral surface.

- ORIGINAL DESCRIPTION: Emmel, Emmel and Mattoon, *Systematics of Western North American Butterflies*, pp. 159-160 (1998i)
- TYPE LOCALITY: Hunter Mountain, east of the Nelson Range, Inyo County, California, at 6800' elevation in a small meadow along a stream 0.4 air mile southeast of peak 7107 (USGS map). Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is found along the east slope of the Sierra Nevada just above the floor of Owens Valley in Inyo County and Mono County (at Rock Creek), and extends eastward to Hunter Mountain at the southeast end of the Inyo Mountains, as well as to the Panamint Range. It may eventually be found in the Coso Range southwest of Hunter Mountain, where its foodplant is known to occur.
- ELEVATION RANGE: From 5,000' to 8,000' elevation.
- HABITAT AND PLANT COMMUNITIES: Slopes, flats, and canyon bottoms within the Pinion-Juniper Woodland and Sagebrush Scrub plant communities.
- PHENOLOGY: Adults fly from mid-June to early August, depending on elevation and progression of the season.
- FOODPLANTS: This subspecies is closely associated with *Ceanothus greggii* Gray ssp. (J. F. Emmel, unpublished data), and this plant is presumed to be the larval host.

f. *S. s. caliginosum* Emmel, Emmel and Mattoon

- DIAGNOSIS: This subspecies (whose name is Latin for "dark" or "gloomy") is immediately distinguished by its very dark underside. In particular, the very dark medial three-fifths of the wing contrasts sharply with the light tan distal two-fifths of the wing. It is somewhat similar to the coastal subspecies *chlorophora* (Watson & W. P. Comstock); in this latter taxon, there is also a two-tone contrasting aspect to the wing, but it is not nearly so striking and the postmedian band of spots ventrally is not nearly so prominent.
- ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 160-161 (1998i).
- TYPE LOCALITY: Boxwood Park, San Luis Obispo County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is known from a limited area of the San Luis Obispo County coast in the vicinity of Baywood Park. Specimens with a virtually identical phenotype have been taken on Santa Cruz Island off the Santa Barbara County coast, ca. 80-90 air miles to the south of the type locality. The presumed *Ceanothus* foodplant on Santa Cruz Island has not been determined as to species.
- ELEVATION RANGE: From sea level to 200' elevation on sand hills.
- HABITAT AND PLANT COMMUNITIES: The known localities are on the immediate coast and are subject to a mild maritime climate with cool moist winters and relatively mild, frequently foggy or overcast summers.

The sandhill plant community here is a coastal chaparral habitat in which *Ceanothus cuneatus* (Hook.) Nutt. var. *fascicularis* (McMinn) Hoover is locally common.

PHENOLOGY: This subspecies flies in a single brood from mid June to mid July, with a peak flight at the end of June and the first part of July.

FOODPLANTS: *Ceanothus cuneatus* (Hook.) Nutt. var. *fascicularis* (McMinn) is the presumed larval foodplant for this subspecies.

g. *S. s. rubrotenebrosum* Emmel, Emmel and Mattoon

DIAGNOSIS: This more northern coastal subspecies is found in the San Bruno Mountains on the south edge of San Francisco, is similar to the preceding *caliginosum*, but it differs in its smaller size, the reddish cast of the ventral surface in contrast to the more grayish cast of *caliginosum*, the more obscure submarginal markings ventrally, and the overall darker ventral appearance in contrast to the two-tone contrast of the ventral wings in *caliginosum*. The name *rubrotenebrosum* is a Latin construction meaning “red darkness,” in reference to the dark ventral surface of this subspecies with its reddish cast.

It is of interest to note that the ventral surface of this *saepium* hairstreak subspecies resembles the ventral aspect of *Incisalia mossii bayensis* (R. M. Brown, 1969), another endemic hairstreak of the San Bruno Mountains. Presumably this dark ventral surface is a reflection of the influence of the moist and cooler maritime climate, either in producing dark-earth substrates where the adults rest or perhaps in facilitating heat absorption while basking to warm up for flight.

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 161-162 (1998i).

TYPE LOCALITY: San Bruno Mountains (southeast ridge), San Mateo County, California. Holotype in the California Academy of Sciences, San Francisco, California.

DISTRIBUTION: This subspecies is known only from the San Bruno Mountains and the north end of the Santa Cruz Mountains (one specimen, from Edgewood Park), San Mateo County. To the south, on the east slope of the Santa Cruz Mountains in Santa Clara County, the phenotype of *S. saepium* populations is closest to *S. s. chalcis*. The San Bruno Mountains are located in the northern part of that county, on the San Francisco peninsula, where this range is exposed to a maritime climate, consisting of cooler moist winters and frequent cool fogs during the summer months.

ELEVATION RANGE: From 400 to 1300' elevation.

HABITAT AND PLANT COMMUNITIES: This butterfly is typically found on steep slopes of ridges within the Northern Coastal Scrub plant community.

PHENOLOGY: *Satyrium saepium rubrotenebrosum* flies in a single brood, from mid-June to mid-August; it appears to have a more prolonged flight period compared to other *S. saepium* populations, presumably due to the cooler summers in its habitat.

FOODPLANTS: The presumed larval host is *Ceanothus thyrisflorus* Esch., the only *Ceanothus* species to occur in the San Bruno Mountains.

124. *Satyrium tetra* (W. H. Edwards)

This gray hairstreak is known only from California, extreme western Nevada, and southern Oregon. In some Chaparral areas of southern California, the butterfly is often seen in large numbers on flowers of Chaparral shrubs. Only the nominate subspecies is known.

DIAGNOSIS: The dorsal surface of this hairstreak is slaty grey and the ventral surface has a white medial line, with outer white suffusion.

ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Entomological Society*, 3: 19 (1870).

TYPE LOCALITY: "California" by implication, restricted to Arroyo Bayo, Santa Clara County, California by F. M. Brown and Clench, in F. M. Brown, *Transactions American Ent. Soc.*, 96: 34-36 (1970). Neotype in Carnegie Museum, designated by F. M. Brown and Clench, in F. M. Brown (1970). This butterfly was synonymized some years ago with *Satyrium adenostomatis* (Henry Edwards), which was described later (in 1877) with a type locality of Tehachapi Pass, California. The holotype of that butterfly is in the American Museum of Natural History.

DISTRIBUTION: From extreme southern Oregon south through California and extreme western Nevada to San Diego County, occurring in the mountains and foothills. Along the eastern edge of its range, populations are known in the Little San Bernardino Mountains, as well as in the Warner Mountains; otherwise, it does not penetrate significantly into the desert areas.

ELEVATION RANGE: From near sea level in San Diego County to approximately 6,500' in the San Bernardino Mountains and in the north from 100' in the Sacramento Valley floor to 6,500' in the Warner Mountains. Most colonies seem to lie at an elevation range of 3,000 to 5,000'.

HABITAT AND PLANT COMMUNITIES: Like its close relative, *S. saepium*, this butterfly is largely confined to the Chaparral belt.

PHENOLOGY: From early June to early August in the southern part of the state, depending on elevation, with a peak flight in early July. Slightly later in the north, with a peak flight in the Warner Mountains in August extending to September. There is only a single brood.

ADULT BEHAVIOR: Males perch on shrubs to await females. Adults can be taken in large numbers in some localities as they visit *Eriogonum fasciculatum* Benth. or *Apocynum* flowers.

LIFE HISTORY: The life history was first described by Comstock and Dammers (1935c). This hairstreak overwinters in the egg stage, although the egg has not been described in a publication. The mature larva is pale apple-green. Each segment bears four bluish-white raised bands, covered with erect short orange hairs. The distinctive cervical shield has a broad orange band on each side of the mid-dorsal line. The head is brown. Pupation takes place on the foodplant in early June, and the pupa is suspended by the usual silken girdle and cremasteric button. The pupa is pale mahogany brown with heavy black blotching. The head, thorax, and body are covered with short white hairs. The adults begin emerging in about two weeks.

FOODPLANTS: Mountain mahogany, *Cercocarpus betuloides* Nutt. ex T. & G. (Rosaceae) is the long-reported sole food source (Emmel and Emmel, 1973). Johnson (1982) found

a larva of *Satyrrium tetra* on *Quercus dumosa* Nutt. near Lake Elsinor in western Riverside County in southern California

PARASITES/PREDATORS: Comstock and Dammers (1930c) state that their field-collected larvae (from beating *Cercocarpus* bushes near Forest Home in the San Bernardino Mountains of southern California) were heavily parasitized by the ichneumonid wasp, *Anisobas bicolor* Cush.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: Males can sometimes be confused with males of *Satyrrium auretteum*, with which it flies in the North Coast Range Mountains. *S. tetra* can be distinguished by the grayer aspect of the dorsal wing surfaces and by a more rounded shape of the hind wings..

GEOGRAPHIC AND SEASONAL VARIATION: There is but one annual brood of adults. However, one interesting record was of a fresh male in the dry low 3,000' edge of the Scott Valley on August 16, 1981, showing a protracted emergence period. Geographically, this species is spread over almost the entire state and yet shows no significant geographic variation, except in San Diego County, where the underside is a relatively lighter gray.

GENERAL REMARKS: This species, *Satyrrium tetra*, was named in 1870, and seven years later Henry Edwards named specimens from further south in California as a different species, *S. adenostomatis*. This latter name is probably derived from the generic name of one of the common Chaparral shrubs where the species occurs. In fact, Comstock (1927a) erroneously lists the shrub *Adenostoma* as the foodplant; it is merely a common Chaparral associate of *Cercocarpus*, the primary foodplant used by this hairstreak species.

125. *Satyrrium behrii behrii* (W. H. Edwards)

This is an easily recognized hairstreak that occurs throughout the western United States, though in widely separated population areas.

DIAGNOSIS: This butterfly has extensive brownish-orange areas on the uppersides of the wings, with a broad dark brown border. On the underside, there is a pattern of heavy black spotting bordered by white, giving somewhat of a checkered appearance to the underside of the hindwing. The butterfly has more rounded wings than most of our California hairstreak species. It is a widespread species in the western states.

ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Ent. Soc.*, 3: 18-19 (1870).

TYPE LOCALITY: "Lake Mono" (equals Mono Lake, Mono County), California. Neotype in Carnegie Museum, designated by Opler, in F. M. Brown, *Transactions American Ent. Soc.*, 96: 30 (1970).

DISTRIBUTION: This species basically occurs east of the Sierran Cascade Crest, although in some areas it can be found on the west slope of these mountains. It occurs sporadically from the Modoc County area southward along the east slope of the Sierra Nevada through the higher mountains of the Death Valley region, southward along the desert edge to the north slope of the San Gabriel and San Bernardino Mountains. It does not occur in western Riverside County, or in eastern San Diego County, nor in the mountain ranges of the eastern Mojave Desert, all of which are areas where at least one foodplant is known to occur.

- ELEVATION RANGE:** From approximately 3,500 to 8,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** This butterfly is typically at home in the Sagebrush Scrub or Pinyon-Juniper Woodland communities of the Sierran east slope and western edge of the Great Basin. Within these plant communities, the two *Purshia* species foodplants (*P. glandulosa* Curran and *P. tridentata* (Pursh) DC.) are frequently abundant and may, in favored localities, be the dominant shrubs.
- PHENOLOGY:** This species is strictly univoltine, with records ranging from early June to early September, depending on elevation. For most populations, the peak flight period seems to be early to mid-July.
- ADULT BEHAVIOR:** The adults are avid flower visitors, and are often seen visiting the flowers of *Eriogonum fasciculatum* Benth., *E. nudum*, *E. umbellatum* Torr., and *Angelica lineariloba* Gray. The males frequently perch on low shrubs, awaiting passing females. This perching behavior tends to be noted more commonly on hilltops.
- LIFE HISTORY:** The eggs are greenish-white, turning white with maturation. They are laid singly on host twigs or sometimes on the leaves. The species overwinters in the egg stage. The larva and pupa were first described by Comstock (1928a). The mature larva is predominantly green. On each segment, a dark green area lies to either side of a narrow whitish mid-dorsal line, as well as diagonal lines of yellow, white, and green. The lower lateral lines on the sides of the body are yellow and dark green. The entire body is covered with minute short yellowish hairs. The pupa is light tan with blotches of dark brown and a few scattered short hairs on the head and dorsal surface.
- FOODPLANTS:** *Purshia glandulosa* Curran in southern California and *P. tridentata* (Pursh) DC. in northern California (family Rosaceae).
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** None; this is a very distinctive, tailless hairstreak species.
- GEOGRAPHIC AND SEASONAL VARIATION:** The species is univoltine, with adults flying in a single brood, so there is no seasonal variation. There is also no significant geographic variation within California, and the two subspecies named from other areas (*crossi* from the southern Rocky Mountains and *columbia* from the Pacific Northwest) are rather weakly defined.
- GENERAL REMARKS:** The foodplant, *Purshia glandulosa* Curran, is abundant in the mountain ranges of the eastern Mojave Desert, and it is strange that this hairstreak has not yet been discovered in those mountain ranges.

126. *Satyrrium fuliginosum* (W. H. Edwards)

- ADULT BEHAVIOR:** In the Trinity Alps, where populations of *fuliginosum* are virtually restricted to the sub-alpine zone, the males perch on shrubs, especially *Quercus vaccinifolia* Kell. and *Cercocarpus ledifolius* Nutt., on rocky summits. Shapiro et al. (1981) notes that their aerial chases after other males and females are swift and spectacular, often poised in the air over sheer cliffs of 300 feet or more. There, both sexes visit flowers of *Eriogonum*, *Monardella*, and *Chrysothamnus*, whereas females fly but little.

A number of lepidopterists have noted that *fuliginosum* is consistently found in association with another *lycaenid* species, *Plebejus icarioides*, throughout its range. They often feed on the same *Lupine* species as larvae. The females of many *icarioides* populations bear a remarkable resemblance to *fuliginosum* males and females, both in the facies of the underside and the flight characteristics of the adults. However, the *Icarioides* Blue will almost always have at least some degree of blue scaling at the base of the uppersides of the wings, which will differentiate the two species. Their behavior is remarkably similar, also. Research into the parallel evolution that has occurred in behavior ecology and phenotype of these two *lycaenids*, from different tribes within the family, would be particularly interesting.

LIFE HISTORY: The eggs are greenish-white in color, and are laid singly on a lupine host or on debris at its base. This species overwinters in the egg stage. The mature larva (from Mono Lake, Mono County material) is green in basic ground color. Along each side is a bright white stripe running the length of the body just below the level of the spiracles. There is a broad green mid-dorsal area, and on either side of this a virtually continuous broad white line broken only briefly at each segmental junction. This line is edged with light purple shading. Between each dorsal-lateral line and the dorsal band of white, there are a series of faint white and purple diagonal lines trailing posteriorly on each segment. Usually, there are two of these diagonal markings between a dorsal white line and the lateral white line on each side of the body. The head is green and lightly marked with soft white and purple on the side. There is a dark green chevron in the center of the dorsal part of the head. The pupa is undescribed.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: This species is unique among our North American hairstreaks. It may be confused only with females of some *Plebejus icarioides* populations, as discussed above in the Adult Behavior section.

GEOGRAPHIC AND SEASONAL VARIATION: This butterfly is very variable across its wide geographic range, so it is not surprising that five distinct segregates have evolved within California in the diverse environments that they inhabit. No seasonal variation has been noted through the extended emergence period of the single brood.

GENERAL REMARKS: Larvae of this species of hairstreak at Donner Pass, California were observed to be heavily attended by ants. In many populations, where this species is in association with *Plebejus icarioides*, both species may be attended by ants and careful study needs to be made of the possible symbiotic relationships between the ants and these two sympatric species.

This butterfly, with the common name of Sooty Hairstreak, is characterized by the rounded forewings, the sooty-brown dorsal surfaces, and the dingy colored white-brown undersides, with a few postmedian and postbasal spots. It is a drab, tailless hairstreak that occurs in scattered localities throughout the western United States, although it is often absent from regions that appear to contain ideal habitats for the insect. In California we have representatives of five subspecies present in different areas.

a. *S. f. fuliginosum* (W. H. Edwards)

DIAGNOSIS: In males of the nominotypical subspecies, the ground color of the upperside is usually a uniform medium dark brown; the forewing scent patch does not stand

out from the ground color as it does in other subspecies. The slightly dimorphic female is lighter. The dorsal fringe in both sexes of this subspecies is a lighter brown than the ground color. Ventrally, the ground color is a light tannish-brown, appearing lustrous from evenly distributed lighter tan scales. The fringe is lighter brown. A very vague, almost unnoticed submarginal row of spots is incomplete on the primaries but usually complete on the secondaries. Only the dark macules of this row on the hindwing are margined inwardly by scattered white scales. On the primaries, these macules are vague dots or linearly aligned dashes, while on the secondaries these become very minute, obscure, and somewhat delta-shaped, dark to rusty points. There is also a postmedian row of spots, quadrate to circular in shape, on the primaries, and sometimes incomplete or very vague tiny dots that are almost unnoticeable on the secondaries; spots in this row are margined inwardly by a few scattered white scales which are limited to the forewing spots in the male.

ORIGINAL DESCRIPTION: W. H. Edwards, *Proceedings Academy Natural Sciences Philadelphia*, 15: 164 (1861).

TYPE LOCALITY: "California", restricted to Norden, El Dorado County, California by F. M. Brown, *Transactions American Ent. Soc.*, 96: 25-28 (1970). Re-restricted to Gold Lake, Sierra County, California by Emmel, Emmel, and Mattoon (1989). Neotype in Carnegie Museum designated by P. A. Opler, in F. M. Brown, *Transactions American Ent. Soc.*, 96: 28 (1970).

DISTRIBUTION: This subspecies is found in the northern Sierra Nevada, from approximately Sierra County northward through the Mt. Lassen region to the area just east of Mt. Shasta. At the northwest end of its range, there is a blending with the Klamath Mountains Assemblage, *S. f. nigrescens*. There appears to be no extension of the nominotypical subspecies into southern Oregon. At the southern end of its range in the Donner Pass and Lake Tahoe region, there is a blendzone with the subspecies to the south, *S. f. maculatum*.

ELEVATION RANGE: From 4,000 to 8,500' elevation.

HABITAT AND PLANT COMMUNITIES: This butterfly is found on open montane slopes, with *Lupinus* species and *Wyethia* usually being two of the most abundant species in the habitat. These areas are usually located within the Montane Coniferous Forest or Sub-Alpine Forest plant communities. They are often exposed in such a way that they are free of snow early in the season.

PHENOLOGY: Records extend from early July to mid-August, with a peak flight period in early August.

FOODPLANTS: For the nominotypical subspecies, the butterfly seems regularly associated with *Lupinus arbustus* Dougl. in Lindl. ssp. *silvicola* (Heller) D. Dunn.

b. *S. f. semiluna* Klots

DIAGNOSIS: This subspecies in California is found throughout the lowland Sagebrush Scrub along the Great Basin fringe into the Modoc Plateau. It represents the westernmost distribution of the Rocky Mountain subspecies *S. f. semiluna*. *Semiluna* is the predominant subspecies of arid zone *fuliginosum* and it is characterized by a browner ground color on the upperside, with a noticeable male forewing scent patch, and a lighter tan underside interspersed with enough randomly placed white scales to give the ground color a tannish gray grizzled appearance. Ventrally, the black spots of both the submarginal and postmedian

macular rows are margined or encircled by white, as is the vague cell end bar on both primaries and secondaries. In *semiluna*, there tends to be a suppression to almost obliteration of at least the black macular aspect of the hindwing submarginal row. In some specimens, all that remains is white crescentic arrowhead-shaped marks, these sometimes absent. Our western populations differ mainly in a slightly greater extent of suppression or absence of white in this row, while the black macules of the hindwing postmedian row are often bolder and less encircled by white. Western populations also average slightly browner with a larger wing size, but appear more closely related to *semiluna* than to the geographically adjacent *S. f. maculatum*.

- ORIGINAL DESCRIPTION: Klots, *Bull. Brooklyn Ent. Soc.*, 25: 161 (1930).
- TYPE LOCALITY: Half Moon Ranch, Moose P. O., Jackson Hole, Wyoming. Holotype in American Museum of Natural History.
- DISTRIBUTION: In California, this butterfly is found in scattered populations through the western Great Basin fringe area northward on the lower slopes of Basin ranges from the Susanville region in Lassen County northward to the Warner Mountains in Modoc County, and westward through the Modoc Plateau to the lower slopes north of Mount Shasta, Siskiyou County. Here, blending with subspecies *S. f. nigrescens* occurs. Blending also takes place with the higher elevation subspecies *S. f. maculatum* along the east slopes of the Warner Mountains. Discovery of similar contact is anticipated along the lower eastern Sierra Nevada and adjacent mountains in Nevada.
- ELEVATION RANGE: 4,500 to 6,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This butterfly is typically found on slopes where *Artemisia tridentata* Nutt. is the dominant plant within the Sagebrush Scrub plant community.
- PHENOLOGY: We have records from late June to early August, depending on elevation, with an apparent peak flight period in late July for most populations.
- FOODPLANTS: This subspecies is usually associated with *Lupinus caudatus* Kell., and this plant is suspected to serve as the larval host.

c. *S. f. maculatum* Tilden, Austin, and Mattoon

- DIAGNOSIS: This high elevation subspecies of the extreme western Great Basin is currently known in California from the east slopes of the Sierra Nevada Mountains and the adjacent mountains in western Nevada. Populations are also found along the crest of the Warner Mountains in extreme northeastern California. This subspecies differs from *semiluna* by its darker brown ground color on the upperside, and a darker grayish underside with increased white scaling which is so evenly interspersed as to give the ground color a light frosted appearance. *Maculatum* has an increased extent of white margining or ringing of the black macules of both the submarginal and postmedian rows. The ringed macules give somewhat of an "eyespot" appearance to these markings. The white halo often persists where the dark macule are vague or lacking. A clothing of white hairs give the basal area a whiter appearance, especially in males. The contrasting effect of the bolder white markings against a darker gray background readily separates *maculatum* from *semiluna*.

- ORIGINAL DESCRIPTION: Tilden, Austin, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1989).
- TYPE LOCALITY: Nevada: Lyon County; Sweetwater Mountains, west slopes of East Sister, T. & N., R. 24 E., S.28. This is a high flat saddle immediately west of the final, relatively steep slope to the peak of East Sister.
- DISTRIBUTION: The presently known principal distribution for the *maculatum* phenotype is in extreme western Nevada in the Wassuk Range in Mineral County, the Sweetwater Mountains in Lyon and Douglas counties, Pine Nut Mountains in Douglas County, the Carson Range in Douglas and Washoe counties and Carson City, and in the Peavine Peak and Red Rock areas of Washoe County. In California, it occurs along the east slope of the Sierra Nevada, occasionally to the crest in the vicinity of some mountain passes, from approximately the Convict Lake area in Mono County northward to the Donner Pass and Lake Tahoe area of Nevada County. This subspecies again occurs along the high crest of the Warner Mountains, so far only in Modoc and Lassen counties, California, but it is expected to occur in the Warner Mountains in Lake County, Oregon as well.
- ELEVATION RANGE: From 7,900' up to 8,762' elevation.
- HABITAT AND PLANT COMMUNITIES: This subspecies is typically found in the Sagebrush Scrub community of the ridge crests, mesas, and wind-swept flat uplands of the mountains within its range. The vegetation is mostly *Artemisia tridentata* with a grass and herb understory. Such areas may be adjacent to or interspersed between coniferous forest stands at the upper edges of its distribution.
- PHENOLOGY: This butterfly begins flying in early June, extending into the first weeks of August, with a peak flight during the month of July.
- FOODPLANTS: Undetermined for this population, but *Lupinus caudatus* Kell. is a suspected host.

d. *S. f. tildeni* Austin and Mattoon

- DIAGNOSIS: This is a subspecies primarily of the Siskiyou Mountains of extreme northern California and adjacent southern Oregon. *Nigrescens* has the darkest ground color and largest size of all *fuliginosum* subspecies, and has broad, highly angled forewings, especially in females. Dorsally, males are a uniform dark brown with no discernable forewing scent patch. The sexually dimorphic females are uniform medium brown. The dorsal fringes are a slightly lighter brown than the ground color in males, but are noticeably lighter brown (tending toward white) in females. Ventrally, the ground color in *nigrescens* males is blackish-dark brown, randomly interspersed with light tan scaling over the secondaries and outside the postmedian macular row on the primaries, with wing fringes again slightly lighter than the ground color. Occasionally, the lighter overscaling invades inwardly through the cell where a vague quadrate cell end-bar macule can usually be seen. Some males are unusually light tan, occasionally appearing dull white. The tendency toward white gradually increases southward into the Trinity Alps where Shapiro et al. (1979) aptly described many of the features of *nigrescens*, pointing out the white forewing apex and hindwing overscaling, even suggesting it gave the wings an "ice green effect." The postmedian spot row in males of this subspecies is a complete but indistinct row of round to quadrate dark macules which are lightly margined outwardly by white, while the unmarginated submarginal row is very vague and often lacking from the primaries or is reduced to a few faint linearly arranged dashes there, and limited to minute circular dots in the posterior end of the row on the secondaries. The underside of females, which lacks the variable

tan or white markings of the males, is a uniform light tan on both fore and hind wings. The maculation differs only on the primaries, where the postmedian macules tend to be slightly larger and stand out on the lighter background. The cell end-bar macule is also missing.

ORIGINAL DESCRIPTION: Tilden, Austin, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1989).

TYPE LOCALITY: Siskiyou Mountains, 5000' to crestline from Dry Lake Mountain, T. 47N., R. 9W., S 19, Siskiyou Co., California. Open lupine-covered gravelly glades surrounded by Coniferous Forests.

DISTRIBUTION: This subspecies is currently known from the eastern half of the Siskiyou Mountains of northern Siskiyou County, extending from the summits of Scraggy and Dry Lake Mountain northeastward along the crest of the range to the Mount Ashland summit area in Jackson County, Oregon. It also extends southward in the Klamath Mountain Assemblage, particularly in the higher passes and crestline of the Scott Mountains, and with slight modification still referable to *nigrescens* into the Trinity Alps. Populations should be sought to the south in the Yolla Bolly Mountains where there is a probable blend zone with the north Coast Range subspecies of *fuliginosum*. In the southeastern extent of its known distribution, *nigrescens* reaches the Mount Shasta region along the Shasta-Trinity Divide, there blending with nominotypical *fuliginosum*. North of Mount Shasta, in the Grass Lake area on Mount Hebron in the Cascade Range, populations are found that appear intermediate between *nigrescens* and *semiluna*.

ELEVATION RANGE: From 5,000' to at least 8,500' elevation.

HABITAT AND PLANT COMMUNITIES: Populations of this subspecies occupy rabbitbush and lupine-covered slopes, ridge tops, and openings in an otherwise predominantly Montane Coniferous Forest plant community. As with other *S. fuliginosum* localities, the sites chosen by this particular butterfly tend to be free of snow rather early in the season. In general, the habitat in the Klamath Mountains Assemblage is more mesic than that found in the Sierran or Warner Mountain populations.

PHENOLOGY: This subspecies flies from early July to late August, with a peak flight period in late July and early August.

FOODPLANTS: Shapiro, *et al.* (1979) has recorded *Lupinus croceus* Eastw. as the host in the Trinity Alps. Oviposition was observed by J. Emmel and O. Shields (in litt.) on a *Lupinus* species that was subsequently identified as *L. albicaulis* Dougl. ex Hook. at two localities in the Trinity Alps; however, the distribution of this Lupine species correlates poorly with that of *S. fuliginosum* in this area, so the proper identification of this plant specimen is in doubt.

e. *S. f. albolineata* Austin and Mattoon

DIAGNOSIS: This strikingly marked subspecies was recently discovered by Richard Kelson in the north Coast Range Mountains of California. This is the third in a group of montane, forest dwelling subspecies that includes *S. f. fuliginosum* and *S. f. nigrescens*. Dorsally, the coloration is similar to that of *nigrescens* in both sexes. Ventrally, the most distinguishing feature is the extensive development of white scaling in the males, which in some individuals occurs along the wing veins, giving a lined or rayed appearance to the wings. In females, the ventral ground

color is a uniform golden brown with darker markings but without the distinct patterning seen in the males.

ORIGINAL DESCRIPTION: Tilden, Austin, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1989).

TYPE LOCALITY: Kneecap Ridge, Forest Route 20N02 from the junction of Bear Wallow Ridge Road (T20N-R8W-S5), Glenn County, California, hence southwestward to Kneecap (rocky outcropping), (T20N-R8W-S19), Lake County, California. Elevation 5,300' (1,615 m) to 5,500' (1,676 m) in gravelly, lupine-clad glades along the ridgecrest. The paratypes were collected along this ridge.

DISTRIBUTION: This subspecies is known in several populations found along the higher ridges of the north Coast Range Mountains in Colusa, Glenn, and Lake counties. These populations are all located in the mountains north and northeast of Lake Pillsbury, but *albolineata* should also be found in adjacent Mendocino County and northward to at least Tehama County, especially in the Yolla Bolly Wilderness Area.

ELEVATION RANGE: From 3,700 to 5,000' elevation, but mostly at the higher sites.

HABITAT AND PLANT COMMUNITIES: All populations so far have been located in gravelly, open ridge crest glades in a mixed Coniferous Forest setting. The habitat surrounding the breeding areas is primarily a combination of *Pinus ponderosa* Dougl. ex P. & C. Lawson and *Pseudotsuga menziesii* (Mirb.) Franco. The small, low-growing host lupine usually occurs in heavy stands in the open glades.

PHENOLOGY: This subspecies tends to have an earlier flight period than any other *fuliginosum* subspecies. Emergence of adults begins in late June and the flight period extends through the month of July.

FOODPLANTS: Unknown. Oviposition has been observed on the dry woody basal area of a lupine species by Mattoon.

127. *Ministrymon leda* (W. H. Edwards)

DIAGNOSIS: This small hairstreak species has a sky-blue dorsal surface, a highly grizzled grayish ventral surface, and a variable ventral hindwing marking, including either dashes or a dark median band, depending on the season.

ORIGINAL DESCRIPTION: W. H. Edwards, *Papilio*, 2: 23-24 (1882).

TYPE LOCALITY: Prescott, Arizona. Lectotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Ent. Soc.*, 96: 51 (1970).

DISTRIBUTION: This species is found in the lower desert areas of southern California from the lower Colorado River Valley, the Imperial Valley, and the desert areas of eastern San Diego County, northward to the Mojave River area eastward to the Big Miria Mountains, just north of Blythe. Occasionally, strays are taken in the mountains such as at Boiling Springs, in the Laguna Mountains or at Forest Home in the San Bernardino Mountains. Although recorded foodplants of this species are found in the lower elevations of the Death Valley region, we have no records for the species from that area.

- ELEVATION RANGE: From 200' below sea level in the Salton Sink to approximately 5,500', with most populations below 3,500'.
- HABITAT AND PLANT COMMUNITIES: The butterfly is typically found along desert washes and in riparian situations where the foodplant is locally common. This is usually within the Creosote Bush Scrub plant community of the desert.
- PHENOLOGY: The species is bivoltine and perhaps multivoltine, depending on rainfall patterns, with the first brood normally emerging in April or May and then with subsequent records recorded for the months of June, July, August, September, October, and November, with the majority of records for September and October.
- ADULT BEHAVIOR: The adults have a nervous, skittish, rapid flight during which they dash out from a perching place on the Mesquite bushes and fly around, and then usually return to the same area.
- LIFE HISTORY: The early stages were first described by Comstock and Dammers (1936). The eggs are pale green with white reticulations, and blend well with the Mesquite blossoms on which they are laid. The ground color of the mature larva is apple-green. The body is sparingly covered with short, thick, chestnut-colored hairs. On the dorsal surface, there is a series of yellowish-white chevron markings. The pupa is pale olive-brown and chestnut, with black stippling and blotching.
- FOODPLANTS: Honey Mesquite, *Prosopis juliflora* (Sw.) DC. var. *torreyana* L. Benson (Family Leguminosae).
- CHROMOSOME NUMBER: Unknown.
- SIMILAR SPECIES: None in our area.
- GEOGRAPHIC AND SEASONAL VARIATION: There are two different forms of this species which have received separate names. The typical form "*leda*" has a light blue upperside suffused with black over the distal two-thirds of the forewing. In the female, this black extends further towards the body and also onto the outer half of the hindwing. On the ventral surface, the gray ground color is marked by a medial band that is strongly red on the hindwing, and there are one or two red anal spots. In the form "*ines*", the dorsal coloration is very similar, while the ventral gray ground color is marked only by a black median line, and no red along that line or at the anal spots. For many years, the two supposed seasonal forms of this butterfly were considered to be separate subspecies or even separate species. Unpublished studies of Killian Rover have indicated otherwise (Emmel, 1975, p. 298-299). The spring form, flying from May at least into July, is *M. leda*, f. "*leda*." This form sometimes is found in the same population area on into the late fall. The autumn or "winter" form appears in late September and October and sometimes into late November, and is called *M. leda*, f. "*ines*." The principal difference between the two, then, is that the winter form lacks the red markings above. However, we have records for both forms occurring in the same population on the same day in late September in Berrego Valley. It appears that the two forms may have a genetic basis and not simply be a response to changing length of day (photoperiod).
- GENERAL REMARKS: Even though Mesquite, the foodplant, is present fairly far north in our deserts, the butterfly appears to be a tropical species (ranging from Mexico up into southern

Arizona and Baja California) and reaches the northern end of its limit in southeastern California.

128. *Incisalia eryphon* (Boisduval)

- ADULT BEHAVIOR:** Males of this species perch on Pine trees or other conifers, usually at the edges of clearings or meadows or along streamsides. They are also frequently seen perching on willows along streams. Both sexes are avid flower visitors and have been recorded on the flowers of *Salix* species, and *Ceanothus cordulatus* Kell.
- LIFE HISTORY:** The only published descriptions are from populations to the north of California, on San Vancouver Island (Hardy, 1959) and from central Washington (Newcomer, 1973). The larva coloration pattern differs slightly from the California material that we have seen, perhaps in part because of the different host trees utilized. The chalky-white egg is a somewhat flattened sphere in shape, and the eggs are laid singly at the base of young needles. On Vancouver Island, the mature (fourth instar) larva is slug-like and is a rich velvet green with paired subdorsal and spiracular cream stripes. There, the species uses Lodgepole Pine (*Pinus contorta* Dougl. ex Loud). In central Washington, where the larvae fed on *Staminate catkins* of the Yellow Pine (*P. ponderosa* Dougl. ex P. & C. Lawson), the egg is described as light green, and the mature larva has a ground color of green with the head and thoracic shield being light brown. A latero-dorsal white stripe runs on each side of the dorsal surface. In the White Mountains of Mono County, where this species feeds on Pinyon Pine (*P. monophylla* Torr. & Frem.), the larva is a light green in ground color, with a pair of latero-dorsal white stripes running either side of the darker green dorsal surface, that surface containing a diffuse light patch at the junction of each body segment. On the side of each larva runs another whitish stripe the length of the body, and between the two stripes on each side are a series of large light-colored blotches in the center of each segment, with the reddish rimmed spiracle in the center of each of these areas. This cryptic coloration pattern matches well the blotchy epidermal coloration of the pine needles. The pupa is a uniform dark brown, and is secured by a cremaster and a silken girdle around the thorax. This species diapauses in the pupal stage until the following spring. A small tuft of short undifferentiated hairs replaces the more definite cremaster structure of most species of butterflies. The head and abdominal segments of the pupa are covered with fine hairs which are absent on the thorax and the wingcases.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** None in our area.
- GEOGRAPHIC AND SEASONAL VARIATION:** This species is strictly univoltine, so there is no seasonal variation. There may be somewhat of a broad blendzone between the North Coastal near *sheltonensis* populations and nominotypical *eryphon* of the western Sierra Nevada, in the Klamath Mountains region and North Coast Ranges, as individuals from this area tend to be somewhat darker than typical *eryphon*. Similarly, there may be a blendzone between nominotypical *eryphon* and the Great Basin subspecies *pallidus* on the east slope of the Sierra Nevada.
- GENERAL REMARKS:** Today there are populations of *Incisalia eryphon* near *sheltonensis* on the Pine trees in the Presidio in the northern part of the city of San Francisco. Yet Williams (1910) did not record this species among the forty-three species given as inhabiting San Francisco at that date (*Cercyonis sthenele sthenele* had already gone extinct). The question arises, then, as to whether this species has spread to

the Presidio from the north across the Bay and perhaps also to the Monterey Peninsula further south, since the planting of Pine trees there. Alternatively, this species may have been introduced to this city by eggs or larvae being carried in on landscaping trees in nurseries or even Christmas trees. Perhaps this mystery will never be solved, but it could be examined genetically by electrophoretic analysis of enzyme variation in the populations involved.

These Pine forest hairstreaks, with highly patterned cryptic undersides, are found in three sets of populations within California.

a. *I. e. eryphon* (Boisduval)

- DIAGNOSIS:** The upperside of this tailless hairstreak is a dull grayish-brown in the male, and a rich chestnut brown in the female. The ventral surface is heavily patterned on the hindwing with purplish and dark brown markings, as shown in the color plate. The forewing is a lighter brown in ground color with purplish-black and white markings.
- ORIGINAL DESCRIPTION:** Boisduval, *Ann. Soc. Ent. France*, (2)10: 290 (1852).
- TYPE LOCALITY:** "California". Type locality restricted to Upper Feather River Canyon, Plumas County, California by Emmel, Emmel, and Mattoon, *Journal Research Lepidoptera*, : (1988). Holotype in U. S. National Museum.
- DISTRIBUTION:** From the San Bernardino and San Gabriel Mountains in southern California, northward on the west slope of the Sierra Nevada to the Warner Mountains, Mount Shasta region, and Klamath Mountains Assemblage.
- ELEVATION RANGE:** 2,000 to 10,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** This species is typically found in the Montane-Coniferous Forest, and prefers the edges of open clearings or meadows or streamsides for its perching activities and flower visiting. One particularly frequent nectar source is *Ceanothus cordulatus* Kell., an early blooming forest species whose bloom period coincides perfectly with the flight period of *eryphon*.
- PHENOLOGY:** From early May to mid-July, depending on elevation, with most specimens being taken in the month of June.
- FOODPLANTS:** This species feeds on several pines in the Family Pinaceae; in the Sierra Nevada species used include *P. ponderosa* Dougl. ex P. & C. Lawson, *P. contorta* Dougl. ex Loud., *P. flexilis* James.

b. *I. e. near sheldonensis* F. Chermock and Frechin

- DIAGNOSIS:** We use the name *sheldonensis* to refer to the coastal populations of *eryphon* in California from Monterey north to the Oregon border. Individuals in these populations are not typical *sheldonensis*, but come closer to that named subspecies than any other. They are small, with decreased orange-brown scaling on the upperside of the females and a darker than nomotypical *eryphon* on the underside, with the ground color of the ventral hindwing being a more blackish-brown than the reddish-brown seen in typical *eryphon*.
- ORIGINAL DESCRIPTION:** F. Chermock and Frechin, *Pan-Pacific Entomologist*, 24: 212 (1948).

- TYPE LOCALITY: Shelton, Washington. Holotype in Carnegie Museum.
- DISTRIBUTION: This subspecies is found along the immediate coast in California, from the Monterey Peninsula northward to the Oregon border. It is also found in several inland localities in Marin County which also appear to be this subspecies.
- ELEVATION RANGE: From near sea level to approximately 1,000' elevation.
- HABITAT AND PLANT COMMUNITIES: Near *Pinus* species, either introduced or native, usually at the borders of Closed-Cone Pine forests.
- PHENOLOGY: Populations referable to this subspecies fly from early April to mid-May, depending on rainfall patterns and exposure.
- FOODPLANTS: At least one documented foodplant for these coastal populations is *Pinus muricata* D. Don; it is also associated with *P. contorta* Dougl. ex Loud on the Samoa Peninsula in Humboldt County.

c. *I. e. ssp. (Great Basin) Austin*

- DIAGNOSIS: This is a large, pale subspecies of the western Great Basin. It is characterized by greatly expanded and lighter orange areas on the uppersides of the females, and a pale underside with the ground color being a yellowish-tan and great reduction of the black markings on the underside.
- ORIGINAL DESCRIPTION: Austin, 1988, *Journal Research Lepidoptera*, : (1988).
- TYPE LOCALITY: Jet Canyon, Toiyabe Mountains, Nye County, Nevada.
- DISTRIBUTION: Within California, this subspecies is found in the Inyo Mountains of Inyo County and in the White Mountains to the north in Inyo and Mono counties.
- ELEVATION RANGE: From 6,000 to 9,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This butterfly is at home in the Pinyon-Juniper Woodland of the western Great Basin ranges. It tends to be found in areas where there is more or less a pure *Pinus monophylla* Torr. & Frem. forest, where it prefers Riparian situations, often being found near moisture.
- PHENOLOGY: This subspecies flies from mid-May to late June, with a peak flight in late May.
- FOODPLANTS: Although oviposition has not yet been recorded on *Pinus monophylla* Torr. & Frem., this species is undoubtedly the host, as it is the only pine species in the areas where these populations of *eryphon* are found.

129. *Incisalia augustus iroides* (Boisduval)

This little brown Elfin is one of the early spring butterflies in California and flies throughout the mountain areas. While it is most common in the Chaparral, it also occurs on the Coastal Plains as well as in the higher Pine forests, and even in the ranges of the eastern Mojave Desert. There is only one subspecies represented in California.

- DIAGNOSIS: This species is characterized by the reddish-brown underside of the hindwing, with a slightly darker basal area. There is no multi-colored banding as on the preceding species, *Incisalia eryphon*.
- ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 289 (1852).
- TYPE LOCALITY: "California". Restricted to Lower Feather River Canyon, Butte County, California by Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990). Holotype in U. S. National Museum.
- DISTRIBUTION: This species is found throughout cismontane California west of the Sierran Crest, and it extends northward widely throughout the northern counties except the plateau region of Modoc County. It is most common in the foothills and coastal areas and occurs on the valley floor in the Sacramento Valley. The butterfly is absent from our desert regions, although it occasionally shows up along the northern Great Basin fringe. A previous record for this species occurring in the Providence Mountains of the eastern Mojave Desert is now thought to be in error, based on a very atypical specimen of *Incisalia fotis*.
- ELEVATION RANGE: From near sea level to 7,600' elevation.
- HABITAT AND PLANT COMMUNITIES: This species is found in a variety of habitats from riparian situations in the mountains or on the Sacramento Valley floor, where it usually occurs along streamsides, to open mountain slopes in the foothills and mid-elevations. Plant communities in which the species occurs include Chaparral, Coastal Sage Scrub (these first two being the favored habitats), Montane Coniferous Forests, Foothill Woodland, Valley Grassland, and Riparian Woodland.
- PHENOLOGY: The butterfly is apparently at least bivoltine, with captures recorded from January through July at several low-elevation California localities. This is one of earliest butterflies, with the first adults appearing in February and March at the lower elevations, to June or early July at the highest elevations of its range. There are records for late January (Mix Canyon, Solano County, 2,000' elevation, and Auburn Ravine, Placer County, 1,000' elevation). Records for the months August through December are lacking, indicating that the butterfly does not breed continuously through the greater part of the year. The extent of a second brood in a given year may be dependent on rainfall patterns, host conditions, etc.
- ADULT BEHAVIOR: The Western Elfin, as this butterfly is often called, frequently visits flowers such as those of *Rhus trilobata* Nutt. ex T. & G., *Arctostaphylos* sp., *Ceanothus* sp., and *Salix* sp., and it occasionally sips water at mud. Scott (1973) has recorded that adults will often move in considerable numbers down from ridges during the morning to take nectar or sip water from mud and then move back up the ridges in the afternoon. The mate-locating behavior of *I. augustus iroides* has been described by Powell (1968a). Males will perch on a small tree in a hillside clearing or an opening on a ridge from about 10:30 a.m. to dusk. Mating occurs in the afternoon, following a courtship display in which the male vibrates his wings before copulating. Males may await females in these clearings for many days at one perching site; males can live up to sixteen days in nature.
- LIFE HISTORY: The echinoid egg is a rich drab green, and has features resembling the egg of a *Plebejus* blue more than a hairstreak (Comstock and Dammers, 1933). The first and second instars are yellowish-green in ground color, with brown hairs. The mature larva (fifth instar, according to Comstock but probably fourth instar

according to Ziegler, 1953, from New Jersey material of another subspecies) is quite variable in color, with a ground color of olive, light green, or apple-green (with yellowish bars). The olive type of larva is figured from Comstock and Dammers' illustration. The raised triangular area on each segment is bordered with a white band. White, red, and pale grayish-violet markings are placed in a subdued but complicated pattern. Minute brown hairs cover the larva. The pupa is pale brown, speckled with black on the head, thorax, and wing cases. The abdomen is bright chestnut, and bears seven longitudinal lines of dark blotches centered in each abdominal segment.

FOODPLANTS: In the western United States, the foodplants of *Incisalia augustus iroides* include species from four plant families: Rosaceae, Rhamnaceae, Polemoniaceae, and Liliaceae (Powell, 1968b). The eastern U. S. subspecies uses plants of the genera *Vaccinium*, *Kalmia*, and *Arctostaphylos uva-ursi* Spreng., in the family Ericaceae (Ziegler, 1953), a family which appear to be most commonly used in the lower chaparral belt of northern California. Certain species of *Arctostaphylos* act as both larval host and nectar source for the spring brood, and also as the site for perching.

In California, the yellow vine-like parasitic plant, Dodder (*Cuscuta* species) (family Cuscutaceae), seems to be most extensively used in the Chaparral of southern California. A second host in southern California is *Ceanothus* species (Rhamnaceae). Powell found larva in Lake County in central California on *C. cuneatus* (Hook.) Nutt. Mattoon, Miller, Collins, and MacNeill found a larva on *Arctostaphylos* at Lake Berryessa, Yolo County, April 1972, which was reared to a second-brood adult. Larvae have also been found in Nevada County, California, on *Chlorogalum pomeridianum* (DC.) Kinth. (Liliaceae), where they were feeding on the flowers and buds. Powell also found the first record on the use of an Ericaceae in the west, when a nearly mature larva was collected on *Arbutus menziesii* Pursh at China Camp in Marin County. Comstock's (1927) record of a *Sedum* species refers to a host plant for *Incisalia mossii windi* in northern California, erroneously recorded for *iroides*.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: None in our area.

GEOGRAPHIC AND SEASONAL VARIATION: There is no seasonal variation between the spring brood and the phenotype of the later brood, and only limited geographic variation despite the wide distribution over a wide range of habitats. Populations on *Arctostaphylos uva-ursi* (L.) on the Samoa Peninsula of extreme coastal Humboldt County average slightly darker (in series of specimens) than typical *iroides*.

130. *Incisalia mossii* (Hy. Edwards)

This is a complex of extremely local spring butterflies that have strongly contrasting ventral coloration on the hindwings, usually with a distinctive whitish area edging the dark basal patch. Clench (1961) combined the *I. mossii* group with *I. fotis* under the latter name, and subsequent authors described subspecies of *mossii* under *I. fotis*. However, more detailed studies of foodplants and the immature stages (see Emmel, Emmel, and Mattoon, 1998i, p. 162) have revealed that these two entities are separate species and that *I. fotis* is restricted to the higher mountains of our desert regions while *I. mossii* occurs in more mesic habitats across the western states.

The major biological differences between these two species groups are as follows: (1) the sexes of the *mossii* show dorsal color dimorphism (males are gray, and females are orange to brown) while the sexes of *I. fotis* are both gray brown, with occasional females showing some reddish brown scaling; (2) the larvae foodplants of *I. mossii* populations are always Crassulaceae, while the sole foodplant of *I. fotis* is a member of the Rosaceae plant family, *Purshia stansburiana* (= *Cowania mexicana* var. *stansburiana*); (3) the larvae of the two species show consistent differences in morphology and color pattern (Ballmer and Pratt, 1989). Other recent authors (Scott, 1986; Ferris and Brown, 1981) have also treated *I. fotis* and *I. mossii* as separate species on the basis of these differences.

Overall, then, *I. mossii* occurs as a series of at least eight subspecies or major geographic segregates in mesic coastal or montane habitats from British Columbia south to southern California. *I. fotis* is a nearly monotypic species found in the high desert regions of southern Nevada, Utah, northwestern New Mexico, northern Arizona, and southeastern California.

ADULT BEHAVIOR: Adults of this species have a rather feeble flight and tend to be rather sedentary in their habits, probably a result of the usual extremely local nature of the foodplant utilized. Males perch on small shrubs near the larval host or open cleared areas between vegetation, sometimes on dead stalks of host *Sedum*, and tend to patrol out over a watercourse if one is adjacent. Females tend to spend most of their time sitting on the foodplant or on nearby vegetation between ovipositions. Females display very short, infrequent flights, mostly crawling in the foodplant during extended oviposition periods of up to 45 minutes. A nectar source for subspecies *bayensis* is *Lomatium utriculatum* (Nutt.) Coult. & Rose. For many *I. mossii* populations recorded for California, adults have never been observed in the wild. This is because adults are difficult to locate and the species is far easier to collect as larvae. Thus, collectors are usually in the favored habitats after the adult flight period, during the time in which larvae are developing.

LIFE HISTORY: Of the six named subspecies in our state, the life history of only one of the sets of the populations, *I. m. bayensis*, has been described in publications (Brown, 1969b; Emmel and Ferris, 1972; Arnold, 1983). The most detailed description for this subspecies is given by Emmel and Ferris (1972). Material, however, is at hand for description of the other subspecies and will be presented following the *bayensis* synopsis.

The eggs are pale green in color and oblate spheroids in shape, approximately 0.8 millimeters in diameter. The egg stage lasts five to six days. The egg turns opaque white prior to emergence of the larva. The first instar larvae are pale yellow-green, with clear hairs upon emergence from the eggs. They do not eat the eggshells. The second instar is pink with pale hairs. The third instar is initially a dark cream or straw color, with considerable pink mottling, and is covered with short black spines. During this stage, various colormorphs develop, as will be described for the fourth instar. The mature larva (fourth instar) exhibits three colormorphs from the beginning. About 71% of the *bayensis* larvae are cherry-red, about 6% are light orange, and about 24% are yellow. These all have short dark bristles across the body surface. There are pronounced chevron markings dorsally on the segments, first being a similar but darker color than the background. Later, the chevrons turn dark cherry-red in all morphs except some of the yellow larvae, which have very light or absent chevron markings. The pupa is pale pink, initially, but quickly turns to pale brown. Short hairs are scattered across the dorsal surface. Pupation occurs on the soil in the debris at the base of the host plant. Pupae of *windi* have a stridulatory organ, with which a creaking sound has been detected upon occasion in some *windi* populations. While late

instar larvae are feeding, they remain relatively motionless with head burrowed into the leaves of the host plant.

The above description applies to the *bayensis* subspecies in the San Bruno Mountain area. *Incisalia mossii windi* from Donner Pass in the Sierra Nevada, as with most *windi* populations, are virtually all of a dark red morph in the mature larval stage. This morph is entirely bright cherry-red, with short translucent hairs scattered across the surface. Populations of *windi* in Butte County, California, that feed in part on *Sedella pomila* are, however, polychromatic, ranging from yellow to mostly the red morph. In the high-elevation southern California forms, the subspecies *hidakupa* tends to be a dull pink to pinkish-red in ground color. On the coast in Monterey County, the subspecies *doudoroffi* has a mature larva that is principally green in color, with soft magenta chevrons off the dorsal line, in one form, whereas the other form found in the same population is a dull cherry-red with slight whitish and green marked chevrons coming off the dorsal surface.

The larva of true *Incisalia mossii mossii* from Cape Foulweather (Lincoln County), Oregon, is a deep olive-green with short magenta and light green chevrons coming off the dorsal surface, whereas the (Del Norte County) California Enderts Beach larvae are all red morph, similar to *windi*. In Colorado and Wyoming *Incisalia mossii schryveri* Cross, the larvae feed on *Sedum lanceolatum* Torrey flowers and have a pattern of rose-pink and white or cream, with no extensive polymorphism or instar changes noted (Ferris and Stanford, 1970).

The chromatic polymorphism in *I. m. bayensis* has been analyzed from San Bruno Mountain material in San Mateo County by Orsak and Whitman (1987). They examined wild fourth-instar larvae with a colorimeter and spectrophotometer and found an even greater range of color hues than reported from laboratory rearing. Their conclusion was that genetic color-determining mechanisms seem to be supplemented by an environment-derived factor (such as eating yellow flowers or red bracts), and producing the broad range of color hues found in wild larvae. While no direct connection exists between the color of ingested plant parts and resultant larval colors, there are indications that diet does have an influence on color. The actual function of this color polymorphism in nature is uncertain, since the most frequently occupied substrate is usually yellow and most of the full-grown larvae are red in color. Observations of the Butte County *Sedella*-feeding population suggests that chromatic polymorphism may be more associated, if not limited to, *Sedella* than in *Sedum spathulifolium*-feeding larvae found in the same population.

One clue to the function of color variation comes from the fact that the third and fourth instar larvae are myrmecophilous. At least nine ant species tend the larvae, and each ant species appears to tend primarily one larval colormorph (Arnold, 1983). Because the larvae may be reared in the lab without ants, the larvae are facultative myrmecophiles (i.e., the symbiosis is not essential for maturation).

In most subspecies, especially *I. m. windi*, eggs are predominantly placed on flower bud clusters before bloom. The larvae, after emerging, burrow into and feed within a flower bud where they are protected. Feeding within buds continues until larval size prohibits it. The later instars continue feeding on the flower heads where red morphs stand out in stark contrast to yellow flower color as bloom advances. Larvae apparently only burrow in first and second instar, even in subspecies that more actively oviposit on bracts or basal leaf whorls. In later instars, the body remains exposed, although much more camouflaged by similar shape and color of the host's leaves.

PARASITES/PREDATORS: Despite their symbiotic association with ants, 55 to 82% of the mature larvae studied by Arnold (1983) were parasitized by a tachinid fly, *Aplomya theclarum* (Scutter). The tachinid larva emerges from the fourth instar larva of *I. m. bayensis*, drops to the ground, and immediately pupates. Other *mossii* populations do not seem to display such a high rate of parasitism, but disease seems to be an important factor in some southern California populations.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: The subspecies *windi*, *hidakupa*, and *doudoroffi*, all may be possibly confused with *I. augustus iroides*, particularly with worn specimens. In *augustus*, the post-median area of the wing is usually a fairly uniform ground color, and tends to lack the whitish scaling in this area which is present at least to a slight degree in *mossii* specimens. Additionally, the fringe in *augustus* tends to be rather uniform-appearing, whereas in the *mossii* subspecies it tends to have a scalloped appearance because of the presence of dark scaling at the end of each hindwing vein. The median-macular band on the ventral surface is usually edged with white scales, at least scantily in *mossii* subspecies, whereas in *augustus* this white scaling is usually absent.

GEOGRAPHIC AND SEASONAL VARIATION: In addition to the entities differentiated above, it should be mentioned that many of the populations in the North Coast Ranges in the Mt. Diablo region show considerable variability, and do not fit neatly into any particular subspecific name category. All populations known are strictly univoltine, so there is no seasonal variation.

GENERAL REMARKS: It ought to be noted that the *Sedum* foodplant genus for this butterfly has been well-studied in North America and reviewed by Clausen (1975). There are apparently many chromosomal and biochemical differences, in addition to visible phenotypic differences, between populations of even the same species in this genus. It would be interesting to carry out an intensive study of the variation in the host plants simultaneously with variation in the butterflies, similar to the kinds of studies being pursued by Gordon F. Pratt and Gregory Balmer on species of the genus *Euphilotes* and the races of *Apodemia mormo*.

a. *I. m. near mossii* (Hy. Edwards)

DIAGNOSIS: Populations approaching nominotypical *mossii* occur on our northern coast. These populations are characterized by having a rather dark underside coloration, with the discal half of the hindwing a dark chocolate-brown with greenish overscaling. The post-median half of the hindwing is sharply contrasted with the discal half in that it is separated by a band of whitish scaling, distal to which is another dark area of brownish-black scaling. Sub-marginally there is often a sharp line of whitish scales. The total effect of this is to give a sharply contrasting banding effect to the underside of the hindwing. The sexes in all subspecies of this complex are markedly dimorphic, with the males tending to be a slaty-gray above, and the females varying shades of brown or orangish-brown. In the nomotypical subspecies, the males are a flat slaty-gray superiorly, and the females are a dull, light brown superiorly.

ORIGINAL DESCRIPTION: Henry Edwards, *Papilio*, 1: 54 (1881).

TYPE LOCALITY: Esquimalt, Vancouver Island, British Columbia. Holotype in American Museum of Natural History.

- DISTRIBUTION:** In California, this subspecies is found only along the immediate coast in Del Norte County at Enderts Beach near Crescent City, California, and several miles south at Wilson Creek. From here, it ranges northward along the coast of Oregon and Washington to the coastal areas of British Columbia and Vancouver Island.
- ELEVATION RANGE:** From sea level to approximately 50' for the California populations.
- HABITAT AND PLANT COMMUNITIES:** This butterfly is found on steep cliffs overlooking the ocean breakers within the Coastal Strand Plant community. On these steep cliffs, *Sedum spathulifolium* is abundant. Larvae of nominotypical *mossii*, more than seen in other subspecies, tend to feed on the basal whorls of fleshy leaves, which the red larvae match closely in red color and shape. They also feed on the blooms and stand out conspicuously against the yellow flower color.
- PHENOLOGY:** *Mossii* is one of the earliest spring fliers emerging in April in this harsh coastal marine environment with adult flight completed by the first weeks of May. In contrast, an unusual situation occurs where populations of subspecies *windi*, found from seven to ten air miles inland and two thousand or more feet above on the first coastal ridges, fly in late May and June, although the habitat is warmer, less foggy, and much less harsh. Larvae of *mossii* at Enderts Beach are in third and fourth instar by mid-May.
- FOODPLANTS:** The host of this subspecies in the California population is *Sedum spathulifolium* Hook. ssp. *pruinatum* (Britton) Clausen & Uhl. (Crassulaceae).

b. *I. m. windi* Clench

- DIAGNOSIS:** Populations falling under this subspecies name are widely distributed through California on the west slope of the Sierra Nevada, in the Klamath Mountains, and in the North Coast Ranges. It is the most variable set of populations to fall under a single name, but these populations have enough characters in common to lump them under a single subspecific name at this time. This butterfly is characterized by males having a light brownish-gray upperside, and females having a very yellowish-brown to dull, almost reddish-brown upperside with thin dark borders at the edges of the wings. On the underside, the contrast between the discal area of the hindwing and the post-median area is not nearly as pronounced as it is in typical *mossii*. The underside ranges from a dull yellowish-brown to a soft reddish-brown. The post-median row of dark spots is also more prominent in this subspecies.
- ORIGINAL DESCRIPTION:** Clench, *Canadian Entomologist*, 75: 185 (1943).
- TYPE LOCALITY:** Placer County, California. Holotype in American Museum of Natural History.
- DISTRIBUTION:** This subspecies in its most typical form is found in the Sierra Nevada foothills in mid-elevations, from approximately the Yosemite region northward to the Mt. Shasta region. West of here there are widely scattered, closely related populations in the Klamath Mountains Assemblage, and in the North Coast Ranges as far south as Sonoma and Napa counties.
- ELEVATION RANGE:** From approximately 250' elevation to 8,000', but most prevalently up to 3,000'.
- HABITAT AND PLANT COMMUNITIES:** There are basically two ecotypes that fall under the subspecies *windi*. One is a very widespread, lower elevation insect which is usually associated with *Sedum spathulifolium* Hook, which is found on north-

facing, or valley-facing, usually partially to heavily shaded slopes, within foothill woodland, Chaparral, Northern Oak Woodland, and the lower edges of the Montane-Coniferous Forest. Higher elevation populations in the the Klamath Mountains Assemblage and in the Sierra Nevada are associated with *Sedum obtusatum* Gray, which typically grows on open rocky slopes and flats, particularly on granitic substrates within the Montane Coniferous Forest community.

PHENOLOGY: For the lower elevation populations, emergence begins in late March and flight period continues into late April to early May, depending on elevation. For the higher elevation populations, the flight period is from mid-May to late June, again depending on elevation and exposure. Rearing studies have shown that this early-emerging butterfly often encounters long periods of stormy weather at emergence time and will eclose in response to the light (and possibly slight temperature increase) of a new day, even under totally cloudy, even rainy, conditions.

FOODPLANTS: For low-elevation populations, *Sedum spathulifolium* Hook ssp. *spathulifolium* Hook, and subspecies *yosemitense* Britton (family Crassulaceae). Additionally, *windi* populations are known to use *S. albomarginatum*, *S. laxum perplexum* (Britton) Berger, and *S. radiatum* (Wats.) Clausen. In northern Mendocino County, *windi* uses *Sedum* (RSA sample #285). *Dudleya cymosa* (Lenn.) Britt. & Rose and *Parvisedum pumilum* (Benth.) Clausen (Formerly in *Sedum* or *Sedella*) may be used by *windi* when in association with *Sedum spathulifolium*. At Alburn Ravine, Placer County, California, *windi* has been reared from *Dudleya cymosa* in areas far removed from any *S. spathulifolium*, using the same plants upon which *Philotes sonorensis* fed earlier in the year. The incidence of such usage is very low and hard to detect, but it may provide the clue as to how contact can be made for occasional gene exchange between otherwise widely separated and isolated *windi* populations. *Dudleya* is a much more widely distributed host than is *spathulifolium*. In Siskiyou County, on Crawford Creek near Cecilville, an unusual *Sedum*, *S.* (R.S.A. plant sample #201) is utilized where it grows in conjunction with the also-used *S. spathulifolium*. On cliffs in Humboldt County, the unusual occurrence of a sizeable population of typical-appearing *windi* is found on *Sedum laxum* (Britton) Berger, a host with seasonal growth development much later than that of *S. spathulifolium*. Late-instar larvae occupy the blooms of this plant which flowers after *spathulifolium* has gone to seed and is drying. Earlier in the season, *windi* uses *spathulifolium* at adjacent locations in this area. It would be most interesting to determine if a similar utilization is taking place with the *spathulifolium* at this location. *Mossii* is very likely adapted to a close timing of adult emergence with proper seasonal development of the available *Sedum* host. If two separate populations can be found using separate *Sedum* species on the same cliffs in Humboldt County, mitochondrial DNA or electrophoretic analysis of genetic and biochemical differences between the populations might be most revealing.

c. *I. m. hidakupa* Emmel, Emmel, and Mattoon

DIAGNOSIS: This subspecies of the Transverse Ranges in southern California is similar to *windi*, with the males having light brownish-gray uppersides and the females tending to be more of a dull reddish-brown on the upperside, and not as yellowish-brown as *windi* females. On the underside, the median-macular band is more pronounced, in most individuals being virtually continuous and broader than that seen in *windi*. The ground color of the underside is a very dull grayish-tan. The post-median band of spots tends to be less pronounced than that seen in *windi*. On the forewing, the macular band markings are nearly obliterated.

- ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 162-163 (1998i).
- TYPE LOCALITY: East Fork Mountain Home Creek, 5,040-5,200', San Bernardino Mountains, San Bernardino County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is found in the San Gabriel and San Bernardino Mountains of southern California.
- ELEVATION RANGE: From 3,000 to 5,500' elevation.
- HABITAT AND PLANT COMMUNITIES: This subspecies is typically found on steep, rocky, north-facing slopes within the Montane Coniferous Forest (Southern Mixed Evergreen Forests), usually near a stream-bottom or watercourse bottom. The foodplant is locally abundant on rocky outcroppings within this habitat.
- PHENOLOGY: This subspecies flies from late March to early May, depending on elevation and exposure, with an apparent peak flight in early May. It is univoltine.
- FOODPLANTS: The sole host is *Sedum spathulifolium* Hook ssp. *yosemitense* Britton (Crassulaceae).

d. *I. m. doudoroffi* dos Passos

- DIAGNOSIS: In this subspecies of the South Coast Ranges, males tend to be a very pale brownish-gray on the upperside, while females are very pale yellowish-brown to orangish-brown on the upperside, with very minimal dark border the outer margins of the wings. On the underside, the color ranges from a very light reddish-brown to a rich chocolate-brown. There tends to be greater contrast between the discal half of the wing and the post-median half of the wing on the ventral hindwing, with a whitish scaling in the post-median area, giving a greater contrasting effect. The post-median band of spots is usually fairly well-developed on both the forewing and the hindwing ventrally.
- ORIGINAL DESCRIPTION: dos Passos, *Canadian Entomologist*, 72: 168 (1940).
- TYPE LOCALITY: Big Sur, Monterey County, California. Holotype in American Museum of Natural History.
- DISTRIBUTION: This subspecies is apparently confined to the Santa Lucia Range in Monterey and northwestern San Luis Obispo counties. This subspecies was originally taken along the immediate coast near Big Sur, but investigation in recent years has revealed a number of colonies away from the coast in more Montane settings.
- ELEVATION RANGE: From near sea level to approximately 3,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The coastal populations are found on steep slopes with abundant growth of *Dudley cymosa*, the foodplant of these populations. In the interior areas, the habitat is more typical steep, rocky, north-facing slopes within Oak Woodland or a Mixed Coniferous Forest setting, where *Sedum spathulifolium* Hook is locally abundant.
- PHENOLOGY: The interior populations tend to fly earlier than the coastal ones, usually showing emergence in early April and flying through the month of April. On the coast, emergence does not begin until mid-May and continues into early June.

FOODPLANTS: *Dudley cymosa* (Lenn.) Britt. & Rose ssp. *minor* (Rose) Moran, for the interior populations, *Sedum spathulifolium* Hook ssp. *yosemitense* Britton is used.

e. *I. m. bayensis* (R. M. Brown)

DIAGNOSIS: In this subspecies, males are a light brownish-gray above, and females tend to be a very dull reddish-brown with expansion of the dark borders along the margins of the wings. Ventrally, the discal half of the hindwing tends to be a dark, rich, reddish-brown. In the post-median area, there is an increased amount of white overscaling, which gives this area of the wing a whitish or gray appearance, and contrasts sharply with the discal area of the wing. The post-median macular band is usually edged outwardly with white scaling, making it stand out more than in most of the other California subspecies of this butterfly. The post-median band of spots tends to be less-developed than that seen in other subspecies, sometimes to the point of being completely obliterated.

ORIGINAL DESCRIPTION: R. M. Brown, *Journal Lepidopterist Society*, 23: 95-96 (1969).

TYPE LOCALITY: San Bruno Mountains, San Mateo County, California. Holotype in California Academy of Sciences.

DISTRIBUTION: This subspecies is found in at least three different sets of populations, the largest number probably being in the San Bruno Mountains in extreme northern San Mateo County. Southwest of these populations, there is a population along Sharp Park Road in Pacifica; south of here there are several populations on Montara Mountain at the extreme northern end of the Santa Cruz Mountains. A population of *I. mossii*, which appears somewhat phenotypically intermediate between the subspecies *bayensis* and *doudoroffi*, occurs on Mt. Diablo in Contra Costa County in the East Bay area.

ELEVATION RANGE: From 400 to 1,300' elevation.

HABITAT AND PLANT COMMUNITIES: This subspecies is typically found on steep north-facing slopes within the Northern Coastal Sage Scrub plant community. A more detailed description of the habitat can be found in J. Emmel and C. Ferris (1972).

PHENOLOGY: Emergence of adults takes place primarily during the month of March, but in some years a few adults may emerge as early as late February. The adults continue to fly into mid-April. It is strictly univoltine.

FOODPLANTS: The apparently sole foodplant of this subspecies is *Sedum spathulifolium* Hook. ssp. *spathulifolium* Hook.

f. *I. m. marinensis* Emmel, Emmel, and Mattoon

DIAGNOSIS: This subspecies is distinguished by both its large size and very golden brown ventral surface. It is geographically closest to *I. m. windi* populations to the north and east; *windi*, however, is distinguished by its smaller size and much duller ground color and less distinct markings ventrally. To the south, the San Francisco Peninsula subspecies, *I. m. bayensis*, is characterized by its smaller size, its darker and more mahogany brown ventral surface, and copious gray scaling in the distal one-third of the ventral hindwing.

In this subspecies, as noted, adults tend to be larger than those in other *I. mossii* populations. The dorsal ground color of the males is a light tannish-gray, and in the females it is a yellowish to orangey, dull brown with fairly broad chocolate-brownish borders at the margins of the wings. Ventrally, the discal area tends to be a yellowish-brown to rich red-brown, with greenish or grayish overscaling. In the post-median area of the wing, the ground color is often a yellowish to orangish-brown with an overscaling of long golden brown scales in the posterior half, and the wing tends to have much less white overscaling than in subspecies *bayensis* to the south. The median macular band is usually edged anteriorly on both wings with white, but tends to become obsolescent in the posterior half of the hindwing. The post-median band of spots is well-developed in some specimens, almost completely absent in others.

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 163-164 (1998i).

TYPE LOCALITY: Along highway at confluence of Lagunitas Creek and San Geronimo Creek, 200' elevation, southwest of Lagunitas, Marin County, California. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This subspecies is known from only a few Redwood Forest localities within Marin County. Populations just to the north in Sonoma County and to the northeast in Napa County show some blending towards the subspecies *marinensis*, but have a closer affinity to *I. m. windi* populations of the North Coast Ranges.

ELEVATION RANGE: 200 to 600' elevation.

HABITAT AND PLANT COMMUNITIES: This subspecies is typically found on steep, gravelly to rocky, north-facing slopes within Redwood forests and Douglas Fir forests. All the populations located so far are along canyon bottoms, usually near roads.

PHENOLOGY: Adults fly in a single brood from early to mid-April.

FOODPLANTS: *Sedum spathulifolium* Hook ssp. *spathulifolium* Hook is the only known foodplant for this subspecies.

131. *Incisalia fotis mojavensis* Austin

As noted earlier, *Incisalia fotis* (which feeds on the larval host *Purshia stansburiana* in the Rosaceae) is abundantly distinct from *Incisalia mossii* (which feeds on *Sedum* and *Dudleya* larval hosts in the family Crassulaceae). We have one newly-recognized subspecies of *fotis* in California.

DIAGNOSIS: This desert *Incisalia* species is readily identified by the whitish-gray outer half of the hindwing on the underside. The upperside is usually gray and in both sexes, although occasionally orangish in females.

ORIGINAL DESCRIPTION: Austin, *Systematics of Western North American Butterflies*, pp. 546-547 (1998c).

TYPE LOCALITY: Spring Mountains, 2 miles north of Red Cloud Mine, 1829m elevation, Clark County, Nevada. Holotype in Nevada State Museum.

DISTRIBUTION: This species is widespread in the higher mountains of the eastern portions of our deserts, from the extreme southern end of the White Mountains in northern Inyo County southward through the Inyo Mountains, Argus Range, the Grapevine Mountains, the Panamint Range, to the mountains of the eastern Mojave Desert,

including the Kingston Range, Clark Mountain, the Ivanpah Mountains, the New York Mountains, and the Providence Mountains.

- ELEVATION RANGE: From 3,200 to 8,800' elevation, with the majority of populations below 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This butterfly is typically found in canyons or on rocky slopes where the rock substrate is limestone. This is usually within Pinyon-Juniper Woodland or the upper edge of the Creosote Bush Scrub plant community.
- PHENOLOGY: Adults fly in a single brood from late March to late May, depending on elevation.
- ADULT BEHAVIOR: The males frequently perch on tall shrubs in the canyon bottoms, particularly on individuals of the *Cowania* foodplant. Often, males will select small hilltops or ridgetops as perching sites, still actually perching on shrubs rather than on the soil or rocks.
- LIFE HISTORY: The egg of this subspecies is undescribed. (Notes by Newcomer, 1973, on the life history of "*I. fotis*" refer to *I. mossii*.) In California material from the Last Chance Range, the mature larva is superbly camouflaged on its *Purshia* foodplant. The ground color is an intense dark green. There is a lateral white band running just below the spiracles, broken slightly at each segmental junction. This white band is edged slightly by black. In the center of the dorsal surface is a faint white band accompanied on either side by a broad white triangular chevron trailing posteriorly on each segment. The center of each white triangle has yellow pigmentation and the side closest to the dorsal line is tinged with magenta. The pupa is a pale tan to medium brown, sometimes with slight green tinting. This species estivates in the pupal stage.
- FOODPLANTS: Cliff Rose, *Purshia stansburiana*.
- CHROMOSOME NUMBER: Unknown.
- SIMILAR SPECIES: This is the only Desert Elfin in our area, and the one record of a *Incisalia augustus iroides* from the Providence Mountains is believed to have been an aberrant specimen of *fotis*.
- GEOGRAPHIC AND SEASONAL VARIATION: This species is strictly univoltine, and within California there is no significant geographic variation.
- GENERAL REMARKS: This species occurs eastward to southwestern Colorado and northwestern New Mexico. It has been frequently confused with *Incisalia mossii* in the past; Clench (1957, 1961) thought the western representatives treated herein were all one species, for example. Its only known host plant is *Purshia stansburiana* (family Rosaceae).

132. *Callophrys dumetorum* (Boisduval)

- SPECIES SYNOPSIS: This is the butterfly that in more recent years has been called *C. viridis* (e.g., Brown and Clench, 1969). A careful examination of the Boisduval syntypes of *C. dumetorum* in the U. S. National Museum (Emmel, Emmel, and Mattoon, 1998I: pp. 164-165), as well as improved knowledge of the areas in which the collector of the types, Lorquin, collected (Emmel, Emmel, and Mattoon, 1998a), has led to the determination that *C. viridis* (W. H. Edwards) is a synonym of *C. dumetorum* (Boisduval), both names referring to the coastal northern California

Callophrys species. As *dumetorum* is the older name, it represents these populations. No subspecies of *C. dumetorum* are recognized currently.

DIAGNOSIS: Additionally, field studies of sympatric populations of this coastal *Callophrys dumetorum* species and the taxon *C. perplexa* Barnes and Benjamin at the Marina Dunes in Monterey County indicate that they are best treated as two species (Emmel, Emmel, and Mattoon, 1998i: p. 165). This second California species, *C. perplexa*, also has significant differences from the eastern U.S. species *C. affinis* (though Scott, 1986, treated *perplexa* as a subspecies of *affinis*). *Callophrys perplexa* is more widely distributed than the coastal *C. dumetorum* and has developed three subspecies across California.

On the upperside, *dumetorumj* males tend to be a uniform slaty-gray, while females are either slaty-gray or shaded with varying amounts of dull reddish-brown. On the underside, there is variation in the shade of the green ground color, with some specimens being a vivid blue-green and others being either a dull dark green or yellowish-green. In most individuals, there is a well-developed white median macular band on the underside. The fringes of the wings are usually white in contrast to that of *C. perplexa*, in which it is usually brown. Additionally, on the underside of the forewing, the green usually covers at least the anterior half of the wing, whereas in *C. perplexa* this area may be invaded by orange scaling, and the green scaling is confined to an area less than half the surface area of the forewing.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 291 (1852).

TYPE LOCALITY: "California". Restricted by Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies* (1998a), to San Francisco, California. Holotype in U. S. National Museum.

DISTRIBUTION: This species is distributed along the immediate coast of northern California from the Marina Dunes in Monterey County northward through the San Francisco Peninsula along the coast to as far north as Juan Creek, north of Westport, Mendocino County.

ELEVATION RANGE: From sea level to 1,300' elevation.

HABITAT AND PLANT COMMUNITIES: This butterfly is found in the North Coastal Sage Scrub and Coastal Strand plant communities of the northern California coast. It is typically found on open rocky or gravelly slopes and ridge tops, on low hills or cliffs above the ocean breakers.

PHENOLOGY: Although this butterfly is single-brooded in a given locality, because of the close proximity to the moderating effect of the ocean, flight period tends to be drawn out over a long period of time. In most populations, emergence of adults begins in mid- to late March and continues into early May. In some localities where fog is especially prevalent, the flight period may extend into early June.

ADULT BEHAVIOR: The adult behavior is described in detail by Gorelick (1971). Males tend to perch on small shrubs, usually near a small cleared area on a slope or ridge top. Females tend to be more sedentary, spending much time alighted on the foodplant or on adjacent small shrubs. When ovipositing, females will usually land on several *Eriogonum* plants, tapping several leaves on each with the antennae. After a period of time of flying from plant to plant, the female will finally alight on an *Eriogonum* leaf and, after touching the underside of the leaf with the antennae, bends the abdomen underneath and deposits a single egg.

- LIFE HISTORY:** The eggs are approximately 0.4 millimeters in diameter and are ovoid in shape, with a green ground color and a fine reticulation over the entire surface. They are deposited singly on the underside of *Eriogonum* leaves near the base of the plant or bloom stalk (Brown and Opler, 1967). Almost none of the host plants are in bloom when the adults are in flight; the larvae feed on the subsequently developing flower parts. The mature larva, as described from material taken from the San Bruno Mountains populations, is a pale yellow-green to whitish-green in ground color. The most prominent feature (and a character which separates it from *C. perplexa*) are the sawtooth-like ridges arising from the subdorsal area and continuing laterally around each segment. Arising from the crest of each ridge is a white chevron marking that recedes posteriorly towards the mid-dorsal line, in the form of a right triangle. As the rear point of this triangle touches the next segment, a new broad triangular base arises off of the next ridge. From a dorsal view, then, there is a broad whitish band on the mid-dorsal line and then a series of right triangles heading off each side to the lateral surface. Below the spiracles on each side, there is a lateral band of white from the head to the tail end of the larva, and on all of the abdominal segments this band is edged on both sides with reddish-brown. The white dorsal chevrons have a small area of reddish-brown in the center of each. A small dark dot lies between the dorsal chevrons and the lateral white line on each segment. The pupa is a light brown in ground color, with slightly darker brown fine mottling. The wing pads are relatively smooth. Over the entire surface, except for the wingcases, are small translucent white hairs.
- FOODPLANTS:** The major foodplant of this species is *Eriogonum latifolium* Sm. (Coast Buckwheat). A secondary host in San Francisco, and possibly along the west base of the San Bruno Mountains, is *Lotus scoparius* (Nutt. in T. & G.) Ottley (Fabaceae).
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** Some individuals of *C. dumetorum* can be very similar to *C. perplexa*, however, there is only one known area where the two species seem to overlap, and this is in the Marina Dunes in Monterey County. Even in this area, the adults of both species tend to be fairly readily separable on the basis of the characters described under Diagnosis of this species. Additionally, in this locality, *C. perplexa* tends to have an earlier flight period from late February to late March, while *C. dumetorum* tends to fly from the months of April through early June (J. Emmel, unpublished data).
- GEOGRAPHIC AND SEASONAL VARIATION:** Because the species is univoltine, there is no seasonal variation. Most of the populations of *C. dumetorum* tend to be fairly similar in their phenotype; however, in San Francisco, there tends to be a greater percentage of *perplexa*-like individuals which may possibly represent some gene flow from *C. perplexa* populations in the past which were established on more extensive *Lotus scoparius* (Nutt. in T. & G.) Ottley biomass on the east side of the San Francisco Peninsula. Through the progressive urbanization of San Francisco, much of this former habitat has been lost, and there is not enough remaining *Lotus scoparius* (Nutt. in T. & G.) Ottley biomass to maintain an ongoing *C. perplexa* population on the east side of the Peninsula.
- GENERAL REMARKS:** It should be noted that this is one of the nearctic hairstreaks whose pupa has been shown to have stridulatory organs between the fourth and fifth abdominal segments, and fifth and sixth abdominal segments. Sounds have not been heard

yet in these pupae. It should be noted that we are treating the four *Callophrys* as separate semi-species in this book. A case could be made for grouping them all within one species, or splitting them even further than four species. But we note that, for example on the eastern slope of the Sierras, *C. comstocki* meets *C. perplexa* in a blendzone and again in northern California *perplexa* meets populations of *lemberti* in a blendzone. Additionally, even topotypical *lemberti* populations show *perplexa*-like facies. We separate *C. dumetorum* and *C. perplexa* because the two entities coexist on the Marina Dunes, where they have different flight periods, different foodplants (*C. dumetorum* there uses *Eriogonum latifolium* Sm., and *C. perplexa* there uses *Lotus scoparius* (Nutt. in T. & G.) Ottley), and the adults remain phenotypically distinct. While there is some hybridization occurring between these two entities on the Marina Dunes, the majority of specimens of either taxon seem to sort out satisfactorily into the diagnostic characters for that particular species.

133. *Callophrys perplexa* Barnes and Benjamin

SPECIES SYNOPSIS: As noted in the preceding species account, extensive field work and rearing studies in the western U.S. of the members of the genus *Callophrys* lead us to recognize (Emmel, Emmel, and Mattoon, 1998I) 7 species groups originally defined by J. W. Tilden (1963) as best representing the taxonomic status of the genus. These are: *C. dumetorum* (Boisduval) [= *viridis* (W. H. Edwards)], *C. perplexa* Barnes and Benjamin [= *C. dumetorum* Auctorum (not Boisduval)], *C. affinis* (W. H. Edwards), *C. apama* (W. H. Edwards), *C. sheridanii* (W. H. Edwards), *C. comstocki* Henne, *C. lemberti* Tilden. Four of these (*dumetorum*, *perplexa*, *comstocki*, and *lemberti*) occur within California, and of these, *C. perplexa* is the most widely distributed and phenotypically diverse, with three geographic subspecies named.

ADULT BEHAVIOR: *Callophrys perplexa* adults fly within three or four feet of the ground and alight repeatedly on both *Lotus scoparius* (Nutt. in T. & G.) Ottley and *Eriogonum fasciculatum* Benth. in San Gabriel Canyon in southern California. At Antioch in central California, however, females seem to land frequently on *Lotus* but ignore the *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes subspecies present. This latter plant is probably not used as a host. Males show aggressive behavior, especially when another butterfly species enters the area. Sometimes males will even perch within one or two inches of each other and "scuffle" with each other by flying around each other up to twenty feet in the air (apparently competing for a given territory while in flight), returning to separate leaves on the same plant or adjacent plants (Gorelick, 1971: 15-16). Courtship behavior begins as early as mid-morning, when an individual male approaches a female in flight and apparently forces the female to land. The male will vigorously vibrate its wings while standing on a leaf behind the one occupied by the female and then move behind the female to copulate. The entire courtship process lasts less than fifteen seconds.

LIFE HISTORY: The eggs are green in color, finely reticulated, ovoid in shape, and about 0.4 millimeters in diameter. They are deposited singly on the various host plants, usually, in the tip of the new shoot between the new leaves of the *Lotus* host. Four larval instars occur. The mature larva varies somewhat in the different subspecies. In *C. p. pseudodumetorum*, the larva is a rich velvety apple-green, with a pair of subdorsal yellow stripes that are broken at each segment, and a more continuous bright yellow lateral stripe running the length of the larva. Along the mid-dorsal line is a faint dark green band. Otherwise, there are no markings on the larva in this subspecies (described from Del Puerto Canyon, Stanislaus County material).

In subspecies *superperplexa*, the mature larva tends to approach the phenotype of the larva of *Callophrys comstocki*. The last-instar larva is a dull olive-green in ground color, with a pale, broad yellow lateral band on each side below the spiracles, and two faint yellow dorso-lateral bands, broken at each segment, which form the inner part of a faint chevron marking on either side in each segment (described from Simmes Creek, Inyo County material).

The mature larva of the typical subspecies occurs in several color forms, these being correlated with the coloration of the particular host on which it is feeding. The light color form is a pale whitish-green in ground color, with a broad white stripe occurring below the spiracles and a darker green stripe immediately dorsal to it. On the upper surface of this form, a pair of broad white dorso-lateral bands runs the length of the larva.

Sometimes the larval ground color is almost a gray in intensity. This light form of typical *perplexa* feeds on *Eriogonum* plants. The dark form of typical *perplexa* larvae is a bright apple-green in color and has a narrow yellow band extending the length of each side below the spiracles. Dorsally, there are two faint yellow dorso-lateral lines broken at each segment. The most notable feature in the mature larvae of the *perplexa* subspecies is the absence of subdorsal and segmental ridges. Likewise, the red spots that are associated with *dumetorum* larvae on the subdorsal ridges are absent. The marked red accentuation of the white areas on *dumetorum* larvae is absent in the *perplexa* larvae.

The ground color of the pupa is dark brownish-black, with pronounced sculpturing across the wing pad.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: See *Callophrys dumetorum* (Diagnosis and Life History) for distinguishing features of these two similar species.

GEOGRAPHIC AND SEASONAL VARIATION: This species is strictly univoltine in all of its populations, and there is no seasonal variation. In populations of *C. p. perplexa* in northern California, from the lower elevations of the Klamath Mountains eastward to Lassen County, the white spotting pattern on the ventral surface is often reduced from that seen in more typical southern California *perplexa*. There is considerable variation in these populations, but they seem closer to *C. p. perplexa* than to any other described subspecies of *C. perplexa* and are thus included here under that subspecies. On the west slope of the Sierra Nevada, particularly from the Yosemite region northward, females of *C. p. perplexa* tend to be more uniformly yellowish-brown above, with minimal dark suffusion at the edges of the wings.

GENERAL REMARKS: It should be noted that geographic variation in adult coloration and pattern varies somewhat independently of the notable variation in larval ground color and pattern, and the latter is somewhat related to the foodplant on which the larva feeds.

SUBSPECIES: This species of green hairstreak occurs through California north into Oregon. In California, three subspecies have been recognized.

a. *C. p. perplexa* Barnes and Benjamin

DIAGNOSIS: Clench (1944) first applied the name *dumetorum* Boisduval (1852) to California *Callophrys* populations other than those that Boisduval named *dumetorum* along the immediate North Coast. Subsequently, because these interior *Callophrys* populations were seemingly identical to the taxon *perplexa* which Barnes and Benjamin named from San Diego in 1923, *perplexa* was synonymized under *dumetorum* by several recent workers. However, in light of the name *dumetorum* being properly applied to the North Coastal *Callophrys*, these more interior populations of *Callophrys* then fall under the resurrected name *perplexa*.

The nominotypical subspecies name is usually applied to populations that are mostly west of the Sierran Cascade Axis in California, typically in foothill or lowland situations, where populations are associated with *Lotus crassifolios* (Benth.) Greene, *L. scoparius* (Nutt. in T. & G.) Ottley and/or *Eriogonum fasciculatum* Benth. The typical wing characters of these populations are as follows. Males have a fairly uniform olive-gray to brown-gray on the dorsal surface, while females are dark gray-brown with a variable amount of yellow-brown suffusion over the dorsal surface. On the underside, the ground color is a soft or dull yellow-green, sometimes olive-green. On the antennae there are alternating rings of black and white, whereas in *C. dumetorum* the antennae tend to be all white scaled when viewed dorsally. On the ventral surface of the forewing, the green scaling never goes beyond the CU₁ vein, whereas in *C. dumetorum* the green scaling almost always reaches the CU₁ vein or goes beyond it to the CU₂ vein of the forewing. Lastly, the macular band of white spots on the ventral surface of the hindwing tends to be reduced in *C. p. perplexa*, often consisting of only two or three spots and sometimes almost completely absent.

ORIGINAL DESCRIPTION: Barnes and Benjamin, *Contributions Natural History Lepidoptera North America*, 5: 65 (1923).

TYPE LOCALITY: San Diego, California. Holotype in U. S. National Museum.

DISTRIBUTION: From the mountains and foothills of southern California northward along the west slope of the Sierra Nevada, both slopes of the Cascade Range, and through the South Coast Ranges and North Coast Ranges to the lower elevations of the Klamath Mountains region. From California, the species ranges northward into Oregon and probably south central Washington.

ELEVATION RANGE: From near sea level to 6,500' elevation.

HABITAT AND PLANT COMMUNITIES: In the lower foothill situations, this species is commonly found in the Coastal Sage Scrub and Chaparral plant communities, generally in cleared areas and the *Lotus scoparius* (Nutt. in T. & G.) Ottley foodplant grows abundantly as a "weedy" colonizer. It is also found on the Coastal Strand plant community of the sand dunes such as at the Marina Dunes in Monterey County, or the Oso Flaco Dunes in San Luis Obispo County and Santa Barbara County. Along the western edge of the California deserts, populations are found in Pinyon-Juniper Woodland and Joshua Tree Woodland plant communities where *Eriogonum fasciculatum* Benth. is locally abundant. In northern California, it inhabits open ridge tops and banks or openings on canyonsides in Transition Zone forests where *Lotus crassifolios* grows, usually above 2,500' elevation.

PHENOLOGY: The species is strictly univoltine, with adults first appearing in late February at the lower elevations and emergence continuing into early May at the higher

elevations. In northern California mountains, the flight period is late April through June.

FOODPLANTS: The butterfly uses both *Lotus scoparius* (Nutt. in T. & G.) Ottley and *L. crassifolios* (Benth.) Greene (Fabaceae), and *Eriogonum fasciculatum* ssp. *fasciculatum* Benth., *polifolium* (Benth.) S. Stokes, *foliolosum* (Nutt.) S. Stokes, and *elongatum* Benth. (Polygonaceae). These are the principal foodplants of this butterfly; in a given locality, one species may be present or both may be present. If both are present, the butterfly will use both species.

b. *C. p. pseudodumetorum* Emmel, Emmel, and Mattoon

DIAGNOSIS: This subspecies of the Inner Coast Range is characterized by usage of *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes as a larval host plant, uniform gray uppersides of both sexes, and a bluish-green underside with a fairly well-developed white macular band on the secondaries ventrally. The black annular rings on the white antennae are narrower than they are in the nominotypical *perplexa* adults.

The close resemblance in adult coloration between *C. p. pseudodumetorum* and *C. dumetorum* is remarkable. (It caused Gorelick [1971] to treat the Del Puerto Canyon, Stanislaus County population as an inland colony of the coastal *C. dumetorum* [= *C. viridis*].) The explanation may be convergent evolution based on the color of similar host plants; the coastal *C. dumetorum* feeds on *Eriogonum latifolium*, a close relative of *E. nudum*. The adults frequently perch on the leaves of the host, and the leaf color of *E. nudum* is very close to that of *E. latifolium*. (In contrast, the more yellowish green *C. p. perplexa* perches on its primary host, *Lotus scoparius*, a plant which has yellowish green to grass green leaves as opposed to the gray-green or bluish green of the *Eriogonum nudum* or *latifolium* leaves). While *C. p. pseudodumetorum* occurs in close proximity to populations of *C. p. perplexa*, no areas of sympatry are known.

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 165-166 (1998i).

TYPE LOCALITY: Ruth Reservoir in the North Coast Ranges, Trinity County, California. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This butterfly is found in two fairly localized areas of the Inner Coast Range in California. The first area is in the vicinity of Ruth Reservoir, in Trinity County in the North Coast Ranges. The second area is on the east side of the Mt. Hamilton Range, such as Del Puerto Canyon, in Stanislaus County.

ELEVATION RANGE: From approximately 2,000 to 5,000' elevation.

HABITAT AND PLANT COMMUNITIES: In the Mt. Hamilton Range, this butterfly is found in canyon bottoms or on steep rocky slopes within a chaparral association. In the Ruth Reservoir area, the habitat is in canyon-bottom chaparral associations, with Northern Oak Woodland on adjacent lower slopes, and extending up into a modified Mixed Evergreen Forest setting. The host, *Eriogonum nudum*, occupies open hillsides or gravelly banks throughout these areas, as well as sandy banks on open slopes, and the males fly into the adjacent chaparral to perch and challenge, or nectar on understory flowers. Higher in the North Coast Range, the hostplant's habitat changes from one dominated by Northern Oak Woodland to Mixed Evergreen or even Douglas Fir Forests, where the host grows in similar hillside settings. However, the adults are drawn to ridgecrests clad with grasses, small

shrubs and a blooming legume vine which acts as the primary nectar source and location for adult mating interaction.

PHENOLOGY: This butterfly is univoltine, with a flight period from late March to late April in the more southern populations, and mid-April to mid-May for the more northern populations.

FOODPLANTS: This subspecies uses *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes (Polygonaceae) in both the Ruth Reservoir and Hamilton Range localities.

c. *C. p. superperplexa* Emmel, Emmel, and Mattoon

DIAGNOSIS: This subspecies of the eastern slope of the southern Sierra Nevada is characterized by smaller size compared to other *C. perplexa* subspecies, the uniform gray upperside of both sexes, a dull grayish-green ground color of the underside, and a well-developed but very thin white macular band on the secondaries approaching the shape seen in that of *Callophrys comstocki*. Although superficially resembling *C. comstocki*, biological characters, and the existence of a contiguous cline to the south with typical *perplexa*, indicates that this taxon is most closely related to *C. perplexa*.

C. p. superperplexa differs from *C. comstocki* by its slightly larger size, somewhat more brownish upperside, and greener underside (a less gray green). Additionally, while the ventral macular band is well developed for a *perplexa* subspecies, it is not as well defined as it typically is in *C. comstocki*. The larval characters are somewhat intermediate between those of *C. comstocki* and nominotypical *perplexa* populations on the east flank of the Piute Mountains in Kern County. Also, it is strictly univoltine, in contrast to the sometimes multivoltine *C. comstocki*.

C. p. superperplexa is distinguished from nominotypical *perplexa* by the more grayish green ventral surface, the well defined macular band ventrally, the more consistent whitish fringe, and the brownish gray surface of females in contrast to *C. p. perplexa* which frequently has females with varying degrees of fulvous scaling, particularly in the basal areas. *C. p. superperplexa* is also similar to *C. lemberti* in the Sierra Nevada, but differs in having a more well-defined macular band, and the more brownish gray dorsal surface, in contrast to the usually grayer *lemberti*. Additionally, the foodplant and habitat of *superperplexa* are in marked contrast to the Alpine Fellfields or Subalpine Forest rocky slope habitats of *lemberti*.

Because this subspecies combines characters of three different *Callophrys* species (*perplexa*, *lemberti*, and *comstocki*), the name *superperplexa* aptly reflects its somewhat uncertain taxonomic status.

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, p. 166 (1998i).

TYPE LOCALITY: Big Pine Creek, 9 roadmiles west of Big Pine, 6,500' elevation, east slope of the Sierra Nevada, Inyo County, California.

DISTRIBUTION: This subspecies is found on the east slope of the southern Sierra Nevada from approximately Little Lake Canyon at the south end of its range, north to approximately Bishop Creek at the north end of its range.

ELEVATION RANGE: From 3,000 to 7,000' elevation.

- HABITAT AND PLANT COMMUNITIES: This butterfly is typically found on steep granitic soil slopes or in small dry canyons on the east slope of the Sierra Nevada in areas where the dominant low shrub covering the slopes is the larval foodplant, *Eriogonum fasciculatum* Benth. This foodplant and habitat are more similar to those of nominotypical *C. p. perplexa* populations to the south. In contrast, *C. comstocki* usually occupies limestone canyons and utilizes *Eriogonum heermanni* Dur. & Hilg. as a larval foodplant.
- PHENOLOGY: This species flies from mid-March to late April, depending on elevation.
- FOODPLANTS: The apparent sole host of this subspecies is *Eriogonum fasciculatum* Benth. ssp. *polofolium* (Benth.) S. Stokes.

134. *Callophrys comstocki* Henne

This demure little *Callophrys* species was described in 1940 from material taken in the Providence Mountains of the eastern Mojave Desert. For many years *Callophrys comstocki* was known only from the Providence Mountains, but has recently been found to have a considerably more extensive distribution. It even ranges into Nevada (Callaghan, 1970). Additionally, in contrast to the other two *Callophrys* species we have considered so far, Comstock's Hairstreak is multiple-brooded.

- DIAGNOSIS: This desert species is characterized by its smaller size, its uniform light gray uppersides and the uniformly grayish-green undersides, with a well-developed medial macular band of linear white markings.
- ORIGINAL DESCRIPTION: C. Henne, *Bulletin Southern California Academy Sciences*, 39: 71 (1940).
- TYPE LOCALITY: Providence Mountains, San Bernardino County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This species is widely distributed in our desert mountains, from the Benton Range in southeastern Mono County southward through the White Mountains and Sherwin Summit area through the Inyo Mountains, the Grapevine Mountains, the Coso Range, the Argus Range, the Panamint Range, the Nopa Range, to the mountains of the Eastern Mojave Desert, namely the Kingston Range, the New York Mountains, the Ivanpah Mountains, the Providence Mountains, Hackberry Mountains, and the Granite Mountains north of Amboy. Additionally, the butterfly occurs in the Ord Mountains southeast of Barstow, a somewhat disjunct set of populations in the western Mojave Desert.
- ELEVATION RANGE: 3,000 to 9,000' elevation, with most populations in the 4,000 to 6,000' range.
- HABITAT AND PLANT COMMUNITIES: Typically found in desert canyons within the Pinyon-Juniper Woodland plant community, or in the Shadscale Scrub plant community. Most populations are found in limestone mountains, where growth of the principal foodplant, *Eriogonum heermanni* Dur. & Hilg., is abundant.
- PHENOLOGY: Unlike other California *Callophrys* species, *C. comstocki* is multivoltine, with the size of the second and third broods dependent in part on both winter and summer rainfall patterns. In years of very wet winters, the spring generation, which begins flying in mid- to late March, flies through April or even into early May, depending on elevation. Subsequently, a second generation appears in June and July, and a

third generation in mid- to late August into September. Even in years of low winter rainfall, these summer broods apparently occur, but are decidedly diminished in number over the spring brood. Summer rainfall may also influence the size of the late summer brood.

- ADULT BEHAVIOR:** Males perch in the desert canyon bottoms, usually in small cleared areas within a wash, landing either on the soil, on rocks, or on low shrubs along the sides of the wash. Females tend to stay in the areas where the foodplant grows, higher up on the canyon slopes. Both sexes are fond of flowers, visiting such blooming species as *Rhus trilobata* Nutt. ex T. & G. and *Prunus fasciculata* (Torr.) Gray.
- LIFE HISTORY:** The egg is undescribed. The remaining early stages have not been published previously. The mature larva has slight development of the sub-dorsal ridges, more or less intermediate between the condition observed in *C. perplexa* (absence) and *C. dumetorum* (strongly present). The general ground color is a dull, dark grayish-green. There are two dorso-lateral rows of short, inwardly curved whitish semi-circles, one to a segment and each with a small yellow-colored center. These form the inner side of a rough triangle extending downward and composed of a thin white band (the center of each triangle is green ground color). These hollow triangles form a series of scallops on either side of the center of the larva down its length. They are roughly comparable to the outline of the triangles present on *Callophrys dumetorum* larvae, but of course lack the intense red centers and broader development in that species. Laterally on the mature *comstocki* larva, there is a thick band of pale yellow segments located below the spiracles on each segment. The larva is covered with short stout pale yellow hairs. The pupa of this species is a uniform light brown in ground color.
- FOODPLANTS:** The principal host is apparently *Eriogonum heermannii* Dur. & Hilg., as this plant is almost invariably present in the majority of *C. comstocki* populations. In several instances larvae have been found feeding on this particular *Eriogonum* (Pratt and Emmel, unpublished data). Additionally, the following *Eriogonum* species have been documented as foodplants of *C. comstocki*: *E. umbellatum* Torr. ssp. _____ (G. Pratt and J. Emmel, unpublished data), and *E. fasciculatum* Benth. ssp. *polifolium* (Benth.) S. Stokes (G. Ballmer, personal communication); *E. microthecum* Nutt. ssp. _____ (J. Emmel and G. Pratt, unpublished data); *E. kennedyi* Porter in Wats. ssp. _____ (G. Pratt, personal communication).
- SIMILAR SPECIES:** A closely related *Callophrys* which may be mistaken for *C. comstocki* is *C. p. superperplexa* along the east slope of the Sierra Nevada. In this subspecies the macular band tends to be less strongly bowed outward in the center of the hindwing, and is often less developed than that seen in *C. comstocki*. In all *C. comstocki* populations, no other *Callophrys* species is present, so the possibility of confusing it with another species within its range is minimal.
- GEOGRAPHIC AND SEASONAL VARIATION:** The phenotype of *C. comstocki* is remarkably uniform in virtually all populations within California. However, there is a marked seasonal variation. In the spring brood, adults have a uniformly gray-green underside ground color; however, in the summer broods, the ventral surface is covered with varying degrees of light yellow overscaling, giving some individuals a very yellowish appearance beneath.
- GENERAL REMARKS:** This species is apparently closely related to *C. sheridanii*, which occurs from southern New Mexico and eastern Arizona north into central Colorado and the Bighorn Mountains of Wyoming. That species is single-brooded and flies in the

early spring from late March to April in central Colorado. That small species has a ventral post-median band on the hindwing which is solid and unbroken.

135. *Callophrys lemberti* Tilden

DIAGNOSIS: This high to mid-elevation species is characterized by the upperside of the males being uniformly gray, the upperside of the females usually being uniform gray but sometimes invaded by varying degrees of fulvous coloration; on the ventral surface, the ground color varies from a soft gray-green to a dark yellowish-green. The median macular band of linear white markings is reduced from that seen in *C. comstocki* to a very thin broken line, often becoming obsolete. In some populations, there are individuals which totally lack any of these white markings.

ORIGINAL DESCRIPTION: Tilden, *Journal Research on the Lepidoptera*, 1: 292-298 (1963).

TYPE LOCALITY: West above Tioga Pass, Yosemite National Park, California. Holotype in California Academy of Natural Sciences.

DISTRIBUTION: This species is found at the mid- and higher elevations of the Sierra Nevada from Tulare County northward to the Mt. Shasta region and the Klamath Mountains Assemblage. It is also found in the higher elevations of the Warner Mountains, and in the White Mountains of Inyo and Mono counties, above 9,000' elevation in that particular range. It ranges northward into the higher elevations of the southern Cascades; the precise northern limits of its range are undetermined. Eastward from California it is found in the highest elevations of the Wassuk Range in western Nevada, and higher elevations in mountains along Nevada's northwestern border.

HABITAT AND PLANT COMMUNITIES: This butterfly is usually found in small ravines or on gravelly slopes, usually in somewhat open or cleared areas within the Montane Coniferous Forest, Sub-Alpine Forest, or the Arctic Alpine Fellfields plant communities. It also occupies such locations at lower elevations along the eastern base of the Sierra Nevada and through the Modoc Plateau in the Artemisia-Juniper Woodland or Artemisia-Scrub plant associations.

PHENOLOGY: This species is strictly univoltine, with adults flying from late April to early August, depending on elevation, with most populations flying during the month of May or early June.

ADULT BEHAVIOR: Males tend to perch on open patches of ground, in small gullies, or on gentle gravelly slopes. Adults will sip moisture from wet sand or mud. Both sexes visit the flowers of several montane *Eriogonum* species, as well as small *Composites*, and are especially fond of pussypaws (*Eriogonum* sp.)

LIFE HISTORY: The egg is undescribed and the later stages of the life history have been unreported previously. The mature larva has been observed from three geographic areas and shows some degree of variation. In the Sierra Nevada, the mature larva is a velvety apple-green in ground color, with a strong and continuous light yellow lateral band below the spiracles and a very faint, slightly lighter green pair of dorso-lateral bands above, with one on either side of the dorsal area. This is the predominant morph in the Sierras, but a second morph also occurs which is reddish-purple in ground color. This morph has a single mid-dorsal light gray band, with no strong lines on either the lateral surface or the dorso-lateral area. However, there are faint grayish blotches in the dorso-lateral area on each side.

In the Klamath Mountains Assemblage, the ground color of the mature larva is a dull gray-green. There is a white lateral band below the spiracles. Dorsally, there are two dashed yellow dorso-lateral bands, often with a diffuse yellow connecting area between them on each segment. In this population also, the reddish-purple morph exists and both morphs have been reared from eggs of the same female.

Finally, in the White Mountains east of the Sierra Nevada, the mature larva exhibits a very pale green, somewhat broken pale yellow band in the dorso-lateral area on each side. The inner parts of this band form the bases of faint posteriorly-facing hollow triangles of there pale lines, each triangle having a green center. As in the other two geographic sets of larvae observed, the spiracles are a dull reddish color but tend to stand out more on this light green background in the White Mountains larvae.

The pupae are light brown to olive-brown in ground color, covered with short translucent hairs, except on the wing cases, and spotted with small brown markings. The pupae are larger than those of *Callophrys comstocki*.

FOODPLANTS: This species uses several montane *Eriogonum* species as foodplants including *E. incanum* (T. & G.) Jones, *E. umbellatum* Torr., *E. marifolium* T. & G., *E. nudum* (Dougl. ex Benth.) S. Stokes, and *E. hirtellum*. *Astragalus andersonii* appears to be a usable host (Mattoon, unpublished). Eggs were found in abundance on both *Eriogonum incanum* (T. & G.) Jones and the *Astragalus* near Fredricksburg, Alpine County. *Callophrys lemberti* were reared from both hosts, and the last instars also successfully fed in the laboratory on *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes from the Chico, California area..

CHROMSOME NUMBER: Unknown.

SIMILAR SPECIES: Although this *Callophrys* species is not sympatric with any others within its range, there are several localities where populations are situated fairly close geographically. Individuals in some populations can look remarkably like *C. perplexa perplexa*, particularly in the Sierran and Klamath Mountains Assemblage populations. Usually, however, there is more development of a linear macular band ventrally in *lemberti* than in *C. perplexa*, and the ventral ground color in *lemberti* tends to be a duller gray-green in contrast to the more yellowish-green of *C. perplexa*. Females in some *C. lemberti* populations may have fulvous scaling dorsally, again resembling some females of *C. perplexa*. In these instances, usually, elevational differences and host plant association differences can be used to separate the two species.

GEOGRAPHIC AND SEASONAL VARIATION: As the species is strictly univoltine, there is no seasonal variation. There is considerable variation, as noted above, in the ventral macular band in California populations of *C. lemberti*. In the Warner Mountains of Modoc County (and in adjacent Nevada mountains to the east), and in the White Mountains, the macular band is often very thin or obsolescent in contrast to the Sierran populations in which a fairly well-defined but very thin white macular band is usually present.

GENERAL REMARKS: The disjunct high elevation *C. lemberti* populations in the White Mountains and the Wassuk Range in Nevada are of interest because one finds typical *C. comstocki*, associated with *Eriogonum heermannii* Dur. & Hilg., in the lower canyons of these Great Basin mountain ranges. The high elevation *lemberti* populations utilize *Eriogonum umbellatum* Torr. ssp. _____, at least in the White Mountains populations studied. This may hold true also for populations on the high pass on Nevada Highway 81 in Washoe County. There is no apparent

intermediate population between these two entities in either mountain range. This situation would tend to lend support to the idea that two separate but closely related species are involved here.

136. *Mitoura siva* (W. H. Edwards)

- ADULT BEHAVIOR:** Nectar sources in the form of blooming wildflowers are apparently essential for emerging adults, even though the larval host is evergreen. Thus, the emergence of the spring, summer, and fall broods when found may be highly dependent on winter rainfall to provide the proper conditions for the nectar source foodplants. Adults fly around the side branches and tops of the Juniper trees and frequently alight, perching to await the passage of a female. In the spring in a Juniper forest, these Hairstreaks are often quite abundant, but unless one taps the branches to scare up perched adults or finds a stand of blooming yellow composites where the butterflies are feeding, this species will rarely be seen.
- LIFE HISTORY:** The early stages were first described by Coolidge (1924), where they were incorrectly identified as "*M. loci*", from material collected in Mint Canyon, the type locality of *juniperaria*. The early stages of the four subspecies are very similar, and a single description will suffice. The echinoid egg is green and is covered with deep triangular reticulations. The mature larva resembles the small terminal twigs of the foodplant with incredible perfection. The ground color is green with darker green patches of raised bumps on either side of a narrow yellow mid-dorsal line, and another green raised patch on the dorso-lateral edge of the body above a yellow lateral band extending the length of the larva just below the spiracles. The ground color between these dark green patches is a light green, with yellowish areas mixed in. When viewed from above, these lighter areas form a series of irregular almost lemon-yellow crescents on either side of the mid-dorsal area. Minute brown hairs cover the body. The pupa is dark chestnut brown and is covered with short hairs except on the wing cases and the facial portions.
- CHROMSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** Occasional individuals in *juniperaria* populations resemble individuals of *Mitoura loki*. See Diagnoses of the two species for the differentiating characters.
- GEOGRAPHIC AND SEASONAL VARIATION:** The summer brood specimens tend to have a yellowish cast to the underside of the hindwing, much as in *Callophrys comstocki*.
- GENERAL REMARKS:** A postulated zone of hybridization between *M. s. juniperaria* and *M. loki* on the northeastern slope of the San Bernardino Mountains has not been found. In this area an interesting situation with potential foodplants occurs. An "island" of *Juniperus osteosperma* (Torr.) Little occurs as an altitudinal band in the northeastern San Bernardino Mountains between *J. occidentalis* Hook *australis* (which has an associated *Mitoura* species, probably *M. barryi* ssp.) and above a belt of *J. californica* Carr. (which has *Mitoura loki* associated with it). Repeated visits to this stand of *J. osteosperma* (Torr.) Little from March to July (John Lane, *in litt.*) failed to turn up any *Mitoura* associated with this *J. osteosperma* (Torr.) Little. Unfortunately, the band of *Juniperus californica* Carr. on the north slope of the San Bernardino Mountains and again at the east end of this range is not contiguous in the area of the northeastern base of these mountains and hence, there is not a continuous habitat in which the two entities come together and possibly form a blendzone or zone of hybridization.

These six species of *Mitoura* (136 through 141) have been variously treated, most extremely by Scott (1986) who lumps them all into one species across the United

States with other eastern species of *Mitoura*. The occurrence of sibling species in this genus (Remington and Pease, 1955), such as the extremely closely related species *Mitoura gryneus* (Hubner) and *M. hesseli* Rawson & Ziegler which utilize different hosts in the eastern coastal area of the U.S., lends a cautionary note to such broadscale synonomization, however. In the laboratory, these foodplant preferences can break down and *M. hesseli* will feed on *Juniperus virginiana* (like *M. gryneus*) instead of its normal host, *Chamaecyparis thyroides* (L.) B.S.P., as shown by Johnson (1983).

We feel that the taxonomic treatment given herein is conservative in retaining some entities which probably could be grouped as subspecies under others, but until further intensive life history and biosystematic work as well as hybridization studies are carried out in both the field and laboratory, this treatment will fairly reflect the best knowledge we have at the present time of this interesting group of Hairstreaks.

This group of small Hairstreaks is closely associated with *juniperus* across the western United States. In California, we have populations representing four subspecies.

a. *M. s. siva* (W. H. Edwards)

DIAGNOSIS: The typical subspecies occurs from Colorado to Arizona and penetrates our state in the Eastern Mojave Desert. The dorsal surface of the male is a deep brown, with diffuse orangish markings on the lower half of the forewing and the anal angle area of the hindwing. In the female, these orangish-brown areas are much more extensive across the wings, bordered by a darker brown. On the underside of the wings the typical subspecies is characterized by having a uniform green ground color all the way to the body, and a relatively straight post-median white line starting at the forward edge of the hindwing. Along the wing margin there is a fine black line, bordered inwardly by an expanded bluish field extending more than half way along the margin, which is actually a mixture of black and white scales. In this field is a orange ocellus-type marking with a black center. Other black spots in this area are usually obsolescent. The basal area of the ventral hindwing is always a uniform green, with no evidence of a proximal brown area as in subspecies *juniperaria*.

ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Ent. Soc.*, 5: 110-111 (1874).

TYPE LOCALITY: "Wingate, Arizona", probably near Fort Wingate, Arizona. Neotype in Carnegie Museum, designated by F. M. Brown and Clench, in F. M. Brown, *Transactions American Ent. Soc.*, 96: 61 (1970).

DISTRIBUTION: The typical subspecies of *Mitoura siva* occurs commonly from the Rocky Mountains through Arizona and penetrates our area in the mountains of the Eastern Mojave Desert and the Death Valley region. Specific mountain ranges in California in which the nomotypical species has been taken include the Providence Mountains, the New York Mountains, Clark Mountain, the Kingston Range, and the Panamint Range. No *Mitoura* have yet been taken in the Granite Mountains north of Amboy or in the Old Woman Mountains of the Eastern Mojave Desert. If *Mitoura* do exist in either of these ranges, it will be of great interest to see what species is involved, as the *Juniper* species present in the Old Woman Mountains is *J. californica* Carr and in the Granite Mountains both *J. californica* Carr and *J. osteosperma* (Torr.) Little are present. Since nomotypical *siva* in our state has only been recorded on *J. osteosperma* (Torr.) Little, and *M.*

loki has only been found on *J. californica* Carr, the phenotype of any *Mitoura* from these latter two mountain ranges should prove most interesting.

- ELEVATION RANGE: From 4,000 to 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is typically found in the Pinyon-Juniper Woodland plant community; within this plant community there tends to be some segregation of Junipers toward the lower elevations of the plant community and *Pinus monophylla* Torr. & Frem. to be more prevalent in the upper elevations of the plant community. The butterflies are found on open slopes and in canyon bottoms, usually closely associated with the host Juniper.
- PHENOLOGY: Apparently multivoltine, with the second and third broods being very small and almost undetectable in some years. Adults of the spring brood fly primarily during the month of April or into mid-May at the higher elevations, sometimes into late May or early June in the higher elevations of the Panamint Range. The second and third broods, if present, fly in June and then again in mid-August to mid-September.
- FOODPLANTS: The sole host of populations in our area is the Utah Juniper, *Juniperus osteosperma* (Torr.) Little (*Cupressaceae*).

b. *M. s. juniperaria* J. A. Comstock

- DIAGNOSIS: This subspecies is found in the Juniper forests along the western and southern borders of the Mojave Desert and into the mountains to the west. It is characterized by the coloration pattern on the ventral surface of the hindwings. The line occurs along the edge of the wing as in *siva*. Interior to this is a much more pronounced bluish field than in *siva*, which covers the outer part of the lower half of the hindwing. Within this field is a minute black ocellus, which is about one fourth of the area of the equivalent ocellus in *siva*. There is no pronounced orange lunule around this spot as is found in typical *siva*. Interior to this blue field is an area of green and along the margins of the blue and green fields are a series of black ovate spots. These are typically four in number. The medial band is more irregular than in *siva*. The basal area of green has a brownish proximal area by the body.
- ORIGINAL DESCRIPTION: J. A. Comstock, *Bulletin Southern California Academy Sciences*, 24: 37 (1925).
- TYPE LOCALITY: Mint Canyon, Sierra Madre Mountains, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is found along the southern and western borders of the Mojave Desert from the north slope of the San Bernardino Mountains (just east of Cajon Pass) west to the Mt. Pinos region of Ventura and Kern counties, then north to the Walker Pass area and west from there to the Bodfish region in Kern County.
- ELEVATION RANGE: 2,000 to 5,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This butterfly is found in areas where the dominant large plant is individuals of *Juniperus californica* Carr in the upper areas of the Joshua Tree Woodland community; in most of these areas Pinyon (*Pinus monophylla* Torr. & Frem.) is absent. So this is not Pinyon-Juniper Woodland in the "classical" sense.

PHENOLOGY: This subspecies is multivoltine, with the largest brood being the first or spring brood appearing in late March to May; this first brood is often closely associated with the maximum blooming period of the composite *Haplopappus linearifolius* DC. The second brood flies in June and is generally somewhat smaller than the spring brood; a third brood, if present, flies in September.

FOODPLANTS: California Juniper (*Juniperus californica* Carr) (Cupressaceae). Additionally, this subspecies may use *J. osteosperma* (Torr.) Little in a very limited area in the vicinity of Phelan on the north slope of the San Gabriel Mountains. In this area, *Juniperus californica* Carr is the dominant small tree but individuals of *J. osteosperma* (Torr.) Little are present here, and the adults seem to perch on this Juniper as frequently as they do on the *J. californica* Carr found in the same area.

c. *M. s. mansfieldi* Tilden

DIAGNOSIS: This is a central Californian subspecies that occurs to the northwest of the range of *juniperaria*. The principal difference in this subspecies is the quality of the green color of the underside. In *mansfieldi* this green tends to be a very deep, dark green or gray-green in most individuals in contrast to the somewhat more yellowish-green of *juniperaria*. Also, the white margination of the median-macular band is markedly wider than that seen in *juniperaria* or *siva*, standing out in bold contrast to the ground color. There is usually no evidence of basaler markings on the ventral hindwing as there is in some specimens of *juniperaria*, and the small black ovoid spots in the post-median area of the hindwing tend to be similar to the pattern seen in *juniperaria*.

ORIGINAL DESCRIPTION: Tilden, *Bulletin Southern California Academy Sciences*, 50: 96 (1951).

TYPE LOCALITY: Seven miles west of Simmler, San Luis Obispo County, California. Holotype in California Academy of Sciences.

DISTRIBUTION: This subspecies is found in the La Panza Range in San Luis Obispo County (the type locality), in the Temblor Range of San Luis Obispo and Kern counties, and in the Figueroa Mountain area in the San Rafael Mountains of Santa Barbara. Specimens from the Upper Cuyama Valley northwest of Ojai in Ventura County seem transitional between *M. s. mansfieldi* and *M. s. juniperaria*.

ELEVATION RANGE: From 1,500 to 3,800' elevation.

HABITAT AND PLANT COMMUNITIES: Typically found in Juniper Woodland on dry slopes, flats and canyon bottoms. In these areas an annual composite species popularly known as Gold Fields (*Baeria* species) is often present and serves as a springtime nectar source for adults of the first brood.

PHENOLOGY: This subspecies is at least bivoltine, with the first brood flying from late March to early May, with a peak in early to mid-April. The second brood is often overlooked and may be dependent in part on winter rainfall patterns.

FOODPLANTS: *Juniperus californica* Carr. (Cupresaceae).

d. *M. s. chalcosiva* Clench

DIAGNOSIS: This butterfly, named from Utah, penetrates our area in the Mono Lake area south to the White Mountains and perhaps the Inyo Mountains. It is characterized by a distinctive underside, where all the green areas of nominate *siva* are replaced by

a coppery brown. In strong light and at an angle, this brown is iridescent, sometimes violet and sometimes greenish. In many respects this color is like that of the far western species *Mitoura nelsoni*. Occasional specimens show a slight amount of green basally on both wings. The post-median line on the ventral hindwing has a very thick and strong white quality. It follows the same course as typical *siva*, and is less irregular than *juniperaria*. The tails are as long as in nominate *siva* and longer than those of *siva juniperaria* and *M. nelsoni*. The common evolution of brown underside color was undoubtedly independently acquired in *nelsoni* and *chalcosiva* by parallel evolution, rather than shared genes.

- ORIGINAL DESCRIPTION: Clench, *Bulletin Allyn Museum*, 64: 11-14 (1981).
- TYPE LOCALITY: South Willow Creek, Stansbury Mountains, Tooele County, Utah.
- DISTRIBUTION: In California this subspecies has been taken in the White Mountains of Inyo and Mono counties and in the Benton Range in Mono County. A presumed blendzone between this subspecies and typical *siva* is presumed to exist through the Inyo Mountains, connecting the White Mountains populations with those of typical *siva* in the Panamint Range, but specimens are lacking. This subspecies can also be expected to be found on the stands of Juniper around Mono Lake and in extreme northeastern Mono County, but again specimens are lacking from these areas.
- ELEVATION RANGE: 6,000' to 8,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This species is typically found in the Pinyon-Juniper Woodland of the western Great Basin. At least one nectar source is *Eriogonum umbellatum* Torr. ssp. *subaridum* (S. Stokes) Mumz (for the sporadic summer brood) and *Viguiera multiflora* (Nutt.) Blake (for the spring brood).
- PHENOLOGY: Mostly univoltine, but with an occasional small summer brood in some years. The first brood flies from mid-May to mid-June; the second brood, if present, flies from mid-July to mid-August.
- FOODPLANTS: These populations are associated with *Juniperus osteosperma* (Torr.) Little (Utah Juniper).

137. *Mitoura loki* (Skinner)

Skinner's Hairstreak is a rare species in collections, although it is rather common at times in its isolated populations in southern California. This species may be distinguished from *Mitoura siva* by its continuous row of submarginal spots on the ventral hindwing surface and the presence of elaborate brown mottling across the inner half of the same wing.

- DIAGNOSIS: The main difference between *M. loki* and the closely related *M. siva* is in the underside coloration and markings. In *loki* there are invariably some post-basal markings on the hindwing. Secondly, there is a full row of small black dots in the post-median area, which is usually very reduced in *juniperaria* and virtually absent in typical *siva*. Additionally, the quality of the ground color beneath may be a dense and heavy green or that the green scaling may be reduced, allowing considerable brown ground color to show. Occasional spring specimens have very little green and a great deal of dark reddish-brown on the ventral hindwing. However, in series *loki* is distinctly green and not so brown as *M. thornei*, the other southern California *Mitoura* which is very similar to *loki* in general wing

pattern. The overall appearance of the underside of *loki* is to give a sort of "banding" pattern.

ORIGINAL DESCRIPTION: Skinner, *Entomological News*, 18: 378 (1907).

TYPE LOCALITY: Mt. Springs [Mountain Spring, 6 airmiles northeast of Jacumba], San Diego County, California. Holotype in Carnegie Museum.

DISTRIBUTION: *M. loki* is found only in California and Baja California, along the western border of the Colorado Desert; it also occurs just west of the mountains bordering the desert in the vicinity of the Gavilan Hills, Riverside County around Redlands, and Hemet to the south. Along the northern border of its range it occurs from Morongo Valley eastward to Twenty-nine Palms, and southward from there through the higher mountains of Joshua Tree National Monument. Although there are two records of its capture in the northwest end of the Sheephole Mountains in San Bernardino County, no Junipers have been found in this range, and these probably represent stray individuals. In Baja California it occurs at least as far south as the San Pedro Martir Range. *M. loki* is not known from the Los Angeles Basin or San Fernando Valley, even though old records exist for *Juniperus californica* Carr. at the southern base of the San Gabriel Mountains. Specimens of *M. loki* taken by the Sperry's and labelled "Azusa" were probably not taken near there (even though there are old records for Juniper in that general area), because on the same date they took a long series of *M. s. juniperaria* from the Mojave Desert. A number of specimens of various butterfly species collected by the Sperry's are known to be mis-labelled (J. F. Emmel, unpublished data; but see Opler, 1966e, for a contrasting opinion). This is believed to represent another instance of their mislabelling. The host, *Juniperus californica* Carr., is found in a fairly large stand at the east end of the Granite Mountains north of Amboy, and also extensively through the Old Woman Mountains in the Eastern Mojave Desert; however, repeated searches of these two stands of Juniper have failed to turn up *M. loki*, or any other *Mitoura* species for that matter.

ELEVATION RANGE: From approximately 2,000 to 4,500' elevation.

HABITAT AND PLANT COMMUNITIES: In the more coastal localities for this butterfly it is found in the Coastal Sage Scrub plant community in which Junipers are scattered. Along the western edge of the desert, it is found at the upper edge of the Creosote Bush Scrub plant community or at the lower edge of Pinyon-Juniper Woodland in which the Pinyons are absent and Juniper is the only representative of the two present. In parts of Joshua Tree National Monument, the butterfly is found in the Joshua Tree Woodland plant community where Junipers are scattered, or in true Pinyon-Juniper Woodland just above this plant community.

PHENOLOGY: This species is multivoltine, with two to three broods most years, with the size of the second and third brood smaller than the spring brood and probably closely correlated with amount of winter rainfall and possibly summer rainfall. The first brood flies from early March to late April, depending on elevation and winter rainfall pattern; a second generation can be taken during the months of June and early July, and again there are records from late July, August, and September.

ADULT BEHAVIOR: Males of this species perch on the Juniper host rather regularly; mating pairs have been found resting on the outer branches of the host Juniper. The species has a tendency to stray from its usual habitat, as evidenced by the two records mentioned above from the Sheephole Mountains. Additionally, stray specimens are known from near Onyx Peak in the San Bernardino Mountains (nearly 9,000'

elevation!), from the summits of the Laguna Mountains in San Diego County, and several records from high elevations in the San Pedro Matir Range in Baja California. Perhaps some of these specimens represent hilltopping males.

LIFE HISTORY: The life history of this species was first described by Comstock and Dammers (1932b). The egg is a delicate light green, with raised portions of a whitish shade and with small structural differences from the egg of *M. siva juniperaria*. The raised points are not as clearly defined in the region of the micropyle, and are more pronounced at the outer circumference of the egg. These points do not show a tendency to regular alignment to the same extent as in the egg of *juniperaria*. The egg stage lasts five days. The eggs are laid singly on the tender tips of the Juniper host. The mature larva (fourth instar) is a vivid green in ground color with a series of raised protrusions that are a darker green. A lemon-yellow broken longitudinal line, or series of irregular crescents, occurs on each side of the center dorsal area (in two dorso-lateral lines). Laterally, there is a similar creamy white line along the edge of the overlapping fold, just below the spiracles. The segmental creases are deep, throwing each segment into rounded relief. Additionally, these segments have a series of bumps and depressions in regular form on each segment, like those in *siva*. The pupa is a dark chestnut brown with fine mottling and a hairy coat, except on the wing covers and facial portions. The life cycle passes in two months. This species then diapauses as a pupa.

FOODPLANTS: The sole host of this butterfly is *Juniperus californica* Carr. (Cupressaceae).

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: See discussion under *M. siva*.

GEOGRAPHIC AND SEASONAL VARIATION: The summer brood specimens tend to be much lighter ventrally than spring brood specimens, with a yellowish or light brownish overscaling on the underside. September specimens may or may not have this light color, sometimes appearing more like spring brood specimens. Although, in any given locality, the species tend to be quite variable in both ground color of the underside and in the pattern of markings on the underside, there is no apparent geographic variation from one locality to another throughout its range (i.e., all populations seem to show a similar range of variation within a given locality).

GENERAL REMARKS: There are two chemical races of *Juniperus californica* Carr, called Chemical Race A and Chemical Race B. *M. s. juniperaria* feeds on Chemical Race A. *M. loki* feeds on Chemical Race B. It has been suggested that Chemical Race A has actually been derived from Chemical Race B and introgression of genes from *Juniperus osteosperma* (Torr.) Little, through hybridization. This evolution of the phenotypic characteristics of the host plant races perhaps parallels the phenotypic relationships of three *Mitoura* here. The subspecies *M. s. juniperaria* combines features of both *Mitoura siva siva* and *Mitoura loki*, perhaps indicating that the butterfly, *juniperaria*, has resulted from introgression of *loki* genes into the *siva siva* genotype. In other words, there may have been an evolutionary pattern of development of the host plant species for *juniperaria* similar to the pathway that the butterfly itself has followed.

138. *Mitoura thornei* J. Brown

This is a recently described species which superficially looks like a brown version of *loki*, and is known only from Otay Mountain, San Diego County, the type

locality. Its host, in the genus *Cupressus*, is different from those of the butterfly's near relatives.

- DIAGNOSIS: In this species, the underside pattern is identical to *loki*, but the color is essentially brown. In series, the distinctness from *loki* is obvious, but individual *thornei* can be as green as many *loki*, and some *loki* (especially spring brood) can be as brown as many *thornei*. When *loki* and *thornei* are reared side by side in controlled temperature chambers, the color distinction between the two persists (John Lane, unpublished data).
- ORIGINAL DESCRIPTION: J. W. Brown, *Journal Research Lepidoptera*, 21: 245-254 (1983).
- TYPE LOCALITY: Little Cedar Canyon, north slope of San Ysidro Mountains (Otay Mountain), east end of Little Otay Lake, 200 meters, 32° 37' N, 116° 52' W, San Diego County, California.
- DISTRIBUTION: At present, the species is known only from the Otay Mountain area in San Diego County.
- ELEVATION RANGE: 600 to 700' elevation.
- HABITAT AND PLANT COMMUNITIES: The host for the Otay Mountain *Mitoura* is Tecate cypress, a closed-cone conifer which occurs on the Xeric slopes in the Chaparral. This tree is restricted to a relatively few isolated stands, extending from the Santa Ana Mountains of Orange County south into Baja California. Fire is important in the natural ecology of these trees, as it is the major factor that initiates cone-opening and seed dispersal. Brown (1983) notes that Chaparral fires have undoubtedly caused great fluctuations in the population of both the cypress and the associated *Mitoura thornei*. To date, the Hairstreak species has not been found in the other known stands of Tecate cypress, *Cupressus forbesii* Jeps..
- PHENOLOGY: *Mitoura thornei* appears to be at least double-brooded; adults fly in March and again in June. However, the second brood is a much reduced one in size.
- ADULT BEHAVIOR: Males generally perch near the top branches of the cypress and are quite easily disturbed. Their quick, erratic flight makes them difficult to capture. Adults visit flowers of Manzanita (*Arctostaphylos otayensis* Wies. * Schreib.), California or Flat-top Buckwheat (*Eriogonum fasciculatum* Benth.), and *Yerba santa* (Eriodictyon species).
- LIFE HISTORY: The early stages of *M. thornei* have been described in Brown (1983). The eggs are light green in color and echinoid in shape, and are laid singly on the new growth of the host. The egg stage lasts seven to fourteen days. The newly hatched larvae bore into the young stems of the host but become external feeders as they develop. Mature larvae closely resemble the terminal twigs on which they feed. The ground color is vivid green with two irregular white crescents on each segment, one on either side of the mid-dorsal crest; the markings together form a longitudinal stripe on each dorso-lateral side of the body. Additionally, there is a thinner, more continuous longitudinal white stripe above the pro-legs on each side of the larva. The entire body is covered with minute brown hairs. Thus, the larval stage of *thornei* closely resembles those described already for *siva* and *loki*. In the laboratory, the larval stages require 26-35 days to pupation. The pupae are dark chestnut brown with fine mottling, and are covered with fine brown hairs; the wing cases are bare. Pupation generally occurs in the debris at the base of the host trees.

- FOODPLANTS: The sole known foodplant in the wild is the endemic Tecate cypress (*Cupressus forbesii* Jepson). In the laboratory, although females exhibit a distinct ovipositional preference for *Cupressus forbesii* Jeps., larvae will develop normally on California juniper (*Juniperus californica* Carr.).
- CHROMOSOME NUMBER: Unknown.
- SIMILAR SPECIES: Differentiated in the Diagnosis.
- GEOGRAPHIC AND SEASONAL VARIATION: Phenotypically, the two broods are similar, the summer brood being just slightly darker in color.
- GENERAL REMARKS: As southern California has long had one of the greatest concentrations of lepidopterists in the country, it is remarkable that this new Hairstreak species remained undiscovered until 1972, when the first specimens were taken. Inaccessibility to this remote Otay Mountain area was undoubtedly the major deterrent. Despite the superficial appearance to *Mitoura loki*, based on the complex phenotypic characters, highly selective host preference, and a unique ecological association, this Otay Mountain *Mitoura thornei* appears to represent a distinct species. The relationship between *thornei* and the *loki* populations both to the north and south of its location would be a particularly interesting problem for lepidopterists to investigate in detail. It is interesting that the use of a *Cupressus* species as the larval host suggests a close affinity with *M. nelsoni* and *M. muiri*. However, *M. thornei* has quite a different appearance and southern California populations of *nelsoni* are all univoltine. Although no sympatry occurs, *M. thornei* is separated from the nearest *M. loki* population by only about 36 miles, and from the nearest *M. nelsoni* population by about 30 miles. In southern California then, the closest relative of *thornei* appears to be *M. loki*, which it resembles in voltinism (multiple-brooded), phenotype, and genitalic characters. It is distinguishable from *loki* in host preference and in the color of the ventral hindwing surface.

139. *Mitoura nelsoni* (Boisduval)

This species is abundant through the mountains of the Sierra Nevada and the higher mountains of southern California, wherever Incense cedar is common. The typical subspecies occurs in our state, and a former *nelsoni* subspecies, *muiri*, has been separated as a distinct species.

- DIAGNOSIS: The upperside of this Hairstreak is brown. The underside is brown laved with lilac, especially on the hindwing. Fresh specimens often have a slightly metallic luster in this pink or reddish sheen. A few specimens will actually have an almost greenish tint. Specimens with any amount of wear will lack these tints, and with additional wear become more uniformly brown or dark flat brown. In this species the post-median band tends towards obsolescence, especially in its most posterior parts. Many specimens have a prominent white band only on the most anterior cells, which the post-median band traverses. The post-median band could be rather straight or rather irregular and jagged; it is mostly brown, sometimes thinly white and usually rather subdued, not standing boldly out of the brown ground color. The post-median band on the ventral surface of the forewing is rather straight and similarly subdued. The other brown *Mitoura*, which might be confused with *nelsoni* usually have bolder post-median bands which are more prominently highlighted by white or black scaling.

- ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. Belgique*, 12: 43 (1869).

- TYPE LOCALITY: "California", the French translating to "Great Forest of the Interior". Restricted by Emmel, Emmel, and Mattoon, Journal Research Lepidoptera, : (1988) to Lower Feather River Canyon, Butte County, California. Holotype in U. S. National Museum.
- DISTRIBUTION: From the Laguna Mountains of San Diego County northward through Palamar Mountain, the San Jacinto Mountains, the Santa Rosa Mountains, to the San Gabriel and San Bernardino Mountains northward through the Tehachapi Mountains northward through the west slope of the Sierra Nevada and Cascade Range to the Klamath Mountains region, the North Coast Ranges. From California it goes northward into the Cascades of Oregon.
- ELEVATION RANGE: From 2,000 to 7,500' elevation.
- HABITAT AND PLANT COMMUNITIES: This species is found in areas of Mixed Coniferous forests, where the foodplant, Incense Cedar (*Calocedrus decurrens*) is found. Within these forests, *nelsoni* is usually seen at the edges of clearings perching on *Calocedrus* or other trees; it is also frequently encountered in meadow situations where it is attracted to nectar sources.
- PHENOLOGY: This butterfly is strictly univoltine, flying from early May to mid-July, depending on elevation, with the majority of records showing a peak flight period in mid-June.
- ADULT BEHAVIOR: The males frequently perch on Incense cedar or other conifers at the edges of meadows and clearings within the forest. The adults are avid flower visitors, and the majority of them are taken by collectors while engaged in nectaring. A primary nectar source in northern California is Wild Lilac, *Ceanothus integerrimus* H. & A.
- LIFE HISTORY: The early stages of this species were first described from southern California material taken on the crest of the Greenhorn Mountains, Kern County, by Comstock and Dammers (1932c). The egg is green, of about the same shade as the Incense cedar twigs. It is covered with minute star-shaped points of a lighter shade, from which low partitions radiate to join those from neighboring points. The shape is echinoid, with a deeply depressed micropyle. These stellate points on the egg are slightly less pronounced than the egg of *M. s. juniperaria*, and do not show quite the same degree of alignment. The mature larva very closely resembles those of *Mitoura siva juniperaria* and *M. loki*. The larva is vivid green with darker green raised lobulations. A series of irregular lemon-yellow crescents occur as a band on each side of the dorsal area. Minute brown hairs occur over the body. The pupa is blackish-brown and covered with minute brown hairs. No silk girdle was noted. The winter is passed in the pupal stage.
- FOODPLANTS: The sole host known to date is Incense cedar, *Calocedrus decurrens*.
- CHROMOSOME NUMBER: Unknown.
- SIMILAR SPECIES: The butterfly may be confused with *M. barryi* subspecies which may occur in close proximity to *nelsoni* populations. Very worn specimens of *M. barryi* may be virtually impossible to distinguish from *nelsoni*; in fresher individuals, *barryi* tend to have a more well-developed white macular band on the ventral surface of both the forewings and hindwings, and the ground color of the hindwings tends to be slightly more greenish or flat light brown in contrast to the more purplish-brown of the underside of *nelsoni*.

GEOGRAPHIC AND SEASONAL VARIATION: Because the species is univoltine, no seasonal variation is present. Geographically, the species is surprisingly constant throughout its rather wide range.

GENERAL REMARKS: The relation of this butterfly to *Mitoura muiri* is unclear. *Muiri* has been treated as a subspecies of *M. nelsoni* in recent years, but ecological data suggest that *muiri* is best treated as a specific entity. Similarly, the relationship of *M. barryi* to *M. nelsoni* is poorly understood, but on the basis of marked ecological differences between the two entities, we prefer to treat them as separate species.

140. *Mitoura muiri* (Hy. Edwards)

LIFE HISTORY: Reared by John Lane but not recorded to date.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: See discussion under *Mitoura nelsoni*.

GEOGRAPHIC AND SEASONAL VARIATION: In a given population of *muiri*, the phenotype tends to be quite variable with varying shades of the ventral surface being purplish red-brown to dark greenish-brown or reddish-brown. The percentages of these different phenotypes in the various populations has not been studied, so at this time we are unable to make any assessment as to any particular trends in geographic variation.

GENERAL REMARKS: The genetic relationship of the *Cupressus* and *Juniper*-feeding populations of this butterfly in the South Coast Ranges should be explored further, particularly with regard to hybridization studies and foodplant choice experiments using ovipositing females.

Until recently, this species was included under *Mitoura nelsoni* as a coastal subspecies. We differentiate two subspecies of this species in California.

a. *M. m. muiri* (Hy. Edwards)

DIAGNOSIS: This *Mitoura* is distinguished by the red-purplish-brown underside coloration, with blue-green or grayish-green overscaling on some specimens, with a fairly well-delineated median macular band of white. Superficially, the species resembles *M. nelsoni* but differs from it by the more rich brown or purplish-brown underside, often with greenish overscaling and the more well-defined macular white band.

ORIGINAL DESCRIPTION: Henry Edwards, *Papilio*, 1: 53 (1881).

TYPE LOCALITY: Mendocino County, California. Holotype in American Museum of Natural History. John Lane (*in litt.*) notes that the type specimens are labelled and cross-referenced to Henry Edwards' catalog entry giving "Tamalpais" as the location of capture by Dunn. This is consistent with the phenotype of *muiri* presently taken at Mt. Tamalpais in Marin County.

DISTRIBUTION: This species is limited to the inner and outer Coast Ranges, from Mendocino and Colusa counties to San Luis Obispo County, where it is always associated with *Cupressus sargentii* Jeps. and occasionally with *Juniperus californica* Carr.

- ELEVATION RANGE: From 1,000 to approximately 3,000' elevation, with most populations in the 1,000 to 2,000' range.
- HABITAT AND PLANT COMMUNITIES: Populations of this subspecies are virtually always located in areas of serpentine soils, which favor the growth of the *Cupressus* host. Usually on these serpentine slopes, there is sparse Chaparral with Digger Pine association. Tilden (1952) mentions the dark volcanic rocks of the Mt. St. Helena district in Lake and Napa counties where *muiri* has been taken.
- PHENOLOGY: This butterfly is apparently univoltine, with captures recorded from late March to mid-June, depending on elevation.
- FOODPLANTS: *Cupressus sargentii* Jeps., and perhaps occasionally on *Juniperus californica* Carr. in the inner North Coast Range.

b. Inner South Coast Range Segregate

- DIAGNOSIS: This butterfly is almost phenotypically indistinguishable from typical *muiri*, except for specimens with greenish coloration such as those seen in Marin and Sonoma counties. These populations are associated with *Juniperus californica* Carr. and unpublished hybridization studies by John Lane indicate some reproductive isolation between this entity and the *Cupressus*-feeding *muiri* of the outer South Coast Range.
- DISTRIBUTION: This subspecies is found in the inner South Coast Ranges from San Luis Obispo County northward to approximately Stanislaus County, where it is associated with *Juniperus californica* Carr.
- ELEVATION RANGE: From 1,500 to 2,500' elevation.
- HABITAT AND PLANT COMMUNITIES: Usually found on serpentine soils, with sparse Chaparral and scattered stands of *Juniperus californica* Carr.
- PHENOLOGY: This butterfly is apparently univoltine in most years, but laboratory rearings indicate that a second generation is possible. We have no field documentation of a second generation occurring in this butterfly.
- FOODPLANTS: *Juniperus californica* Carr., similar to the other *Mitoura* species.

141. *Mitoura barryi* K. Johnson

- ADULT BEHAVIOR: The adults of *barryi* behave similarly to other *Mitoura*, staying in close proximity to the host plants and exhibiting perching behavior on the higher portions of the trees. At least one frequently used nectar source is *Ceanothus cordulatus* Kell., whose blooming period is closely correlated with the emergence of the adults of this *Mitoura*.
- LIFE HISTORY: Undescribed, although reared by Greg Ballmer (University of California, Riverside).
- CHROMOSOME NUMBER: Unknown.
- SIMILAR SPECIES: Worn specimens of *M. barryi* may be extremely similar to specimens of *M. nelsoni*. In the San Bernardino Mountains and probably in the southern Sierra

Nevada populations, *M. nelsoni* on *Callocedrus* probably occurs within close proximity, and in localities located on the borders of these two entities one might expect to get specimens that are difficult to place with either taxon with certainty. In the Great Basin fringe of Lassen County (Frenchman Lake), forested areas containing abundant Incense Cedar intermix with Juniper. In this area, adults of *barryi* and *nelsoni* appear to associate with their respective hosts which grow side by side, with a comingling of both species at nectar in the understory. The two insects (if in fact they really are distinct species) are all but impossible to differentiate.

**GEOGRAPHIC AND
SEASONAL VARIATION:**

As the species is univoltine, there is no seasonal variation. The populations within our area show surprisingly little difference between the populations in the northeastern corner of the state and those in southern California.

GENERAL REMARKS:

The disjunct distribution of the foodplants for these two population areas of *barryi* suggests that at one time the butterfly may have enjoyed a wider distribution when its host plant had a more extensive range through the mountains of California. Although populations of *Juniperus occidentalis* Hook are scattered through the higher elevations of the Sierra Nevada today, dense or contiguous populations of this species of host plant are not prevalent as in the other hosts used by other *Mitoura* species.

This species was not recognized and described until 1976. At that time the nominotypical subspecies was known to be represented by populations from Oregon northeastward into Idaho east of the Deschutes Plateau. The other subspecies, *M. barryi acuminata*, occurs westward along the edge of the Deschutes Plateau and Cascade Mountains, and then southward in the Cascades to southern Oregon and northward to Vancouver Island. In California, populations of *Mitoura* which appear to represent this species are found in the Modoc County and northern Lassen County region of California, and disjunct populations occur in the southern Sierra Nevada of Tulare County and the San Bernardino Mountains of southern California.

a. *M. b. acuminata* K. Johnson

DIAGNOSIS:

The upper surface of the male is deep brown, while the female is a lighter brown. The under surfaces lack the yellow coloration found in typical *barryi*; there is a white submarginal line on the forewing, and a continuous mesial line (white outside, black in the center, and brown on the body side) across the hindwing. Four or five black spots occur outside this line near the tail, followed by orange and then blue-gray scaling next to the tail area. The most distinctive features, however, are in the pointed shape of the characteristic broad and wide-rimmed anterior valval structure of the male genitalia (Johnson, 1976).

ORIGINAL DESCRIPTION:

K. Johnson, *Bulletin Allyn Museum*, 38: 20-21 (1976).

TYPE LOCALITY:

Butte Falls, Jackson Co., Oregon. Holotype male in American Museum of Natural History.

DISTRIBUTION:

Populations representing typical *M. acuminata* occur in the northeastern corner of California from eastern and northern Lassen County northward through Modoc County.

ELEVATION RANGE:

From approximately 5,000 to 6,500' elevation in California.

HABITAT AND PLANT COMMUNITIES:	This species is typically found in the Northern Pinyon-Juniper Woodland plant community.
PHENOLOGY:	This subspecies is apparently strictly univoltine, flying from late May to mid-July with an apparent peak flight in late June.
FOODPLANTS:	The butterfly is closely associated with <i>Juniperus occidentalis</i> Hook ssp. <i>occidentalis</i> ; this is almost certainly the foodplant within California. The larval foodplant in the Northwest is unknown; the butterfly occurs there where either <i>Thuja plicata</i> or <i>Juniperus occidentalis</i> are present (Johnson, 1976).

b. *M. b.* ssp.: Southern California Segregate

DIAGNOSIS:	We consider populations of <i>Mitoura</i> of high elevations in the southern Sierra Nevada and San Bernardino Mountains to be representative of <i>M. barryi</i> . In these populations the phenotype is similar to <i>M. b. barryi</i> , but they tend to lack the reddish tints on the underside and many have a greenish aspect. This green is not metallic, but rather a flat, dull almost grayish-green.
DISTRIBUTION:	This butterfly is found in the southern Sierra Nevada of Tulare County and at high elevations in the eastern San Bernardino Mountains, where it is associated with <i>Juniperus occidentalis</i> Hook ssp. <i>australis</i> .
ELEVATION RANGE:	From 7,000 to 10,000' elevation.
HABITAT AND PLANT COMMUNITIES:	These populations are usually associated with a sparse Mixed Coniferous Forest with <i>Juniperus occidentalis</i> Hook usually being the dominant tree.
PHENOLOGY:	Apparently univoltine, with adults flying from late May to late June.
FOODPLANTS:	The species is closely associated with <i>Juniperus occidentalis</i> Hook ssp. <i>australis</i> ; in captivity, females of this entity will readily oviposit on this plant.

142. *Xamia xami* (Reakirt)

See **Appendix** for discussion of the single record for this species from the Providence Mountains in the eastern Mojave Desert.

143. *Mitoura spinetorum* (Hewitson)

This rather large, handsome Hairstreak ranges throughout the West from the Rocky Mountains to the California coast, north to southern British Columbia and south to northern Baja California and Jalisco in Mexico. It is usually rather rare and encountered only in small numbers in the Upper Sonoran and Transition Zones wherever conifers with the proper dwarf mistletoes grow.

DIAGNOSIS:	This Hairstreak may be immediately identified by the steel blue dorsal surface and the reddish-brown undersides. There is a prominent white post-median band on both wings ventrally, bordered interiorly with black. The adults are tailed. An excellent review of this species, including its distribution habits and variation, is given by Shields (1965).
ORIGINAL DESCRIPTION:	Hewitson, <i>Ill. Diurn. Lepid. Lyc.</i> ; 1: 94 (1867).

- TYPE LOCALITY: "California". Holotype in British Museum (although Shields states it is in the U. S. National Museum). Hewitson described the butterfly from one female collected somewhere in California by Lorquin.
- DISTRIBUTION: This species is found along the North Coast Range mountains north of San Francisco Bay in scattered locations to Del Norte County, and then again to the south starting in Santa Barbara County and throughout the cismontane areas of southern California into northern Baja California. From there our records include localities along both sides of the Sierra Nevada and several of the eastern Mojave Mountain ranges north through the Cascade Range and parts of the Klamath Mountain assemblage to the Oregon border in scattered locations.
- ELEVATION RANGE: Our California *spinetorum* populations are found from near sea level (Monterey Peninsula, Monterey County) to over 8,000' (Minereal King, Tulare County).
- HABITAT AND PLANT COMMUNITIES: The larvae of this butterfly feed on parasitic mistletoes that live in conifer trees. Most of the locations where this species occurs are located in Pinyon-Juniper Woodland up through Chaparral with Yellow Pine forests to Mixed Coniferous Forests or Red Fir forests in the mountains. The butterfly is uncommonly taken in all localities, perhaps because the mistletoe foodplants grow high in their host trees, drawing the butterflies away from the usual collecting haunts of lepidopterists.
- PHENOLOGY: The butterfly has been recorded from March to September, with a concentration of records in July and August. Apparently this species is multivoltine, inasmuch as specimens have been recorded from April to the end of August in the Laguna Mountains of San Diego County.
- ADULT BEHAVIOR: Mud and flowers attract adults, and they commonly hilltop, as in the desert mountain ranges. In northern California, *spinetorum* can become quite abundant, especially in certain drier years along open Digger Pine (*Pinus sabiniana*) or Ponderosa Pine (*Pinus ponderosa*)-clad serpentine ridges in the Foothill Woodland plant community. In Northern Juniper Woodland-Pinyon Pine country of the Basin fringe, large numbers of adults can occasionally be encountered.
- LIFE HISTORY: The first description of the early stages was by Comstock and Dammers (1938). The egg is the usual echinoid shape in the genus, with a reticulation of raised walls over the surface. The mature larva is exceptionally cryptically colored on its foodplant. The ground color is a yellow-olive with a mid-dorsal pale olive band. Subdorsally on most segments, there occurs an oblique off-white bar proceeding to either side. The lower edges of these bars are tinged with dark magenta; above each bar is a large raised waxy orange patch (fifth to ninth segments). Only the abdomen bears short colorless hairs. The pupa is a dark chestnut brown, with heavy black mottling. Pupation occurs within the foodplant mass and no silken attachment has been observed. In northern California, Cascade Range foothill populations have shown a tendency to use the Pine Dwarf Mistletoe which grows on the southeast aspect of Digger Pine trees (S. Mattoon, personal observation).
- FOODPLANTS: Exclusively species of the Dwarf mistletoe genus, *Arceuthobium* (Family Loranthaceae), which occur only on conifer host trees in the family Pinaceae. Mistletoe species used include: *A. campylopodum* Engelm. in Gray; *A. vaginatum* f. *cryptopodum* on *Pinus ponderosa* Dougl. ex P. & C. Lawson; *A. americanum* Nutt. ex Engelm. in Gray on *Pinus contorta*; *A. campylopodum* Engelm. in Gray on *Pinus jeffreyi* Grev. & Balf. in A. Murr, *Abies concolor*, *Pinus reflexa*, *Pinus aristata* Engelm., *Pinus monophylla* Torr. & Frem., *Pinus sabiniana*, and other

host species outside our area. In nearby areas of Arizona, it has been found on *Arceuthobium vaginatum* Willd. f. *cryptopodum* in Ponderosa Pines and in Pinyon Pines (Remington, 1958).

PARASITES AND PREDATORS:	Shields (1965) records a Tachinid fly, <i>Masphyomyia paralis</i> , that parasitized larvae in Tuolumne County and San Diego County. Remington (1958) records a braconid larval parasite in Arizona and an undescribed <i>Apanteles</i> braconid wasp parasite from pupae in Colorado. Adults of this Hairstreak occasionally have clipped wings and beak-marked wings, indicating bird predation.
CHROMOSOME NUMBER:	Unknown.
SIMILAR SPECIES:	<i>Mitoura johnsoni</i> is rather similar in appearance on the underside, but the dorsal coloration is quite brown in <i>johnsoni</i> and steely blue in <i>spinetorum</i> adults.
GEOGRAPHIC AND SEASONAL VARIATION:	Though this species ranges from the Rocky Mountains to the Pacific Coast and north into Canada, only the typical subspecies has been named over this range. There is a Mexican subspecies (<i>millerorum</i>) that ranges south to Durango and Hidalgo. No seasonal variation has been detected in this species.
GENERAL REMARKS:	The butterflies visit a wide variety of nectar sources; at least 28 genera of nectar sources are listed by Shields (1965). Hilltopping behavior of males is strongly pronounced in this species.

144. *Mitoura johnsoni* (Skinner)

Mitoura johnsoni was described by Skinner in 1904 from a female from British Columbia and a male from Seattle, Washington. Since that date it has been considered a very rare species and is only occasionally found in collections (Opler, 1962). The best review of the species' ecology distribution and variation is by Shields (1965).

ORIGINAL DESCRIPTION: Skinner, *Entomological News*, 15: 298 (1904).

TYPE LOCALITY:	Seattle, Washington and British Columbia. Syntypes in Carnegie Museum.
DISTRIBUTION:	Our only California records are from Lassen County, Plumas County, El Dorado County, Del Norte County, Glenn County, Butte County, Mariposa County, Placer County, Sierra County, Solano County, Siskiyou County, Tehama County, Napa County, and Tuolumne County.
ELEVATION RANGE:	From 1,200' to 8,000'.
HABITAT AND PLANT COMMUNITIES:	Coniferous forest areas where appropriate host plants occur.
PHENOLOGY:	From mid-March to mid-August, with a peak during most of the month of July.
ADULT BEHAVIOR:	Both males and females are drawn to moisture at various localities. In some areas this involves down-valley flight of the adults during the morning hours and return in the afternoon (Scott, 1973). It should be noted that Scott's observations of <i>johnsoni</i> involved over 100 individuals at Thompson Canyon, Yolo County between March 18 and 21, 1972, a very early time. These represent the spring brood, not often observed in such numbers. <i>Mitoura johnsoni</i> adults visit flowers

of *Arctostaphylos*, *Calyptridium umbellatum* (Torr.), *Ceanothus*, *Cornus*, Dandelion, *Fragaria*, *Rorippa*, and *Spraguea* (Opler, 1962; Shields, 1965), as well as *Eriodictyon californicum* (H. & A.) (=Yerba Santa).

LIFE HISTORY: The first male of this species was described from an adult that emerged from a larva collected in Washington, and larvae and eggshells were found on the host plant by McCorkle (1962). The following descriptions are based on ova and larvae collected at Thompson Canyon, Yolo County, California from a wild female (J. Emmel, unpublished). Eggs are laid directly on conifer bark near the base of tiny *Arceuthobium* mistletoe plants. As many as four to six eggs may be attached to the bark within several square inches. The egg is pale green in color and is the typical *Mitoura* echinoid shape, with fine reticulations of raised walls over the surface, and a deep micropyle. The first instar larva is pale yellow-green. The second and third instars have a light green ground color with two rows of yellow protruberances on the raised dorsal surface of each segment; these yellowish bumps lie in two dorso-lateral rows extending the length of the larva. In the fourth (mature) instar, the larva is olive-green in color with a prominent triangular yellow area dorso-laterally to either side of the mid-dorsal line. Each of these yellow triangles is edged anterior-laterally with a white band and then a magenta band, except on the third thoracic segment which retains a diffuse reddish-yellow spot on top of the protuberance which is also characteristic of that segment in the second and third larval instars. Laterally there is a well-marked yellow band just below the spiracles with faint purplish shading above it on each segment. The yellowish and white portions of this larval pattern are more restricted, especially on the rear most abdominal segments in *johnsoni* than in the rather similar mature larva of *Mitoura spinetorum*. Nevertheless, the two patterns are close and both provide superb camouflage on the chosen mistletoe host. The pupa, previously undescribed is

[T.C.E.]

FOODPLANTS: C. V. Piper, the collector of the original male specimen which Skinner (1904) described as *johnsoni*, reared the adult from larvae found on the mistletoe, *Arceuthobium campylopodium* Engelm. in Gray f. *tsugensis* (Rosend.) Gill., a parasite on a western Hemlock tree (*Tsuga heterophylla* (Raf.) Sarg.) near Seattle, Washington. The eggshells and larvae were found by David McCorkle on this same form of *Arceuthobium campylopodium* Engelm. in Gray. The subspecies of this mistletoe is not known to occur in at least several low-elevation California localities, suggesting another host plant is being utilized. The mistletoe used in Thompson Canyon in Yolo County is *Arceuthobium occidentale*, a parasite on Digger Pine (*Pinus sabiniana* Dougl.). The *arceuthobium* on Digger Pine in Butte County has been identified as *campylopodium* but may be *occidentale*.

CHROMSOME NUMBER: Unknown.

SIMILAR SPECIES: See *Mitoura spinetorum*.

GEOGRAPHIC AND SEASONAL VARIATION: No geographic subspeciation has been observed to date, perhaps because of the rarity of specimens in collections. The overall distribution ranges from extreme southern British Columbia south through the western half of Washington, with one record in Oregon, and then in northern and central montane populations in California. No seasonal variation has been observed yet. From the range of records, it would be expected that this butterfly would be multivoltine, but insufficient records exist for any one locality to be certain.

GENERAL REMARKS: This butterfly will undoubtedly be found in a number of additional populations that will better fill in the present known set of distribution records, especially if larvae and eggs are sought on the host plants in prospective population areas. It is of interest to note how often *spinetorum* and *johnsoni* have been recorded from the same exact location. The same host is used by both in Butte County, California.

145. *Atlides halesus estesi* Clench

This is the Great Blue Hairstreak, which occurs across much of the southwestern United States and north into Oregon. The species also has a geographically separate distribution on the East and Gulf Coast. Our California subspecies is *A. h. estesi*.

DIAGNOSIS: This Hairstreak is readily identified by the very large size, the blue dorsal surfaces, and the mostly black ventral surfaces with red basal spots next to the body on both wings. There are several iridescent green spots near the anal margin of the hindwing, as well as some iridescent blue spots along the margin.

ORIGINAL DESCRIPTION: Clench, *Entomological News*, 53: 219 (1940).

TYPE LOCALITY: Riverside, California. Holotype in Museum of Comparative Zoology, Harvard University.

DISTRIBUTION: The subspecies *estesi* Clench occurs from the Mississippi Valley westward to the Pacific Coast, and it also flies in northern Mexico. In California, we have abundant records from throughout the southern California area from Topanga Canyon and San Gabriel Canyon in Los Angeles County, south to the eastern part of San Diego County, and north through all of Riverside County and San Bernardino County (including the eastern Mojave Mountain ranges: Providence Mountains, Sheephole Mountains), and from there north through the coastal counties of Santa Barbara, Monterey, Santa Clara, Contra Costa, Alameda, Lake, Yolo, Yuba, Solano, Sacramento, to Shasta counties north of the Central Valley. From Kern County, in the southern Sierra Nevada, the butterfly extends in scattered colonies up the western slope of the Sierran foothills and Cascade Range into Oregon.

ELEVATION RANGE: From near sea level in San Diego County to 5200' on Breckenridge Mountain in Oak Chaparral communities near Bakersfield in Kern County.

HABITAT AND PLANT COMMUNITIES: This spectacular iridescent hairstreak is found rather sparingly in the Lower Sonoran, Upper Sonoran, Juniper Woodland, and Transition Zone oak belts in California, particularly in the deserts, foothills, and cismontane areas. It is most numerous along watercourses where its mistletoe foodplants are abundant on Cottonwoods and Sycamores. It is found in valley riparian areas, agricultural areas, cities and towns where Black Walnut, *Juglans*, supports the mistletoe.

PHENOLOGY: The species has been recorded as early as mid-February in the Santa Barbara area to as late as mid-November in the Scissors Crossing area and Anza Desert area of San Diego County. There are at least two broods in northern California, flying from April to October.

ADULT BEHAVIOR: Although adults are usually taken as singletons, occasionally one finds fairly good numbers on flowers, especially on *Baccharis* in the north during the fall. The species is multiple-brooded, and males can live up to twenty-four days, from

marking experiments by John Alcock (1983, 1985) in Arizona. Males perch on treetops along washes or on hilltops in the afternoon to await females, and will return to the same tree day after day, Alcock has found.

LIFE HISTORY: The larvae eat the male flowers and leaves of the *Phoradendron* parasitic mistletoes. The mature larva is velvety green with a yellowish lateral stripe and traces of reddish along with a darker mid-dorsal line. The body is covered by short orange hairs, except on the center portion of the cervical shield. The pupa is brown and heavily mottled with black. Short yellow-orange hairs are scattered over the pupal surface except on the wing cases. Pupation takes place under the bark of or at the base of trees on which the mistletoe grows. Pupae can sometimes be found in large numbers at the bases of isolated trees with heavy growths of mistletoe. The species hibernates in the pupal stage.

FOODPLANTS: The foodplants in California are all in the broad-leaved parasitic mistletoe genus, *Phoradendron*, including the following species; *P. flavescens* (Pursh) Nutt. var. *macrophyllum* Engelm. in Rothr., *P. bolleanum* (Seem.) Eichler var. *densum* (Torr.) Fosc., *P. californicum* Nutt., and *P. juniperinum* Engelm. (all in the Family *Loranthaceae*). These mistletoes are found on host plants as diverse as *Populus*, *Platanus*, *Juglans*, *Fraxinus*, *Quercus*, *Olneya*, *Prosopis*, *Conifers*, and *Junipers* (*Juniperus*).

CHROMOSOME NUMBER:

SIMILAR SPECIES: No similar species in our fauna.

GEOGRAPHIC AND SEASONAL VARIATION: There is a western U. S. subspecies (*estesii*) and an eastern U. S. subspecies (typical *halesus*). Otherwise, there is no geographic or seasonal variation in the United States.

GENERAL REMARKS: While the butterfly is usually considered fairly rare and local in the western United States, large numbers of pupae may be collected under trees supporting mistletoe. Along the Santa Ana River in Riverside County, as many as 420 pupae have been collected under one tree.

146. *Strymon melinus* Hubner

ADULT BEHAVIOR: The adults visit many kinds of flowers to sip nectar. The males will perch on small trees and shrubs during the afternoon to await females. While perched, they frequently rub their hindwings together, vibrating the two anal-margin tails.

LIFE HISTORY: The flattened egg is pale green in color. Eggs are normally laid on the host inflorescences and are laid singly. The larvae usually feed on flowers and fruits, and only rarely on young leaves. The mature larva is quite variable in color. The most common morph is green with diagonal markings of diverse colors on each segment, but the larva may be tan-colored, pink, reddish-brown, purplish-white, or yellowish-brown with various pale marks. The surface is covered with short yellowish-brown hairs. The pupa is a delicate brown, heavily mottled with dark brown spots of various sizes.

FOODPLANTS: Many genera and several families are used. These include *Malva* and flowers of cultivated hibiscus in urban areas (family *Malvaceae*), *Humulus* (*Moraceae*), a *Morpha* (*Leguminosae*), *Nolina* (*Agavaceae*), *Phaseolus* (*Leguminosae*), *Polygonum* and *Eriogonum* (*Polygonaceae*). The species sometimes becomes a pest in commercial bean fields. Guppy (1959) found that on Vancouver Island, British Columbia, *Strymon melinus* fed on the flowers of two *Trifolium* clover

species in the spring brood and on *Anaphalis margaritacea* Benth. during the summer brood. The latter would also oviposit on and eat the flower of a wild strawberry, *Fragaria loracteata* Heller, in the lab. It appears that the larvae of this hairstreak can feed on the flower parts of many species, and opportunistically selects them according to the species in bloom locally at time of oviposition.

CHROMOSOME NUMBER: n = 24 (Emmel and Eliazar, unpublished).

SIMILAR SPECIES: This species closely resembles *Strymon avalona*, an endemic species found only on Santa Catalina Island off the coast of southern California. However, *S. melinus* does not occur on that Island, although it does occur in great abundance on Santa Cruz Island to the north (records in April and June) where *S. avalona* is absent.

GEOGRAPHIC AND SEASONAL VARIATION: The six subspecies that have been described for *Strymon melinus* are weakly differentiated, and there is no seasonal variation despite the multivoltine character of the species.

GENERAL REMARKS: This is the most widespread species in the genus *Strymon* north of Mexico. The weak differentiation between the six described subspecies is because of the variable nature of individuals in the same population through the year. Almost every phenotype can be found in a population if one collects enough specimens.

This dark gray Hairstreak occurs throughout the lowlands of California and up to mid-elevations in the mountains. It is more scarce in desert areas. The typical subspecies does not occur in California but two other subspecies are represented.

a. *S. m. pudica* (Hy. Edwards)

DIAGNOSIS: This subspecies ranges from southern Oregon through California west of the Sierras to Baja California. The upperside is blackish with a conspicuous hindwing spot. The ventral surface is pale gray and the post-median band is narrow and lined with black, with considerable red in the hindwing post-medial band area.

ORIGINAL DESCRIPTION: Henry Edwards, *Proceedings California Academy Sciences*, 7: 172 (1876).

TYPE LOCALITY: Contra Costa County, California. Holotype in American Museum of Natural History.

DISTRIBUTION: We have hundreds of records of thousands of specimens collected in virtually every county west of the crest of the Sierra Nevada and north on the east side of the Sierras to Inyo County. It occurs from the coast up into mid-elevations in the mountains.

ELEVATION RANGE: From sea level to approximately 7,000 feet elevation.

PHENOLOGY: The flight period of this subspecies extends from February to November, although we have captures even in early January and mid-December as isolated individuals. The butterfly goes through a series of broods in all localities except perhaps the highest mountain populations.

b. *S. m. setonia* McDunnough

DIAGNOSIS: This subspecies is found in semi-arid areas from eastern Oregon across the Great Basin to Colorado. It is similar to the previously described subspecies except that

the post-median band on the hindwing ventral surface is more broadly edged with black. In California, this subspecies occurs in the state's northeastern corner.

- ORIGINAL DESCRIPTION: McDunnough, *Canadian Entomologist*, 59: 160 (1927).
- TYPE LOCALITY: Seton Lake, Lillooet, British Columbia. Holotype in Canadian National Collection.
- DISTRIBUTION: This butterfly is distributed from British Columbia south through eastern Oregon to the Great Basin Desert in Nevada and elsewhere in the west. In California it is found only in Modoc (and probably Lassen) counties.
- ELEVATION RANGE: From 4,000 to 7,000 feet elevation.
- HABITAT AND PLANT COMMUNITIES: This subspecies flies in Great Basin Sagebrush Scrub in its California range.
- PHENOLOGY: At present, most of our records are from July.

147. *Strymon avalona* (W. G. Wright)

This Hairstreak is one of the world's most restricted species, being found only on Santa Catalina Island off the coast of southern California.

- DIAGNOSIS: It rather resembles *Strymon melinus*, but is smaller in size and lacks the heavy wavy black post-median line that *melinus* has on the ventral surface. Instead it has a series of small black spots. Additionally, the red-orange hindwing spot is reduced both dorsally and ventrally.

ORIGINAL DESCRIPTION: W. G. Wright, *Butterflies of the West Coast*: 209 (1905).

- TYPE LOCALITY: Avalon, Catalina Island, California. Lectotype in California Academy of Sciences, designated by Tilden, *Occasional Papers California Academy Sciences*, 118: 32 (1975).
- DISTRIBUTION: *Strymon avalona* is common in select localities such as the hills around Avalon, the type locality. Meadows (1936) states that perhaps the best collecting locality is around common sumac (*Rhus laurina*) along the road to Renton Mine, south of Avalon in early March. Other localities where it has been recorded are Pebbly Beach, Jewfish Point, the Isthmus, hills west of Avalon, and a hillside 1/2 to 3/4 miles west of Avalon. All of these localities are on Santa Catalina Island off the Los Angeles coast.
- ELEVATION RANGE: Sea level to 200' elevation.
- HABITAT AND PLANT COMMUNITIES: The favored habitat is grassy areas and Chaparral, where the adults frequently perch on bushes.
- PHENOLOGY: Captures have been reported in every month of the year, with the first brood primarily occurring from mid-February to April, a second brood in July and August, and a third brood flying from September to November.
- ADULT BEHAVIOR: Besides visiting flowers of common sumac, the adults also visit the flower of the Giant Buckwheat, *Eriogonum giganteum* Wats.

- LIFE HISTORY:** The life history was first described by Comstock and Dammers (1933). The egg is of the usual echinoid form, with a large and deeply depressed micropyle and the characteristic reticulated network of raised walls enclosing cells of an irregular hexagonal type. Spiny projections come off the walled junctions as with other related species. The color is a gray-green with a bluish cast. The eggs are laid singly, usually in the terminal buds or on immature flowers of the foodplant. The mature larva shows considerable variation in ground color, ranging from a pale apple-green to pale pink. The pale apple-green form has no special markings or shadings except on the cervical shield, which has a pale green band down its center and the upper half speckled with black. The entire body of the larva, except the cervical shield, is covered with short white fine hairs. The pupa is pale pinkish-brown or wood-brown, shading to buff on the abdomen. Superimposed on this background color are markings of various shades of olive-green. Pupation occurs at the base of the foodplant, with the usual support of a delicate silk girdle. The head, thorax, and body of the pupa are covered with short yellow hairs.
- FOODPLANTS:** *Lotus argophyllus* (Gray) Greene var. *ornithopus* (Greene) Ottley, and *Lotus scoparius* (Nutt.) Ottley (Leguminosae).
- CHROMOSOME NUMBER:** (See Gorelick paper.)
- SIMILAR SPECIES:** See discussion under *Strymon melinus*.
- GEOGRAPHIC AND SEASONAL VARIATION:** None has been noted on Santa Catalina Island.
- GENERAL REMARKS:** Scott (1976) asserts that *melinus* has been introduced to Santa Catalina Island and that Glenn Gorelick has found intermediates there, suggesting that the introduced *melinus* may be absorbed by the *avalona* population. This is apparently incorrect, from all information available to us from other lepidopterists who have collected on the Channel Islands.

148. *Strymon columella clenchi* Austin and Emmel

- This Hairstreak is quite scarce in southern California and has only been taken in the Colorado Desert, particularly the Coachella, Imperial, and Colorado River Valleys.
- DIAGNOSIS:** The adults are distinguished from other *Strymon* species in California by the single pair of tails on the hindwings and the ventral markings, with a small-sized, pale underside and a poorly developed red spot.
- ORIGINAL DESCRIPTION:** Reakirt, *Proceedings Academy Natural Sciences Philadelphia*, [1988]: 339 (1866).
- TYPE LOCALITY:** "Near Vera Cruz, Mexico". Location of type not known (not in Field Museum of Natural History; Miller and Brown, 1981).
- DISTRIBUTION:** This butterfly has been taken in the Colorado Desert portions of Riverside County, Imperial County, and San Diego County, and once on the coast at Laguna Beach in Orange County. There are also several old records to the city of San Diego area in San Diego County, which may indicate a former coastal population (all coastal records are from September 1928). The only coastal colony with records later than this is in the El Cajon area of San Diego County.
- ELEVATION RANGE:** From below sea level to mid-elevations in the Laguna Mountains.

HABITAT AND PLANT
COMMUNITIES:

PHENOLOGY: The flight period extends from mid-March to early November in the desert areas, and in August to September at El Cajon.

ADULT BEHAVIOR:

LIFE HISTORY: The early stages were first described by Comstock and Dammers (1935b). The flattened egg is pea-green in color. The eggs hatch in about seven days. In the laboratory, the larvae will eat Mallow. The mature larva (said to be fifth instar) is dark green with a slightly darker mid-dorsal line, and a soiled white cervical shield (maroon shading in its center). The body is covered with translucent white points, from which arise translucent hairs of a glistening chestnut brown. The pupa is a pink-buff in ground color, heavily sprinkled with minute brown specks. There is a greenish mid-dorsal band on the abdomen which bifurcates and curves to either side on the last three segments.

FOODPLANTS: *Sida hederaceae* (Dougl.) Torr. (Malvaceae), at the California Lakes in Imperial County. Along the western edge of the Colorado Desert the butterfly uses two Malvaceous plants: *Hibiscus denudatus* Benth., and *Sphaeralcea ambigua* Gray. The eggs are usually laid between the sepals and the unfolding flower buds; the young larvae then feed on the flower parts and ultimately on the maturing seeds of these two plants.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: None in our area.

GEOGRAPHIC AND SEASONAL VARIATION: There are no apparent color pattern differences in individuals taken at different times during the year. There is no geographic variation within our populations of this species.

GENERAL REMARKS: This butterfly may not be a permanent resident of southern California. Populations may be established from individuals flying in from Mexico or southern Arizona, and if conditions are favorable, these may persist for several years before dying out due to unusually cold weather or an unusually dry winter or summer. A diapause stage is not known for this butterfly.

149. *Erora quaderna sanfordi* dos Passos

See **Appendix** for details of the one record in the Providence Mountains in the eastern Mojave Desert (Emmel and Emmel, 1973; Klots and dos Passos, 1982).

Subfamily **Lycaeninae** Leach

153. *Lycaena phlaeas alpestris* Emmel and Pratt

This small Copper is a California representative of a species that occurs across the temperate zones of the New World and Old World, and in the United States is restricted mostly to the eastern half of the country, as well as a few populations in the northwest part of Canada and Alaska.

DIAGNOSIS: The uppersides of this butterfly are a brassy copper, with somewhat of a dusky aspect, especially in males. Beneath, the ground color of the hindwing is an ashy-gray with wide and distinct orange borders on the hindwing. The post-median row of black spots on the ventral hindwing is distinct, with only a suggestion of white edging distally.

ORIGINAL DESCRIPTION: Emmel and Pratt, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990).

TYPE LOCALITY: North slope of Mt. Dana, 11,000 to 11,500' elevation, Tuolumne County, California. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This subspecies is found in the Sierra Nevada and the adjacent White Mountains of Mono County. In the Sierra Nevada, it is known from the area of Palaccede Glacier west of Big Pine northward to Sonora Pass. It undoubtedly occurs south of the Palaccede Glacier locality, and probably to the north of Sonora Pass as well, as the foodplant is found north and south of the known range of the butterfly. In the White Mountains, the butterfly has so far only been taken at one locality, in a cirque east of White Mountain peak, but the lack of records in the remainder of the White Mountains is probably due to the general inaccessibility of much of the potential habitat for the butterfly.

ELEVATION RANGE: From 11,000 to 13,000' elevation.

HABITAT AND PLANT COMMUNITIES: The butterfly is found within the Arctic Alpine Fellfields plant community. It is typically found on a north-facing, rocky slope, often just above a rock slide or talus slope particularly in glacial cirques.

PHENOLOGY: The species in California is apparently univoltine (although the eastern *L. phlaeas* is known to be multivoltine). Adults fly from mid-July to late August, depending on elevation, exposure, and depth of snow pack for a given year.

ADULT BEHAVIOR: Males tend to perch on rocks or on open patches of ground in small depressions on the north-facing rocky slopes. Females usually show unidirectional flight over the rocky slopes, landing on the *Oxyria* foodplants and spending most of their time either resting on or near the foodplant or on adjacent vegetation. Several alpine flowers have been noted as nectar sources of this butterfly in the White Mountains, namely

[JFE, FILL IN.]

LIFE HISTORY: The eggs are deposited on or near the foodplant, frequently on rock surfaces within several millimeters of the foodplant. The few hatched eggshells of this butterfly that have been found in the wild were placed on rocks within one centimeter of parts of the plant, and usually near the base of the foodplant. Eggs hatch within five days under laboratory conditions and the larvae feed to the third instar, in which they diapause the first winter. In the following year, the larvae molt and feed up to mature size in the fourth instar. Evidently, this larval stage goes into a second diapause until the following year when the diapausing larva pupates after snowmelt in the spring, and adults then emerge from the pupae within a two-week period (about ten days under laboratory conditions).

However, this California *Lycaena* does not have an obligate diapause. The larvae are able to tolerate winter cold much more consistently than adults or pupa, however. In addition, Ballmer and Pratt (1989a) have demonstrated that instar

number in this subspecies is variable in the White Mountains: four instars are prevalent under warm, long-day (late summer) conditions while five instars predominate when days are cooler and shorter in fall. The number of instars is apparently fixed at oviposition, and developmental time is greater for five-instar larvae than for four-instar larvae.

The eggs are greenish-white and are laid singly, as related above. The mature larva in California populations shows some variability, but not to the extent of other populations throughout the temperate regions of the world as described by Scott (1986). Specifically, in populations on Mt. Dana in the Sierra Nevada and in the White Mountains, the mature larva may vary from a almost totally green form to a darker green form with intense violet markings. The basic ground color above the spiracles is a dull green, with a mid-dorsal, dull purplish-red line. Just below there is a pale purplish lateral line starting faintly on the first thoracic segment, and intensifying by the first abdominal segment. The ventral half of the body, including the legs and prolegs, is also green in this color form. At the other extreme in these populations, the larva is a dull green from the spiracles up to an intense purplish-red mid-dorsal line. The entire ventral half of the body below the spiracles is a dull purplish-red with an intense bright purple lateral line running the length of the body just below the spiracles. Even the prolegs are a dull purplish-red in this color form. The head is black in both larval color forms. The pupa is a purplish-brown in ground color, with heavy but diffuse black blotches over the entire surface except the wingcases, where the wing venation is the purplish ground color while the intervein spaces are filled with black blotching. The cremaster area is the pale purplish ground color. The species as noted above is biannual in California, with hibernation in the third instar larva and again in the fourth instar larva. In Japan, Sakai and Masaki (1965; see also Endo et al., 1985) found that the onset of diapause in *L. p. daimo* Seite (or at least similar lengthened larval development and extra molts) is triggered by a shortening photoperiod and low temperature. Japanese adults of this species live up to fourteen days in nature.

FOODPLANTS: The only known foodplant of this species in California is *Oxyria digyna* (L.) Hill (Polygonaceae). J. Emmel and G. Pratt (1990) found larvae on this plant on the north slope of Mt. Dana and in the White Mountains in a cirque east of White Mountain peak. In the laboratory, larvae can be readily reared on *Rumex acetosella* L.

CHROMOSOME NUMBER: $n = 24$ (Emmel, Pratt, and Eliazar, 1990).

SIMILAR SPECIES: The species may fly in close proximity to Alpine populations of *Lycaena cupreus*, a superficially similar species which may be readily distinguished by the fact that on *cupreus* the dorsal surface of the hindwing is mostly copper-colored, whereas in *L. phlaeas*, this area of the wing is largely a brownish-charcoal gray.

GEOGRAPHIC AND SEASONAL VARIATION: As there is only one brood each year, there is no apparent seasonal variation. The populations in the White Mountains appear to be phenotypically identical to those found in the Sierra Nevada. The California *L. phlaeas* populations are the southernmost of any Arctic-Alpine *L. phlaeas* in North America. They are the only subspecies to be univoltine, apparently monophagous on *Oxyria digyna*, and confined to arctic-alpine habitats in the central Sierra Nevada and White Mountains. These areas are exposed to extreme and unpredictable weather for much of the year, especially cold (even in the summer, frost and occasional snow occur). The restricted range of this subspecies is especially strange in view of the fact that suitable hosts (*Rumex* species) are widespread at lower elevations in California where

they are utilized by other *Lycaena* species (Ballmer and Pratt, 1989a). Those subspecies of *L. phlaeas* in Asia, Europe and eastern North America are multivoltine, polyphagous (primarily on *Rumex* species). Their characters in relation to the other alpine subspecies of *phlaeas* are described by Ferris (1974). Life-history details in Ballmer and Pratt (1989b) were published under the name of *L. phlaeas hypophlaeus* (Boisduval).

GENERAL REMARKS: Our populations have gone under the subspecific name *hypophlaeas* Boisduval since 1852 (Dod, 1907; Klots, 1951; Shields and Montgomery, 1966; Ferris, 1974). An examination of the type specimen of *hypophlaeas* in the U. S. National Museum has revealed that the phenotype of this specimen is identical with *L. phlaeas* from lowland northeastern United States; it is not-at-all consistent with the facies of the California populations of *L. phlaeas*. At the time Boisduval named *hypophlaeas* (1852), he apparently had specimens from eastern North America and assumed that the species also occurred in California, describing its locality as "North of California. It is found in all the northern United States." No precise type locality was indicated, but certainly it was not in California. We have absolutely no evidence that Lorquin, the supplier of most of Boisduval's California material, ever got into the high Alpine areas of the Sierra Nevada (Emmel, Emmel, and Mattoon, 1990). Thus, the eastern subspecies name, *americana* Harris, falls as a junior synonym of *hypophlaeas* Boisduval. We leave the matter of fixing a type locality for this taxon to someone working with the lowland populations of *L. phlaeas* in the eastern United States.

This species in California is easily overlooked by collectors. The primary reason is that its favored habitat is rarely visited by the average collector, because of its usual inaccessibility and treacherous footing. Furthermore, there are few other butterflies in this habitat, making it an unattractive area for most lepidopterists to visit.

151. *Lycaena cupreus cupreus* (W. H. Edwards)

DIAGNOSIS: This small Copper has a bright reddish-orange dorsal ground color, with a metallic sheen to it and dark brown borders on the outer margins of the wings. Males are spotted on both forewings and hindwings with brownish-black small spots, whereas in females these spots are greatly expanded in comparison to the males. Ventrally, the forewing is a light orange, with a grayish outer margin. The outer margin is edged inwardly with a series of dark brown dashes or crescent-shaped markings, and the remainder of the forewing is marked with large brownish-black spots edged with white scaling. The ventral hindwing is a grayish-white with large black spots, and there is a sub-marginal broken orange line along the outer margin.

ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Ent. Soc.*, 3: 20-21 (1870).

TYPE LOCALITY: "Oregon". Lectotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Ent. Soc.*, 95: 176 (1969).

DISTRIBUTION: This species is widely distributed in the Sierra Nevada from Tulare County northward to Plumas County, and from there westward to the region around Bartle in extreme southeastern Siskiyou County. Outside of California, the species ranges to the southern edge of Alaska and eastward to the Rocky Mountains.

ELEVATION RANGE: From 3,600' to 12,500'.

- HABITAT AND PLANT COMMUNITIES:** The highest elevation populations are found in Arctic-Alpine Fellfield situations, usually on rocky or gravelly slopes or ravines where the *Rumex* foodplants are locally abundant. Low to mid-elevation populations occur in meadows or along streambanks or roadsides within Montane Coniferous forests.
- PHENOLOGY:** The species is usually univoltine, but some August records for several low to mid-elevation populations suggest that it may be bivoltine in some localities, depending on precipitation amounts and length of the potential summer flight season.
- ADULT BEHAVIOR:** Males perch on rocks or on open patches of ground on the rocky or gravelly slopes, or in small ravines, or along roadsides. Females tend to be more sedentary, frequently landing on the foodplant or on the ground adjacent to foodplants. The adults are frequently seen nectaring at the flowers of Pussypaws (*Calyptidium umbellatum* (Torr.) Greene).
- LIFE HISTORY:** The eggs are laid on the foodplant, usually on the lower stems or leaf undersides near the base of the plant. In some instances, oviposition may occur on debris or small rocks near the base of the plant. The eggs hatch within five to six days in the laboratory, probably taking a week or more under field conditions. The larvae feed to the third instar, in which they go into diapause. The following season, diapause is broken, the larvae feed through the fourth instar, pupate, and emerge within ten to fourteen days under laboratory conditions.
- The egg is undescribed. The mature larva as seen in the population in Calaveras County on *Rumex acetosella* L., is dull green in ground color, with a diffuse lighter area on the dorsal surface, culminating in two diffuse yellowish-green stripes on either side of the mid-dorsal line of green. There are no other markings on this soft green larva; even the spiracles are pale green, except for reddish centers. This color exactly matches the background leaf color of the *Rumex* species with which they were associated with in the field. The pupal stage is a light ivory tan in ground color, with several longitudinal rows of blackish-brown spots on the abdomen and across the dorsal surface of the thorax. The wings are lightly marked with alternating stripes of tan and dark brownish pigment. The antennae, proboscis, and eye cases are dark brown. There is a dark brown mid-dorsal line running the length of the pupa, also.
- FOODPLANTS:** The native foodplant of this species in California is *Rumex paucifolius* Nutt. ex Wats. ssp. *paucifolius* and ssp. *gracilescens* (Rech. f.) Rech. f. (J. Emmel, G. Pratt, and G. Ballmer, unpublished data). Additionally, many populations at mid-elevations and low elevations, particularly those in the extreme northern Sierra Nevada and southeastern Siskiyou County are associated only with the introduced *Rumex acetosella* L. (Sheep Sorrel).
- CHROMOSOME NUMBER:** n= from Tioga Pass material ().
- SIMILAR SPECIES:** The coloration and wing pattern of this species is distinctive, and it is not easily confused with any other Copper species. Occasionally, populations of this Copper may exist in close proximity to populations of *L. phlaeas alpestris*; see Similar Species section under that species for a discussion of the differences between *L. cupreus* and *L. phlaeas*.
- GEOGRAPHIC AND SEASONAL VARIATION:** In the few instances where there has been an apparent small late summer second brood, no phenotypic difference has been noted between the spring-flying individuals and summer-flying individuals in

that particular locality. At the northwest edge of this species' range in California, namely in Plumas County and southeastern Siskiyou County, specimens tend to be larger, slightly more heavily marked with the black markings, and females tend to be suffused with dark scaling over the orange ground color dorsally. We have seen no significant differences between the populations in the White Mountains and those in the Sierra Nevada.

A curious feature of this species is the number of populations, particularly at mid-elevations on the west slope of the Sierra Nevada, or at various elevations in the extreme northern Sierra Nevada and southeastern Siskiyou County, as all of these populations appear to use the introduced *Rumex acetosella* L. as their sole foodplant. This *Rumex* species is a weedy colonizer of disturbed areas such as roadsides, railroad right-of-ways, and other human disturbed areas. Thus, we may be witnessing the rapid expansion of the range of *L. cupreus* in California into areas not occupied by the butterfly before the coming of the first European settlers. It is of particular interest to note that Lorquin, collecting extensively in the northern Sierra Nevada in the 1850's, did not collect specimens of *L. cupreus*, to our knowledge. It is possible that virtually all of the northern Sierra Nevada *cupreus* populations (i.e., north of Lake Tahoe) have become established within the last 100 years.

152. *Lycaena mariposa mariposa* (Reakirt)

This is a local species, occurring in the high Canadian Zone from southern Alaska and British Columbia south in the Rocky Mountains to Colorado, and in the Sierra Nevada to northern California.

DIAGNOSIS: This is a strongly sexually dimorphic Copper, with the ground color of the upperside of males being a dark brownish-purplish color, with a dark border and a small orangish crescent-shaped marking near the anal angle. The female upperside is a dull dark brown with light orange patterning on the forewing broken by several irregular dark rows of spots. On the hindwing, there are several patches of light orange scaling with a border of light orange crescents along the submarginal area. The underside is the most distinctive feature of this Copper, in that the ground color of the hindwing is a light gray with several irregular lines composed of black crescent shapes or roundish spots, giving a banding affect to the wing pattern. The basal area of the wing is darker than the post-median area. On the ventral forewing, the ground color is a light orange, bordered by a sub-marginal area of dark brownish-gray, and there are scattered dark spots within the light orange area.

ORIGINAL DESCRIPTION: Reakirt, *Proceedings Ent. Soc. Philadelphia*, 6: 149 (1866).

TYPE LOCALITY: "California". Syntypes in Field Museum of Natural History, Chicago.

DISTRIBUTION: Within California, this species is found in scattered populations in the northern Sierra Nevada and Klamath Mountains region. The southernmost Sierra Nevada populations occur in Tuolumne County and extend northward to the Gold Lake area in Sierra County. In the Klamath Mountains region, colonies are known in the Trinity Alps, Mt. Eddy, and Scott Mountain.

ELEVATION RANGE: From 4,500 to 10,000' elevation.

HABITAT AND PLANT COMMUNITIES: This species is found at the edges of boggy meadows, often among Lodgepole Pines, or in open glades in the forest and in small sub-

Alpine meadows on open slopes, all within the Montane Coniferous forest or sub-Alpine forest plant communities.

- PHENOLOGY:** Adults fly from early July to late August, depending on elevation and snowpack conditions. This species is univoltine and overwinters as an egg.
- ADULT BEHAVIOR:** Shapiro et al (1979) notes at least two nectar sources for this species: *Helenium digelovii* Gray (a plant rarely visited by butterflies) and *Aster alpinus* (T. & G.) Gray ssp. *andersonii* (Gray) Onno (Asteraceae). Opler (1975) also notes *Fragaria* as a nectar source. Males are attracted to mud or moist ground, particularly along partially shaded trails. Males will perch on low vegetation.
- LIFE HISTORY:** The egg was described by Coolidge (1910a), but the larva and pupa have not been described previously. The mature larva (based on Siskiyou County material collected by G. Pratt and G. Ballmer) has a velvety medium-green ground color over the entire body, except for a faintly darker mid-dorsal line and a light yellowish lateral line on either side below the spiracles. The spiracles are yellow, and the entire body surface is covered by short yellowish hairs. The pupa is a somewhat duller green in ground color, with a darker green mid-dorsal band and a lighter green abdomen. The positions of the abdominal spiracles are marked by yellow spots, forming a necklace of yellow dots extending laterally around the abdomen.
- FOODPLANTS:** *Vaccinium arbuscula* (Gray) Merriam in the family Ericaceae is the only known host (Pratt and Ballmer, 1986). Other hosts have been listed erroneously in the past literature, and the reader is referred to the Pratt and Ballmer paper for explanation as to why they are not valid host records.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** The combination of ventral forewing and hindwing coloration patterns will distinguish this *Lycaena* from its other congeners in California.
- GEOGRAPHIC AND SEASONAL VARIATION:** Shapiro *et al.* (1979) note that specimens from the Klamath Mountains region tend to be more heavily marked beneath than Sierran ones from similar elevations and habitats.
- GENERAL REMARKS:** The limited distribution of this butterfly, in contrast to the more widespread distribution of its known foodplant, is puzzling. Guppy (1964) notes that one reason collectors have considered *L. mariposa* to be a scarce butterfly throughout its range is its very late season of flight. Above timberline in British Columbia, for instance, it is not likely to be seen before August 20th, long after most other alpine species have flowered.

153. *Lycaena nivalis* (Boisduval)

- ADULT BEHAVIOR:** The adults of *nivalis* have been observed visiting the flowers of Yarrow (*Achillea millefolium* L.), Woolly Sunflower (*Eriophyllum lanatum* (Pursh) Forbes), often on blooms of several *Eriogonum* species and other flowers near the foodplant. Males frequently perch all day on the ground and open areas to await females.
- LIFE HISTORY:** The life history of *Lycaena nivalis* was first described by Newcomer (1911, 1964) from material taken at Deerpark, near Lake Tahoe from females ovipositing on *Polygonum douglasii* Greene. The egg is pale bluish in color and 0.85 millimeters in diameter. The shape is that of a depressed spheroid, ornamented with deep, polygonal pits. There are four larval instars, which initially are brownish-yellow

and then become pale green. The mature larva is pale green with a dorsal line of rose or purplish color. A narrow whitish line occurs to either side on the dorsal surface. The cervical shield is sunken on full-grown larva, and is in the shape of a double diamond. The body is covered with short brownish-hairs. The dorsal surface is covered with small white, hairless tubercles. The head is dark brown. More recently obtained material from Tioga Pass (J. Emmel) shows a mature larval coloration of a soft green across the entire body surface, with a very faint mid-dorsal purplish line and two very faint bands on either side of this line, yellowish-green in color. Just below the spiracles on either side, occurs a lateral line of diffuse yellow color. The pupa is pale tan in ground color, with a large number of minute brown striations over the entire surface. There is a prominent purplish mid-dorsal line across the abdominal segments, turning to dark brown as across the thoracic and head areas. Tiny minute hairs, resembling miniature trumpets, are scattered thickly on the dorsal surface of the head, and more sparingly across the thorax and abdomen, appearing like minute tacks stuck into the surface of the pupa. The species overwinters in the egg stage.

**GEOGRAPHIC AND
SEASONAL VARIATION:**

This species is single-brooded, so there is no seasonal variation. Geographic variability in this species has been discussed over its broad range by Newcomer (1964). He looked at the populations from northern Washington to the Warner Mountains in northern California, and observed the more brilliant yellow and pink undersides occurred in populations where precipitation was high (at least 40 inches annually), whereas specimens from areas with light spring rainfall and an annual precipitation of less than 20 inches tended to have a washed out light cream underside, with a tinge of pinkish on the hindwings, but no evidence of yellow. He suggested that in the areas where intense coloration in this species occurs, there would be less sunlight due to frequent cloudiness, and this may be a factor in determining the intensity of the colors. In areas where the colors beneath are less intense, there is more sunlight. He also examined the change in temperatures over this gradient and decided that neither temperature nor elevation was a factor that correlated with color variations found in *nivalis*.

GENERAL REMARKS:

Newcomer also noted that because the foodplant is an annual, the newly hatched larvae the following spring must seek out seedling plants sprouting from seeds produced by the *Polygonum* plants on which oviposition occurred the previous year. Despite the hazards of extreme temperatures during the winter and the spring search for newly sprouting seedlings, the species is relatively successful and quite common at times in its colonies.

Within its range, from the Rocky Mountains to California and north into British Columbia, this species is widespread in mountainous areas and rather variable in adult coloration (e.g., Brown, 1961). There are three subspecies found within our state.

a. *L. n. nivalis* (Boisduval)

DIAGNOSIS:

This species is strongly sexually dimorphic, like most of the other Coppers. The upperside of males is a light brown with a purplish sheen, and there is a scalloped light orange border along the outer margin of the hindwing. Females tend to be light orange with a pattern of dark brown spots on the upperside and dark marginal and basal areas on both wings. On the underside, the forewing is a pale cream in ground color, with dark brown markings. The hindwing ventral surface is a pinkish-gray, of fairly uniform coloration from the basal area to the post-median

area of the wing. Black spotting on the hindwing is usually reduced to rather small spots, often becoming obsolete in this subspecies.

- ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. Belgique*, 12: 44 (1869).
- TYPE LOCALITY: "California". Suggested as probably Sierra, Nevada, Placer or El Dorado County by dos Passos (1938). Restricted by Emmel, Emmel, and Mattoon, : (1990) to Gold Lake, Sierra County, California. Holotype in U. S. National Museum.
- DISTRIBUTION: The nominotypical subspecies is widely distributed in the Sierra Nevada from the Mineral King area of Tulare County northward to Plumas County. From there it extends northwestward along the eastern portion of the Mt. Shasta region to the westernmost distribution of subspecies *warnermontana* in the Goosenest District area of the Cascade Range in northern Siskiyou County.
- ELEVATION RANGE: 4,500 to 10,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This species is most commonly encountered in dry meadows within the Montane Coniferous Forest plant community. One adult nectar source which is frequently visited is Pussypaws (*Calyptridium umbellatum* (Torr.) Greene) (Portulacaceae).
- PHENOLOGY: This species is univoltine, but has a fairly long flight period extending from late June to early September, depending on elevation, exposure, and snowpack. The peak flight period seems to be late July to early August, in most localities.
- FOODPLANTS: For the Sierran populations, *Polygonum douglasii* Greene (Polygonaceae) (Newcomer, 1964).

b. *L. n. bicolor* Emmel and Pratt

- DIAGNOSIS: In this subspecies, both sexes are much like Sierran *nivalis* on the uppersides, with the exception of the females having somewhat more extensive dark brown basally on both forewing and hindwing. The most striking difference is in the coloration of the underside. The forewing ground color is a lemon-yellow, with a slight orangish flush in the posterior half of the submarginal area. On the hindwing, there is a striking "two-tone" quality to the wing coloration, with the proximal half of the wing lemon-yellow and the distal half a mauve or grayish-pink color.
- ORIGINAL DESCRIPTION: Emmel and Pratt, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990).
- TYPE LOCALITY: Mt. Eddy, Siskiyou County, California.
- DISTRIBUTION: This subspecies is found throughout the Klamath Mountains Assemblage and northward into the southern Cascade Range of Oregon, specifically in Linn and Jackson counties. To the north and east, in Washington, Idaho, Wyoming and Utah, occurs *L. nivalis browni* dos Passos (1938), which has duller brown males with a brilliant violet reflection that hides the brown seen in typical *nivalis*.
- ELEVATION RANGE: From 5,000 to 9,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This subspecies is common in dry meadows, on rocky slopes, and along trails, usually in full sun, within the Montane Coniferous Forest and Sub-Alpine Forest plant communities (Shapiro, 1979).

PHENOLOGY: Records range from mid-June to mid-September, indicating a very long flight period in the Klamath Mountains area.

FOODPLANTS: This subspecies is closely associated with *Polygonum spergulariaeforme* Meissn., and this plant is very strongly suspected to be the foodplant.

c. *L. n. warnermontana* Emmel and Pratt

DIAGNOSIS: In this subspecies, the males are much like Sierran *nivalis*, except that on the underside the post-median row of black spots on the hindwing is noticeably more prominent. The most marked differences occur in the females, which are noticeably more melanic than their Sierran counterparts. In some females, the forewings and hindwings on the upperside are largely obscured by dark brown scaling, with the light orange pattern reduced to a few patches in some specimens. On the underside, the spotting pattern is noticeably more prominent, particularly on the hindwings where the post-median row of black spots stands out very strongly. Otherwise, the ventral ground color is much like that of Sierran *nivalis*.

ORIGINAL DESCRIPTION: Emmel and Pratt, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990).

TYPE LOCALITY: Bidwell Peak, near Dismal Swamp, 6 air miles east of Highway 395 at New Pine Creek, Modoc County, California.

DISTRIBUTION: This subspecies appears to be largely confined to the Warner Mountains in northeastern California and extreme southern Oregon. It is also abundant in the uplands of the Goosenest District of the Klamath National Forest in the Cascade Range, a block of high mountains just south of the Oregon state line between Highway I-5 and Highway 97.

ELEVATION RANGE: 6,000 to 8,200' elevation.

HABITAT AND PLANT COMMUNITIES: This butterfly, wherever found, breeds in the more mesic areas of the *Artemisia* scrub at elevations above 6,000'. The habitat is one of sagebrush within which springtime water-catch flats produce grassy meadows with abundant *Eriogonum* sp., sunflowers, lupines, and wildflowers in the surroundings. These areas are often adjacent to yellow pine or mixed with Red Fir forest stands where snowbanks accumulate in winter to feed the moisture out and produce the flower-studded *nivalis* habitat. Occasional wet permanent meadows marked by Quaking Aspen and willow will result. The larval host of *warnermontana* will often become dense stands of this tiny *Polygonum*.

PHENOLOGY: Records for this species extend from late June to mid-August, again indicating a fairly long flight period for this univoltine species.

FOODPLANTS: The foodplant is unknown for the Warner Mountains populations, but *Polygonum douglasii* Greene is common in the Warner Mountains and Goosenest District and is the likely host. Although it is not the only *Polygonum* in the habitat, it is the most abundant, and is always in association with the flight area of this subspecies.

154. *Lycaena helloides* (Boisduval)

This species, known as the Purplish Copper, occurs from southern California to Alaska and east to almost the northeastern states. In our state, it is found in the form of the nominotypical subspecies.

DIAGNOSIS: Males of this species have a purplish ground color above, with dark brownish-black borders and a scalloped reddish-orange sub-marginal border on the hindwing, accentuated near the anal angle. Females, on the upperside, have varying amounts of the light orange ground color and the dark brown markings; in some, the light orange ground color predominates and there is a dark brown border and a series of dark brownish-black spots on both wings, with brown scaling basally and a scalloped orange sub-marginal band as in the male. However, some females are much darker, with the dark brown ground color predominating and the light orange areas broken up by enlarged dark brown spots and markings. On the underside, the most characteristic feature is the orangish-gray or ruddy-gray ground color of the hindwing. The forewing is usually yellowish to yellowish-orange on the underside, with dark black markings. There is a rather fine reddish scalloped line submarginally on the ventral hindwing, also.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 291 (1852).

TYPE LOCALITY: "San Francisco, California." Holotype in U. S. National Museum.

DISTRIBUTION: This species is widespread in a variety of habitats in California, absent only from the Mojave and Colorado Deserts. It is found from the Mexican border northward through San Diego County, through the lowlands and mountains of southern California northward, through the Coast Ranges, Central Valley, and Sierra Nevada to the Oregon border. This species is also found on Santa Cruz Island in the Channel Islands.

ELEVATION RANGE: From near sea level to 7,700' elevation.

HABITAT AND PLANT COMMUNITIES: This species is usually found in moist bottomlands, such as along rivers and canals or other man-made watercourses, particularly in valley bottoms. It is also found in scattered populations in similar habitats in the foothills and mountains. Some of its foodplants are introduced European weeds, and this probably accounts for the tendency to find this butterfly in areas where human disturbance is more marked. Its associated plant communities include Freshwater Marsh, Valley Grassland, Riparian Woodland, suburban-agricultural areas, Chaparral, Coastal Sage Scrub, Sagebrush Scrub, Montane Coniferous Forest, Foothill Woodland, and Subalpine Forests.

PHENOLOGY: This species is multivoltine, with captures ranging from early March to late November.

ADULT BEHAVIOR: Males usually perch on low vegetation to await passing females. When females are forced to land by a pursuing male, they invariably fan their wings intermittently in response to the activity of the male. Shapiro (1973c) observed an attempted interfamilial mating between a fresh male *Lycaena helloides* (Lycaenidae) and a fresh female *Cynthia annabella* (Nymphalidae) in a vacant lot at Southport in Yolo County. The male courted the female for nine minutes without success; the *C. annabella* was estimated to be fully twice the size of a *L. helloides* female, and resembled it superficially only in general color.

LIFE HISTORY: The early stages were first described by Comstock (1927b, 1929). The echinoid egg is somewhat more flattened than those of the other *Lycaena* species, and

especially differs in the less extreme reticulation and presence of nodules instead of thin high walls and deep cells. The mature larva is grass-green and has a bright yellow lateral stripe, as well as a broken bright yellow line on each side of the mid-dorsal region. A faint yellow oblique dash occurs on the side of each segment. The body hairs are colorless, and somewhat longer than those of other *Lycaena* species. The pupa is greenish, with brown and black markings, and has numerous pale green low warty tubercles, bearing bristles. The life history was also described but not illustrated by Coolidge (1924b).

FOODPLANTS: The following species of Polygonaceae have been given as foodplants: *Polygonum aviculare* L., *P. lapathifolium* L., *P. persicaria* L., *P. punctatum* Ell., and *Rumex crispus* L. This species is also associated with *Potentilla egedei* Wormsk. (Rosaceae) in the Suisun Marsh in central California (Shapiro, 1974a and 1974b) and with *P. fruticosa* at high elevations. Other species of Polygonaceae have been documented for *L. helloides* populations outside of California (e.g., Chambers 1963), and undoubtedly some of our populations use these same foodplants.

CHROMSOME NUMBER: Unknown.

SIMILAR SPECIES: Very worn specimens of *L. helloides* may resemble *L. nivalis*. Since the two species are largely allopatric, there is unlikely to be any confusion, but in the few montane localities where the two might occur sympatrically, *L. helloides* is identified by the more orangish-gray underside of the hindwing in contrast to the flatter pinkish-gray of *L. nivalis*.

**GEOGRAPHIC AND
SEASONAL VARIATION:** None.

GENERAL REMARKS: This is a "weedy" species and may be expected to colonize many human-disturbed areas in the state. Subalpine specimens are smaller, with more gray ventrally on the secondaries, and tend to resemble *L. dorcas*. Kirby. Chambers (1963) has suggested that the high-altitude univoltine *florus* Edwards of Colorado may not be referable to either *L. dorcas* Kirby or *L. helloides* Boisduval, having biological differences in host preference, elevation, and number of broods. Our California material deserves further field study as well.

155. *Lycaena gorgon* (Boisduval)

ADULT BEHAVIOR: The adults avidly visit *Eriogonum* flowers. Adults of the Warner Mountains and Lower Rock Creek populations avidly visit flowers of *Apocyanum* species. Males perch along small ravines, on open patches of soil, or along roadsides, particularly at the bases of road cuts.

LIFE HISTORY: The early stages were first described by Comstock and Dammers, in 1934. The eggs are laid singly, or occasionally in pairs or threes, at the forks of the flowering stems of the host plant. They then diapause until the following spring. The egg is echinoid, flattened at the base, with a deep micropyle at the top, with a size of about .48 millimeters high by .84 millimeters in diameter. The surface of the egg is extraordinarily deeply ribbed into a series of about 22 longitudinal folds, which are then connected by lower horizontal partitions. The cells enclosed by these walls are deep and unlike the appearance of the other members of the genus. The color at first is a delicate green, but later the ridges assume a glistening white and the general color of the egg is a creamy white. The mature larva is a pale turquoise green, becoming extremely light in the Warner Mountains. This basic ground color is largely obscured by a covering of dense long white hairs. This gives the

larva a protective coloration matching the leaves of the foodplant. Underneath these hairs, on the ground color of the larva, are a row of whitish diagonal dashes, one on each segment and protruding out from the dorsal midline in a posterior direction. Thus, these form two parallel rows on the dorsal surface of white, rearward angling bars. The spiracles are pale tan in color. There is a narrow white band running laterally below the spiracles. The legs are colorless, and the prolegs are pale green with light brown claspers. The head is pale buff, with brown mouthparts. Pupation takes place late in May on the foodplant, with the support of a delicate silk girdle. The pupa is pale blue-green in ground color with a slight yellowish shading on the abdominal segments. All surfaces but the wingcases are thickly studded with minute fungoid or trumpet-shaped white protrusions, although these are absent in four longitudinal rows of circular patches on the dorsal surface of the abdomen (appearing darker green than in the dorsal view).

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: Although the males superficially resemble those of other *Lycaena* species on the dorsal surface, both sexes are distinctively colored on the ventral surface from other *Lycaena*.

GEOGRAPHIC AND SEASONAL VARIATION: Within any given locality, there is considerable variation in the adult pattern, both upperside and underside. However, for the nomotypical subspecies the range of this pattern seems fairly constant from population to population throughout most of the state.

GENERAL REMARKS: This Copper species is almost entirely confined to California, and is a distinctive species of our fauna.

The metropolis of this western Copper species is in California, with a slight extension into southern Oregon. It is found in foothill woodland and chaparral areas. Within our state, three subspecies have been identified.

a. *L. g. gorgon* (Boisduval)

DIAGNOSIS: In this species, the males on the upperside have a light violet-brown ground color, with a purplish sheen and a dark brown border along the outer margins with a white fringe. Near the anal angle, there is a varying sized area of light orange markings, usually in somewhat of a scalloped pattern. The upperside of the females is a pale yellowish-orange, with light grayish-brown suffusion at the base of both wings, and a light grayish-brown wide border along the outer margin of the forewing. There are a series of dark brown spots on both the forewing and hindwings, rendering somewhat of a checkered pattern. Along the outer margin of the hindwing are a series of pale orange crescent-shaped markings, each enclosing a round dark brown spot. The outer fringes are also white in the females. On the underside, the usual ground color is a light grayish-tan and there is a pattern of dark brown to black spots scattered over both forewing and hindwing. Along the outer margin of the hindwing, there is a series of red-orange markings, usually crescent-shaped, with a dark spot distal to them and an arrow-shaped edging of dark scaling proximally.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 292 (1852).

TYPE LOCALITY: Mountains of California. Restricted by Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1988) to Lower Feather River Canyon, Butte County, California. Type in U. S. National Museum.

- DISTRIBUTION:** The typical subspecies of *gorgon* is widespread in Cismontane California from San Diego County northward through the foothills and mountains of southern California through the Sierra Nevada foothills and the Coast Ranges to the Mt. Shasta region. From here it ranges into extreme southwestern Oregon.
- ELEVATION RANGE:** From 400 to 4,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** This species is usually found in canyons or on dry slopes within the Chaparral or Coastal Sage Scrub plant communities, rarely entering the lower edges of the Montane Coniferous forest.
- PHENOLOGY:** Strictly univoltine. The majority of our records range from late April to early July, with an apparent peak flight period during the month of May. There is one late March record.
- FOODPLANTS:** The nomotypical subspecies uses both *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes, and *E. elongatum* Benth.

b. *L. g. megapunctata* Emmel and Pratt

- DIAGNOSIS:** This subspecies is readily characterized by the greatly enlarged dark spots on the underside of both sexes. On the uppersides, the pattern in males is similar to that seen in typical *gorgon*; in the females, there is a tendency for expansion of the light yellowish-orange areas, giving a "blond" appearance to some specimens. On the underside, the ground color ranges from a light tannish-gray to a yellowish-tan. All of the black spots on the underside are markedly enlarged from that seen in the nomotypical subspecies.
- ORIGINAL DESCRIPTION:** Emmel and Pratt, *Journal Research Lepidoptera*, : (1988).
- TYPE LOCALITY:** Pine Creek Canyon, County Road 2, 3 roadmiles east of New Pine Creek, Modoc County, California.
- DISTRIBUTION:** This subspecies is found in the Warner Mountains of northeastern Modoc County, extending northward into extreme southern Oregon in the same range. From here it extends westward to northeastern Siskiyou County in the Goosenest District.
- ELEVATION RANGE:** From 5,000 to 6,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** This *gorgon* subspecies has habitat requirements similar to those described for Warner Mountain *nivalis* except that the *Artemisia* scrub within which it flies is slightly drier, lacking the grassy rain-catch flats with seeps that are more abundant on the higher portions of its montane distribution. *Megapunctata* utilizes the lower, drier slopes and foothills of the range which are still moist enough to produce abundant sunflowers, occasional thistles and junipers, along with patches of *Apocynum*. Here on the gravelly, sometimes lava-rubble slopes, the host *Eriogonum nudum* grows in abundance as do lupine species. While most abundant on lower slopes, this *gorgon* subspecies also follows such habitat upwards into the Coniferous Forest areas, and often the Dogbane or *Monardella* nectar sources attract *megapunctata* within forested areas, to feed where these plants grow more prolifically. In all areas where we have taken this insect, there have been coniferous, oak, and chaparral mixed forests nearby, but it breeds out on the drier slopes.

PHENOLOGY: From late June to early August, with a peak flight period in mid-July.

FOODPLANTS: *Eriogonum nudum* ssp. .

c. *L. g. obliterata* Emmel and Pratt

DIAGNOSIS: This subspecies is characterized by its smaller size and reduction or obsolescence of the black spots on the underside of both sexes. In the males, on the upperside there is expansion of the orange areas near the anal angle, in comparison to that seen in nomotypical *gorgon*. Females tend to be more lightly marked above than typical *gorgon*, with expansion of the pale yellowish-orange areas of the wings. On the underside, the ground color tends to be a paler shade than that seen on nomotypical *gorgon*.

ORIGINAL DESCRIPTION: Emmel and Pratt, *Journal Research Lepidoptera*, : (1988).

TYPE LOCALITY: South-facing slope above Lower Rock Creek, 6,150-6,200' elevation, 0.8 airmiles NNW of Sherwin Summit, Mono County, California. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This subspecies is found on the east slope of the Sierra Nevada, from the region of Butterbreidt Peak in Kern County northward to Lower Rock Creek in Mono County.

ELEVATION RANGE: From 4,500 to 6,200' elevation.

HABITAT AND PLANT COMMUNITIES: This subspecies flies on open granitic sand slopes, often south-facing, within the Sagebrush Scrub plant communities or Jeffrey Pine forest plant communities in the Rock Creek region, and in sparse Joshua Tree woodland in the Butterbreidt Peak area and Ninemile Canyon areas of the southern Sierra Nevada. Within this habitat, *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes ssp. is locally abundant.

PHENOLOGY: This butterfly flies from early May to mid-June, with an apparently peak flight period in late May to early June, depending on elevation.

FOODPLANTS: *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes ssp. (Polygonaceae).

156. *Lycaena heteronea* (Boisduval)

ADULT BEHAVIOR: Males avidly perch and both sexes roost on Great Basin Sage whenever this species is present, although other shrubs may also be used. Orsak (1977) found by mark-release experiments that while some adults move very little within the population sites, others would move a great deal. Male movement appears to vary with the density and location of adults in the population. In the population center, territorial interactions are frequent, whereas on the periphery of the population male movement is very slight. The presence of females is a better indicator of the breeding site than is male presence, since males tend to disperse also into the surrounding habitat.

Nectar sources in the southern California populations are primarily the larval host plant, *Eriogonum fasciculatum* Benth., which blooms only once a year at the time of adult emergence. At the beginning of the flight season, adults may visit *Lotus scoparius* (Nutt. in T. & G.) Ottley and at the end of the flight season, they may

visit *Encelia* species. The presence of Great Basin stage (*Artemisia tridentata* Nutt.) as the preferred perching substrate appears important in southern California populations. Adult butterflies were never observed to fly through unsuitable habitats, such as a Pinyon Pine or Oak woodland, suggesting that these vegetational formations might form natural buffers to minimize adult dispersal (Orsak, 1977). Females stay close to the *Eriogonum* foodplants in all populations, from the coast to the sub-Alpine areas of its distribution. Males patrol in the morning and perch after 1:00 p.m.; matings occur from 9:00 a.m. to as late as 5:30 p.m. A pair may stay in copula for as long as 3-4 hours. Of ten females dissected, nine had single spermatophores present and one female had two, indicating most females mate only once.

LIFE HISTORY: The larva and pupa of nominotypical *heteronea* were described from Marin County material by Williams (1910). The egg of the southern California race, *clara*, was described by Comstock (1927a). Orsak (1977) gives a very generalized life history. Thus, the following account is drawn from material that we have observed, as well as the earlier published accounts. The egg (based on *clara* material) is a delicate light green, changing immediately after ovi-position to clear white. The eggs are nearly spherical in shape and the small micropyle is a deep pit with abrupt walls. The egg surface is covered by irregular depressions, separated by thin upright walls which gives the entire egg a spiny appearance with low relief. The eggs are usually placed on the underside of the leaves of the host, and form the diapause stage until the following spring. The mature larva in the Marin County material examined by Williams, and Mt. Lassen and Warner Mountains material examined by us, shows a ground color of pale grayish-green, nearly the color of the dorsal surface of its foodplant. There is a pale median line on the dorsal surface, flanked on either side by a broader pale band, extending the length of the larva also. Arising from each of these lateral bands are two diagonal posteriorly-facing white bars on each segment. These dorsal markings are all very faint in appearance. From a lateral view, the two diagonal stripes on each segment form two wavy bands extending the length of the larva on each side. At the level of the spiracles is another very pale, barely visible light band running horizontally along the length of the larva. Below the spiracles is a stronger pale yellow band running the length of each side. This lower lateral line is the plainest of the markings, and is whitish in all populations.

The pupa has a similar ground coloration of light whitish-green. The wing covers are almost white, and are reticulated with grayish-white. There is a pale green dorsal thoracic line which becomes darker where it meets the first abdominal segment, and then becomes more obscure on the abdomen until it reaches a darker line near the cremaster end of the pupa. The entire surface of the pupa bears numerous white spots, with the exception of the wing covers.

CHROMOSOME NUMBER: $n = 68$ in Colorado material (Emmel, Eliazar, and Harris, 1990).

SIMILAR SPECIES: This is the only Copper species with a blue male. Dark females of *heteronea* can resemble the females of *Lycaena rubidus* in the Warner Mountains.

GEOGRAPHIC AND SEASONAL VARIATION: There is considerable phenotypic variation of this butterfly within any given locality and virtually all populations show this extreme variability. In our geographic subspecific scheme, there are a number of populations which do not neatly fit into a particular described subspecies, but tend to represent intermediate populations. In the North Coast Ranges, particularly in the Yolla Bolly Mountains region, populations there seem to be intermediate between nominate *heteronea* and the subspecies *submaculata*. Along the crest of the Sierra Nevada

there are some populations which show characters of both the subspecies *immaculata* and *submaculata*. In the southern Sierra Nevada on the western slope in Tulare County, populations show characters of the subspecies *clara*. Reference to the Distribution Map will help clarify some of these distributional patterns.

GENERAL REMARKS: The southern California subspecies, *L. h. clara*, has been suggested as a potential candidate for an endangered species classification because of the destruction of habitat in some of its remaining population areas. Today there are 30 or fewer populations, and most are located in the Cuddy Valley area of the Tehachapi Mountains, near Gorman. This is a site for extensive mountain-cabin resort development and also for the conversion of sagebrush areas to pasture land. Orsak (1977) presents a cogent argument for habitat and population management of this species in order to avert its extinction in the future.

This bright blue Copper is found in the Great Basin and the Sierra Nevadas and in a disjunct population in southern California. It is extraordinary for having a brilliant blue color in the males instead of the usual coppery tone.

a. *L. h. heteronea* (Boisduval)

DIAGNOSIS: The nominotypical subspecies of *heteronea*, found in Marin and Sonoma counties north of San Francisco Bay, is the largest of the California subspecies of *heteronea*. The male's dorsal surface is a lilac-blue with a violaceous sheen. On the upperside of the females, the ground color of the wings varies from a yellowish-tan to a dull gray-brown. On both forewing and hindwing, there are varying amounts of blue scaling in the medial two-thirds of the wing, often fairly prominent. The submarginal area of the hindwing is marked by a series of orangish-tan markings, usually each containing a small black spot. Inwardly, these are marked with crescentic-shaped areas of dark brown spots, giving a sort of "scalloped" appearance to this band on the hindwing. On the underside, the ground color of the males is a pale grayish-white and on the females a pale grayish-cream. The pattern of black spots on the forewing is relatively reduced and there are no black spots on the hindwing, but there are several patches of brownish-gray scales, giving a very faint spotting pattern.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 298 (1852).

TYPE LOCALITY: Mountains of California. Restricted by Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990) to Bodega Bay, Sonoma County, California. Holotype in U. S. National Museum.

DISTRIBUTION: This subspecies is found along the immediate coast from southern Marin County northward to southern Sonoma County. It may be expected to occur at other points along the coast as the foodplant extends as far north as southern Oregon in various coastal localities.

ELEVATION RANGE: From sea level to approximately 100' elevation.

HABITAT AND PLANT COMMUNITIES: This subspecies is found within the Coastal Strand or North Coastal Sage Scrub plant communities along the immediate coast. In these habitats, the foodplant, *Eriogonum latifolium* Sm., is often locally abundant.

PHENOLOGY: This subspecies has a long flight period from early May to early July, depending on the degree of summer fog, winter rainfall patterns, etc.

FOODPLANTS: The apparent sole host of this set of populations is *Eriogonum latifolium* Sm. (Polygonaceae).

b. *L. h. clara* (Hy. Edwards)

DIAGNOSIS: This southern California subspecies is characterized by its smaller size, reduction of black markings on the underside of the forewings, the very pale underside in both sexes, and the very extensive blue scaling seen on the upperside of females. This blue scaling is a silvery powder blue and usually extends over the medial two-thirds of the forewing, sometimes extending even into the submarginal area of the forewing and scattered over the entire wing on the hindwings. On the upperside of the males, the ground color is a light lilac blue with a metallic sheen.

ORIGINAL DESCRIPTION: Henry Edwards, *Pacific Coast Lepidoptera*, (26): 1 (1880).

TYPE LOCALITY: "Colorado and the mountains of California," but all syntypes are from Tehachapi, California. Syntypes in American Museum of Natural History.

DISTRIBUTION: This subspecies ranges from the Tejon Range in extreme southwestern Kern County and northern Ventura County northeastward through the Tehachapi Mountains to the Piute Mountains of the extreme southern Sierra Nevada. Records of this species from the Silverwood Lake area of the San Bernardino Mountains we consider to be mislabelled. In recent years, *L. h. clara* has not been found at its type locality in the Tehachapi Mountains (including former colony sites in Antelope Canyon, Double Mountain, and the Tehachapi Mountain County Park), where it may be extinct now. It may still occur on private property on the eastern and southern slopes of the Tehachapi Mountains.

ELEVATION RANGE: From 3,000 to 7,000', with the majority of populations from 4,000 to 6,000' elevation.

HABITAT AND PLANT COMMUNITIES: Orsak (1977) summarizes the general habitat and plant associations as follows. Populations are nearly always located in montane valleys, occasionally on mountain slopes. They usually occur in the Sagebrush Scrub community, sometimes with scattered trees such as Pinyon Pine (*Pinus monophylla* Torr. & Frem.) or Canyon Oak (*Quercus chrysolepis* Liebm.). They are rarely found in forest clearings, in contrast to the nominotypical subspecies of this butterfly. Populations are always located on well-drained soils in areas with adequate moisture; *clara* is almost never found on south-facing or other arid slopes. Many populations are located in or adjacent to dry, gravelly washes or gullies.

PHENOLOGY: Records range from late June to early July, with a peak flight period in early to mid-July.

FOODPLANTS: The following *Eriogonum* species have been documented as foodplants of this butterfly: *E. heermannii* Dur. & Hilg. (probably the most commonly used host), *E. umbellatum* Torr. ssp. *munzii* (Reveal) Thorne, and *E. fasciculatum* Benth. ssp. *polifolium* (Benth.) Stokes. The usage of *Eriogonum fasciculatum* Benth. is apparently confined to plants that are especially robust and succulent.

c. *L. h. immaculata* Emmel and Pratt

- DIAGNOSIS:** This is a high montane subspecies of the Sierra Nevada, White Mountains, and Warner Mountains in California. It is characterized by relatively small size and the virtual absence of dark markings on the underside of the hindwing in both sexes, giving an "immaculate" appearance. The ground color of the upperside of the males varies from a pale cyanic blue to a pale lilac blue with a metallic sheen. On the females, the ground color of the upperside ranges from a dull gray-brown to a pale yellowish-tan. Varying amounts of blue scales are scattered over the medial half of the forewing and hindwing in the females, but generally never to the degree seen in nomotypical *heteronea*. Along the submarginal area of the hindwing, there is usually absence of the tannish-orange markings seen in nomotypical *heteronea* or if present, this is represented by a series of obsolescent tan crescents bordering very small dark brown spots. The underside ground color is a very pale whitish-cream in both males and females, with the females having a slightly deeper tint. The markings on the hindwings, if present, are reduced to very small patches of grayish-tan scales.
- ORIGINAL DESCRIPTION:** Emmel and Pratt, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990).
- TYPE LOCALITY:** Chiatovich Flats, White Mountains, 10,400 to 11,200' elevation, Mono County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION:** This subspecies is found in the White Mountains, along the east slope of the Sierra Nevada, from approximately the area west of Lone Pine, northward to the Warner Mountains of Modoc County.
- ELEVATION RANGE:** From 6,000 to 11,200' elevation.
- HABITAT AND PLANT COMMUNITIES:** This butterfly is typically found in the Sagebrush Scrub plant community, where it is found on dry slopes and open ridgetops, particularly where *Artemisia tridentata* Nutt. is the dominant vegetation.
- PHENOLOGY:** Records range from early July to mid-August, depending on elevation, with an apparent peak flight period in late July and early August.
- FOODPLANTS:** The following *Eriogonum* species have been documented as hosts for this subspecies: *E. umbellatum* Torr. ssp. .

d. *L. h. submaculata* Emmel and Pratt

- DIAGNOSIS:** This subspecies of the west slope of the Sierra Nevada is characterized by a prominence of the dark markings on the underside of both the forewing and the hindwing in both sexes, but not to the extreme degree shown in the Rocky Mountain subspecies, *gravenotata* (Klots). It tends to be smaller in size than nominotypical *heteronea*. The upperside ground color of males ranges from a pale cyanic blue to a light lilac blue with a metallic sheen. On females, the upperside ground color ranges from a pale yellowish-tan to an orangish-tan with considerable dull gray-brown scaling in the basal area of both wings and along the outer margin of the forewing. The band of tannish orange lunules along the submarginal area of the hindwing tends to be poorly defined, and does not stand out significantly from the ground color of the adjacent areas of the wing. On the underside, the ventral ground color is a very light gray in males, and a very light tannish-gray in females. On the forewings, ventrally, there is increased prominence of the black markings in both the basal area of the wing, as well as in

the submarginal areas. On the hindwing, the spotting pattern is well-developed, with the post-median band of brownish-black spots being the most prominent.

ORIGINAL DESCRIPTION: Emmel and Pratt, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990).

TYPE LOCALITY: Warner Valley, at southern boundary of Lassen National Park, Plumas County, California. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This subspecies is widely distributed over the west slope of the Sierra Nevada, from Tulare County in the south northward to Plumas County. From here it extends northwestward to populations in the southern Mt. Shasta region and eastern Klamath Mountains region.

ELEVATION RANGE: 4,500 to 9,000' elevation.

HABITAT AND PLANT COMMUNITIES: This subspecies occurs in a somewhat more mesic habitat than its close relative, *L. h. immaculata*. It is usually found on open slopes or in ravines within the Montane Coniferous forest community.

PHENOLOGY: Records for this subspecies range from early July to late August, depending on elevation and exposure.

FOODPLANTS: The primary foodplant of this subspecies seems to be *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes. However, other *Eriogonum* species such as *E. umbellatum* Torr., are present in the habitats of this subspecies and may serve as additional hosts.

e. *L. h. umbrosa* Emmel and Pratt

DIAGNOSIS: This subspecies was named for the dark, obscured upperside appearance of the females, which gives it a "shadowed" effect. This subspecies of the east slope of the Cascade Range in Oregon is found in extreme northern Siskiyou County in its southernmost extension. This butterfly is characterized by a heavy spotting pattern on the underside in some specimens, approaching that of the Rocky Mountain subspecies *gravenotata*. On the upperside of males the ground color is a deep lilac blue with a metallic sheen, with fairly prominent black borders along the edges of the wings. In the females, the upperside tends to be a uniform dull dark gray-brown with some blending of the darker spots into the background pattern. The pattern of orangish-tan markings along the submarginal area of the hindwing of the female may be completely obscured or only faintly present, or occasionally fairly well-developed in some individuals. Blue scaling is absent from the females. On the underside, in both sexes there is a marked accentuation of the black spotting pattern with all groups of the black spots enlarged from that seen in the other California subspecies of *heteronea*.

ORIGINAL DESCRIPTION: Emmel and Pratt, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990).

TYPE LOCALITY: Five road miles west of Martin's Dairy Campground, Goosenest District, Klamath National Forest, Siskiyou County, California. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This butterfly is found in scattered populations along the east side of the Cascade Range from Siskiyou County, California northward to at least Wasco County, Oregon.

- ELEVATION RANGE: 5,000 to 6,000' for the populations in our area; apparently down to as low as 500' elevation in some of the Oregon populations.
- HABITAT AND PLANT COMMUNITIES: *Umbrosa* is found on open rocky hillsides predominantly within the Yellow Pine Forest plant community, but extending higher to the Ball Mountain and Goosenest Mountain summits where areas of this open volcanic habitat arise in Lodgepole Pine, Red Fir, and Subalpine Forest settings. The breeding habitat is characterized by grasses and sagebrush scrub, *Artemisia tridentata*, in which an abundance of the suspected larval host plant, *Eriogonum hirtellum*, is found, along with other *Eriogonum* species such as *E. umbellatum*. A steadfast close association strictly with *E. hirtellum* suggests it is the larval host. *Haplopappus bloomeri* is an abundant nectar source which grows with *Monardella odoratissima* more commonly in the forested areas adjacent to the open habitat. But the *umbrosa* copper remains close to *Eriogonum hirtellum*, with both males and females nectaring on this plant.
- PHENOLOGY: Adults fly from early July to mid-August.
- FOODPLANTS: Unknown.

157. *Lycaena rubidus* (Behr)

- ADULT BEHAVIOR: Males perch on low shrubs and streamside vegetation in wet meadows, and appear to defend territories while waiting for passing females. In Arizona observations (Funk, 1975), each ovipositing female would hover near a *Rumex hymenosepalus* Torr. (Polygonaceae), alight on one of the leaves, and walk down the leaf toward the base of the plant. When she reached a height of about 2-8 cm above the ground, she laid an egg, which fell to the ground (covered with sparse plant litter), sometimes bouncing on one or more of the leaves on its way. After laying each egg, the female then walked back toward the top of the plant. After resting a minute or more, she would either walk back down to lay another egg, or fly to another plant. Each egg was laid singly. Small black ants, *Formica altipetens* Wheeler, actually followed these ovipositing females and either seized eggs as soon as they were extruded by the females and before they fell to the ground, or picked up the eggs on the ground. It is unknown whether these observations indicate predation or a more complex symbiotic interaction; the eggs were carried away but not into the nest. This same ant species was found tending aphids in North Dakota.
- LIFE HISTORY: Undescribed. The mature larva (from material in Mono County and Alpine County) has an almost concolorless green ground coloration. Along the midline is a broad, faint purplish dorsal stripe bordered laterally on either side by a faint whitish line. The entire body is covered generally by tiny yellow punctae and short orangish hairs. Laterally, below the spiracles, there is a slightly darker green lateral line, but not on all larvae. The pupa is a light tan and is covered by irregularly shaped and randomly placed dark brown spots and short lines. The pupal skin is not covered by hairs in this species.
- CHROMOSOME NUMER: $n = 24$ in Colorado material (Emmel and Eliazar, 1990).
- SIMILAR SPECIES: While the underside is mostly white, as in *Lycaena heteronea*, the upperside of the male is unmistakable in its orange coloration and the female always has an orange border on the hindwing dorsally that is lacking in *heteronea*.

GEOGRAPHIC AND SEASONAL VARIATION: We find the treatment of geographic variation in this species by Johnson and Balogh (1977) highly unsatisfactory in describing the geographic variation and biology of this species. Thus, their treatment is not followed precisely here. Further investigation of the geographic variation in this butterfly with larger numbers of specimens, particularly females, is definitely needed.

GENERAL REMARKS: G. Pratt and G. Ballmer (personal communication) note that the larva of *L. rubidus* is extremely similar to that of *L. xanthoides*. In fact, there are more similarities between the larvae of these two species than there are between the larvae of *L. xanthoides* and *L. editha*, which has been considered a subspecies of *xanthoides* by J. Scott (1986).

This bright, showy orange Copper is widely distributed through the west from the Rocky Mountains to the Pacific Coast and north into southern Canada. In California, we have segregates of populations representing three named subspecies.

a. *L. r. rubidus* (Behr)

DIAGNOSIS: Males have a light orange ground color dorsally. On the hindwing, this is of a slightly more brownish shade than that on the forewing, giving the hindwing a darker appearance. The upperside of the female is relatively dark, with extensive grayish-brown scaling and patches of buff of varying sizes on the forewing, particularly in the discal area. On the hindwing, the submarginal orange markings are reduced to an irregular line of thin crescents. On the underside, the ground color of the male is a pale buff-gray, while on the female it is more of a dirty cream color. The underside of the forewing has a pattern of black spots similar to other Copper species. On the hindwing, it is essentially devoid of any markings ventrally.

ORIGINAL DESCRIPTION: Behr, *Proc. Ent. Soc. Philadelphia*, 6: 208.

TYPE LOCALITY: "Interior of Oregon", suggested as from Klamath Basin by K. Johnson and Balogh, *Bull. Allyn Museum*, 43: 20-21 (1977). Neotype in Carnegie Museum, designated by K. Johnson and Balogh (1977).

DISTRIBUTION: This subspecies is found in the extreme northeastern corner of the state in Modoc County and in adjacent south central Oregon.

ELEVATION RANGE: 4,500 to 5,500' elevation.

HABITAT AND PLANT COMMUNITIES: This butterfly is typically found in moist situations, such as along streams or in wet meadows in valley bottoms within the Sagebrush Scrub plant community.

PHENOLOGY: Univoltine, with adults flying from mid-July to mid-August.

FOODPLANTS: None documented for the nomotypical subspecies.

b. *L. r. sirius* (W. H. Edwards)

DIAGNOSIS: The central and northern Sierra Nevada populations and White Mountains populations of *L. rubidus* in California were lumped under the subspecies, *sirius*

(W. H. Edwards), by K. Johnson, 1977. In our opinion, these populations seem to show a much greater affinity to the subspecies *monachensis* Johnson and Balogh (1977). In these north and central Sierran and White Mountains populations, females are variable but tend to have a bright orange ground color with marked reduction of the melanic overscaling seen on females of typical *rubidus* from the northeastern corner of the state. On the underside, the pattern is much like that of nominotypical *rubidus*, but perhaps paler in ground color.

- ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Ent. Soc.*, 3: 270 (1871).
- TYPE LOCALITY: "Colorado", restricted to near Twin Lakes, Lake County, Colorado, by F. M. Brown, *Transactions American Ent. Soc.*, 95: 166-167 (1969). Lectotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Ent. Soc.*, 95: 168-169 (1969).
- DISTRIBUTION: In the central and northern Sierra Nevada from Mono County northward to Donner Pass, extending eastward to the Sweetwater Mountains of extreme northern Mono County, and from there south into the White Mountains of Mono and Inyo counties.
- ELEVATION RANGE: 5,300 to 10,000' elevation.
- HABITAT AND PLANT COMMUNITIES: Usually along streams or in wet meadows within the sub-Alpine forest plant community.
- PHENOLOGY: Records extend from mid-July to mid-September, with an apparent peak in mid-August.
- FOODPLANTS: At least one documented host of this set of populations is *Rumex transitorius* Rech. F.(Polygonaceae) (J. Emmel and O. Shields, unpublished data).

c. *L. r. monachensis* (K. Johnson and Balogh)

- DIAGNOSIS: In this subspecies of the southern Sierra Nevada, there is general reduction in the size of the black markings on both upperside and underside of both sexes. Females tend to be a bright yellowish orange with a greater amount of the upperside wing surface covered by these light orange scales.
- ORIGINAL DESCRIPTION: K. Johnson and Balogh, *Bulletin Allyn Museum*, 43: 38-40 (1977).
- TYPE LOCALITY: Monache Meadows, Tulare County, California. Holotype in American Museum of Natural History.
- DISTRIBUTION: This subspecies is found in the southern Sierra Nevada in the Monache Meadows area of Tulare County. A single record of *L. rubidus* from Mineral King in Tulare County probably also represents this subspecies, although we have not personally looked at the specimen.
- ELEVATION RANGE: From approximately 7,500 to 8,500' elevation.
- HABITAT AND PLANT COMMUNITIES: This butterfly flies near streamsides in an extensive system of meadows within the Montane Coniferous plant community.
- PHENOLOGY: Adults fly from early July to at least mid-August, with the majority of specimens having been taken in early August.

FOODPLANTS: Unknown.

158. *Lycaena xanthoides* (Boisduval)

ADULT BEHAVIOR: Males perch on vegetation from a few feet off the ground to as much as six or seven feet above the ground. Females tend to be more sedentary, spending much time landed on the foodplant or near potential foodplants. Courtship occurs from 9:00 a.m. to 4:30 p.m.; the male pursues a passing female, and hovers over her, beating his wings with wide amplitude about seven times a second. He then lands behind the female and bends his abdomen laterally to copulate. Of 26 females dissected near the end of the flight period (mid July at Point Richmond, Contra Costa County), 6 females had not mated, 18 had mated once, and two had mated twice (Scott and Opler, 1975).

Yellow composites (such as *Grindelia*) are heavily visited by the adults. Other nectar sources in California and elsewhere are listed by Scott and Opler (1975). In their capture-recapture study of *xanthoides* in a small field at Berkeley in Alameda County, the average lifespan found by those authors is nine days for males and fourteen days for females. Scott and Opler noted that the lifespan of *L. xanthoides* was much greater than the lifespan of *L. arota* in a similar study (Scott, 1974a). Both sexes bask by spreading their wings 20 to 60 degrees from vertical and facing away from the sun. Basking tended to occur at cool temperatures, primarily during the morning and late afternoon hours.

LIFE HISTORY: The eggs are laid singly on sticks, dead leaves, and debris at the base of the larval foodplant in June. The egg is echinoid in shape with rather small pits between irregular walls. The color when first laid is a pale green, immediately changing to white as the egg matures. The larval instars are described from southern California material in detail by Comstock and Dammers (1935c). When not feeding, they rest near the base of the plant among litter or dead leaves. The mature larvae are polymorphic, there being an apple-green morph, a yellowish-green form, and a dark orange form bearing bands and bars of magenta! The cervical shield is green, with slight mauve shading around its margins. A narrow bluish-white bar bisects the shield, and the whole body is sparsely covered with white punctate points. In northern California material from Mendocino County the predominant larval form is apple-green, with a deep red mid-dorsal band and a medium red flush extending as a band on either side of the mid-dorsal line the length of the larva. The total reddish area covers about one third of the dorsum of the larva. On the side of the Mendocino County larval form, there is a very faint yellowish-green lateral line, extending the length of the larva well below the spiracles. The spiracles themselves are red in color. The larva is covered with small yellowish punctate in this form.

Surprisingly, for a butterfly species, Comstock and Dammers found that when the larva prepares to pupate it forms "a loosely woven silk cocoon on the floor of the breeding cage, into which it incorporated particles of soil. This cocoon formation by a Lycaenid is a most unusual feature, and the first of its kind encountered in our breeding of diurnals." The pupa in the southern California populations is pink-buff in color, and is spotted and blotched everywhere with irregular black markings. The surface is covered with minute colorless hairs, except on the wingcases. In the northern California material that J. Emmel reared, pupating larva did not have opportunity from materials in its enclosure to make a cocoon, if indeed it planned to do. (In the San Bruno Mountains, however, J. Emmel found pupae at the base of the foodplants with no indication of a cocoon being made prior to pupation.) The Mendocino County pupae have a medium tan ground color and have medium dark brown blotching over the entire surface. In the San

Bruno Mountains, the larval form resembles the larval form from Mendocino County and the pupae are somewhat variable in the degree of dark blotching on an olive-tan ground color. The mid-dorsal line in the San Bruno Mountain pupae is composed solely of dark brown blotches and no purple pigment as in the Mendocino County pupae appears.

CHROMOSOME NUMBER:

SIMILAR SPECIES: The only species with which *xanthoides* might be confused is the phenotypically similar *L. editha*, a smaller species. In addition to the smaller size, *editha* specimens can be fairly readily distinguished from *xanthoides* by the following character differences. The spots in the post-median row of spots on the hindwing tend to be about twice the diameter of the post-median black spots on the forewing on the underside; in *xanthoides* the post-median spots on the ventral hindwing are about the same diameter or sometimes even smaller than the post-median black spots on the ventral forewing.

GEOGRAPHIC AND SEASONAL VARIATION: As the species is univoltine, there is no seasonal variation. As noted above, we consider the name *luctuosa* to be a synonym of nominate *xanthoides*. There is some variability in the populations that we consider to fall under the nominate subspecies. Specimens from the east San Francisco Bay area, such as Berkeley, tend to have slightly larger spots beneath and darker ground colors. Specimens from the northern Sacramento Valley often have rather large black spots beneath, and further investigation of these populations may show them to be a distinct geographic subspecies.

GENERAL REMARKS: Although Scott (1980, 1986) treated *L. editha* as a subspecies of *L. xanthoides* on the basis of supposed intermediate populations, we feel there is sufficient justification to separate these two entities as distinct species. G. Pratt and G. Ballmer (personal communication) have studied the larvae of all the California *Lycaena* species and have found that the larvae of *L. editha* and *L. xanthoides* differ consistently in several characters, and that the larvae of *L. xanthoides* and *L. rubidus* are extremely similar, almost indistinguishable from one another. Thus, although *L. xanthoides* and *L. rubidus* are readily distinguishable in the adult stage, *L. xanthoides* and *L. editha* are readily distinguishable in the larval stage. Secondly, there are biological differences between these two entities. *Xanthoides* is typically found in situations where its foodplant grows, in areas near some sort of permanent moisture as a spring or stream, etc. *L. editha*, on the other hand, prefers dry slopes or flats and feeds on several species of herbaceous annual or biennial *Rumex* species. Lastly, the adults differ consistently in the size ratio of spotting on the underside of the forewings to that on the underside of the hindwings. The so called "intermediate" populations of *Lycaena* at Dunsmore in California have larvae that are indistinguishable from larvae in other *L. editha* populations, and we consider them to be a subspecies of *L. editha* rather than an intermediate form between the species *editha* and *xanthoides*.

This large Copper has a dark gray dorsal surface which resembles some Hairstreaks, except for the lack of tails. It is found primarily in grasslands and grassy foothills throughout California, north into Oregon. There are three subspecies groups identified in our state.

a. *L. x. xanthoides* (Boisduval)

DIAGNOSIS: The typical subspecies was named by Boisduval from California. It is characterized by males of this species having a brownish-gray upperside with a

varying amount of orange scaling in the submarginal area of the hindwing, tending to be most accentuated near the anal angle. This orange scaling occurs as a scalloped border, with a series of small black spots within the arches of the scallops. The upperside of the females is a more brownish-gray, somewhat lighter in shade than that of the male, with patches of light orange scaling on the forewing, primarily in the median area of the wing and on the hindwing in the post-median area. On the forewing, there is a pattern of black dots of varying size, and on the hindwing there is an orange band in the submarginal area similar to that of the males, except that it is much more fully developed and often extends onto the forewing along the outer margin posteriorly. On the underside, the female ground color is similar to the male except of a more yellowish cast. On the underside, both sexes have a pattern of black spots on the forewing, which is more accentuated in the females with larger spots and more of them developed. On the hindwing there is also a pattern of black spots, with the most prominent ones being in the post-median area but in a number of individuals these spots have grayish-tan centers, which in some cases renders virtually the entire spot grayish-tan rather than black, although it still stands out from the background color. The orange banding in the submarginal area of the hindwing is largely confined to the area near the anal angle and is thinner than on the upperside. Included under nominotypical *xanthoides* is the subspecies *luctuosa* Watson and Comstock (1920), which we consider a synonym. In analyzing the characters of a long series of *L. xanthoides* from the Tehachapi Mountains (the type locality) and other southern California mountain ranges, we are unable to see any consistent differences between these populations and nominotypical *L. xanthoides* from northern California.

- ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 292 (1852).
- TYPE LOCALITY: "Mountains of California". Type locality restricted to Sacramento, California, by Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990). Holotype in U. S. National Museum.
- DISTRIBUTION: This species is widely distributed through the state at low to mid-elevations from San Diego County northward through the foothills and mountains of southern California through the Coast Ranges, Central Valley, and west slope of the Sierra Nevada to the north end of the Sacramento Valley. It is also found in the northern Owens Valley and in several adjacent canyons of the east slope of the Sierra Nevada and the western slope of the White Mountains in extreme southern Mono County and northern Inyo County.
- ELEVATION RANGE: From near sea level to 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES: *L. xanthoides* is usually found in dryish meadows near some sort of water source such as a spring or intermittent stream or permanent stream. It is also found in canyon bottoms and valleylands where there may not be any water on the surface nearby, but where drainage supports a reasonably moist soil for the *Rumex* foodplants of this species that prefer such situations.
- PHENOLOGY: Species is strictly univoltine, with adults recorded from mid-May to mid-July and an apparent peak of flight activity in mid-June.
- FOODPLANTS: For nominotypical *xanthoides*, the following *Rumex* species (Polygonaceae) have been recorded as foodplants: *R. hymenosepalus* Torr., *R. pulcher* L., *R. californicus* Rech. F., *R. crispus* L., and *R. conglomeratus* Murr.

b. *L. x. obsolescens* Emmel and Pratt

- DIAGNOSIS:** This isolated desert population of *L. xanthoides* is characterized by an extreme reduction in the size of the black markings on the underside, with many spots disappearing completely in some specimens. Additionally, the males tend to have a paler orange aurora on the submarginal area of the hindwing dorsally, and in the females this orange aurora tends to be expanded from that seen in typical *xanthoides*, as well as having smaller black spots within it than is seen in the typical insect. Females of this subspecies are almost uniformly grayish-brown on the forewing, with only very reduced areas of light orange scaling just distal to the end of the discal cell and near the posterior angle of the forewing.
- ORIGINAL DESCRIPTION:** Emmel and Pratt, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990).
- TYPE LOCALITY:** Hunter Mountain, at extreme southeastern end of Saline Valley, Inyo County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION:** So far as is known, this subspecies is confined to the Hunter Mountain area.
- ELEVATION RANGE:** 6,000 to 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** The butterfly occurs in small, dry meadows, usually near springs or with an intermittent stream source nearby, within an admixture of Pinyon-Juniper Woodland and Sagebrush Scrub plant communities. The periphery of these small meadows and springy areas supports a fairly abundant growth of *Angelica lineariloba* Gray, an important nectar source which comes into full bloom at the time this Copper is flying.
- PHENOLOGY:** Adults begin flying in late June and continue into early August, with the peak abundance during the first half of July.
- FOODPLANTS:** G. Ballmer and G. Pratt (personal communication) found larvae of this subspecies on *Rumex salisifolius* Weinm. (Polygonaceae).

159. *Lycaena editha* (Mead)

- ADULT BEHAVIOR:** Males perch in open spaces on the gravelly or rocky slopes, or small clearings in meadows, or along roadsides or trails, usually in full sun. The species is frequently sympatric with *Lycaena cupreus*, which uses both the same native and introduced *Rumex* species as does *L. editha*; however, they are usually allochronically separated, as *L. editha* overwinters as an egg and the main flight is in late July to early August, whereas *L. cupreus* overwinters as a half-grown larva and completes development more rapidly the following year, usually emerging in June.
- LIFE HISTORY:** The early stages have not previously been described. The eggs are laid on or near the *Rumex* plants; if laid on the plants, they are usually deposited on the stems near the base of the plant. If not laid on the stems, the eggs are usually deposited on vegetative debris or small rocks in the immediate vicinity of the stem of the foodplant. The eggs overwinter and the larvae hatch immediately after snowmelt the following spring.

The following descriptions of the mature larva and the pupa pertain to material reared from the Mt. Shasta and Dunsmuir areas in Siskiyou County. The larva is apple-green in ground color. Running the length of the mid-dorsal line is a reddish-purple band bordered laterally on either side by a diffuse white area, and then a yellow area that proceeds to blend into the green ground color. The overall effect of the dorsal coloration is to accentuate the red stripe. On the sides, there is a pale yellowish-green or whitish lateral band running below the spiracles the length of the body. The larva is covered with yellow punctae and short yellowish hairs arising independently from the skin. The pupa is a very light tan, with light mottling of darker brown speckles across the entire surface. There is a faintly darker pigmentation, suggesting a dorsal band of brown across the abdomen. Some inter-individual variability occurs in the extent of brown speckling across the tan ground color.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: See discussion under General Remarks in *Lycaena xanthoides* section.

GEOGRAPHIC AND SEASONAL VARIATION: As the species is univoltine, there is no seasonal variation. Specimens of this butterfly from the White Mountains tend to have slightly larger spots on the underside than populations at similar elevations in the Sierra Nevada. Specimens from the Manache Meadows area of Tulare County are somewhat lighter above in the females and have a stronger yellowish or orangish cast to the ground color of the underside. Further investigations of these sets of populations may reveal enough consistent differences that some sort of subspecific delineation is warranted.

GENERAL REMARKS: As noted above under the section on Foodplants, many populations of this butterfly in California feed on an introduced *Rumex* species and do not seem to have a native foodplant in these localities. Thus, it is possible that many of the populations that we are seeing at the low to mid-elevations in the Sierra Nevada and in the Mt. Shasta region are rather recent, perhaps colonized within the last 100 years. Of particular interest to note is the recent discovery by S. Mattoon of a colony of this butterfly in the North Coast Range. [STERLING, PLEASE FILL IN LOCALITY HERE.]. Since there are not previous records for this species in the Coast Range and this newly discovered population appears to be associated with an introduced *Rumex*, we may be witnessing the continued expansion of the range of this species as it follows the weedy *Rumex acetosella* L. into appropriate montane habitats.

SUBSPECIES: This small Copper occurs typically in dry sagebrush amid mixed open conifer situations in California eastward to northwestern Colorado and north into southeastern Washington, Idaho, and Montana. It is essentially a montane species throughout its range. There are two subspecies within our state.

a. *L. e. editha* (Mead)

DIAGNOSIS: This species is similar to *L. xanthoides*, but is noticeably smaller. The ground color of the upperside is usually a slightly lighter shade of brownish-gray than that seen in nomotypical *xanthoides*. Also, the pale orange scalloped aurora in the submarginal area of the hindwing is markedly reduced in the males and even absent in some specimens. On the females, the overall pattern of brownish-gray ground color, dark spots, and patches of yellowish-orange scaling is similar to that seen in *xanthoides*, except that the yellowish areas tend to be more extensive in *editha*. On the underside, *editha* has a rather bold pattern of dark spots on the

forewing and very large grayish-brown spots on the hindwing, edged with darker scales. The size of the hindwing spots ventrally is noticeably larger than the post-median curved band of black spots on the forewing, usually at least twice the diameter of these spots, whereas in *xanthoides* the spots on the two wings are approximately equal in size. Also, the ground color of *editha* is darker, more of a grayish-tan on the hindwings in the males with white overscaling; in the females, the white scaling is more extensive on the underside of the hindwing and the forewings tend to have a yellowish flush to the ground color.

- ORIGINAL DESCRIPTION: Mead, *Canadian Entomologist*, 10: 198 (1878).
- TYPE LOCALITY: Near Carnelian Bay, Lake Tahoe, California. Syntypes in Field Museum of Natural History, Chicago.
- DISTRIBUTION: Within California, typical *L. editha* is found in the mid- to higher elevations of the Sierra Nevada, in the higher elevations of the White Mountains, and in the Warner Mountains of Lassen and Modoc counties.
- ELEVATION RANGE: 4,000 to 12,000' elevation.
- HABITAT AND PLANT COMMUNITIES: Typically found in dry meadows, roadsides, or along trails, sometimes on rocky or gravelly slopes within the Montane Coniferous forest, Sub-Alpine forest, or Arctic Alpine Fellfield communities.
- PHENOLOGY: Strictly univoltine, but with a rather long flight period with specimens recorded from late June to mid-September, with one early October record.
- FOODPLANTS: For the higher elevation populations in the Sierra Nevada and White Mountains, the foodplant is *Rumex paucifolius* Nutt. ex Watts. (Polygonaceae). We believe records for *Potentilla* and *Horkelia* (Rosaceae) to be erroneous. At the mid-elevation populations, the butterfly is known to use an introduced *Rumex*, *R. acetosella* L.. In many of these mid-elevation populations, this *Rumex* appears to be the only foodplant with no native species being used. This could indicate that many of these populations are of recent introduction following the introduction of the European weedy *Rumex*.

b. *L. e. robusta* Emmel and Pratt

- DIAGNOSIS: This is a large, low-elevation subspecies of *L. editha* occurring in the Mt. Shasta region. In addition to its larger size, it is characterized by having reduced size of spots on the underside in comparison to typical higher elevation *editha*. The relationship of the ratio of the size of the hindwing spots being much larger than the post-median black spots of the forewing on the ventral surface is maintained in this set of populations. It also differs from typical *editha* in that the females tend to be darker, with reduction of the yellowish scaling on both forewings and hindwings and a similar reduction in the prominence of the orange aurora on the submarginal area of the hindwing. The larvae of this subspecies are virtually indistinguishable from the larvae of Sierran *L. editha*, and are readily distinguishable from the larvae of *L. xanthoides* (G. Pratt and G. Ballmer, unpublished studies).

- ORIGINAL DESCRIPTION: Emmel and Pratt, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990).

- TYPE LOCALITY: Railroad Park, Dunsmuir, Shasta County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is found in the Mt. Shasta region from northern Shasta County and possibly northwestern Plumas County northward through Siskiyou County to southern Oregon.
- ELEVATION RANGE: 3,500 to 5,000' elevation.
- HABITAT AND PLANT COMMUNITIES: [S. MATTOON, PLEASE FILL IN.]
- PHENOLOGY: This subspecies flies from mid-June to early August, depending on elevation and rainfall pattern for the year.
- FOODPLANTS: At the type locality, larvae of this subspecies have been collected on *Rumex acetosella* L. (G. Ballmer, personal communication).

160. *Lycaena hermes* (W. H. Edwards)

One of our most famous endemic butterflies, *Lycaena hermes* has an exceedingly restricted range. Its known distribution in the United States includes only part of San Diego County. It also occurs south of the border almost 100 miles, to a point 18 miles south of Santo Tomas in Baja California. Everywhere, the Hermes Copper colonies are closely associated with and confined to the vicinity of the host plant, which itself has a much broader range throughout the Coast Ranges in California. The use of a rhamnaceous host plant by *hermes* is unique in the genus *Lycaena*, a presumably ancient worldwide genus of relatively few, phenotypically similar species.

- DIAGNOSIS: This is one of the two tailed Copper species in our state, the other one being *L. arota*. *Hermes* is rather readily distinguished by the dark dull ground color of the upperside with the extensive bright yellow area in the medial part of the forewing, the yellow bordering in the anal area extending into the tail, and the very distinctive deep lemon-yellow underside ground color. There is sexual dimorphism, but it is not nearly so marked as in all of the other California *Lycaena* species.
- ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Ent. Soc.*, 3: 21 (1870).
- TYPE LOCALITY: "California", restricted to vicinity of San Diego, San Diego County, California by F. M. Brown, *Transactions American Ent. Soc.*, 95: 165 (1969). Neotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Ent. Soc.*, 95: 166 (1969).
- DISTRIBUTION: In California, this species is wholly confined to San Diego County, where it occurs from near the coast to a point about 40 miles inland from the coast and a northernmost point about 50 miles north of the Mexican border. From San Diego County it extends southward into Baja California approximately 100 miles.
- ELEVATION RANGE: From near sea level to approximately 3,500' elevation.
- HABITAT AND PLANT COMMUNITIES: Mostly in Coastal Sage Scrub or Chaparral plant communities, where *Rhamnus crocea* Nutt. in T. & G. is common.

- PHENOLOGY:** Records range from May 20 to July 20, with a peak flight for males around June 10 and a peak flight for females about June 20 (Thorne, 1963).
- ADULT BEHAVIOR:** Males perch on the foodplant, but according to Thorne, are not particularly aggressive. A possible type of cryptic mimicry protecting the adults was first noted by Thorne (1959). Because the Redberry foodplant (*Rhamnus crocea*) is evergreen, its leaves mature singly. During the flight season of *L. hermes*, a mature leaf will appear here and there on the plant as a bright yellow spot against the background of dark green foliage. At a short distance, such a leaf appears to the collector's eye very much like a perched *hermes* in size and color. But the yellow leaves are much more common than the butterfly, and after repeated disappointments they no longer attract the collector. Presumably, potential predators such as birds also are deflected from searching for the butterflies by this cryptic yellow resemblance. Both sexes are avid flower visitors and the nectar source of choice is *Eriogonum fasciculatum* Benth.
- LIFE HISTORY:** The life history was first described by Comstock and Dammers (1935b), with additional details in Thorne (1963). The eggs are laid on the stems of *Rhamnus crocea* Nutt. in T. & G. and overwinter until the following spring. The white echinoid egg is covered with deep pits created by high irregular ridges. The physical appearance of the egg is very similar to that of *Lycaena gorgon*. The micropyle area is deeply depressed. The mature larva is apple-green in ground color with a mid-dorsal band of darker green bordered with yellowish-green in a broken irregular band. Laterally on each segment, there are two faint and indistinct yellow diagonal marks, a third faint yellow mark arising from the region around the spiracle, and a fourth one (very indistinct) below that on each segment. The ventral surface is pale green and the spiracles are dark brown. The body is sparingly covered with silvery white dots which, under high magnification, are observed to be pillar-shaped stout projections with rounded ends. The body is also completely covered by minute short brown hairs which are not erect and can only be seen with a strong hand lens. Those on the front of the first segment and on the caudal end are much longer. The head is a dirty yellow color, with the mouth parts brown. The ocelli are white on a black field. The cervical shield is quite distinctive and is shaped like a double barb spear point. The basal color is brown, bisected by a bluish-white bar across the center. The pupa is grass-green in color and has a narrow mid-dorsal yellow stripe extending from the fifth to ninth segments. Subdorsally, a second yellow band runs longitudinally over the thorax and abdomen and bends abruptly at each segmental juncture edging this junction for some distance laterally. Each abdominal segment is also crossed laterally by three diagonal yellow bars. The spiracles are a soiled orange in color. The entire surface is lightly covered with olive-brown spots of various sizes. Mid-dorsally on the fourth segment, there is a black triangle. On the ninth to the caudal segments in the mid-dorsal line occurs a black quadrate spot on each segment, those placed near the tail shading off to brown. The entire pupa, except for the wing cases, is sparingly covered with minute silvery white processes which appear under magnification as trumpet-shaped projections. The butterfly is single-brooded and overwinters in the egg stage.
- FOODPLANTS:** Red Berry, *Rhamnus crocea* Nutt. in T. & G. (Rhamnaceae), is the only known foodplant.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** This *Lycaena* species is unique in North America.
- GEOGRAPHIC AND**

SEASONAL VARIATION: None.

GENERAL REMARKS: The existing populations are apparently quite stable from year to year, with no wide fluctuation in numbers noted by Thorne (1959, 1963) or later lepidopterists. While there does not seem to be need at this point in time to place the species on an endangered or threatened species list, the situation with potential loss of habitat in populous San Diego County certainly bears continued monitoring.

161. *Lycaena arota* (Boisduval)

ADULT BEHAVIOR: Males of all three subspecies perch in small clearings in many different situations from sagebrush to gulleys to ridgetops and valleys. They begin perching at about 0715 and actively perch until about 1100 hours (at least in Colorado). Scott (1974) has described the mating behavior. The male darts after a passing female and flies about 14 centimeters off the ground for several meters. Then the female lands on a branch, the male lands behind and then starts flicking his wings and vibrating them. The female remains quiescent, the male then crawls alongside and bends his abdomen either right or left to attempt copulation. Unreceptive females will flap their wings ten or more times a second while sitting. Males in Colorado may move as far as 214 meters in several days, but most individuals of both sexes do not move at all from day to day. In Colorado, males and females live an average of only four days. In northern California, they are believed to be longer-lived (Mattoon, personal communication).

Both sexes feed commonly on flowers and may even be found visiting mud.

LIFE HISTORY: The life history was first described by Comstock (1927b for egg; 1928a for other stages). The turban-shaped egg is off-white in color and has about fourteen heavy vertical ribs that stand up above the surface and have shallow cross-ribbing with no deep depressions like in *hermes* or *gorgon*. The mature larva is green in ground color, somewhat darker at the head end. The surface is covered with minute white granulations. Minute yellowish-white hairs arise from the skin surface but not from the tiny granules. A very faint double light colored line occurs dorsally and there is a fine single yellowish lateral line below the spiracles. The larva of both the typical race and *nubila* are shown in the accompanying figures. The variably colored pupa is brown or mottled yellow-brown. There are minute hairlike processes with flaring trumpet-shaped ends scattered over the surface. The pupa is supported by a silk girdle around the thorax.

CHROMOSOME NUMBER:

SIMILAR SPECIES: This is one of the only two tailed Coppers in our California fauna, the other being the very distinctive *Lycaena hermes*.

GEOGRAPHIC AND SEASONAL VARIATION: Despite the widespread populations of the nomotypical subspecies within our state, and the diverse habitats utilized, there seems to be little if any geographic variation from one area to another.

GENERAL REMARKS: It is curious that this species has not shown up in the mountain ranges of the eastern Mojave Desert, where one of its foodplants, *Ribes velutinum* Greene, is locally common in some of the canyons.

SUBSPECIES: This tailed Copper occurs in montane areas throughout the west, from southern California north to southern Oregon and eastward to the Rocky Mountains of Colorado and central New Mexico. Within our state occur three of the four known subspecies.

a. *L. a. arota* (Boisduval)

- DIAGNOSIS:** This is the most widespread subspecies in California. In the males the dorsal surface is a dull tan with a purplish sheen. There is a dark border on both forewing and hindwing, and a scalloped orange aurora near the anal angle and the tail. The upperside of the female is pale orange, with extensive dark brown markings and a more extensive orange aurora in the submarginal area of the hindwing. Ventrally, the forewing ground color is a whitish tan-gray with an orangish flush in the post-median area; the ground color of the hindwing ventrally is a dull tannish-gray. A pattern of variously shaped brownish-black markings in the proximal two-thirds of both wings and a pattern of whitish markings in the distal one-third of both wings defines the general wing pattern on both sexes. An irregular reddish to orangish line is found in the submarginal area near the tail and the anal angle of the hindwing.
- ORIGINAL DESCRIPTION:** Boisduval, *Ann. Soc. Ent. France*, (2)10: 293 (1852).
- TYPE LOCALITY:** "California", restricted to Juba Mountains by W. P. Comstock and Huntington, *Journal New York Entomological Society*, 67: 79 (1959). Re-restricted by Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990) to Lower Feather River Canyon, Butte County, California. Holotype in U. S. National Museum.
- DISTRIBUTION:** This subspecies is widely distributed through cismontane California from San Diego County northward through the San Jacinto Mountains, San Bernardino Mountains, and thence northwestward to the Tehachapi and Tejon Ranges in Kern County. From there it is found northward through the Coast Ranges and the west slope of the Sierra Nevada to the Klamath Mountains Assemblage and the Mt. Shasta region.
- ELEVATION RANGE:** From 250' elevation to 7,600' elevation.
- HABITAT AND PLANT COMMUNITIES:** Found in several different plant communities, depending on elevation, including Montane Coniferous Forest, Chaparral, Foothill Woodland, and Northern Oak Woodland. The butterfly is found on dry slopes and in canyon bottoms, particularly near watercourses.
- PHENOLOGY:** This species is strictly univoltine, with records ranging from late May to mid-September, depending on elevation and other local habitat conditions.
- FOODPLANTS:** Various species of *Ribes* are recorded as foodplants including the following species in California: *R. roezlii* Regel., *R. quercetorum* Greene, *R. californicum* H. & A., *R. aureum* Pursh, and *R. divaricatum* Dougl.

b. *L. a. virginiensis*

- DIAGNOSIS:** This is a weakly differentiated subspecies of the Great Basin which enters our area on the east slope of the Sierra Nevada. In this subspecies the ground color of the underside on the hindwing tends to be more brown and the forewing ventrally on the male has an orange flush. Also, there is a tendency for the white markings in the post-median area of the hindwing and forewing to be slightly larger than in nominotypical *arota*. Additionally, females in these populations tend to be slightly more lightly marked than in typical *arota*.

- ORIGINAL DESCRIPTION: E. H. Edwards, *Transactions American Ent. Soc.*, 3: 21 (1870).
- TYPE LOCALITY: Virginia City, Nevada. Neotype in American Museum of Natural History, designated by F. M. Brown, *Transactions American Ent. Soc.*, 95: 164 (1969).
- DISTRIBUTION: In our area, this subspecies is found along the east side of the Sierra Nevada from Inyo County to Mono County; it is also found in the Sweetwater Mountains of Mono County and in the White Mountains and Inyo Mountains of Mono and Inyo counties. It is also found in the Coso Range and on Hunter Mountain in the western Death Valley region.
- ELEVATION RANGE: From 6,000 to 9,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This butterfly typically is found along watercourses in the Pinyon-Juniper Woodland plant community of the western Great Basin. It also occurs within areas of Sagebrush Scrub.
- PHENOLOGY: Records range from mid-June to early September, with apparent peak of abundance in early to mid-July.
- FOODPLANTS: For subspecies *virginiensis*, the following *Ribe* species have been documented as foodplants: *R. velutinum* Greene and *R. aureum* Pursh.

c. *L. a. nubila* J. A. Comstock

- DIAGNOSIS: This coastal southern California subspecies is characterized by the generally darker ground color of the dorsal surface and extensive dark markings on the female, and a wider dark marginal band on both sexes. On the underside, it is also a darker brownish-gray than typical *arota*.
- ORIGINAL DESCRIPTION: J. A. Comstock, *Bulletin Southern California Academy Sciences*, 25: 34 (1926).
- TYPE LOCALITY: Griffith Park, Los Angeles, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is found in the Santa Monica Mountains of Ventura and Los Angeles counties, the western foothills of the San Gabriel Mountains, and in the Santa Ana Mountains. There is an apparent blendzone with typical *arota* on the south slope of the San Gabriel Mountains.
- ELEVATION RANGE: From 1,000 to 2,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This butterfly is found in moist coastal canyons, with heavy growth of either Chaparral, or Southern Oak Woodland, or Riparian Woodland. The butterfly is typically found along canyon bottoms where males perch on medium-sized shrubs, usually near small streams or trails.
- PHENOLOGY: We have records from late May to mid-August, with the majority of specimens taken during the latter part of June and the first week in July.
- FOODPLANTS: The recorded foodplant of this subspecies is *Ribes aureum* Pursh ssp. *gracillimum* (Cov. & Britt.) Jeps.

Subfamily Polyommatainae Swainson

162. *Leptotes marina* (Reakirt)

This medium-sized Blue is found throughout the lowlands of southern California, and sporadically in the central and northern portions of the state. In our parks and suburban areas, it often flies abundantly, due to the extensive planting of *Plumbago* perennials as ornamentals.

DIAGNOSIS: A medium-sized lycaenid, with males having bright blue uppersides and female dorsal surfaces suffused with brown. The underside pattern has a series of apparent rows of brown spots alternating with white bands proceeding outward from the body to the marginal black dots.

ORIGINAL DESCRIPTION: Reakirt, *Proceedings Academy Natural Sciences of Philadelphia*, 20: 87 (1868).

TYPE LOCALITY: "Orizaba nr. Vera Cruz, Mexico". The probable syntypes are in the Field Museum of Natural History, Chicago.

DISTRIBUTION: In southern California this species is found throughout the deserts to the coastal areas, as well as in the Channel Islands on Santa Catalina and Santa Cruz. It becomes more uncommon at middle elevations in the mountains, and as one goes northward in the state. In years of extreme abundance, it may become temporarily established in such areas as the Sacramento Valley or the lower elevations of Mono County on the east side of the Sierra Nevada, but these populations do not persist. It is unclear which, if any, of the southern California populations are permanently established. It seems likely that populations established on *Plumbago* in the urban and suburban areas of coastal southern California are ongoing populations, in view of the fact that in these areas freezes are rare and the butterfly is likely able to survive the winters. To the east in the desert areas, the butterfly may be only transiently established from the spring months to the fall months, as mid-winter records from these areas are lacking and occasional freezes in most of the habitats in these areas may be lethal to potentially overwintering individuals of this sub-tropical species.

ELEVATION RANGE: The majority of records seem to fall into an elevation range from sea level to approximately 6,000' elevation, but there are records of this species as high as 10,000', such as in the White Mountains of Mono County.

134. *Callophrys comstocki* Henne

This demure little *Callophrys* species was described in 1940 from material taken in the Providence Mountains of the eastern Mojave Desert. For many years *Callophrys comstocki* was known only from the Providence Mountains, but has recently been found to have a considerably more extensive distribution. It even ranges into Nevada (Callaghan, 1970). Additionally, in contrast to the other two *Callophrys* species we have considered so far, Comstock's Hairstreak is multiple-brooded.

DIAGNOSIS: This desert species is characterized by its smaller size, its uniform light gray uppersides and the uniformly grayish-green undersides, with a well-developed medial macular band of linear white markings.

ORIGINAL DESCRIPTION: C. Henne, *Bulletin Southern California Academy Sciences*, 39: 71 (1940).

- TYPE LOCALITY: Providence Mountains, San Bernardino County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This species is widely distributed in our desert mountains, from the Benton Range in southeastern Mono County southward through the White Mountains and Sherwin Summit area through the Inyo Mountains, the Grapevine Mountains, the Coso Range, the Argus Range, the Panamint Range, the Nopa Range, to the mountains of the Eastern Mojave Desert, namely the Kingston Range, the New York Mountains, the Ivanpah Mountains, the Providence Mountains, Hackberry Mountains, and the Granite Mountains north of Amboy. Additionally, the butterfly occurs in the Ord Mountains southeast of Barstow, a somewhat disjunct set of populations in the western Mojave Desert.
- ELEVATION RANGE: 3,000 to 9,000' elevation, with most populations in the 4,000 to 6,000' range.
- HABITAT AND PLANT COMMUNITIES: Typically found in desert canyons within the Pinyon-Juniper Woodland plant community, or in the Shadscale Scrub plant community. Most populations are found in limestone mountains, where growth of the principal foodplant, *Eriogonum heermannii* Dur. & Hilg., is abundant.
- PHENOLOGY: Unlike other California *Callophrys* species, *C. comstocki* is multivoltine, with the size of the second and third broods dependent in part on both winter and summer rainfall patterns. In years of very wet winters, the spring generation, which begins flying in mid- to late March, flies through April or even into early May, depending on elevation. Subsequently, a second generation appears in June and July, and a third generation in mid- to late August into September. Even in years of low winter rainfall, these summer broods apparently occur, but are decidedly diminished in number over the spring brood. Summer rainfall may also influence the size of the late summer brood.
- ADULT BEHAVIOR: Males perch in the desert canyon bottoms, usually in small cleared areas within a wash, landing either on the soil, on rocks, or on low shrubs along the sides of the wash. Females tend to stay in the areas where the foodplant grows, higher up on the canyon slopes. Both sexes are fond of flowers, visiting such blooming species as *Rhus trilobata* Nutt. ex T. & G. and *Prunus fasciculata* (Torr.) Gray.
- LIFE HISTORY: The egg is undescribed. The remaining early stages have not been published previously. The mature larva has slight development of the sub-dorsal ridges, more or less intermediate between the condition observed in *C. perplexa* (absence) and *C. dumetorum* (strongly present). The general ground color is a dull, dark grayish-green. There are two dorso-lateral rows of short, inwardly curved whitish semi-circles, one to a segment and each with a small yellow-colored center. These form the inner side of a rough triangle extending downward and composed of a thin white band (the center of each triangle is green ground color). These hollow triangles form a series of scallops on either side of the center of the larva down its length. They are roughly comparable to the outline of the triangles present on *Callophrys dumetorum* larvae, but of course lack the intense red centers and broader development in that species. Laterally on the mature *comstocki* larva, there is a thick band of pale yellow segments located below the spiracles on each segment. The larva is covered with short stout pale yellow hairs. The pupa of this species is a uniform light brown in ground color.
- FOODPLANTS: The principal host is apparently *Eriogonum heermannii* Dur. & Hilg., as this plant is almost invariably present in the majority of *C. comstocki* populations. In several instances larvae have been found feeding on this particular *Eriogonum*

(Pratt and Emmel, unpublished data). Additionally, the following *Eriogonum* species have been documented as foodplants of *C. comstocki*: *E. umbellatum* Torr. ssp. _____ (G. Pratt and J. Emmel, unpublished data), and *E. fasciculatum* Benth. ssp. *polifolium* (Benth.) S. Stokes (G. Ballmer, personal communication); *E. microthecum* Nutt. ssp. _____ (J. Emmel and G. Pratt, unpublished data); *E. kennedyi* Porter in Wats. ssp. _____ (G. Pratt, personal communication).

SIMILAR SPECIES: A closely related *Callophrys* which may be mistaken for *C. comstocki* is *C. p. superperplexa* along the east slope of the Sierra Nevada. In this subspecies the macular band tends to be less strongly bowed outward in the center of the hindwing, and is often less developed than that seen in *C. comstocki*. In all *C. comstocki* populations, no other *Callophrys* species is present, so the possibility of confusing it with another species within its range is minimal.

GEOGRAPHIC AND SEASONAL VARIATION: The phenotype of *C. comstocki* is remarkably uniform in virtually all populations within California. However, there is a marked seasonal variation. In the spring brood, adults have a uniformly gray-green underside ground color; however, in the summer broods, the ventral surface is covered with varying degrees of light yellow overscaling, giving some individuals a very yellowish appearance beneath.

GENERAL REMARKS: This species is apparently closely related to *C. sheridanii*, which occurs from southern New Mexico and eastern Arizona north into central Colorado and the Bighorn Mountains of Wyoming. That species is single-brooded and flies in the early spring from late March to April in central Colorado. That small species has a ventral post-median band on the hindwing which is solid and unbroken.

135. *Callophrys lemberti* Tilden

DIAGNOSIS: This high to mid-elevation species is characterized by the upperside of the males being uniformly gray, the upperside of the females usually being uniform gray but sometimes invaded by varying degrees of fulvous coloration; on the ventral surface, the ground color varies from a soft gray-green to a dark yellowish-green. The median macular band of linear white markings is reduced from that seen in *C. comstocki* to a very thin broken line, often becoming obsolete. In some populations, there are individuals which totally lack any of these white markings.

ORIGINAL DESCRIPTION: Tilden, *Journal Research on the Lepidoptera*, 1: 292-298 (1963).

TYPE LOCALITY: West above Tioga Pass, Yosemite National Park, California. Holotype in California Academy of Natural Sciences.

DISTRIBUTION: This species is found at the mid- and higher elevations of the Sierra Nevada from Tulare County northward to the Mt. Shasta region and the Klamath Mountains Assemblage. It is also found in the higher elevations of the Warner Mountains, and in the White Mountains of Inyo and Mono counties, above 9,000' elevation in that particular range. It ranges northward into the higher elevations of the southern Cascades; the precise northern limits of its range are undetermined. Eastward from California it is found in the highest elevations of the Wassuk Range in western Nevada, and higher elevations in mountains along Nevada's northwestern border.

HABITAT AND PLANT COMMUNITIES: This butterfly is usually found in small ravines or on gravelly slopes, usually in somewhat open or cleared areas within the Montane Coniferous Forest, Sub-Alpine Forest, or the Arctic Alpine Fellfields

plant communities. It also occupies such locations at lower elevations along the eastern base of the Sierra Nevada and through the Modoc Plateau in the Artemisia-Juniper Woodland or Artemisia-Scrub plant associations.

PHENOLOGY: This species is strictly univoltine, with adults flying from late April to early August, depending on elevation, with most populations flying during the month of May or early June.

ADULT BEHAVIOR: Males tend to perch on open patches of ground, in small gullies, or on gentle gravelly slopes. Adults will sip moisture from wet sand or mud. Both sexes visit the flowers of several montane *Eriogonum* species, as well as small *Composites*, and are especially fond of pussypaws (*Eriogonum* sp.)

LIFE HISTORY: The egg is undescribed and the later stages of the life history have been unreported previously. The mature larva has been observed from three geographic areas and shows some degree of variation. In the Sierra Nevada, the mature larva is a velvety apple-green in ground color, with a strong and continuous light yellow lateral band below the spiracles and a very faint, slightly lighter green pair of dorso-lateral bands above, with one on either side of the dorsal area. This is the predominant morph in the Sierras, but a second morph also occurs which is reddish-purple in ground color. This morph has a single mid-dorsal light gray band, with no strong lines on either the lateral surface or the dorso-lateral area. However, there are faint grayish blotches in the dorso-lateral area on each side.

In the Klamath Mountains Assemblage, the ground color of the mature larva is a dull gray-green. There is a white lateral band below the spiracles. Dorsally, there are two dashed yellow dorso-lateral bands, often with a diffuse yellow connecting area between them on each segment. In this population also, the reddish-purple morph exists and both morphs have been reared from eggs of the same female.

Finally, in the White Mountains east of the Sierra Nevada, the mature larva exhibits a very pale green, somewhat broken pale yellow band in the dorso-lateral area on each side. The inner parts of this band form the bases of faint posteriorly-facing hollow triangles of there pale lines, each triangle having a green center. As in the other two geographic sets of larvae observed, the spiracles are a dull reddish color but tend to stand out more on this light green background in the White Mountains larvae.

The pupae are light brown to olive-brown in ground color, covered with short translucent hairs, except on the wing cases, and spotted with small brown markings. The pupae are larger than those of *Callophrys comstocki*.

FOODPLANTS: This species uses several montane *Eriogonum* species as foodplants including *E. incanum* (T. & G.) Jones, *E. umbellatum* Torr., *E. marifolium* T. & G., *E. nudum* (Dougl. ex Benth.) S. Stokes, and *E. hirtellum*. *Astragalus andersonii* appears to be a usable host (Mattoon, unpublished). Eggs were found in abundance on both *Eriogonum incanum* (T. & G.) Jones and the *Astragalus* near Fredricksburg, Alpine County. *Callophrys lemberti* were reared from both hosts, and the last instars also successfully fed in the laboratory on *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes from the Chico, California area..

CHROMSOME NUMBER: Unknown.

SIMILAR SPECIES: Although this *Callophrys* species is not sympatric with any others within its range, there are several localities where populations are situated fairly close

geographically. Individuals in some populations can look remarkably like *C. perplexa perplexa*, particularly in the Sierran and Klamath Mountains Assemblage populations. Usually, however, there is more development of a linear macular band ventrally in *lemberti* than in *C. perplexa*, and the ventral ground color in *lemberti* tends to be a duller gray-green in contrast to the more yellowish-green of *C. perplexa*. Females in some *C. lemberti* populations may have fulvous scaling dorsally, again resembling some females of *C. perplexa*. In these instances, usually, elevational differences and host plant association differences can be used to separate the two species.

GEOGRAPHIC AND
SEASONAL VARIATION:

As the species is strictly univoltine, there is no seasonal variation. There is considerable variation, as noted above, in the ventral macular band in California populations of *C. lemberti*. In the Warner Mountains of Modoc County (and in adjacent Nevada mountains to the east), and in the White Mountains, the macular band is often very thin or obsolescent in contrast to the Sierran populations in which a fairly well-defined but very thin white macular band is usually present.

GENERAL REMARKS:

The disjunct high elevation *C. lemberti* populations in the White Mountains and the Wassuk Range in Nevada are of interest because one finds typical *C. comstocki*, associated with *Eriogonum heermannii* Dur. & Hilg., in the lower canyons of these Great Basin mountain ranges. The high elevation *lemberti* populations utilize *Eriogonum umbellatum* Torr. ssp. _____, at least in the White Mountains populations studied. This may hold true also for populations on the high pass on Nevada Highway 81 in Washoe County. There is no apparent intermediate population between these two entities in either mountain range. This situation would tend to lend support to the idea that two separate but closely related species are involved here.

136. *Mitoura siva* (W. H. Edwards)

ADULT BEHAVIOR:

Nectar sources in the form of blooming wildflowers are apparently essential for emerging adults, even though the larval host is evergreen. Thus, the emergence of the spring, summer, and fall broods when found may be highly dependent on winter rainfall to provide the proper conditions for the nectar source foodplants. Adults fly around the side branches and tops of the Juniper trees and frequently alight, perching to await the passage of a female. In the spring in a Juniper forest, these Hairstreaks are often quite abundant, but unless one taps the branches to scare up perched adults or finds a stand of blooming yellow composites where the butterflies are feeding, this species will rarely be seen.

LIFE HISTORY:

The early stages were first described by Coolidge (1924), where they were incorrectly identified as "*M. loci*", from material collected in Mint Canyon, the type locality of *juniperaria*. The early stages of the four subspecies are very similar, and a single description will suffice. The echinoid egg is green and is covered with deep triangular reticulations. The mature larva resembles the small terminal twigs of the foodplant with incredible perfection. The ground color is green with darker green patches of raised bumps on either side of a narrow yellow mid-dorsal line, and another green raised patch on the dorso-lateral edge of the body above a yellow lateral band extending the length of the larva just below the spiracles. The ground color between these dark green patches is a light green, with yellowish areas mixed in. When viewed from above, these lighter areas form a series of irregular almost lemon-yellow crescents on either side of the mid-dorsal area. Minute brown hairs cover the body. The pupa is dark chestnut brown and is covered with short hairs except on the wing cases and the facial portions.

- CHROMOSOME NUMBER: Unknown.
- SIMILAR SPECIES: Occasional individuals in *juniperaria* populations resemble individuals of *Mitoura loki*. See Diagnoses of the two species for the differentiating characters.
- GEOGRAPHIC AND SEASONAL VARIATION: The summer brood specimens tend to have a yellowish cast to the underside of the hindwing, much as in *Callophrys comstocki*.
- GENERAL REMARKS: A postulated zone of hybridization between *M. s. juniperaria* and *M. loki* on the northeastern slope of the San Bernardino Mountains has not been found. In this area an interesting situation with potential foodplants occurs. An "island" of *Juniperus osteosperma* (Torr.) Little occurs as an altitudinal band in the northeastern San Bernardino Mountains between *J. occidentalis* Hook *australis* (which has an associated *Mitoura* species, probably *M. barryi* ssp.) and above a belt of *J. californica* Carr. (which has *Mitoura loki* associated with it). Repeated visits to this stand of *J. osteosperma* (Torr.) Little from March to July (John Lane, *in litt.*) failed to turn up any *Mitoura* associated with this *J. osteosperma* (Torr.) Little. Unfortunately, the band of *Juniperus californica* Carr. on the north slope of the San Bernardino Mountains and again at the east end of this range is not contiguous in the area of the northeastern base of these mountains and hence, there is not a continuous habitat in which the two entities come together and possibly form a blendzone or zone of hybridization.

These six species of *Mitoura* (136 through 141) have been variously treated, most extremely by Scott (1986) who lumps them all into one species across the United States with other eastern species of *Mitoura*. The occurrence of sibling species in this genus (Remington and Pease, 1955), such as the extremely closely related species *Mitoura gryneus* (Hubner) and *M. hesseli* Rawson & Ziegler which utilize different hosts in the eastern coastal area of the U.S., lends a cautionary note to such broadscale synonomization, however. In the laboratory, these foodplant preferences can break down and *M. hesseli* will feed on *Juniperus virginiana* (like *M. gryneus*) instead of its normal host, *Chamaecyparis thyroides* (L.) B.S.P., as shown by Johnson (1983).

We feel that the taxonomic treatment given herein is conservative in retaining some entities which probably could be grouped as subspecies under others, but until further intensive life history and biosystematic work as well as hybridization studies are carried out in both the field and laboratory, this treatment will fairly reflect the best knowledge we have at the present time of this interesting group of Hairstreaks.

This group of small Hairstreaks is closely associated with *juniperus* across the western United States. In California, we have populations representing four subspecies.

a. *M. s. siva* (W. H. Edwards)

- DIAGNOSIS: The typical subspecies occurs from Colorado to Arizona and penetrates our state in the Eastern Mojave Desert. The dorsal surface of the male is a deep brown, with diffuse orangish markings on the lower half of the forewing and the anal angle area of the hindwing. In the female, these orangish-brown areas are much more extensive across the wings, bordered by a darker brown. On the underside of the wings the typical subspecies is characterized by having a uniform green ground color all the way to the body, and a relatively straight post-median white line starting at the forward edge of the hindwing. Along the wing margin there is a fine black line, bordered inwardly by an expanded bluish field extending more

than half way along the margin, which is actually a mixture of black and white scales. In this field is a orange ocellus-type marking with a black center. Other black spots in this area are usually obsolescent. The basal area of the ventral hindwing is always a uniform green, with no evidence of a proximal brown area as in subspecies *juniperaria*.

- ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Ent. Soc.*, 5: 110-111 (1874).
- TYPE LOCALITY: "Wingate, Arizona", probably near Fort Wingate, Arizona. Neotype in Carnegie Museum, designated by F. M. Brown and Clench, in F. M. Brown, *Transactions American Ent. Soc.*, 96: 61 (1970).
- DISTRIBUTION: The typical subspecies of *Mitoura siva* occurs commonly from the Rocky Mountains through Arizona and penetrates our area in the mountains of the Eastern Mojave Desert and the Death Valley region. Specific mountain ranges in California in which the nomotypical species has been taken include the Providence Mountains, the New York Mountains, Clark Mountain, the Kingston Range, and the Panamint Range. No *Mitoura* have yet been taken in the Granite Mountains north of Amboy or in the Old Woman Mountains of the Eastern Mojave Desert. If *Mitoura* do exist in either of these ranges, it will be of great interest to see what species is involved, as the *Juniper* species present in the Old Woman Mountains is *J. californica* Carr and in the Granite Mountains both *J. californica* Carr and *J. osteosperma* (Torr.) Little are present. Since nomotypical *siva* in our state has only been recorded on *J. osteosperma* (Torr.) Little, and *M. loki* has only been found on *J. californica* Carr, the phenotype of any *Mitoura* from these latter two mountain ranges should prove most interesting.
- ELEVATION RANGE: From 4,000 to 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is typically found in the Pinyon-Juniper Woodland plant community; within this plant community there tends to be some segregation of Junipers toward the lower elevations of the plant community and *Pinus monophylla* Torr. & Frem. to be more prevalent in the upper elevations of the plant community. The butterflies are found on open slopes and in canyon bottoms, usually closely associated with the host Juniper.
- PHENOLOGY: Apparently multivoltine, with the second and third broods being very small and almost undetectable in some years. Adults of the spring brood fly primarily during the month of April or into mid-May at the higher elevations, sometimes into late May or early June in the higher elevations of the Panamint Range. The second and third broods, if present, fly in June and then again in mid-August to mid-September.
- FOODPLANTS: The sole host of populations in our area is the Utah Juniper, *Juniperus osteosperma* (Torr.) Little (*Cupressaceae*).

b. *M. s. juniperaria* J. A. Comstock

- DIAGNOSIS: This subspecies is found in the Juniper forests along the western and southern borders of the Mojave Desert and into the mountains to the west. It is characterized by the coloration pattern on the ventral surface of the hindwings. The line occurs along the edge of the wing as in *siva*. Interior to this is a much more pronounced bluish field than in *siva*, which covers the outer part of the lower half of the hindwing. Within this field is a minute black ocellus, which is about one fourth of the area of the equivalent ocellus in *siva*. There is no pronounced

orange lunule around this spot as is found in typical *siva*. Interior to this blue field is an area of green and along the margins of the blue and green fields are a series of black ovate spots. These are typically four in number. The medial band is more irregular than in *siva*. The basal area of green has a brownish proximal area by the body.

- ORIGINAL DESCRIPTION: J. A. Comstock, *Bulletin Southern California Academy Sciences*, 24: 37 (1925).
- TYPE LOCALITY: Mint Canyon, Sierra Madre Mountains, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is found along the southern and western borders of the Mojave Desert from the north slope of the San Bernardino Mountains (just east of Cajon Pass) west to the Mt. Pinos region of Ventura and Kern counties, then north to the Walker Pass area and west from there to the Bodfish region in Kern County.
- ELEVATION RANGE: 2,000 to 5,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This butterfly is found in areas where the dominant large plant is individuals of *Juniperus californica* Carr in the upper areas of the Joshua Tree Woodland community; in most of these areas Pinyon (*Pinus monophylla* Torr. & Frem.) is absent. So this is not Pinyon-Juniper Woodland in the "classical" sense.
- PHENOLOGY: This subspecies is multivoltine, with the largest brood being the first or spring brood appearing in late March to May; this first brood is often closely associated with the maximum blooming period of the composite *Haplopappus linearifolius* DC. The second brood flies in June and is generally somewhat smaller than the spring brood; a third brood, if present, flies in September.
- FOODPLANTS: California Juniper (*Juniperus californica* Carr) (*Cupressaceae*). Additionally, this subspecies may use *J. osteosperma* (Torr.) Little in a very limited area in the vicinity of Phelan on the north slope of the San Gabriel Mountains. In this area, *Juniperus californica* Carr is the dominant small tree but individuals of *J. osteosperma* (Torr.) Little are present here, and the adults seem to perch on this Juniper as frequently as they do on the *J. californica* Carr found in the same area.

c. *M. s. mansfieldi* Tilden

- DIAGNOSIS: This is a central Californian subspecies that occurs to the northwest of the range of *juniperaria*. The principal difference in this subspecies is the quality of the green color of the underside. In *mansfieldi* this green tends to be a very deep, dark green or gray-green in most individuals in contrast to the somewhat more yellowish-green of *juniperaria*. Also, the white margination of the median-macular band is markedly wider than that seen in *juniperaria* or *siva*, standing out in bold contrast to the ground color. There is usually no evidence of basaler markings on the ventral hindwing as there is in some specimens of *juniperaria*, and the small black ovoid spots in the post-median area of the hindwing tend to be similar to the pattern seen in *juniperaria*.
- ORIGINAL DESCRIPTION: Tilden, *Bulletin Southern California Academy Sciences*, 50: 96 (1951).
- TYPE LOCALITY: Seven miles west of Simmler, San Luis Obispo County, California. Holotype in California Academy of Sciences.

- DISTRIBUTION:** This subspecies is found in the La Panza Range in San Luis Obispo County (the type locality), in the Temblor Range of San Luis Obispo and Kern counties, and in the Figueroa Mountain area in the San Rafael Mountains of Santa Barbara. Specimens from the Upper Cuyama Valley northwest of Ojai in Ventura County seem transitional between *M. s. mansfieldi* and *M. s. juniperaria*.
- ELEVATION RANGE:** From 1,500 to 3,800' elevation.
- HABITAT AND PLANT COMMUNITIES:** Typically found in Juniper Woodland on dry slopes, flats and canyon bottoms. In these areas an annual composite species popularly known as Gold Fields (*Baeria* species) is often present and serves as a springtime nectar source for adults of the first brood.
- PHENOLOGY:** This subspecies is at least bivoltine, with the first brood flying from late March to early May, with a peak in early to mid-April. The second brood is often overlooked and may be dependent in part on winter rainfall patterns.
- FOODPLANTS:** *Juniperus californica* Carr. (Cupresaceae).

d. *M. s. chalcosiva* Clench

- DIAGNOSIS:** This butterfly, named from Utah, penetrates our area in the Mono Lake area south to the White Mountains and perhaps the Inyo Mountains. It is characterized by a distinctive underside, where all the green areas of nominate *siva* are replaced by a coppery brown. In strong light and at an angle, this brown is iridescent, sometimes violet and sometimes greenish. In many respects this color is like that of the far western species *Mitoura nelsoni*. Occasional specimens show a slight amount of green basally on both wings. The post-median line on the ventral hindwing has a very thick and strong white quality. It follows the same course as typical *siva*, and is less irregular than *juniperaria*. The tails are as long as in nominate *siva* and longer than those of *siva juniperaria* and *M. nelsoni*. The common evolution of brown underside color was undoubtedly independently acquired in *nelsoni* and *chalcosiva* by parallel evolution, rather than shared genes.
- ORIGINAL DESCRIPTION:** Clench, *Bulletin Allyn Museum*, 64: 11-14 (1981).
- TYPE LOCALITY:** South Willow Creek, Stansbury Mountains, Tooele County, Utah.
- DISTRIBUTION:** In California this subspecies has been taken in the White Mountains of Inyo and Mono counties and in the Benton Range in Mono County. A presumed blendzone between this subspecies and typical *siva* is presumed to exist through the Inyo Mountains, connecting the White Mountains populations with those of typical *siva* in the Panamint Range, but specimens are lacking. This subspecies can also be expected to be found on the stands of Juniper around Mono Lake and in extreme northeastern Mono County, but again specimens are lacking from these areas.
- ELEVATION RANGE:** 6,000' to 8,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** This species is typically found in the Pinyon-Juniper Woodland of the western Great Basin. At least one nectar source is *Eriogonum umbellatum* Torr. ssp. *subaridum* (S. Stokes) Mumz (for the sporadic summer brood) and *Viguiera multiflora* (Nutt.) Blake (for the spring brood).

PHENOLOGY: Mostly univoltine, but with an occasional small summer brood in some years. The first brood flies from mid-May to mid-June; the second brood, if present, flies from mid-July to mid-August.

FOODPLANTS: These populations are associated with *Juniperus osteosperma* (Torr.) Little (Utah Juniper).

137. *Mitoura loki* (Skinner)

Skinner's Hairstreak is a rare species in collections, although it is rather common at times in its isolated populations in southern California. This species may be distinguished from *Mitoura siva* by its continuous row of submarginal spots on the ventral hindwing surface and the presence of elaborate brown mottling across the inner half of the same wing.

DIAGNOSIS: The main difference between *M. loki* and the closely related *M. siva* is in the underside coloration and markings. In *loki* there are invariably some post-basal markings on the hindwing. Secondly, there is a full row of small black dots in the post-median area, which is usually very reduced in *juniperaria* and virtually absent in typical *siva*. Additionally, the quality of the ground color beneath may be a dense and heavy green or that the green scaling may be reduced, allowing considerable brown ground color to show. Occasional spring specimens have very little green and a great deal of dark reddish-brown on the ventral hindwing. However, in series *loki* is distinctly green and not so brown as *M. thornei*, the other southern California *Mitoura* which is very similar to *loki* in general wing pattern. The overall appearance of the underside of *loki* is to give a sort of "banding" pattern.

ORIGINAL DESCRIPTION: Skinner, *Entomological News*, 18: 378 (1907).

TYPE LOCALITY: Mt. Springs [Mountain Spring, 6 airmiles northeast of Jacumba], San Diego County, California. Holotype in Carnegie Museum.

DISTRIBUTION: *M. loki* is found only in California and Baja California, along the western border of the Colorado Desert; it also occurs just west of the mountains bordering the desert in the vicinity of the Gavilan Hills, Riverside County around Redlands, and Hemet to the south. Along the northern border of its range it occurs from Morongo Valley eastward to Twenty-nine Palms, and southward from there through the higher mountains of Joshua Tree National Monument. Although there are two records of its capture in the northwest end of the Sheephole Mountains in San Bernardino County, no Junipers have been found in this range, and these probably represent stray individuals. In Baja California it occurs at least as far south as the San Pedro Martir Range. *M. loki* is not known from the Los Angeles Basin or San Fernando Valley, even though old records exist for *Juniperus californica* Carr. at the southern base of the San Gabriel Mountains. Specimens of *M. loki* taken by the Sperry's and labelled "Azusa" were probably not taken near there (even though there are old records for Juniper in that general area), because on the same date they took a long series of *M. s. juniperaria* from the Mojave Desert. A number of specimens of various butterfly species collected by the Sperry's are known to be mis-labelled (J. F. Emmel, unpublished data; but see Opler, 1966e, for a contrasting opinion). This is believed to represent another instance of their mislabelling. The host, *Juniperus californica* Carr., is found in a fairly large stand at the east end of the Granite Mountains north of Amboy, and also extensively through the Old Woman Mountains in the Eastern Mojave Desert; however, repeated searches of these two stands of Juniper have failed to turn up *M. loki*, or any other *Mitoura* species for that matter.

- ELEVATION RANGE:** From approximately 2,000 to 4,500' elevation.
- HABITAT AND PLANT COMMUNITIES:** In the more coastal localities for this butterfly it is found in the Coastal Sage Scrub plant community in which Junipers are scattered. Along the western edge of the desert, it is found at the upper edge of the Creosote Bush Scrub plant community or at the lower edge of Pinyon-Juniper Woodland in which the Pinyons are absent and Juniper is the only representative of the two present. In parts of Joshua Tree National Monument, the butterfly is found in the Joshua Tree Woodland plant community where Junipers are scattered, or in true Pinyon-Juniper Woodland just above this plant community.
- PHENOLOGY:** This species is multivoltine, with two to three broods most years, with the size of the second and third brood smaller than the spring brood and probably closely correlated with amount of winter rainfall and possibly summer rainfall. The first brood flies from early March to late April, depending on elevation and winter rainfall pattern; a second generation can be taken during the months of June and early July, and again there are records from late July, August, and September.
- ADULT BEHAVIOR:** Males of this species perch on the Juniper host rather regularly; mating pairs have been found resting on the outer branches of the host Juniper. The species has a tendency to stray from its usual habitat, as evidenced by the two records mentioned above from the Sheephole Mountains. Additionally, stray specimens are known from near Onyx Peak in the San Bernardino Mountains (nearly 9,000' elevation!), from the summits of the Laguna Mountains in San Diego County, and several records from high elevations in the San Pedro Matir Range in Baja California. Perhaps some of these specimens represent hilltopping males.
- LIFE HISTORY:** The life history of this species was first described by Comstock and Dammers (1932b). The egg is a delicate light green, with raised portions of a whitish shade and with small structural differences from the egg of *M. siva juniperaria*. The raised points are not as clearly defined in the region of the micropyle, and are more pronounced at the outer circumference of the egg. These points do not show a tendency to regular alignment to the same extent as in the egg of *juniperaria*. The egg stage lasts five days. The eggs are laid singly on the tender tips of the Juniper host. The mature larva (fourth instar) is a vivid green in ground color with a series of raised protrusions that are a darker green. A lemon-yellow broken longitudinal line, or series of irregular crescents, occurs on each side of the center dorsal area (in two dorso-lateral lines). Laterally, there is a similar creamy white line along the edge of the overlapping fold, just below the spiracles. The segmental creases are deep, throwing each segment into rounded relief. Additionally, these segments have a series of bumps and depressions in regular form on each segment, like those in *siva*. The pupa is a dark chestnut brown with fine mottling and a hairy coat, except on the wing covers and facial portions. The life cycle passes in two months. This species then diapauses as a pupa.
- FOODPLANTS:** The sole host of this butterfly is *Juniperus californica* Carr. (Cupressaceae).
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** See discussion under *M. siva*.
- GEOGRAPHIC AND SEASONAL VARIATION:** The summer brood specimens tend to be much lighter ventrally than spring brood specimens, with a yellowish or light brownish overscaling on the underside. September specimens may or may not have this light

color, sometimes appearing more like spring brood specimens. Although, in any given locality, the species tend to be quite variable in both ground color of the underside and in the pattern of markings on the underside, there is no apparent geographic variation from one locality to another throughout its range (i.e., all populations seem to show a similar range of variation within a given locality).

GENERAL REMARKS: There are two chemical races of *Juniperus californica* Carr, called Chemical Race A and Chemical Race B. *M. s. juniperaria* feeds on Chemical Race A. *M. loki* feeds on Chemical Race B. It has been suggested that Chemical Race A has actually been derived from Chemical Race B and introgression of genes from *Juniperus osteosperma* (Torr.) Little, through hybridization. This evolution of the phenotypic characteristics of the host plant races perhaps parallels the phenotypic relationships of three *Mitoura* here. The subspecies *M. s. juniperaria* combines features of both *Mitoura siva siva* and *Mitoura loki*, perhaps indicating that the butterfly, *juniperaria*, has resulted from introgression of *loki* genes into the *siva siva* genotype. In other words, there may have been an evolutionary pattern of development of the host plant species for *juniperaria* similar to the pathway that the butterfly itself has followed.

138. *Mitoura thornei* J. Brown

This is a recently described species which superficially looks like a brown version of *loki*, and is known only from Otay Mountain, San Diego County, the type locality. Its host, in the genus *Cupressus*, is different from those of the butterfly's near relatives.

DIAGNOSIS: In this species, the underside pattern is identical to *loki*, but the color is essentially brown. In series, the distinctness from *loki* is obvious, but individual *thornei* can be as green as many *loki*, and some *loki* (especially spring brood) can be as brown as many *thornei*. When *loki* and *thornei* are reared side by side in controlled temperature chambers, the color distinction between the two persists (John Lane, unpublished data).

ORIGINAL DESCRIPTION: J. W. Brown, *Journal Research Lepidoptera*, 21: 245-254 (1983).

TYPE LOCALITY: Little Cedar Canyon, north slope of San Ysidro Mountains (Otay Mountain), east end of Little Otay Lake, 200 meters, 32° 37' N, 116° 52' W, San Diego County, California.

DISTRIBUTION: At present, the species is known only from the Otay Mountain area in San Diego County.

ELEVATION RANGE: 600 to 700' elevation.

HABITAT AND PLANT COMMUNITIES: The host for the Otay Mountain *Mitoura* is Tecate cypress, a closed-cone conifer which occurs on the Xeric slopes in the Chaparral. This tree is restricted to a relatively few isolated stands, extending from the Santa Ana Mountains of Orange County south into Baja California. Fire is important in the natural ecology of these trees, as it is the major factor that initiates cone-opening and seed dispersal. Brown (1983) notes that Chaparral fires have undoubtedly caused great fluctuations in the population of both the cypress and the associated *Mitoura thornei*. To date, the Hairstreak species has not been found in the other known stands of Tecate cypress, *Cupressus forbesii* Jeps..

- PHENOLOGY:** *Mitoura thornei* appears to be at least double-brooded; adults fly in March and again in June. However, the second brood is a much reduced one in size.
- ADULT BEHAVIOR:** Males generally perch near the top branches of the cypress and are quite easily disturbed. Their quick, erratic flight makes them difficult to capture. Adults visit flowers of Manzanita (*Arctostaphylos otayensis* Wies. * Schreib.), California or Flat-top Buckwheat (*Eriogonum fasciculatum* Benth.), and *Yerba santa* (*Eriodictyon* species).
- LIFE HISTORY:** The early stages of *M. thornei* have been described in Brown (1983). The eggs are light green in color and echinoid in shape, and are laid singly on the new growth of the host. The egg stage lasts seven to fourteen days. The newly hatched larvae bore into the young stems of the host but become external feeders as they develop. Mature larvae closely resemble the terminal twigs on which they feed. The ground color is vivid green with two irregular white crescents on each segment, one on either side of the mid-dorsal crest; the markings together form a longitudinal stripe on each dorso-lateral side of the body. Additionally, there is a thinner, more continuous longitudinal white stripe above the pro-legs on each side of the larva. The entire body is covered with minute brown hairs. Thus, the larval stage of *thornei* closely resembles those described already for *siva* and *loki*. In the laboratory, the larval stages require 26-35 days to pupation. The pupae are dark chestnut brown with fine mottling, and are covered with fine brown hairs; the wing cases are bare. Pupation generally occurs in the debris at the base of the host trees.
- FOODPLANTS:** The sole known foodplant in the wild is the endemic Tecate cypress (*Cupressus forbesii* Jepson). In the laboratory, although females exhibit a distinct ovipositional preference for *Cupressus forbesii* Jeps., larvae will develop normally on California juniper (*Juniperus californica* Carr.).
- CHROMSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** Differentiated in the Diagnosis.
- GEOGRAPHIC AND SEASONAL VARIATION:** Phenotypically, the two broods are similar, the summer brood being just slightly darker in color.
- GENERAL REMARKS:** As southern California has long had one of the greatest concentrations of lepidopterists in the country, it is remarkable that this new Hairstreak species remained undiscovered until 1972, when the first specimens were taken. Inaccessibility to this remote Otay Mountain area was undoubtedly the major deterrent. Despite the superficial appearance to *Mitoura loki*, based on the complex phenotypic characters, highly selective host preference, and a unique ecological association, this Otay Mountain *Mitoura thornei* appears to represent a distinct species. The relationship between *thornei* and the *loki* populations both to the north and south of its location would be a particularly interesting problem for lepidopterists to investigate in detail. It is interesting that the use of a *Cupressus* species as the larval host suggests a close affinity with *M. nelsoni* and *M. muiri*. However, *M. thornei* has quite a different appearance and southern California populations of *nelsoni* are all univoltine. Although no sympatry occurs, *M. thornei* is separated from the nearest *M. loki* population by only about 36 miles, and from the nearest *M. nelsoni* population by about 30 miles. In southern California then, the closest relative of *thornei* appears to be *M. loki*, which it resembles in voltinism (multiple-brooded), phenotype, and genetical characters.

It is distinguishable from *loki* in host preference and in the color of the ventral hindwing surface.

139. *Mitoura nelsoni* (Boisduval)

This species is abundant through the mountains of the Sierra Nevada and the higher mountains of southern California, wherever Incense cedar is common. The typical subspecies occurs in our state, and a former *nelsoni* subspecies, *muiri*, has been separated as a distinct species.

DIAGNOSIS: The upperside of this Hairstreak is brown. The underside is brown laved with lilac, especially on the hindwing. Fresh specimens often have a slightly metallic luster in this pink or reddish sheen. A few specimens will actually have an almost greenish tint. Specimens with any amount of wear will lack these tints, and with additional wear become more uniformly brown or dark flat brown. In this species the post-median band tends towards obsolescence, especially in its most posterior parts. Many specimens have a prominent white band only on the most anterior cells, which the post-median band traverses. The post-median band could be rather straight or rather irregular and jagged; it is mostly brown, sometimes thinly white and usually rather subdued, not standing boldly out of the brown ground color. The post-median band on the ventral surface of the forewing is rather straight and similarly subdued. The other brown *Mitoura*, which might be confused with *nelsoni* usually have bolder post-median bands which are more prominently highlighted by white or black scaling.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. Belgique*, 12: 43 (1869).

TYPE LOCALITY: "California", the French translating to "Great Forest of the Interior". Restricted by Emmel, Emmel, and Mattoon, *Journal Research Lepidoptera*, : (1988) to Lower Feather River Canyon, Butte County, California. Holotype in U. S. National Museum.

DISTRIBUTION: From the Laguna Mountains of San Diego County northward through Palamar Mountain, the San Jacinto Mountains, the Santa Rosa Mountains, to the San Gabriel and San Bernardino Mountains northward through the Tehachapi Mountains northward through the west slope of the Sierra Nevada and Cascade Range to the Klamath Mountains region, the North Coast Ranges. From California it goes northward into the Cascades of Oregon.

ELEVATION RANGE: From 2,000 to 7,500' elevation.

HABITAT AND PLANT COMMUNITIES: This species is found in areas of Mixed Coniferous forests, where the foodplant, Incense Cedar (*Calocedrus decurrens*) is found. Within these forests, *nelsoni* is usually seen at the edges of clearings perching on *Calocedrus* or other trees; it is also frequently encountered in meadow situations where it is attracted to nectar sources.

PHENOLOGY: This butterfly is strictly univoltine, flying from early May to mid-July, depending on elevation, with the majority of records showing a peak flight period in mid-June.

ADULT BEHAVIOR: The males frequently perch on Incense cedar or other conifers at the edges of meadows and clearings within the forest. The adults are avid flower visitors, and the majority of them are taken by collectors while engaged in nectaring. A primary nectar source in northern California is Wild Lilac, *Ceanothus integerrimus* H. & A.

- LIFE HISTORY:** The early stages of this species were first described from southern California material taken on the crest of the Greenhorn Mountains, Kern County, by Comstock and Dammers (1932c). The egg is green, of about the same shade as the Incense cedar twigs. It is covered with minute star-shaped points of a lighter shade, from which low partitions radiate to join those from neighboring points. The shape is echinoid, with a deeply depressed micropyle. These stellate points on the egg are slightly less pronounced than the egg of *M. s. juniperaria*, and do not show quite the same degree of alignment. The mature larva very closely resembles those of *Mitoura siva juniperaria* and *M. loki*. The larva is vivid green with darker green raised lobulations. A series of irregular lemon-yellow crescents occur as a band on each side of the dorsal area. Minute brown hairs occur over the body. The pupa is blackish-brown and covered with minute brown hairs. No silk girdle was noted. The winter is passed in the pupal stage.
- FOODPLANTS:** The sole host known to date is Incense cedar, *Calocedrus decurrens*.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** The butterfly may be confused with *M. barryi* subspecies which may occur in close proximity to *nelsoni* populations. Very worn specimens of *M. barryi* may be virtually impossible to distinguish from *nelsoni*; in fresher individuals, *barryi* tend to have a more well-developed white macular band on the ventral surface of both the forewings and hindwings, and the ground color of the hindwings tends to be slightly more greenish or flat light brown in contrast to the more purplish-brown of the underside of *nelsoni*.
- GEOGRAPHIC AND SEASONAL VARIATION:** Because the species is univoltine, no seasonal variation is present. Geographically, the species is surprisingly constant throughout its rather wide range.
- GENERAL REMARKS:** The relation of this butterfly to *Mitoura muiri* is unclear. *Muiri* has been treated as a subspecies of *M. nelsoni* in recent years, but ecological data suggest that *muiri* is best treated as a specific entity. Similarly, the relationship of *M. barryi* to *M. nelsoni* is poorly understood, but on the basis of marked ecological differences between the two entities, we prefer to treat them as separate species.

140. *Mitoura muiri* (Hy. Edwards)

- LIFE HISTORY:** Reared by John Lane but not recorded to date.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** See discussion under *Mitoura nelsoni*.
- GEOGRAPHIC AND SEASONAL VARIATION:** In a given population of *muiri*, the phenotype tends to be quite variable with varying shades of the ventral surface being purplish red-brown to dark greenish-brown or reddish-brown. The percentages of these different phenotypes in the various populations has not been studied, so at this time we are unable to make any assessment as to any particular trends in geographic variation.
- GENERAL REMARKS:** The genetic relationship of the *Cupressus* and *Juniper*-feeding populations of this butterfly in the South Coast Ranges should be explored further, particularly with regard to hybridization studies and foodplant choice experiments using ovipositing females.

Until recently, this species was included under *Mitoura nelsoni* as a coastal subspecies. We differentiate two subspecies of this species in California.

a. *M. m. muiri* (Hy. Edwards)

- DIAGNOSIS:** This *Mitoura* is distinguished by the red-purplish-brown underside coloration, with blue-green or grayish-green overscaling on some specimens, with a fairly well-delineated median macular band of white. Superficially, the species resembles *M. nelsoni* but differs from it by the more rich brown or purplish-brown underside, often with greenish overscaling and the more well-defined macular white band.
- ORIGINAL DESCRIPTION:** Henry Edwards, *Papilio*, 1: 53 (1881).
- TYPE LOCALITY:** Mendocino County, California. Holotype in American Museum of Natural History. John Lane (*in litt.*) notes that the type specimens are labelled and cross-referenced to Henry Edwards' catalog entry giving "Tamalpais" as the location of capture by Dunn. This is consistent with the phenotype of *muiri* presently taken at Mt. Tamalpais in Marin County.
- DISTRIBUTION:** This species is limited to the inner and outer Coast Ranges, from Mendocino and Colusa counties to San Luis Obispo County, where it is always associated with *Cupressus sargentii* Jeps. and occasionally with *Juniperus californica* Carr.
- ELEVATION RANGE:** From 1,000 to approximately 3,000' elevation, with most populations in the 1,000 to 2,000' range.
- HABITAT AND PLANT COMMUNITIES:** Populations of this subspecies are virtually always located in areas of serpentine soils, which favor the growth of the *Cupressus* host. Usually on these serpentine slopes, there is sparse Chaparral with Digger Pine association. Tilden (1952) mentions the dark volcanic rocks of the Mt. St. Helena district in Lake and Napa counties where *muiri* has been taken.
- PHENOLOGY:** This butterfly is apparently univoltine, with captures recorded from late March to mid-June, depending on elevation.
- FOODPLANTS:** *Cupressus sargentii* Jeps., and perhaps occasionally on *Juniperus californica* Carr. in the inner North Coast Range.

b. Inner South Coast Range Segregate

- DIAGNOSIS:** This butterfly is almost phenotypically indistinguishable from typical *muiri*, except for specimens with greenish coloration such as those seen in Marin and Sonoma counties. These populations are associated with *Juniperus californica* Carr. and unpublished hybridization studies by John Lane indicate some reproductive isolation between this entity and the *Cupressus*-feeding *muiri* of the outer South Coast Range.
- DISTRIBUTION:** This subspecies is found in the inner South Coast Ranges from San Luis Obispo County northward to approximately Stanislaus County, where it is associated with *Juniperus californica* Carr.
- ELEVATION RANGE:** From 1,500 to 2,500' elevation.

- HABITAT AND PLANT COMMUNITIES: Usually found on serpentine soils, with sparse Chaparral and scattered stands of *Juniperus californica* Carr.
- PHENOLOGY: This butterfly is apparently univoltine in most years, but laboratory rearings indicate that a second generation is possible. We have no field documentation of a second generation occurring in this butterfly.
- FOODPLANTS: *Juniperus californica* Carr., similar to the other *Mitoura* species.

141. *Mitoura barryi* K. Johnson

- ADULT BEHAVIOR: The adults of *barryi* behave similarly to other *Mitoura*, staying in close proximity to the host plants and exhibiting perching behavior on the higher portions of the trees. At least one frequently used nectar source is *Ceanothus cordulatus* Kell., whose blooming period is closely correlated with the emergence of the adults of this *Mitoura*.
- LIFE HISTORY: Undescribed, although reared by Greg Ballmer (University of California, Riverside).
- CHROMOSOME NUMBER: Unknown.
- SIMILAR SPECIES: Worn specimens of *M. barryi* may be extremely similar to specimens of *M. nelsoni*. In the San Bernardino Mountains and probably in the southern Sierra Nevada populations, *M. nelsoni* on *Callocedrus* probably occurs within close proximity, and in localities located on the borders of these two entities one might expect to get specimens that are difficult to place with either taxon with certainty. In the Great Basin fringe of Lassen County (Frenchman Lake), forested areas containing abundant Incense Cedar intermix with Juniper. In this area, adults of *barryi* and *nelsoni* appear to associate with their respective hosts which grow side by side, with a comingling of both species at nectar in the understory. The two insects (if in fact they really are distinct species) are all but impossible to differentiate.
- GEOGRAPHIC AND SEASONAL VARIATION: As the species is univoltine, there is no seasonal variation. The populations within our area show surprisingly little difference between the populations in the northeastern corner of the state and those in southern California.
- GENERAL REMARKS: The disjunct distribution of the foodplants for these two population areas of *barryi* suggests that at one time the butterfly may have enjoyed a wider distribution when its host plant had a more extensive range through the mountains of California. Although populations of *Juniperus occidentalis* Hook are scattered through the higher elevations of the Sierra Nevada today, dense or contiguous populations of this species of host plant are not prevalent as in the other hosts used by other *Mitoura* species.

This species was not recognized and described until 1976. At that time the nominotypical subspecies was known to be represented by populations from Oregon northeastward into Idaho east of the Deschutes Plateau. The other subspecies, *M. barryi acuminata*, occurs westward along the edge of the Deschutes Plateau and Cascade Mountains, and then southward in the Cascades to southern Oregon and northward to Vancouver Island. In California, populations of *Mitoura* which appear to represent this species are found in the Modoc County and northern Lassen County region of California, and disjunct

populations occur in the southern Sierra Nevada of Tulare County and the San Bernardino Mountains of southern California.

a. *M. b. acuminata* K. Johnson

- DIAGNOSIS: The upper surface of the male is deep brown, while the female is a lighter brown. The under surfaces lack the yellow coloration found in typical *barryi*; there is a white submarginal line on the forewing, and a continuous mesial line (white outside, black in the center, and brown on the body side) across the hindwing. Four or five black spots occur outside this line near the tail, followed by orange and then blue-gray scaling next to the tail area. The most distinctive features, however, are in the pointed shape of the characteristic broad and wide-rimmed anterior valval structure of the male genitalia (Johnson, 1976).
- ORIGINAL DESCRIPTION: K. Johnson, *Bulletin Allyn Museum*, 38: 20-21 (1976).
- TYPE LOCALITY: Butte Falls, Jackson Co., Oregon. Holotype male in American Museum of Natural History.
- DISTRIBUTION: Populations representing typical *M. acuminata* occur in the northeastern corner of California from eastern and northern Lassen County northward through Modoc County.
- ELEVATION RANGE: From approximately 5,000 to 6,500' elevation in California.
- HABITAT AND PLANT COMMUNITIES: This species is typically found in the Northern Pinyon-Juniper Woodland plant community.
- PHENOLOGY: This subspecies is apparently strictly univoltine, flying from late May to mid-July with an apparent peak flight in late June.
- FOODPLANTS: The butterfly is closely associated with *Juniperus occidentalis* Hook ssp. *occidentalis*; this is almost certainly the foodplant within California. The larval foodplant in the Northwest is unknown; the butterfly occurs there where either *Thuja plicata* or *Juniperus occidentalis* are present (Johnson, 1976).

b. *M. b. ssp.*: Southern California Segregate

- DIAGNOSIS: We consider populations of *Mitoura* of high elevations in the southern Sierra Nevada and San Bernardino Mountains to be representative of *M. barryi*. In these populations the phenotype is similar to *M. b. barryi*, but they tend to lack the reddish tints on the underside and many have a greenish aspect. This green is not metallic, but rather a flat, dull almost grayish-green.
- DISTRIBUTION: This butterfly is found in the southern Sierra Nevada of Tulare County and at high elevations in the eastern San Bernardino Mountains, where it is associated with *Juniperus occidentalis* Hook ssp. *australis*.
- ELEVATION RANGE: From 7,000 to 10,000' elevation.
- HABITAT AND PLANT COMMUNITIES: These populations are usually associated with a sparse Mixed Coniferous Forest with *Juniperus occidentalis* Hook usually being the dominant tree.
- PHENOLOGY: Apparently univoltine, with adults flying from late May to late June.

FOODPLANTS: The species is closely associated with *Juniperus occidentalis* Hook ssp. *australis*; in captivity, females of this entity will readily oviposit on this plant.

142. *Xamia xami* (Reakirt)

See **Appendix** for discussion of the single record for this species from the Providence Mountains in the eastern Mojave Desert.

143. *Mitoura spinetorum* (Hewitson)

This rather large, handsome Hairstreak ranges throughout the West from the Rocky Mountains to the California coast, north to southern British Columbia and south to northern Baja California and Jalisco in Mexico. It is usually rather rare and encountered only in small numbers in the Upper Sonoran and Transition Zones wherever conifers with the proper dwarf mistletoes grow.

DIAGNOSIS: This Hairstreak may be immediately identified by the steel blue dorsal surface and the reddish-brown undersides. There is a prominent white post-median band on both wings ventrally, bordered interiorly with black. The adults are tailed. An excellent review of this species, including its distribution habits and variation, is given by Shields (1965).

ORIGINAL DESCRIPTION: Hewitson, *Ill. Diurn. Lepid. Lyc.*; 1: 94 (1867).

TYPE LOCALITY: "California". Holotype in British Museum (although Shields states it is in the U. S. National Museum). Hewitson described the butterfly from one female collected somewhere in California by Lorquin.

DISTRIBUTION: This species is found along the North Coast Range mountains north of San Francisco Bay in scattered locations to Del Norte County, and then again to the south starting in Santa Barbara County and throughout the cismontane areas of southern California into northern Baja California. From there our records include localities along both sides of the Sierra Nevada and several of the eastern Mojave Mountain ranges north through the Cascade Range and parts of the Klamath Mountain assemblage to the Oregon border in scattered locations.

ELEVATION RANGE: Our California *spinetorum* populations are found from near sea level (Monterey Peninsula, Monterey County) to over 8,000' (Mineral King, Tulare County).

HABITAT AND PLANT COMMUNITIES: The larvae of this butterfly feed on parasitic mistletoes that live in conifer trees. Most of the locations where this species occurs are located in Pinyon-Juniper Woodland up through Chaparral with Yellow Pine forests to Mixed Coniferous Forests or Red Fir forests in the mountains. The butterfly is uncommonly taken in all localities, perhaps because the mistletoe foodplants grow high in their host trees, drawing the butterflies away from the usual collecting haunts of lepidopterists.

PHENOLOGY: The butterfly has been recorded from March to September, with a concentration of records in July and August. Apparently this species is multivoltine, inasmuch as specimens have been recorded from April to the end of August in the Laguna Mountains of San Diego County.

- ADULT BEHAVIOR:** Mud and flowers attract adults, and they commonly hilltop, as in the desert mountain ranges. In northern California, *spinetorum* can become quite abundant, especially in certain drier years along open Digger Pine (*Pinus sabiniana*) or Ponderosa Pine (*Pinus ponderosa*)-clad serpentine ridges in the Foothill Woodland plant community. In Northern Juniper Woodland-Pinyon Pine country of the Basin fringe, large numbers of adults can occasionally be encountered.
- LIFE HISTORY:** The first description of the early stages was by Comstock and Dammers (1938). The egg is the usual echinoid shape in the genus, with a reticulation of raised walls over the surface. The mature larva is exceptionally cryptically colored on its foodplant. The ground color is a yellow-olive with a mid-dorsal pale olive band. Subdorsally on most segments, there occurs an oblique off-white bar proceeding to either side. The lower edges of these bars are tinged with dark magenta; above each bar is a large raised waxy orange patch (fifth to ninth segments). Only the abdomen bears short colorless hairs. The pupa is a dark chestnut brown, with heavy black mottling. Pupation occurs within the foodplant mass and no silken attachment has been observed. In northern California, Cascade Range foothill populations have shown a tendency to use the Pine Dwarf Mistletoe which grows on the southeast aspect of Digger Pine trees (S. Mattoon, personal observation).
- FOODPLANTS:** Exclusively species of the Dwarf mistletoe genus, *Arceuthobium* (Family Loranthaceae), which occur only on conifer host trees in the family Pinaceae. Mistletoe species used include: *A. campylopodum* Engelm. in Gray; *A. vaginatum* f. *cryptopodum* on *Pinus ponderosa* Dougl. ex P. & C. Lawson; *A. americanum* Nutt. ex Engelm. in Gray on *Pinus contorta*; *A. campylopodum* Engelm. in Gray on *Pinus jeffreyi* Grev. & Balf. in A. Murr., *Abies concolor*, *Pinus reflexa*, *Pinus aristata* Engelm., *Pinus monophylla* Torr. & Frem., *Pinus sabiniana*, and other host species outside our area. In nearby areas of Arizona, it has been found on *Arceuthobium vaginatum* Willd. f. *cryptopodum* in Ponderosa Pines and in Pinyon Pines (Remington, 1958).
- PARASITES AND PREDATORS:** Shields (1965) records a Tachinid fly, *Masphyomyia paralis*, that parasitized larvae in Tuolumne County and San Diego County. Remington (1958) records a braconid larval parasite in Arizona and an undescribed *Apanteles* braconid wasp parasite from pupae in Colorado. Adults of this Hairstreak occasionally have clipped wings and beak-marked wings, indicating bird predation.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** *Mitouri johnsoni* is rather similar in appearance on the underside, but the dorsal coloration is quite brown in *johnsoni* and steely blue in *spinetorum* adults.
- GEOGRAPHIC AND SEASONAL VARIATION:** Though this species ranges from the Rocky Mountains to the Pacific Coast and north into Canada, only the typical subspecies has been named over this range. There is a Mexican subspecies (*millerorum*) that ranges south to Durango and Hidalgo. No seasonal variation has been detected in this species.
- GENERAL REMARKS:** The butterflies visit a wide variety of nectar sources; at least 28 genera of nectar sources are listed by Shields (1965). Hilltopping behavior of males is strongly pronounced in this species.

144. *Mitoura johnsoni* (Skinner)

Mitoura johnsoni was described by Skinner in 1904 from a female from British Columbia and a male from Seattle, Washington. Since that date it has been considered a very rare species and is only occasionally found in collections (Opler, 1962). The best review of the species' ecology distribution and variation is by Shields (1965).

- ORIGINAL DESCRIPTION: Skinner, *Entomological News*, 15: 298 (1904).
- TYPE LOCALITY: Seattle, Washington and British Columbia. Syntypes in Carnegie Museum.
- DISTRIBUTION: Our only California records are from Lassen County, Plumas County, El Dorado County, Del Norte County, Glenn County, Butte County, Mariposa County, Placer County, Sierra County, Solano County, Siskiyou County, Tehama County, Napa County, and Tuolumne County.
- ELEVATION RANGE: From 1,200' to 8,000'.
- HABITAT AND PLANT COMMUNITIES: Coniferous forest areas where appropriate host plants occur.
- PHENOLOGY: From mid-March to mid-August, with a peak during most of the month of July.
- ADULT BEHAVIOR: Both males and females are drawn to moisture at various localities. In some areas this involves down-valley flight of the adults during the morning hours and return in the afternoon (Scott, 1973). It should be noted that Scott's observations of *johnsoni* involved over 100 individuals at Thompson Canyon, Yolo County between March 18 and 21, 1972, a very early time. These represent the spring brood, not often observed in such numbers. *Mitoura johnsoni* adults visit flowers of *Arctostaphylos*, *Calyptridium umbellatum* (Torr.), *Ceanothus*, *Cornus*, Dandelion, *Fragaria*, *Rorippa*, and *Spraguea* (Opler, 1962; Shields, 1965), as well as *Eriodictyon californicum* (H. & A.) (=Yerba Santa).
- LIFE HISTORY: The first male of this species was described from an adult that emerged from a larva collected in Washington, and larvae and eggshells were found on the host plant by McCorkle (1962). The following descriptions are based on ova and larvae collected at Thompson Canyon, Yolo County, California from a wild female (J. Emmel, unpublished). Eggs are laid directly on conifer bark near the base of tiny *Arceuthobium* mistletoe plants. As many as four to six eggs may be attached to the bark within several square inches. The egg is pale green in color and is the typical *Mitoura* echinoid shape, with fine reticulations of raised walls over the surface, and a deep micropyle. The first instar larva is pale yellow-green. The second and third instars have a light green ground color with two rows of yellow protruberances on the raised dorsal surface of each segment; these yellowish bumps lie in two dorso-lateral rows extending the length of the larva. In the fourth (mature) instar, the larva is olive-green in color with a prominent triangular yellow area dorso-laterally to either side of the mid-dorsal line. Each of these yellow triangles is edged anterior-laterally with a white band and then a magenta band, except on the third thoracic segment which retains a diffuse reddish-yellow spot on top of the protuberance which is also characteristic of that segment in the second and third larval instars. Laterally there is a well-marked yellow band just below the spiracles with faint purplish shading above it on each segment. The yellowish and white portions of this larval pattern are more restricted, especially on the rear most abdominal segments in *johnsoni* than in the rather similar mature larva of *Mitoura spinetorum*. Nevertheless, the two patterns are close and both provide superb camouflage on the chosen mistletoe host. The pupa, previously undescribed is

[T.C.E.]

- FOODPLANTS: C. V. Piper, the collector of the original male specimen which Skinner (1904) described as *johnsoni*, reared the adult from larvae found on the mistletoe, *Arceuthobium campylopodum* Engelm. in Gray f. *tsugensis* (Rosend.) Gill., a parasite on a western Hemlock tree (*Tsuga heterophylla* (Raf.) Sarg.) near Seattle, Washington. The eggshells and larvae were found by David McCorkle on this same form of *Arceuthobium campylopodum* Engelm. in Gray. The subspecies of this mistletoe is not known to occur in at least several low-elevation California localities, suggesting another host plant is being utilized. The mistletoe used in Thompson Canyon in Yolo County is *Arceuthobium occidentale*, a parasite on Digger Pine (*Pinus sabiniana* Dougl.). The *arceuthobium* on Digger Pine in Butte County has been identified as *campylopodium* but may be *occidentale*.
- CHROMOSOME NUMBER: Unknown.
- SIMILAR SPECIES: See *Mitoura spinetorum*.
- GEOGRAPHIC AND SEASONAL VARIATION: No geographic subspeciation has been observed to date, perhaps because of the rarity of specimens in collections. The overall distribution ranges from extreme southern British Columbia south through the western half of Washington, with one record in Oregon, and then in northern and central montane populations in California. No seasonal variation has been observed yet. From the range of records, it would be expected that this butterfly would be multivoltine, but insufficient records exist for any one locality to be certain.
- GENERAL REMARKS: This butterfly will undoubtedly be found in a number of additional populations that will better fill in the present known set of distribution records, especially if larvae and eggs are sought on the host plants in prospective population areas. It is of interest to note how often *spinetorum* and *johnsoni* have been recorded from the same exact location. The same host is used by both in Butte County, California.

145. *Atlides halesus estesi* Clench

This is the Great Blue Hairstreak, which occurs across much of the southwestern United States and north into Oregon. The species also has a geographically separate distribution on the East and Gulf Coast. Our California subspecies is *A. h. estesi*.

- DIAGNOSIS: This Hairstreak is readily identified by the very large size, the blue dorsal surfaces, and the mostly black ventral surfaces with red basal spots next to the body on both wings. There are several iridescent green spots near the anal margin of the hindwing, as well as some iridescent blue spots along the margin.
- ORIGINAL DESCRIPTION: Clench, *Entomological News*, 53: 219 (1940).
- TYPE LOCALITY: Riverside, California. Holotype in Museum of Comparative Zoology, Harvard University.
- DISTRIBUTION: The subspecies *estesi* Clench occurs from the Mississippi Valley westward to the Pacific Coast, and it also flies in northern Mexico. In California, we have abundant records from throughout the southern California area from Topanga Canyon and San Gabriel Canyon in Los Angeles County, south to the eastern part

of San Diego County, and north through all of Riverside County and San Bernardino County (including the eastern Mojave Mountain ranges: Providence Mountains, Sheephole Mountains), and from there north through the coastal counties of Santa Barbara, Monterey, Santa Clara, Contra Costa, Alameda, Lake, Yolo, Yuba, Solano, Sacramento, to Shasta counties north of the Central Valley. From Kern County, in the southern Sierra Nevada, the butterfly extends in scattered colonies up the western slope of the Sierran foothills and Cascade Range into Oregon.

- ELEVATION RANGE:** From near sea level in San Diego County to 5200' on Breckenridge Mountain in Oak Chaparral communities near Bakersfield in Kern County.
- HABITAT AND PLANT COMMUNITIES:** This spectacular iridescent hairstreak is found rather sparingly in the Lower Sonoran, Upper Sonoran, Juniper Woodland, and Transition Zone oak belts in California, particularly in the deserts, foothills, and cismontane areas. It is most numerous along watercourses where its mistletoe foodplants are abundant on Cottonwoods and Sycamores. It is found in valley riparian areas, agricultural areas, cities and towns where Black Walnut, *Juglans*, supports the mistletoe.
- PHENOLOGY:** The species has been recorded as early as mid-February in the Santa Barbara area to as late as mid-November in the Scissors Crossing area and Anza Desert area of San Diego County. There are at least two broods in northern California, flying from April to October.
- ADULT BEHAVIOR:** Although adults are usually taken as singletons, occasionally one finds fairly good numbers on flowers, especially on *Baccharis* in the north during the fall. The species is multiple-brooded, and males can live up to twenty-four days, from marking experiments by John Alcock (1983, 1985) in Arizona. Males perch on treetops along washes or on hilltops in the afternoon to await females, and will return to the same tree day after day, Alcock has found.
- LIFE HISTORY:** The larvae eat the male flowers and leaves of the *Phoradendron* parasitic mistletoes. The mature larva is velvety green with a yellowish lateral stripe and traces of reddish along with a darker mid-dorsal line. The body is covered by short orange hairs, except on the center portion of the cervical shield. The pupa is brown and heavily mottled with black. Short yellow-orange hairs are scattered over the pupal surface except on the wing cases. Pupation takes place under the bark of or at the base of trees on which the mistletoe grows. Pupae can sometimes be found in large numbers at the bases of isolated trees with heavy growths of mistletoe. The species hibernates in the pupal stage.
- FOODPLANTS:** The foodplants in California are all in the broad-leafed parasitic mistletoe genus, *Phoradendron*, including the following species; *P. flavescens* (Pursh) Nutt. var. *macrophyllum* Engelm. in Rothr., *P. bolleanum* (Seem.) Eichler var. *densum* (Torr.) Fosc., *P. californicum* Nutt., and *P. juniperinum* Engelm. (all in the Family *Loranthaceae*). These mistletoes are found on host plants as diverse as *Populus*, *Platanus*, *Juglans*, *Fraxinus*, *Quercus*, *Olneya*, *Prosopis*, *Conifers*, and *Junipers* (*Juniperus*).
- CHROMOSOME NUMBER:**
- SIMILAR SPECIES:** No similar species in our fauna.

GEOGRAPHIC AND SEASONAL VARIATION: There is a western U. S. subspecies (*estesi*) and an eastern U. S. subspecies (typical *haesus*). Otherwise, there is no geographic or seasonal variation in the United States.

GENERAL REMARKS: While the butterfly is usually considered fairly rare and local in the western United States, large numbers of pupae may be collected under trees supporting mistletoe. Along the Santa Ana River in Riverside County, as many as 420 pupae have been collected under one tree.

146. *Strymon melinus* Hubner

ADULT BEHAVIOR: The adults visit many kinds of flowers to sip nectar. The males will perch on small trees and shrubs during the afternoon to await females. While perched, they frequently rub their hindwings together, vibrating the two anal-margin tails.

LIFE HISTORY: The flattened egg is pale green in color. Eggs are normally laid on the host inflorescences and are laid singly. The larvae usually feed on flowers and fruits, and only rarely on young leaves. The mature larva is quite variable in color. The most common morph is green with diagonal markings of diverse colors on each segment, but the larva may be tan-colored, pink, reddish-brown, purplish-white, or yellowish-brown with various pale marks. The surface is covered with short yellowish-brown hairs. The pupa is a delicate brown, heavily mottled with dark brown spots of various sizes.

FOODPLANTS: Many genera and several families are used. These include *Malva* and flowers of cultivated hibiscus in urban areas (family Malvaceae), *Humulus* (Moraceae), a *Morpha* (Leguminosae), *Nolina* (Agavaceae), *Phaseolus* (Leguminosae), *Polygonum* and *Eriogonum* (Polygonaceae). The species sometimes becomes a pest in commercial bean fields. Guppy (1959) found that on Vancouver Island, British Columbia, *Strymon melinus* fed on the flowers of two *Trifolium* clover species in the spring brood and on *Anaphalis margaritacea* Benth. during the summer brood. The latter would also oviposit on and eat the flower of a wild strawberry, *Fragaria loracteata* Heller, in the lab. It appears that the larvae of this hairstreak can feed on the flower parts of many species, and opportunistically selects them according to the species in bloom locally at time of oviposition.

CHROMSOME NUMBER: $n = 24$ (Emmel and Eliazar, unpublished).

SIMILAR SPECIES: This species closely resembles *Strymon avalona*, an endemic species found only on Santa Catalina Island off the coast of southern California. However, *S. melinus* does not occur on that Island, although it does occur in great abundance on Santa Cruz Island to the north (records in April and June) where *S. avalona* is absent.

GEOGRAPHIC AND SEASONAL VARIATION: The six subspecies that have been described for *Strymon melinus* are weakly differentiated, and there is no seasonal variation despite the multivoltine character of the species.

GENERAL REMARKS: This is the most widespread species in the genus *Strymon* north of Mexico. The weak differentiation between the six described subspecies is because of the variable nature of individuals in the same population through the year. Almost every phenotype can be found in a population if one collects enough specimens.

This dark gray Hairstreak occurs throughout the lowlands of California and up to mid-elevations in the mountains. It is more scarce in desert areas. The typical subspecies does not occur in California but two other subspecies are represented.

a. *S. m. pudica* (Hy. Edwards)

- DIAGNOSIS: This subspecies ranges from southern Oregon through California west of the Sierras to Baja California. The upperside is blackish with a conspicuous hindwing spot. The ventral surface is pale gray and the post-median band is narrow and lined with black, with considerable red in the hindwing post-medial band area.
- ORIGINAL DESCRIPTION: Henry Edwards, *Proceedings California Academy Sciences*, 7: 172 (1876).
- TYPE LOCALITY: Contra Costa County, California. Holotype in American Museum of Natural History.
- DISTRIBUTION: We have hundreds of records of thousands of specimens collected in virtually every county west of the crest of the Sierra Nevada and north on the east side of the Sierras to Inyo County. It occurs from the coast up into mid-elevations in the mountains.
- ELEVATION RANGE: From sea level to approximately 7,000 feet elevation.
- PHENOLOGY: The flight period of this subspecies extends from February to November, although we have captures even in early January and mid-December as isolated individuals. The butterfly goes through a series of broods in all localities except perhaps the highest mountain populations.

b. *S. m. setonia* McDunnough

- DIAGNOSIS: This subspecies is found in semi-arid areas from eastern Oregon across the Great Basin to Colorado. It is similar to the previously described subspecies except that the post-median band on the hindwing ventral surface is more broadly edged with black. In California, this subspecies occurs in the state's northeastern corner.
- ORIGINAL DESCRIPTION: McDunnough, *Canadian Entomologist*, 59: 160 (1927).
- TYPE LOCALITY: Seton Lake, Lillooet, British Columbia. Holotype in Canadian National Collection.
- DISTRIBUTION: This butterfly is distributed from British Columbia south through eastern Oregon to the Great Basin Desert in Nevada and elsewhere in the west. In California it is found only in Modoc (and probably Lassen) counties.
- ELEVATION RANGE: From 4,000 to 7,000 feet elevation.
- HABITAT AND PLANT COMMUNITIES: This subspecies flies in Great Basin Sagebrush Scrub in its California range.
- PHENOLOGY: At present, most of our records are from July.

147. *Strymon avalona* (W. G. Wright)

This Hairstreak is one of the world's most restricted species, being found only on Santa Catalina Island off the coast of southern California.

- DIAGNOSIS: It rather resembles *Strymon melinus*, but is smaller in size and lacks the heavy wavy black post-median line that *melinus* has on the ventral surface. Instead it

- has a series of small black spots. Additionally, the red-orange hindwing spot is reduced both dorsally and ventrally.
- ORIGINAL DESCRIPTION: W. G. Wright, *Butterflies of the West Coast*: 209 (1905).
- TYPE LOCALITY: Avalon, Catalina Island, California. Lectotype in California Academy of Sciences, designated by Tilden, *Occasional Papers California Academy Sciences*, 118: 32 (1975).
- DISTRIBUTION: *Strymon avalona* is common in select localities such as the hills around Avalon, the type locality. Meadows (1936) states that perhaps the best collecting locality is around common sumac (*Rhus laurina*) along the road to Renton Mine, south of Avalon in early March. Other localities where it has been recorded are Pebbly Beach, Jewfish Point, the Isthmus, hills west of Avalon, and a hillside 1/2 to 3/4 miles west of Avalon. All of these localities are on Santa Catalina Island off the Los Angeles coast.
- ELEVATION RANGE: Sea level to 200' elevation.
- HABITAT AND PLANT COMMUNITIES: The favored habitat is grassy areas and Chaparral, where the adults frequently perch on bushes.
- PHENOLOGY: Captures have been reported in every month of the year, with the first brood primarily occurring from mid-February to April, a second brood in July and August, and a third brood flying from September to November.
- ADULT BEHAVIOR: Besides visiting flowers of common sumac, the adults also visit the flower of the Giant Buckwheat, *Eriogonum giganteum* Wats.
- LIFE HISTORY: The life history was first described by Comstock and Dammers (1933). The egg is of the usual echinoid form, with a large and deeply depressed micropyle and the characteristic reticulated network of raised walls enclosing cells of an irregular hexagonal type. Spiny projections come off the walled junctions as with other related species. The color is a gray-green with a bluish cast. The eggs are laid singly, usually in the terminal buds or on immature flowers of the foodplant. The mature larva shows considerable variation in ground color, ranging from a pale apple-green to pale pink. The pale apple-green form has no special markings or shadings except on the cervical shield, which has a pale green band down its center and the upper half speckled with black. The entire body of the larva, except the cervical shield, is covered with short white fine hairs. The pupa is pale pinkish-brown or wood-brown, shading to buff on the abdomen. Superimposed on this background color are markings of various shades of olive-green. Pupation occurs at the base of the foodplant, with the usual support of a delicate silk girdle. The head, thorax, and body of the pupa are covered with short yellow hairs.
- FOODPLANTS: *Lotus argophyllus* (Gray) Greene var. *ornithopus* (Greene) Ottley, and *Lotus scoparius* (Nutt.) Ottley (Leguminosae).
- CHROMOSOME NUMBER: (See Gorelick paper.)
- SIMILAR SPECIES: See discussion under *Strymon melinus*.
- GEOGRAPHIC AND SEASONAL VARIATION: None has been noted on Santa Catalina Island.

GENERAL REMARKS: Scott (1976) asserts that *melinus* has been introduced to Santa Catalina Island and that Glenn Gorelick has found intermediates there, suggesting that the introduced *melinus* may be absorbed by the *avalona* population. This is apparently incorrect, from all information available to us from other lepidopterists who have collected on the Channel Islands.

148. *Strymon columella clenchi* Austin and Emmel

This Hairstreak is quite scarce in southern California and has only been taken in the Colorado Desert, particularly the Coachella, Imperial, and Colorado River Valleys.

DIAGNOSIS: The adults are distinguished from other *Strymon* species in California by the single pair of tails on the hindwings and the ventral markings, with a small-sized, pale underside and a poorly developed red spot.

ORIGINAL DESCRIPTION: Reakirt, *Proceedings Academy Natural Sciences Philadelphia*, [1988]: 339 (1866).

TYPE LOCALITY: "Near Vera Cruz, Mexico". Location of type not known (not in Field Museum of Natural History; Miller and Brown, 1981).

DISTRIBUTION: This butterfly has been taken in the Colorado Desert portions of Riverside County, Imperial County, and San Diego County, and once on the coast at Laguna Beach in Orange County. There are also several old records to the city of San Diego area in San Diego County, which may indicate a former coastal population (all coastal records are from September 1928). The only coastal colony with records later than this is in the El Cajon area of San Diego County.

ELEVATION RANGE: From below sea level to mid-elevations in the Laguna Mountains.

HABITAT AND PLANT COMMUNITIES:

PHENOLOGY: The flight period extends from mid-March to early November in the desert areas, and in August to September at El Cajon.

ADULT BEHAVIOR:

LIFE HISTORY: The early stages were first described by Comstock and Dammers (1935b). The flattened egg is pea-green in color. The eggs hatch in about seven days. In the laboratory, the larvae will eat Mallow. The mature larva (said to be fifth instar) is dark green with a slightly darker mid-dorsal line, and a soiled white cervical shield (maroon shading in its center). The body is covered with translucent white points, from which arise translucent hairs of a glistening chestnut brown. The pupa is a pink-buff in ground color, heavily sprinkled with minute brown specks. There is a greenish mid-dorsal band on the abdomen which bifurcates and curves to either side on the last three segments.

FOODPLANTS: *Sida hederaceae* (Dougl.) Torr. (Malvaceae), at the California Lakes in Imperial County. Along the western edge of the Colorado Desert the butterfly uses two Malvaceous plants: *Hibiscus denudatus* Benth., and *Sphaeralcea ambigua* Gray. The eggs are usually laid between the sepals and the unfolding flower buds; the young larvae then feed on the flower parts and ultimately on the maturing seeds of these two plants.

CHROMOSOME NUMBER:	Unknown.
SIMILAR SPECIES:	None in our area.
GEOGRAPHIC AND SEASONAL VARIATION:	There are no apparent color pattern differences in individuals taken at different times during the year. There is no geographic variation within our populations of this species.
GENERAL REMARKS:	This butterfly may not be a permanent resident of southern California. Populations may be established from individuals flying in from Mexico or southern Arizona, and if conditions are favorable, these may persist for several years before dying out due to unusually cold weather or an unusually dry winter or summer. A diapause stage is not known for this butterfly.

149. *Erora quaderna sanfordi* dos Passos

See **Appendix** for details of the one record in the Providence Mountains in the eastern Mojave Desert (Emmel and Emmel, 1973; Klots and dos Passos, 1982).

Subfamily **Lycaeninae** Leach

153. *Lycaena phlaeas alpestris* Emmel and Pratt

This small Copper is a California representative of a species that occurs across the temperate zones of the New World and Old World, and in the United States is restricted mostly to the eastern half of the country, as well as a few populations in the northwest part of Canada and Alaska.

DIAGNOSIS:	The uppersides of this butterfly are a brassy copper, with somewhat of a dusky aspect, especially in males. Beneath, the ground color of the hindwing is an ashy-gray with wide and distinct orange borders on the hindwing. The post-median row of black spots on the ventral hindwing is distinct, with only a suggestion of white edging distally.
ORIGINAL DESCRIPTION:	Emmel and Pratt, <i>Natural History Museum of Los Angeles County Contributions in Science</i> , : (1990).
TYPE LOCALITY:	North slope of Mt. Dana, 11,000 to 11,500' elevation, Tuolumne County, California. Holotype in Natural History Museum of Los Angeles County.
DISTRIBUTION:	This subspecies is found in the Sierra Nevada and the adjacent White Mountains of Mono County. In the Sierra Nevada, it is known from the area of Palaccede Glacier west of Big Pine northward to Sonora Pass. It undoubtedly occurs south of the Palaccede Glacier locality, and probably to the north of Sonora Pass as well, as the foodplant is found north and south of the known range of the butterfly. In the White Mountains, the butterfly has so far only been taken at one locality, in a cirque east of White Mountain peak, but the lack of records in the remainder of the White Mountains is probably due to the general inaccessibility of much of the potential habitat for the butterfly.
ELEVATION RANGE:	From 11,000 to 13,000' elevation.

- HABITAT AND PLANT COMMUNITIES:** The butterfly is found within the Arctic Alpine Fellfields plant community. It is typically found on a north-facing, rocky slope, often just above a rock slide or talus slope particularly in glacial cirques.
- PHENOLOGY:** The species in California is apparently univoltine (although the eastern *L. phlaeas* is known to be multivoltine). Adults fly from mid-July to late August, depending on elevation, exposure, and depth of snow pack for a given year.
- ADULT BEHAVIOR:** Males tend to perch on rocks or on open patches of ground in small depressions on the north-facing rocky slopes. Females usually show unidirectional flight over the rocky slopes, landing on the *Oxyria* foodplants and spending most of their time either resting on or near the foodplant or on adjacent vegetation. Several alpine flowers have been noted as nectar sources of this butterfly in the White Mountains, namely

[JFE, FILL IN.]

- LIFE HISTORY:** The eggs are deposited on or near the foodplant, frequently on rock surfaces within several millimeters of the foodplant. The few hatched eggshells of this butterfly that have been found in the wild were placed on rocks within one centimeter of parts of the plant, and usually near the base of the foodplant. Eggs hatch within five days under laboratory conditions and the larvae feed to the third instar, in which they diapause the first winter. In the following year, the larvae molt and feed up to mature size in the fourth instar. Evidently, this larval stage goes into a second diapause until the following year when the diapausing larva pupates after snowmelt in the spring, and adults then emerge from the pupae within a two-week period (about ten days under laboratory conditions).

However, this California *Lycaena* does not have an obligate diapause. The larvae are able to tolerate winter cold much more consistently than adults or pupa, however. In addition, Ballmer and Pratt (1989a) have demonstrated that instar number in this subspecies is variable in the White Mountains: four instars are prevalent under warm, long-day (late summer) conditions while five instars predominate when days are cooler and shorter in fall. The number of instars is apparently fixed at oviposition, and developmental time is greater for five-instar larvae than for four-instar larvae.

The eggs are greenish-white and are laid singly, as related above. The mature larva in California populations shows some variability, but not to the extent of other populations throughout the temperate regions of the world as described by Scott (1986). Specifically, in populations on Mt. Dana in the Sierra Nevada and in the White Mountains, the mature larva may vary from a almost totally green form to a darker green form with intense violet markings. The basic ground color above the spiracles is a dull green, with a mid-dorsal, dull purplish-red line. Just below there is a pale purplish lateral line starting faintly on the first thoracic segment, and intensifying by the first abdominal segment. The ventral half of the body, including the legs and prolegs, is also green in this color form. At the other extreme in these populations, the larva is a dull green from the spiracles up to an intense purplish-red mid-dorsal line. The entire ventral half of the body below the spiracles is a dull purplish-red with an intense bright purple lateral line running the length of the body just below the spiracles. Even the prolegs are a dull purplish-red in this color form. The head is black in both larval color forms. The pupa is a purplish-brown in ground color, with heavy but diffuse black blotches over the entire surface except the wingcases, where the wing venation is the purplish ground color while the intervein spaces are filled with black blotching. The cremaster area is the pale purplish ground color. The species as noted above

is biannual in California, with hibernation in the third instar larva and again in the fourth instar larva. In Japan, Sakai and Masaki (1965; see also Endo et al., 1985) found that the onset of diapause in *L. p. daimo* Seite (or at least similar lengthened larval development and extra molts) is triggered by a shortening photoperiod and low temperature. Japanese adults of this species live up to fourteen days in nature.

FOODPLANTS: The only known foodplant of this species in California is *Oxyria digyna* (L.) Hill (Polygonaceae). J. Emmel and G. Pratt (1990) found larvae on this plant on the north slope of Mt. Dana and in the White Mountains in a cirque east of White Mountain peak. In the laboratory, larvae can be readily reared on *Rumex acetosella* L.

CHROMOSOME NUMBER: $n = 24$ (Emmel, Pratt, and Eliazar, 1990).

SIMILAR SPECIES: The species may fly in close proximity to Alpine populations of *Lycaena cupreus*, a superficially similar species which may be readily distinguished by the fact that on *cupreus* the dorsal surface of the hindwing is mostly copper-colored, whereas in *L. phlaeas*, this area of the wing is largely a brownish-charcoal gray.

GEOGRAPHIC AND SEASONAL VARIATION: As there is only one brood each year, there is no apparent seasonal variation. The populations in the White Mountains appear to be phenotypically identical to those found in the Sierra Nevada. The California *L. phlaeas* populations are the southernmost of any Arctic-Alpine *L. phlaeas* in North America. They are the only subspecies to be univoltine, apparently monophagous on *Oxyria digyna*, and confined to arctic-alpine habitats in the central Sierra Nevada and White Mountains. These areas are exposed to extreme and unpredictable weather for much of the year, especially cold (even in the summer, frost and occasional snow occur). The restricted range of this especially strange in view of the fact that suitable hosts (*Rumex* subspecies is species) are widespread at lower elevations in California where they are utilized by other *Lycaena* species (Ballmer and Pratt, 1989a). Those subspecies of *L. phlaeas* in Asia, Europe and eastern North America multivoltine, polyphagous (primarily on *Rumex* species). Their characters in relation to the other alpine subspecies of *phlaeas* are described by Ferris (1974). Life-history details in Ballmer and Pratt (1989b) were published under the name of *L. phlaeas hypophlaeus* (Boisduval).

GENERAL REMARKS: Our populations have gone under the subspecific name *hypophlaeas* Boisduval since 1852 (Dod, 1907; Klots, 1951; Shields and Montgomery, 1966; Ferris, 1974). An examination of the type specimen of *hypophlaeas* in the U. S. National Museum has revealed that the phenotype of this specimen is identical with *L. phlaeas* from lowland northeastern United States; it is not-at-all consistent with the facies of the California populations of *L. phlaeas*. At the time Boisduval named *hypophlaeas* (1852), he apparently had specimens from eastern North America and assumed that the species also occurred in California, describing its locality as "North of California. It is found in all the northern United States." No precise type locality was indicated, but certainly it was not in California. We have absolutely no evidence that Lorquin, the supplier of most of Boisduval's California material, ever got into the high Alpine areas of the Sierra Nevada (Emmel, Emmel, and Mattoon, 1990). Thus, the eastern subspecies name, *americana* Harris, falls as a junior synonym of *hypophlaeas* Boisduval. We leave the matter of fixing a type locality for this taxon to someone working with the lowland populations of *L. phlaeas* in the eastern United States.

This species in California is easily overlooked by collectors. The primary reason is that its favored habitat is rarely visited by the average collector, because of its usual inaccessibility and treacherous footing. Furthermore, there are few other butterflies in this habitat, making it an unattractive area for most lepidopterists to visit.

151. *Lycaena cupreus cupreus* (W. H. Edwards)

- DIAGNOSIS:** This small Copper has a bright reddish-orange dorsal ground color, with a metallic sheen to it and dark brown borders on the outer margins of the wings. Males are spotted on both forewings and hindwings with brownish-black small spots, whereas in females these spots are greatly expanded in comparison to the males. Ventrally, the forewing is a light orange, with a grayish outer margin. The outer margin is edged inwardly with a series of dark brown dashes or crescent-shaped markings, and the remainder of the forewing is marked with large brownish-black spots edged with white scaling. The ventral hindwing is a grayish-white with large black spots, and there is a sub-marginal broken orange line along the outer margin.
- ORIGINAL DESCRIPTION:** W. H. Edwards, *Transactions American Ent. Soc.*, 3: 20-21 (1870).
- TYPE LOCALITY:** "Oregon". Lectotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Ent. Soc.*, 95: 176 (1969).
- DISTRIBUTION:** This species is widely distributed in the Sierra Nevada from Tulare County northward to Plumas County, and from there westward to the region around Bartle in extreme southeastern Siskiyou County. Outside of California, the species ranges to the southern edge of Alaska and eastward to the Rocky Mountains.
- ELEVATION RANGE:** From 3,600' to 12,500'.
- HABITAT AND PLANT COMMUNITIES:** The highest elevation populations are found in Arctic-Alpine Fellfield situations, usually on rocky or gravelly slopes or ravines where the *Rumex* foodplants are locally abundant. Low to mid-elevation populations occur in meadows or along streamsides or roadsides within Montane Coniferous forests.
- PHENOLOGY:** The species is usually univoltine, but some August records for several low to mid-elevation populations suggest that it may be bivoltine in some localities, depending on precipitation amounts and length of the potential summer flight season.
- ADULT BEHAVIOR:** Males perch on rocks or on open patches of ground on the rocky or gravelly slopes, or in small ravines, or along roadsides. Females tend to be more sedentary, frequently landing on the foodplant or on the ground adjacent to foodplants. The adults are frequently seen nectaring at the flowers of Pussypaws (*Calyptridium umbellatum* (Torr.) Greene).
- LIFE HISTORY:** The eggs are laid on the foodplant, usually on the lower stems or leaf undersides near the base of the plant. In some instances, oviposition may occur on debris or small rocks near the base of the plant. The eggs hatch within five to six days in the laboratory, probably taking a week or more under field conditions. The larvae feed to the third instar, in which they go into diapause. The following season, diapause is broken, the larvae feed through the fourth instar, pupate, and emerge within ten to fourteen days under laboratory conditions.

The egg is undescribed. The mature larva as seen in the population in Calavares County on *Rumex acetosella* L., is dull green in ground color, with a diffuse lighter area on the dorsal surface, culminating in two diffuse yellowish-green stripes on either side of the mid-dorsal line of green. There are no other markings on this soft green larva; even the spiracles are pale green, except for reddish centers. This color exactly matches the background leaf color of the *Rumex* species with which they were associated with in the field. The pupal stage is a light ivory tan in ground color, with several longitudinal rows of blackish-brown spots on the abdomen and across the dorsal surface of the thorax. The wings are lightly marked with alternating stripes of tan and dark brownish pigment. The antennae, proboscis, and eye cases are dark brown. There is a dark brown mid-dorsal line running the length of the pupa, also.

FOODPLANTS: The native foodplant of this species in California is *Rumex paucifolius* Nutt. ex Wats. ssp. *paucifolius* and ssp. *gracilescens* (Rech. f.) Rech. f. (J. Emmel, G. Pratt, and G. Ballmer, unpublished data). Additionally, many populations at mid-elevations and low elevations, particularly those in the extreme northern Sierra Nevada and southeastern Siskiyou County are associated only with the introduced *Rumex acetosella* L. (Sheep Sorrel).

CHROMOSOME NUMBER: n= from Tioga Pass material ().

SIMILAR SPECIES: The coloration and wing pattern of this species is distinctive, and it is not easily confused with any other Copper species. Occasionally, populations of this Copper may exist in close proximity to populations of *L. phlaeas alpestris*; see Similar Species section under that species for a discussion of the differences between *L. cupreus* and *L. phlaeas*.

GEOGRAPHIC AND SEASONAL VARIATION: In the few instances where there has been an apparent small late summer second brood, no phenotypic difference has been noted between the spring-flying individuals and summer-flying individuals in that particular locality. At the northwest edge of this species' range in California, namely in Plumas County and southeastern Siskiyou County, specimens tend to be larger, slightly more heavily marked with the black markings, and females tend to be suffused with dark scaling over the orange ground color dorsally. We have seen no significant differences between the populations in the White Mountains and those in the Sierra Nevada.

A curious feature of this species is the number of populations, particularly at mid-elevations on the west slope of the Sierra Nevada, or at various elevations in the extreme northern Sierra Nevada and southeastern Siskiyou County, as all of these populations appear to use the introduced *Rumex acetosella* L. as their sole foodplant. This *Rumex* species is a weedy colonizer of disturbed areas such as roadsides, railroad right-of-ways, and other human disturbed areas. Thus, we may be witnessing the rapid expansion of the range of *L. cupreus* in California into areas not occupied by the butterfly before the coming of the first European settlers. It is of particular interest to note that Lorquin, collecting extensively in the northern Sierra Nevada in the 1850's, did not collect specimens of *L. cupreus*, to our knowledge. It is possible that virtually all of the northern Sierra Nevada *cupreus* populations (i.e., north of Lake Tahoe) have become established within the last 100 years.

152. *Lycaena mariposa mariposa* (Reakirt)

This is a local species, occurring in the high Canadian Zone from southern Alaska and British Columbia south in the Rocky Mountains to Colorado, and in the Sierra Nevada to northern California.

DIAGNOSIS: This is a strongly sexually dimorphic Copper, with the ground color of the upperside of males being a dark brownish-purplish color, with a dark border and a small orangish crescent-shaped marking near the anal angle. The female upperside is a dull dark brown with light orange patterning on the forewing broken by several irregular dark rows of spots. On the hindwing, there are several patches of light orange scaling with a border of light orange crescents along the submarginal area. The underside is the most distinctive feature of this Copper, in that the ground color of the hindwing is a light gray with several irregular lines composed of black crescent shapes or roundish spots, giving a banding affect to the wing pattern. The basal area of the wing is darker than the post-median area. On the ventral forewing, the ground color is a light orange, bordered by a submarginal area of dark brownish-gray, and there are scattered dark spots within the light orange area.

ORIGINAL DESCRIPTION: Reakirt, *Proceedings Ent. Soc. Philadelphia*, 6: 149 (1866).

TYPE LOCALITY: "California". Syntypes in Field Museum of Natural History, Chicago.

DISTRIBUTION: Within California, this species is found in scattered populations in the northern Sierra Nevada and Klamath Mountains region. The southernmost Sierra Nevada populations occur in Tuolumne County and extend northward to the Gold Lake area in Sierra County. In the Klamath Mountains region, colonies are known in the Trinity Alps, Mt. Eddy, and Scott Mountain.

ELEVATION RANGE: From 4,500 to 10,000' elevation.

HABITAT AND PLANT COMMUNITIES: This species is found at the edges of boggy meadows, often among Lodgepole Pines, or in open glades in the forest and in small sub-Alpine meadows on open slopes, all within the Montane Coniferous forest or sub-Alpine forest plant communities.

PHENOLOGY: Adults fly from early July to late August, depending on elevation and snowpack conditions. This species is univoltine and overwinters as an egg.

ADULT BEHAVIOR: Shapiro et al (1979) notes at least two nectar sources for this species: *Helenium digelovii* Gray (a plant rarely visited by butterflies) and *Aster alpigenus* (T. & G.) Gray ssp. *andersonii* (Gray) Onno (Asteraceae). Opler (1975) also notes *Fragaria* as a nectar source. Males are attracted to mud or moist ground, particularly along partially shaded trails. Males will perch on low vegetation.

LIFE HISTORY: The egg was described by Coolige (1910a), but the larva and pupa have not been described previously. The mature larva (based on Siskiyou County material collected by G. Pratt and G. Ballmer) has a velvety medium-green ground color over the entire body, except for a faintly darker mid-dorsal line and a light yellowish lateral line on either side below the spiracles. The spiracles are yellow, and the entire body surface is covered by short yellowish hairs. The pupa is a somewhat duller green in ground color, with a darker green mid-dorsal band and a lighter green abdomen. The positions of the abdominal spiracles are marked by yellow spots, forming a necklace of yellow dots extending laterally around the abdomen.

- FOODPLANTS: *Vaccinium arbuscula* (Gray) Merriam in the family Ericaceae is the only known host (Pratt and Ballmer, 1986). Other hosts have been listed erroneously in the past literature, and the reader is referred to the Pratt and Ballmer paper for explanation as to why they are not valid host records.
- CHROMOSOME NUMBER: Unknown.
- SIMILAR SPECIES: The combination of ventral forewing and hindwing coloration patterns will distinguish this *Lycaena* from its other congeners in California.
- GEOGRAPHIC AND SEASONAL VARIATION: Shapiro *et al.* (1979) note that specimens from the Klamath Mountains region tend to be more heavily marked beneath than Sierran ones from similar elevations and habitats.
- GENERAL REMARKS: The limited distribution of this butterfly, in contrast to the more widespread distribution of its known foodplant, is puzzling. Guppy (1964) notes that one reason collectors have considered *L. mariposa* to be a scarce butterfly throughout its range is its very late season of flight. Above timberline in British Columbia, for instance, it is not likely to be seen before August 20th, long after most other alpine species have flower.

153. *Lycaena nivalis* (Boisduval)

- ADULT BEHAVIOR: The adults of *nivalis* have been observed visiting the flowers of Yarrow (*Achillea millefolium* L.), Woolly Sunflower (*Eriophyllum lanatum* (Pursh) Forbes), often on blooms of several *Eriogonum* species and other flowers near the foodplant. Males frequently perch all day on the ground and open areas to await females.
- LIFE HISTORY: The life history of *Lycaena nivalis* was first described by Newcomer (1911, 1964) from material taken at Deerpark, near Lake Tahoe from females ovipositing on *Polygonum douglasii* Greene. The egg is pale bluish in color and 0.85 millimeters in diameter. The shape is that of a depressed spheroid, ornamented with deep, polygonal pits. There are four larval instars, which initially are brownish-yellow and then become pale green. The mature larva is pale green with a dorsal line of rose or purplish color. A narrow whitish line occurs to either side on the dorsal surface. The cervical shield is sunken on full-grown larva, and is in the shape of a double diamond. The body is covered with short brownish-hairs. The dorsal surface is covered with small white, hairless tubercles. The head is dark brown. More recently obtained material from Tioga Pass (J. Emmel) shows a mature larval coloration of a soft green across the entire body surface, with a very faint mid-dorsal purplish line and two very faint bands on either side of this line, yellowish-green in color. Just below the spiracles on either side, occurs a lateral line of diffuse yellow color. The pupa is pale tan in ground color, with a large number of minute brown striations over the entire surface. There is a prominent purplish mid-dorsal line across the abdominal segments, turning to dark brown as across the thoracic and head areas. Tiny minute hairs, resembling miniature trumpets, are scattered thickly on the dorsal surface of the head, and more sparingly across the thorax and abdomen, appearing like minute tacks stuck into the surface of the pupa. The species overwinters in the egg stage.
- GEOGRAPHIC AND SEASONAL VARIATION: This species is single-brooded, so there is no seasonal variation. Geographic variability in this species has been discussed over its broad range by Newcomer (1964). He looked at the populations from northern Washington to the Warner Mountains in northern California, and observed the more brilliant yellow and pink undersides occurred in populations where precipitation was high (at least 40 inches annually),

whereas specimens from areas with light spring rainfall and an annual precipitation of less than 20 inches tended to have a washed out light cream underside, with a tinge of pinkish on the hindwings, but no evidence of yellow. He suggested that in the areas where intense coloration in this species occurs, there would be less sunlight due to frequent cloudiness, and this may be a factor in determining the intensity of the colors. In areas where the colors beneath are less intense, there is more sunlight. He also examined the change in temperatures over this gradient and decided that neither temperature nor elevation was a factor that correlated with color variations found in *nivalis*.

GENERAL REMARKS: Newcomer also noted that because the foodplant is an annual, the newly hatched larvae the following spring must seek out seedling plants sprouting from seeds produced by the *Polygonum* plants on which oviposition occurred the previous year. Despite the hazards of extreme temperatures during the winter and the spring search for newly sprouting seedlings, the species is relatively successful and quite common at times in its colonies.

Within its range, from the Rocky Mountains to California and north into British Columbia, this species is widespread in mountainous areas and rather variable in adult coloration (e.g., Brown, 1961). There are three subspecies found within our state.

a. *L. n. nivalis* (Boisduval)

DIAGNOSIS: This species is strongly sexually dimorphic, like most of the other Coppers. The upperside of males is a light brown with a purplish sheen, and there is a scalloped light orange border along the outer margin of the hindwing. Females tend to be light orange with a pattern of dark brown spots on the upperside and dark marginal and basal areas on both wings. On the underside, the forewing is a pale cream in ground color, with dark brown markings. The hindwing ventral surface is a pinkish-gray, of fairly uniform coloration from the basal area to the post-median area of the wing. Black spotting on the hindwing is usually reduced to rather small spots, often becoming obsolete in this subspecies.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. Belgique*, 12: 44 (1869).

TYPE LOCALITY: "California". Suggested as probably Sierra, Nevada, Placer or El Dorado County by dos Passos (1938). Restricted by Emmel, Emmel, and Mattoon, , : (1990) to Gold Lake, Sierra County, California. Holotype in U. S. National Museum.

DISTRIBUTION: The nominotypical subspecies is widely distributed in the Sierra Nevada from the Mineral King area of Tulare County northward to Plumas County. From there it extends northwestward along the eastern portion of the Mt. Shasta region to the westernmost distribution of subspecies *warnermontana* in the Goosenest District area of the Cascade Range in northern Siskiyou County.

ELEVATION RANGE: 4,500 to 10,000' elevation.

HABITAT AND PLANT COMMUNITIES: This species is most commonly encountered in dry meadows within the Montane Coniferous Forest plant community. One adult nectar source which is frequently visited is Pussypaws (*Calyptridium umbellatum* (Torr.) Greene) (Portulacaceae).

PHENOLOGY: This species is univoltine, but has a fairly long flight period extending from late June to early September, depending on elevation, exposure, and snowpack. The peak flight period seems to be late July to early August, in most localities.

FOODPLANTS: For the Sierran populations, *Polygonum douglasii* Greene (Polygonaceae) (Newcomer, 1964).

b. *L. n. bicolor* Emmel and Pratt

DIAGNOSIS: In this subspecies, both sexes are much like Sierran *nivalis* on the uppersides, with the exception of the females having somewhat more extensive dark brown basally on both forewing and hindwing. The most striking difference is in the coloration of the underside. The forewing ground color is a lemon-yellow, with a slight orangish flush in the posterior half of the submarginal area. On the hindwing, there is a striking "two-tone" quality to the wing coloration, with the proximal half of the wing lemon-yellow and the distal half a mauve or grayish-pink color.

ORIGINAL DESCRIPTION: Emmel and Pratt, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990).

TYPE LOCALITY: Mt. Eddy, Siskiyou County, California.

DISTRIBUTION: This subspecies is found throughout the Klamath Mountains Assemblage and northward into the southern Cascade Range of Oregon, specifically in Linn and Jackson counties. To the north and east, in Washington, Idaho, Wyoming and Utah, occurs *L. nivalis browni* dos Passos (1938), which has duller brown males with a brilliant violet reflection that hides the brown seen in typical *nivalis*.

ELEVATION RANGE: From 5,000 to 9,000' elevation.

HABITAT AND PLANT COMMUNITIES: This subspecies is common in dry meadows, on rocky slopes, and along trails, usually in full sun, within the Montane Coniferous Forest and Sub-Alpine Forest plant communities (Shapiro, 1979).

PHENOLOGY: Records range from mid-June to mid-September, indicating a very long flight period in the Klamath Mountains area.

FOODPLANTS: This subspecies is closely associated with *Polygonum spergulariaeforme* Meissn., and this plant is very strongly suspected to be the foodplant.

c. *L. n. warnermontana* Emmel and Pratt

DIAGNOSIS: In this subspecies, the males are much like Sierran *nivalis*, except that on the underside the post-median row of black spots on the hindwing is noticeably more prominent. The most marked differences occur in the females, which are noticeably more melanic than their Sierran counterparts. In some females, the forewings and hindwings on the upperside are largely obscured by dark brown scaling, with the light orange pattern reduced to a few patches in some specimens. On the underside, the spotting pattern is noticeably more prominent, particularly on the hindwings where the post-median row of black spots stands out very strongly. Otherwise, the ventral ground color is much like that of Sierran *nivalis*.

ORIGINAL DESCRIPTION: Emmel and Pratt, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990).

- TYPE LOCALITY: Bidwell Peak, near Dismal Swamp, 6 air miles east of Highway 395 at New Pine Creek, Modoc County, California.
- DISTRIBUTION: This subspecies appears to be largely confined to the Warner Mountains in northeastern California and extreme southern Oregon. It is also abundant in the uplands of the Goosenest District of the Klamath National Forest in the Cascade Range, a block of high mountains just south of the Oregon state line between Highway I-5 and Highway 97.
- ELEVATION RANGE: 6,000 to 8,200' elevation.
- HABITAT AND PLANT COMMUNITIES: This butterfly, wherever found, breeds in the more mesic areas of the *Artemisia* scrub at elevations above 6,000'. The habitat is one of sagebrush within which springtime water-catch flats produce grassy meadows with abundant *Eriogonum* sp., sunflowers, lupines, and wildflowers in the surroundings. These areas are often adjacent to yellow pine or mixed with Red Fir forest stands where snowbanks accumulate in winter to feed the moisture out and produce the flower-studded nivalis habitat. Occasional wet permanent meadows marked by Quaking Aspen and willow will result. The larval host of *warnermontana* will often become dense stands of this tiny *Polygonum*.
- PHENOLOGY: Records for this species extend from late June to mid-August, again indicating a fairly long flight period for this univoltine species.
- FOODPLANTS: The foodplant is unknown for the Warner Mountains populations, but *Polygonum douglasii* Greene is common in the Warner Mountains and Goosenest District and is the likely host. Although it is not the only *Polygonum* in the habitat, it is the most abundant, and is always in association with the flight area of this subspecies.

154. *Lycaena helloides* (Boisduval)

This species, known as the Purplish Copper, occurs from southern California to Alaska and east to almost the northeastern states. In our state, it is found in the form of the nominotypical subspecies.

- DIAGNOSIS: Males of this species have a purplish ground color above, with dark brownish-black borders and a scalloped reddish-orange sub-marginal border on the hindwing, accentuated near the anal angle. Females, on the upperside, have varying amounts of the light orange ground color and the dark brown markings; in some, the light orange ground color predominates and there is a dark brown border and a series of dark brownish-black spots on both wings, with brown scaling basally and a scalloped orange sub-marginal band as in the male. However, some females are much darker, with the dark brown ground color predominating and the light orange areas broken up by enlarged dark brown spots and markings. On the underside, the most characteristic feature is the orangish-gray or ruddy-gray ground color of the hindwing. The forewing is usually yellowish to yellowish-orange on the underside, with dark black markings. There is a rather fine reddish scalloped line submarginally on the ventral hindwing, also.
- ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 291 (1852).
- TYPE LOCALITY: "San Francisco, California." Holotype in U. S. National Museum.
- DISTRIBUTION: This species is widespread in a variety of habitats in California, absent only from the Mojave and Colorado Deserts. It is found from the Mexican border northward

through San Diego County, through the lowlands and mountains of southern California northward, through the Coast Ranges, Central Valley, and Sierra Nevada to the Oregon border. This species is also found on Santa Cruz Island in the Channel Islands.

- ELEVATION RANGE: From near sea level to 7,700' elevation.
- HABITAT AND PLANT COMMUNITIES: This species is usually found in moist bottomlands, such as along rivers and canals or other man-made watercourses, particularly in valley bottoms. It is also found in scattered populations in similar habitats in the foothills and mountains. Some of its foodplants are introduced European weeds, and this probably accounts for the tendency to find this butterfly in areas where human disturbance is more marked. Its associated plant communities include Freshwater Marsh, Valley Grassland, Riparian Woodland, suburban-agricultural areas, Chaparral, Coastal Sage Scrub, Sagebrush Scrub, Montane Coniferous Forest, Foothill Woodland, and Subalpine Forests.
- PHENOLOGY: This species is multivoltine, with captures ranging from early March to late November.
- ADULT BEHAVIOR: Males usually perch on low vegetation to await passing females. When females are forced to land by a pursuing male, they invariably fan their wings intermittently in response to the activity of the male. Shapiro (1973c) observed an attempted interfamilial mating between a fresh male *Lycaena helloides* (Lycaenidae) and a fresh female *Cynthia annabella* (Nymphalidae) in a vacant lot at Southport in Yolo County. The male courted the female for nine minutes without success; the *C. annabella* was estimated to be fully twice the size of a *L. helloides* female, and resembled it superficially only in general color.
- LIFE HISTORY: The early stages were first described by Comstock (1927b, 1929). The echinoid egg is somewhat more flattened than those of the other *Lycaena* species, and especially differs in the less extreme reticulation and presence of nodules instead of thin high walls and deep cells. The mature larva is grass-green and has a bright yellow lateral stripe, as well as a broken bright yellow line on each side of the mid-dorsal region. A faint yellow oblique dash occurs on the side of each segment. The body hairs are colorless, and somewhat longer than those of other *Lycaena* species. The pupa is greenish, with brown and black markings, and has numerous pale green low warty tubercles, bearing bristles. The life history was also described but not illustrated by Coolidge (1924b).
- FOODPLANTS: The following species of Polygonaceae have been given as foodplants: *Polygonum aviculare* L., *P. lapathifolium* L., *P. persicaria* L., *P. punctatum* Ell., and *Rumex crispus* L. This species is also associated with *Potentilla egedei* Wormsk. (Rosaceae) in the Suisun Marsh in central California (Shapiro, 1974a and 1974b) and with *P. fruticosa* at high elevations. Other species of Polygonaceae have been documented for *L. helloides* populations outside of California (e.g., Chambers 1963), and undoubtedly some of our populations use these same foodplants.
- CHROMOSOME NUMBER: Unknown.
- SIMILAR SPECIES: Very worn specimens of *L. helloides* may resemble *L. nivalis*. Since the two species are largely allopatric, there is unlikely to be any confusion, but in the few montane localities where the two might occur sympatrically, *L. helloides* is

identified by the more orangish-gray underside of the hindwing in contrast to the flatter pinkish-gray of *L. nivalis*.

GEOGRAPHIC AND
SEASONAL VARIATION:

None.

GENERAL REMARKS:

This is a "weedy" species and may be expected to colonize many human-disturbed areas in the state. Subalpine specimens are smaller, with more gray ventrally on the secondaries, and tend to resemble *L. dorcas*. Kirby. Chambers (1963) has suggested that the high-altitude univoltine *florus* Edwards of Colorado may not be referable to either *L. dorcas* Kirby or *L. helloides* Boisduval, having biological differences in host preference, elevation, and number of broods. Our California material deserves further field study as well.

155. *Lycaena gorgon* (Boisduval)

ADULT BEHAVIOR:

The adults avidly visit *Eriogonum* flowers. Adults of the Warner Mountains and Lower Rock Creek populations avidly visit flowers of *Apocyanum* species. Males perch along small ravines, on open patches of soil, or along roadsides, particularly at the bases of road cuts.

LIFE HISTORY:

The early stages were first described by Comstock and Dammers, in 1934. The eggs are laid singly, or occasionally in pairs or threes, at the forks of the flowering stems of the host plant. They then diapause until the following spring. The egg is echinoid, flattened at the base, with a deep micropyle at the top, with a size of about .48 millimeters high by .84 millimeters in diameter. The surface of the egg is extraordinarily deeply ribbed into a series of about 22 longitudinal folds, which are then connected by lower horizontal partitions. The cells enclosed by these walls are deep and unlike the appearance of the other members of the genus. The color at first is a delicate green, but later the ridges assume a glistening white and the general color of the egg is a creamy white. The mature larva is a pale turquoise green, becoming extremely light in the Warner Mountains. This basic ground color is largely obscured by a covering of dense long white hairs. This gives the larva a protective coloration matching the leaves of the foodplant. Underneath these hairs, on the ground color of the larva, are a row of whitish diagonal dashes, one on each segment and protruding out from the dorsal midline in a posterior direction. Thus, these form two parallel rows on the dorsal surface of white, rearward angling bars. The spiracles are pale tan in color. There is a narrow white band running laterally below the spiracles. The legs are colorless, and the prolegs are pale green with light brown claspers. The head is pale buff, with brown mouthparts. Pupation takes place late in May on the foodplant, with the support of a delicate silk girdle. The pupa is pale blue-green in ground color with a slight yellowish shading on the abdominal segments. All surfaces but the wingcases are thickly studded with minute fungoid or trumpet-shaped white protrusions, although these are absent in four longitudinal rows of circular patches on the dorsal surface of the abdomen (appearing darker green than in the dorsal view).

CHROMOSOME NUMBER:

Unknown.

SIMILAR SPECIES:

Although the males superficially resemble those of other *Lycaena* species on the dorsal surface, both sexes are distinctively colored on the ventral surface from other *Lycaena*.

GEOGRAPHIC AND
SEASONAL VARIATION:

Within any given locality, there is considerable variation in the adult pattern, both upperside and underside. However, for the nomotypical

subspecies the range of this pattern seems fairly constant from population to population throughout most of the state.

GENERAL REMARKS: This Copper species is almost entirely confined to California, and is a distinctive species of our fauna.

The metropolis of this western Copper species is in California, with a slight extension into southern Oregon. It is found in foothill woodland and chaparral areas. Within our state, three subspecies have been identified.

a. *L. g. gorgon* (Boisduval)

DIAGNOSIS: In this species, the males on the upperside have a light violet-brown ground color, with a purplish sheen and a dark brown border along the outer margins with a white fringe. Near the anal angle, there is a varying sized area of light orange markings, usually in somewhat of a scalloped pattern. The upperside of the females is a pale yellowish-orange, with light grayish-brown suffusion at the base of both wings, and a light grayish-brown wide border along the outer margin of the forewing. There are a series of dark brown spots on both the forewing and hindwings, rendering somewhat of a checkered pattern. Along the outer margin of the hindwing are a series of pale orange crescent-shaped markings, each enclosing a round dark brown spot. The outer fringes are also white in the females. On the underside, the usual ground color is a light grayish-tan and there is a pattern of dark brown to black spots scattered over both forewing and hindwing. Along the outer margin of the hindwing, there is a series of red-orange markings, usually crescent-shaped, with a dark spot distal to them and an arrow-shaped edging of dark scaling proximally.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 292 (1852).

TYPE LOCALITY: Mountains of California. Restricted by Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1988) to Lower Feather River Canyon, Butte County, California. Type in U. S. National Museum.

DISTRIBUTION: The typical subspecies of *gorgon* is widespread in Cismontane California from San Diego County northward through the foothills and mountains of southern California through the Sierra Nevada foothills and the Coast Ranges to the Mt. Shasta region. From here it ranges into extreme southwestern Oregon.

ELEVATION RANGE: From 400 to 4,000' elevation.

HABITAT AND PLANT COMMUNITIES: This species is usually found in canyons or on dry slopes within the Chaparral or Coastal Sage Scrub plant communities, rarely entering the lower edges of the Montane Coniferous forest.

PHENOLOGY: Strictly univoltine. The majority of our records range from late April to early July, with an apparent peak flight period during the month of May. There is one late March record.

FOODPLANTS: The nomotypical subspecies uses both *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes, and *E. elongatum* Benth.

b. *L. g. megapunctata* Emmel and Pratt

- DIAGNOSIS: This subspecies is readily characterized by the greatly enlarged dark spots on the underside of both sexes. On the uppersides, the pattern in males is similar to that seen in typical *gorgon*; in the females, there is a tendency for expansion of the light yellowish-orange areas, giving a "blond" appearance to some specimens. On the underside, the ground color ranges from a light tannish-gray to a yellowish-tan. All of the black spots on the underside are markedly enlarged from that seen in the nomotypical subspecies.
- ORIGINAL DESCRIPTION: Emmel and Pratt, *Journal Research Lepidoptera*, : (1988).
- TYPE LOCALITY: Pine Creek Canyon, County Road 2, 3 roadmiles east of New Pine Creek, Modoc County, California.
- DISTRIBUTION: This subspecies is found in the Warner Mountains of northeastern Modoc County, extending northward into extreme southern Oregon in the same range. From here it extends westward to northeastern Siskiyou County in the Goosenest District.
- ELEVATION RANGE: From 5,000 to 6,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This *gorgon* subspecies has habitat requirements similar to those described for Warner Mountain *nivalis* except that the *Artemisia* scrub within which it flies is slightly drier, lacking the grassy rain-catch flats with seeps that are more abundant on the higher portions of its montane distribution. *Megapunctata* utilizes the lower, drier slopes and foothills of the range which are still moist enough to produce abundant sunflowers, occasional thistles and junipers, along with patches of *Apocynum*. Here on the gravelly, sometimes lava-rubble slopes, the host *Eriogonum nudum* grows in abundance as do lupine species. While most abundant on lower slopes, this *gorgon* subspecies also follows such habitat upwards into the Coniferous Forest areas, and often the Dogbane or *Monardella* nectar sources attract *megapunctata* within forested areas, to feed where these plants grow more prolifically. In all areas where we have taken this insect, there have been coniferous, oak, and chaparral mixed forests nearby, but it breeds out on the drier slopes.
- PHENOLOGY: From late June to early August, with a peak flight period in mid-July.
- FOODPLANTS: *Eriogonum nudum* ssp. .

c. *L. g. obliterated* Emmel and Pratt

- DIAGNOSIS: This subspecies is characterized by its smaller size and reduction or obsolescence of the black spots on the underside of both sexes. In the males, on the upperside there is expansion of the orange areas near the anal angle, in comparison to that seen in nomotypical *gorgon*. Females tend to be more lightly marked above than typical *gorgon*, with expansion of the pale yellowish-orange areas of the wings. On the underside, the ground color tends to be a paler shade than that seen on nomotypical *gorgon*.
- ORIGINAL DESCRIPTION: Emmel and Pratt, *Journal Research Lepidoptera*, : (1988).
- TYPE LOCALITY: South-facing slope above Lower Rock Creek, 6,150-6,200' elevation, 0.8 airmiles NNW of Sherwin Summit, Mono County, California. Holotype in Natural History Museum of Los Angeles County.

- DISTRIBUTION:** This subspecies is found on the east slope of the Sierra Nevada, from the region of Butterbrecht Peak in Kern County northward to Lower Rock Creek in Mono County.
- ELEVATION RANGE:** From 4,500 to 6,200' elevation.
- HABITAT AND PLANT COMMUNITIES:** This subspecies flies on open granitic sand slopes, often south-facing, within the Sagebrush Scrub plant communities or Jeffrey Pine forest plant communities in the Rock Creek region, and in sparse Joshua Tree woodland in the Butterbrecht Peak area and Ninemile Canyon areas of the southern Sierra Nevada. Within this habitat, *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes ssp. is locally abundant.
- PHENOLOGY:** This butterfly flies from early May to mid-June, with an apparently peak flight period in late May to early June, depending on elevation.
- FOODPLANTS:** *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes ssp. (Polygonaceae).

156. *Lycaena heteronea* (Boisduval)

- ADULT BEHAVIOR:** Males avidly perch and both sexes roost on Great Basin Sage whenever this species is present, although other shrubs may also be used. Orsak (1977) found by mark-release experiments that while some adults move very little within the population sites, others would move a great deal. Male movement appears to vary with the density and location of adults in the population. In the population center, territorial interactions are frequent, whereas on the periphery of the population male movement is very slight. The presence of females is a better indicator of the breeding site than is male presence, since males tend to disperse also into the surrounding habitat.

Nectar sources in the southern California populations are primarily the larval host plant, *Eriogonum fasciculatum* Benth., which blooms only once a year at the time of adult emergence. At the beginning of the flight season, adults may visit *Lotus scoparius* (Nutt. in T. & G.) Otterley and at the end of the flight season, they may visit *Encelia* species. The presence of Great Basin sage (*Artemisia tridentata* Nutt.) as the preferred perching substrate appears important in southern California populations. Adult butterflies were never observed to fly through unsuitable habitats, such as a Pinyon Pine or Oak woodland, suggesting that these vegetational formations might form natural buffers to minimize adult dispersal (Orsak, 1977). Females stay close to the *Eriogonum* foodplants in all populations, from the coast to the sub-Alpine areas of its distribution. Males patrol in the morning and perch after 1:00 p.m.; matings occur from 9:00 a.m. to as late as 5:30 p.m. A pair may stay in copula for as long as 3-4 hours. Of ten females dissected, nine had single spermatophores present and one female had two, indicating most females mate only once.

- LIFE HISTORY:** The larva and pupa of nominotypical *heteronea* were described from Marin County material by Williams (1910). The egg of the southern California race, *clara*, was described by Comstock (1927a). Orsak (1977) gives a very generalized life history. Thus, the following account is drawn from material that we have observed, as well as the earlier published accounts. The egg (based on *clara* material) is a delicate light green, changing immediately after ovi-position to clear white. The eggs are nearly spherical in shape and the small micropyle is a deep pit with abrupt walls. The egg surface is covered by irregular depressions, separated by thin upright walls which gives the entire egg a spiny appearance with low relief. The eggs are usually placed on the underside of the leaves of the host,

and form the diapause stage until the following spring. The mature larva in the Marin County material examined by Williams, and Mt. Lassen and Warner Mountains material examined by us, shows a ground color of pale grayish-green, nearly the color of the dorsal surface of its foodplant. There is a pale median line on the dorsal surface, flanked on either side by a broader pale band, extending the length of the larva also. Arising from each of these lateral bands are two diagonal posteriorly-facing white bars on each segment. These dorsal markings are all very faint in appearance. From a lateral view, the two diagonal stripes on each segment form two wavy bands extending the length of the larva on each side. At the level of the spiracles is another very pale, barely visible light band running horizontally along the length of the larva. Below the spiracles is a stronger pale yellow band running the length of each side. This lower lateral line is the plainest of the markings, and is whitish in all populations.

The pupa has a similar ground coloration of light whitish-green. The wing covers are almost white, and are reticulated with grayish-white. There is a pale green dorsal thoracic line which becomes darker where it meets the first abdominal segment, and then becomes more obscure on the abdomen until it reaches a darker line near the cremaster end of the pupa. The entire surface of the pupa bears numerous white spots, with the exception of the wing covers.

CHROMOSOME NUMBER: $n = 68$ in Colorado material (Emmel, Eliazar, and Harris, 1990).

SIMILAR SPECIES: This is the only Copper species with a blue male. Dark females of *heteronea* can resemble the females of *Lycaena rubidus* in the Warner Mountains.

GEOGRAPHIC AND SEASONAL VARIATION: There is considerable phenotypic variation of this butterfly within any given locality and virtually all populations show this extreme variability. In our geographic subspecific scheme, there are a number of populations which do not neatly fit into a particular described subspecies, but tend to represent intermediate populations. In the North Coast Ranges, particularly in the Yolla Bolly Mountains region, populations there seem to be intermediate between nominate *heteronea* and the subspecies *submaculata*. Along the crest of the Sierra Nevada there are some populations which show characters of both the subspecies *immaculata* and *submaculata*. In the southern Sierra Nevada on the western slope in Tulare County, populations show characters of the subspecies *clara*. Reference to the Distribution Map will help clarify some of these distributional patterns.

GENERAL REMARKS: The southern California subspecies, *L. h. clara*, has been suggested as a potential candidate for an endangered species classification because of the destruction of habitat in some of its remaining population areas. Today there are 30 or fewer populations, and most are located in the Cuddy Valley area of the Tehachapi Mountains, near Gorman. This is a site for extensive mountain-cabin resort development and also for the conversion of sagebrush areas to pasture land. Orsak (1977) presents a cogent argument for habitat and population management of this species in order to avert its extinction in the future.

This bright blue Copper is found in the Great Basin and the Sierra Nevadas and in a disjunct population in southern California. It is extraordinary for having a brilliant blue color in the males instead of the usual coppery tone.

a. *L. h. heteronea* (Boisduval)

- DIAGNOSIS:** The nominotypical subspecies of *heteronea*, found in Marin and Sonoma counties north of San Francisco Bay, is the largest of the California subspecies of *heteronea*. The male's dorsal surface is a lilac-blue with a violaceous sheen. On the upperside of the females, the ground color of the wings varies from a yellowish-tan to a dull gray-brown. On both forewing and hindwing, there are varying amounts of blue scaling in the medial two-thirds of the wing, often fairly prominent. The submarginal area of the hindwing is marked by a series of orangish-tan markings, usually each containing a small black spot. Inwardly, these are marked with crescentic-shaped areas of dark brown spots, giving a sort of "scalloped" appearance to this band on the hindwing. On the underside, the ground color of the males is a pale grayish-white and on the females a pale grayish-cream. The pattern of black spots on the forewing is relatively reduced and there are no black spots on the hindwing, but there are several patches of brownish-gray scales, giving a very faint spotting pattern.
- ORIGINAL DESCRIPTION:** Boisduval, *Ann. Soc. Ent. France*, (2)10: 298 (1852).
- TYPE LOCALITY:** Mountains of California. Restricted by Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990) to Bodega Bay, Sonoma County, California. Holotype in U. S. National Museum.
- DISTRIBUTION:** This subspecies is found along the immediate coast from southern Marin County northward to southern Sonoma County. It may be expected to occur at other points along the coast as the foodplant extends as far north as southern Oregon in various coastal localities.
- ELEVATION RANGE:** From sea level to approximately 100' elevation.
- HABITAT AND PLANT COMMUNITIES:** This subspecies is found within the Coastal Strand or North Coastal Sage Scrub plant communities along the immediate coast. In these habitats, the foodplant, *Eriogonum latifolium* Sm., is often locally abundant.
- PHENOLOGY:** This subspecies has a long flight period from early May to early July, depending on the degree of summer fog, winter rainfall patterns, etc.
- FOODPLANTS:** The apparent sole host of this set of populations is *Eriogonum latifolium* Sm. (Polygonaceae).

b. *L. h. clara* (Hy. Edwards)

- DIAGNOSIS:** This southern California subspecies is characterized by its smaller size, reduction of black markings on the underside of the forewings, the very pale underside in both sexes, and the very extensive blue scaling seen on the upperside of females. This blue scaling is a silvery powder blue and usually extends over the medial two-thirds of the forewing, sometimes extending even into the submarginal area of the forewing and scattered over the entire wing on the hindwings. On the upperside of the males, the ground color is a light lilac blue with a metallic sheen.
- ORIGINAL DESCRIPTION:** Henry Edwards, *Pacific Coast Lepidoptera*, (26): 1 (1880).
- TYPE LOCALITY:** "Colorado and the mountains of California," but all syntypes are from Tehachapi, California. Syntypes in American Museum of Natural History.
- DISTRIBUTION:** This subspecies ranges from the Tejon Range in extreme southwestern Kern County and northern Ventura County northeastward through the Tehachapi

Mountains to the Piute Mountains of the extreme southern Sierra Nevada. Records of this species from the Silverwood Lake area of the San Bernardino Mountains we consider to be mislabelled. In recent years, *L. h. clara* has not been found at its type locality in the Tehachapi Mountains (including former colony sites in Antelope Canyon, Double Mountain, and the Tehachapi Mountain County Park), where it may be extinct now. It may still occur on private property on the eastern and southern slopes of the Tehachapi Mountains.

- ELEVATION RANGE:** From 3,000 to 7,000', with the majority of populations from 4,000 to 6,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** Orsak (1977) summarizes the general habitat and plant associations as follows. Populations are nearly always located in montane valleys, occasionally on mountain slopes. They usually occur in the Sagebrush Scrub community, sometimes with scattered trees such as Pinyon Pine (*Pinus monophylla* Torr. & Frem.) or Canyon Oak (*Quercus chrysolepis* Liebm.). They are rarely found in forest clearings, in contrast to the nominotypical subspecies of this butterfly. Populations are always located on well-drained soils in areas with adequate moisture; *clara* is almost never found on south-facing or other arid slopes. Many populations are located in or adjacent to dry, gravelly washes or gullies.
- PHENOLOGY:** Records range from late June to early July, with a peak flight period in early to mid-July.
- FOODPLANTS:** The following *Eriogonum* species have been documented as foodplants of this butterfly: *E. heermannii* Dur. & Hilg. (probably the most commonly used host), *E. umbellatum* Torr. ssp. *munzii* (Reveal) Thorne, and *E. fasciculatum* Benth. ssp. *polifolium* (Benth.) Stokes. The usage of *Eriogonum fasciculatum* Benth. is apparently confined to plants that are especially robust and succulent.

c. *L. h. immaculata* Emmel and Pratt

- DIAGNOSIS:** This is a high montane subspecies of the Sierra Nevada, White Mountains, and Warner Mountains in California. It is characterized by relatively small size and the virtual absence of dark markings on the underside of the hindwing in both sexes, giving an "immaculate" appearance. The ground color of the upperside of the males varies from a pale cyanic blue to a pale lilac blue with a metallic sheen. On the females, the ground color of the upperside ranges from a dull gray-brown to a pale yellowish-tan. Varying amounts of blue scales are scattered over the medial half of the forewing and hindwing in the females, but generally never to the degree seen in nomotypical *heteronea*. Along the submarginal area of the hindwing, there is usually absence of the tannish-orange markings seen in nomotypical *heteronea* or if present, this is represented by a series of obsolescent tan crescents bordering very small dark brown spots. The underside ground color is a very pale whitish-cream in both males and females, with the females having a slightly deeper tint. The markings on the hindwings, if present, are reduced to very small patches of grayish-tan scales.
- ORIGINAL DESCRIPTION:** Emmel and Pratt, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990).
- TYPE LOCALITY:** Chiatovich Flats, White Mountains, 10,400 to 11,200' elevation, Mono County, California. Holotype in Natural History Museum of Los Angeles County.

- DISTRIBUTION:** This subspecies is found in the White Mountains, along the east slope of the Sierra Nevada, from approximately the area west of Lone Pine, northward to the Warner Mountains of Modoc County.
- ELEVATION RANGE:** From 6,000 to 11,200' elevation.
- HABITAT AND PLANT COMMUNITIES:** This butterfly is typically found in the Sagebrush Scrub plant community, where it is found on dry slopes and open ridgetops, particularly where *Artemisia tridentata* Nutt. is the dominant vegetation.
- PHENOLOGY:** Records range from early July to mid-August, depending on elevation, with an apparent peak flight period in late July and early August.
- FOODPLANTS:** The following *Eriogonum* species have been documented as hosts for this subspecies: *E. umbellatum* Torr. ssp. .

d. *L. h. submaculata* Emmel and Pratt

- DIAGNOSIS:** This subspecies of the west slope of the Sierra Nevada is characterized by a prominence of the dark markings on the underside of both the forewing and the hindwing in both sexes, but not to the extreme degree shown in the Rocky Mountain subspecies, *gravenotata* (Klots). It tends to be smaller in size than nominotypical *heteronea*. The upperside ground color of males ranges from a pale cyanic blue to a light lilac blue with a metallic sheen. On females, the upperside ground color ranges from a pale yellowish-tan to an orangish-tan with considerable dull gray-brown scaling in the basal area of both wings and along the outer margin of the forewing. The band of tannish orange lunules along the submarginal area of the hindwing tends to be poorly defined, and does not stand out significantly from the ground color of the adjacent areas of the wing. On the underside, the ventral ground color is a very light gray in males, and a very light tannish-gray in females. On the forewings, ventrally, there is increased prominence of the black markings in both the basal area of the wing, as well as in the submarginal areas. On the hindwing, the spotting pattern is well-developed, with the post-median band of brownish-black spots being the most prominent.
- ORIGINAL DESCRIPTION:** Emmel and Pratt, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990).
- TYPE LOCALITY:** Warner Valley, at southern boundary of Lassen National Park, Plumas County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION:** This subspecies is widely distributed over the west slope of the Sierra Nevada, from Tulare County in the south northward to Plumas County. From here it extends northwestward to populations in the southern Mt. Shasta region and eastern Klamath Mountains region.
- ELEVATION RANGE:** 4,500 to 9,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** This subspecies occurs in a somewhat more mesic habitat than its close relative, *L. h. immaculata*. It is usually found on open slopes or in ravines within the Montane Coniferous forest community.
- PHENOLOGY:** Records for this subspecies range from early July to late August, depending on elevation and exposure.

FOODPLANTS: The primary foodplant of this subspecies seems to be *Eriogonum nudum* (Dougl. ex Benth.) S. Stokes. However, other *Eriogonum* species such as *E. umbellatum* Torr., are present in the habitats of this subspecies and may serve as additional hosts.

e. *L. h. umbrosa* Emmel and Pratt

DIAGNOSIS: This subspecies was named for the dark, obscured upperside appearance of the females, which gives it a "shadowed" effect. This subspecies of the east slope of the Cascade Range in Oregon is found in extreme northern Siskiyou County in its southernmost extension. This butterfly is characterized by a heavy spotting pattern on the underside in some specimens, approaching that of the Rocky Mountain subspecies *gravenotata*. On the upperside of males the ground color is a deep lilac blue with a metallic sheen, with fairly prominent black borders along the edges of the wings. In the females, the upperside tends to be a uniform dull dark gray-brown with some blending of the darker spots into the background pattern. The pattern of orangish-tan markings along the submarginal area of the hindwing of the female may be completely obscured or only faintly present, or occasionally fairly well-developed in some individuals. Blue scaling is absent from the females. On the underside, in both sexes there is a marked accentuation of the black spotting pattern with all groups of the black spots enlarged from that seen in the other California subspecies of *heteronea*.

ORIGINAL DESCRIPTION: Emmel and Pratt, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990).

TYPE LOCALITY: Five road miles west of Martin's Dairy Campground, Goosenest District, Klamath National Forest, Siskiyou County, California. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This butterfly is found in scattered populations along the east side of the Cascade Range from Siskiyou County, California northward to at least Wasco County, Oregon.

ELEVATION RANGE: 5,000 to 6,000' for the populations in our area; apparently down to as low as 500' elevation in some of the Oregon populations.

HABITAT AND PLANT COMMUNITIES: *Umbrosa* is found on open rocky hillsides predominantly within the Yellow Pine Forest plant community, but extending higher to the Ball Mountain and Goosenest Mountain summits where areas of this open volcanic habitat arise in Lodgepole Pine, Red Fir, and Subalpine Forest settings. The breeding habitat is characterized by grasses and sagebrush scrub, *Artemisia tridentata*, in which an abundance of the suspected larval host plant, *Eriogonum hirtellum*, is found, along with other *Eriogonum* species such as *E. umbellatum*. A steadfast close association strictly with *E. hirtellum* suggests it is the larval host. *Haplopappus bloomeri* is an abundant nectar source which grows with *Monardella odoratissima* more commonly in the forested areas adjacent to the open habitat. But the *umbrosa* copper remains close to *Eriogonum hirtellum*, with both males and females nectaring on this plant.

PHENOLOGY: Adults fly from early July to mid-August.

FOODPLANTS: Unknown.

157. *Lycaena rubidus* (Behr)

- ADULT BEHAVIOR:** Males perch on low shrubs and streamside vegetation in wet meadows, and appear to defend territories while waiting for passing females. In Arizona observations (Funk, 1975), each ovipositing female would hover near a *Rumex hymenosepalus* Torr. (Polygonaceae), alight on one of the leaves, and walk down the leaf toward the base of the plant. When she reached a height of about 2-8 cm above the ground, she laid an egg, which fell to the ground (covered with sparse plant litter), sometimes bouncing on one or more of the leaves on its way. After laying each egg, the female then walked back toward the top of the plant. After resting a minute or more, she would either walk back down to lay another egg, or fly to another plant. Each egg was laid singly. Small black ants, *Formica altipetens* Wheeler, actually followed these ovipositing females and either seized eggs as soon as they were extruded by the females and before they fell to the ground, or picked up the eggs on the ground. It is unknown whether these observations indicate predation or a more complex symbiotic interaction; the eggs were carried away but not into the nest. This same ant species was found tending aphids in North Dakota.
- LIFE HISTORY:** Undescribed. The mature larva (from material in Mono County and Alpine County) has an almost concolorless green ground coloration. Along the midline is a broad, faint purplish dorsal stripe bordered laterally on either side by a faint whitish line. The entire body is covered generally by tiny yellow punctae and short orangish hairs. Laterally, below the spiracles, there is a slightly darker green lateral line, but not on all larvae. The pupa is a light tan and is covered by irregularly shaped and randomly placed dark brown spots and short lines. The pupal skin is not covered by hairs in this species.
- CHROMOSOME NUMER:** $n = 24$ in Colorado material (Emmel and Eliazar, 1990).
- SIMILAR SPECIES:** While the underside is mostly white, as in *Lycaena heteronea*, the upperside of the male is unmistakable in its orange coloration and the female always has an orange border on the hindwing dorsally that is lacking in *heteronea*.
- GEOGRAPHIC AND SEASONAL VARIATION:** We find the treatment of geographic variation in this species by Johnson and Balogh (1977) highly unsatisfactory in describing the geographic variation and biology of this species. Thus, their treatment is not followed precisely here. Further investigation of the geographic variation in this butterfly with larger numbers of specimens, particularly females, is definitely needed.
- GENERAL REMARKS:** G. Pratt and G. Ballmer (personal communication) note that the larva of *L. rubidus* is extremely similar to that of *L. xanthoides*. In fact, there are more similarities between the larvae of these two species than there are between the larvae of *L. xanthoides* and *L. editha*, which has been considered a subspecies of *xanthoides* by J. Scott (1986).
- This bright, showy orange Copper is widely distributed through the west from the Rocky Mountains to the Pacific Coast and north into southern Canada. In California, we have segregates of populations representing three named subspecies.

a. *L. r. rubidus* (Behr)

- DIAGNOSIS:** Males have a light orange ground color dorsally. On the hindwing, this is of a slightly more brownish shade than that on the forewing, giving the hindwing a darker appearance. The upperside of the female is relatively dark, with extensive grayish-brown scaling and patches of buff of varying sizes on the forewing, particularly in the discal area. On the hindwing, the submarginal orange markings are reduced to an irregular line of thin crescents. On the underside, the ground color of the male is a pale buff-gray, while on the female it is more of a dirty cream color. The underside of the forewing has a pattern of black spots similar to other Copper species. On the hindwing, it is essentially devoid of any markings ventrally.
- ORIGINAL DESCRIPTION:** Behr, *Proc. Ent. Soc. Philadelphia*, 6: 208.
- TYPE LOCALITY:** "Interior of Oregon", suggested as from Klamath Basin by K. Johnson and Balogh, *Bull. Allyn Museum*, 43: 20-21 (1977). Neotype in Carnegie Museum, designated by K. Johnson and Balogh (1977).
- DISTRIBUTION:** This subspecies is found in the extreme northeastern corner of the state in Modoc County and in adjacent south central Oregon.
- ELEVATION RANGE:** 4,500 to 5,500' elevation.
- HABITAT AND PLANT COMMUNITIES:** This butterfly is typically found in moist situations, such as along streams or in wet meadows in valley bottoms within the Sagebrush Scrub plant community.
- PHENOLOGY:** Univoltine, with adults flying from mid-July to mid-August.
- FOODPLANTS:** None documented for the nomotypical subspecies.

b. *L. r. sirius* (W. H. Edwards)

- DIAGNOSIS:** The central and northern Sierra Nevada populations and White Mountains populations of *L. rubidus* in California were lumped under the subspecies, *sirius* (W. H. Edwards), by K. Johnson, 1977. In our opinion, these populations seem to show a much greater affinity to the subspecies *monachensis* Johnson and Balogh (1977). In these north and central Sierran and White Mountains populations, females are variable but tend to have a bright orange ground color with marked reduction of the melanic overscaling seen on females of typical *rubidus* from the northeastern corner of the state. On the underside, the pattern is much like that of nominotypical *rubidus*, but perhaps paler in ground color.
- ORIGINAL DESCRIPTION:** W. H. Edwards, *Transactions American Ent. Soc.*, 3: 270 (1871).
- TYPE LOCALITY:** "Colorado", restricted to near Twin Lakes, Lake County, Colorado, by F. M. Brown, *Transactions American Ent. Soc.*, 95: 166-167 (1969). Lectotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Ent. Soc.*, 95: 168-169 (1969).
- DISTRIBUTION:** In the central and northern Sierra Nevada from Mono County northward to Donner Pass, extending eastward to the Sweetwater Mountains of extreme northern Mono County, and from there south into the White Mountains of Mono and Inyo counties.
- ELEVATION RANGE:** 5,300 to 10,000' elevation.

- HABITAT AND PLANT COMMUNITIES: Usually along streams or in wet meadows within the sub-Alpine forest plant community.
- PHENOLOGY: Records extend from mid-July to mid-September, with an apparent peak in mid-August.
- FOODPLANTS: At least one documented host of this set of populations is *Rumex transitorius* Rech. F.(Polygonaceae) (J. Emmel and O. Shields, unpublished data).

c. *L. r. monachensis* (K. Johnson and Balogh)

- DIAGNOSIS: In this subspecies of the southern Sierra Nevada, there is general reduction in the size of the black markings on both upperside and underside of both sexes. Females tend to be a bright yellowish orange with a greater amount of the upperside wing surface covered by these light orange scales.
- ORIGINAL DESCRIPTION: K. Johnson and Balogh, *Bulletin Allyn Museum*, 43: 38-40 (1977).
- TYPE LOCALITY: Monache Meadows, Tulare County, California. Holotype in American Museum of Natural History.
- DISTRIBUTION: This subspecies is found in the southern Sierra Nevada in the Monache Meadows area of Tulare County. A single record of *L. rubidus* from Mineral King in Tulare County probably also represents this subspecies, although we have not personally looked at the specimen.
- ELEVATION RANGE: From approximately 7,500 to 8,500' elevation.
- HABITAT AND PLANT COMMUNITIES: This butterfly flies near streambanks in an extensive system of meadows within the Montane Coniferous plant community.
- PHENOLOGY: Adults fly from early July to at least mid-August, with the majority of specimens having been taken in early August.
- FOODPLANTS: Unknown.

158. *Lycaena xanthoides* (Boisduval)

- ADULT BEHAVIOR: Males perch on vegetation from a few feet off the ground to as much as six or seven feet above the ground. Females tend to be more sedentary, spending much time landed on the foodplant or near potential foodplants. Courtship occurs from 9:00 a.m. to 4:30 p.m.; the male pursues a passing female, and hovers over her, beating his wings with wide amplitude about seven times a second. He then lands behind the female and bends his abdomen laterally to copulate. Of 26 females dissected near the end of the flight period (mid July at Point Richmond, Contra Costa County), 6 females had not mated, 18 had mated once, and two had mated twice (Scott and Opler, 1975).

Yellow composites (such as *Grindelia*) are heavily visited by the adults. Other nectar sources in California and elsewhere are listed by Scott and Opler (1975). In their capture-recapture study of *xanthoides* in a small field at Berkeley in Alameda County, the average lifespan found by those authors is nine days for males and fourteen days for females. Scott and Opler noted that the lifespan of *L. xanthoides* was much greater than the lifespan of *L. arota* in a similar study (Scott, 1974a). Both sexes bask by spreading their wings 20 to 60 degrees from vertical

and facing away from the sun. Basking tended to occur at cool temperatures, primarily during the morning and late afternoon hours.

LIFE HISTORY: The eggs are laid singly on sticks, dead leaves, and debris at the base of the larval foodplant in June. The egg is echinoid in shape with rather small pits between irregular walls. The color when first laid is a pale green, immediately changing to white as the egg matures. The larval instars are described from southern California material in detail by Comstock and Dammers (1935c). When not feeding, they rest near the base of the plant among litter or dead leaves. The mature larvae are polymorphic, there being an apple-green morph, a yellowish-green form, and a dark orange form bearing bands and bars of magenta! The cervical shield is green, with slight mauve shading around its margins. A narrow bluish-white bar bisects the shield, and the whole body is sparsely covered with white punctate points. In northern California material from Mendocino County the predominant larval form is apple-green, with a deep red mid-dorsal band and a medium red flush extending as a band on either side of the mid-dorsal line the length of the larva. The total reddish area covers about one third of the dorsum of the larva. On the side of the Mendocino County larval form, there is a very faint yellowish-green lateral line, extending the length of the larva well below the spiracles. The spiracles themselves are red in color. The larva is covered with small yellowish punctate in this form.

Surprisingly, for a butterfly species, Comstock and Dammers found that when the larva prepares to pupate it forms "a loosely woven silk cocoon on the floor of the breeding cage, into which it incorporated particles of soil. This cocoon formation by a Lycaenid is a most unusual feature, and the first of its kind encountered in our breeding of diurnals." The pupa in the southern California populations is pink-buff in color, and is spotted and blotched everywhere with irregular black markings. The surface is covered with minute colorless hairs, except on the wingcases. In the northern California material that J. Emmel reared, pupating larva did not have opportunity from materials in its enclosure to make a cocoon, if indeed it planned to do. (In the San Bruno Mountains, however, J. Emmel found pupae at the base of the foodplants with no indication of a cocoon being made prior to pupation.) The Mendocino County pupae have a medium tan ground color and have medium dark brown blotching over the entire surface. In the San Bruno Mountains, the larval form resembles the larval form from Mendocino County and the pupae are somewhat variable in the degree of dark blotching on an olive-tan ground color. The mid-dorsal line in the San Bruno Mountain pupae is composed solely of dark brown blotches and no purple pigment as in the Mendocino County pupae appears.

CHROMOSOME NUMBER:

SIMILAR SPECIES: The only species with which *xanthoides* might be confused is the phenotypically similar *L. editha*, a smaller species. In addition to the smaller size, *editha* specimens can be fairly readily distinguished from *xanthoides* by the following character differences. The spots in the post-median row of spots on the hindwing tend to be about twice the diameter of the post-median black spots on the forewing on the underside; in *xanthoides* the post-median spots on the ventral hindwing are about the same diameter or sometimes even smaller than the post-median black spots on the ventral forewing.

GEOGRAPHIC AND SEASONAL VARIATION: As the species is univoltine, there is no seasonal variation. As noted above, we consider the name *luctuosa* to be a synonym of nominate *xanthoides*. There is some variability in the populations that we consider to fall under the nominate subspecies. Specimens from the

east San Francisco Bay area, such as Berkeley, tend to have slightly larger spots beneath and darker ground colors. Specimens from the northern Sacramento Valley often have rather large black spots beneath, and further investigation of these populations may show them to be a distinct geographic subspecies.

GENERAL REMARKS: Although Scott (1980, 1986) treated *L. editha* as a subspecies of *L. xanthoides* on the basis of supposed intermediate populations, we feel there is sufficient justification to separate these two entities as distinct species. G. Pratt and G. Ballmer (personal communication) have studied the larvae of all the California *Lycaena* species and have found that the larvae of *L. editha* and *L. xanthoides* differ consistently in several characters, and that the larvae of *L. xanthoides* and *L. rubidus* are extremely similar, almost indistinguishable from one another. Thus, although *L. xanthoides* and *L. rubidus* are readily distinguishable in the adult stage, *L. xanthoides* and *L. editha* are readily distinguishable in the larval stage. Secondly, there are biological differences between these two entities. *Xanthoides* is typically found in situations where its foodplant grows, in areas near some sort of permanent moisture as a spring or stream, etc. *L. editha*, on the other hand, prefers dry slopes or flats and feeds on several species of herbaceous annual or biennial *Rumex* species. Lastly, the adults differ consistently in the size ratio of spotting on the underside of the forewings to that on the underside of the hindwings. The so called "intermediate" populations of *Lycaena* at Dunsmore in California have larvae that are indistinguishable from larvae in other *L. editha* populations, and we consider them to be a subspecies of *L. editha* rather than an intermediate form between the species *editha* and *xanthoides*.

This large Copper has a dark gray dorsal surface which resembles some Hairstreaks, except for the lack of tails. It is found primarily in grasslands and grassy foothills throughout California, north into Oregon. There are three subspecies groups identified in our state.

a. *L. x. xanthoides* (Boisduval)

DIAGNOSIS: The typical subspecies was named by Boisduval from California. It is characterized by males of this species having a brownish-gray upperside with a varying amount of orange scaling in the submarginal area of the hindwing, tending to be most accentuated near the anal angle. This orange scaling occurs as a scalloped border, with a series of small black spots within the arches of the scallops. The upperside of the females is a more brownish-gray, somewhat lighter in shade than that of the male, with patches of light orange scaling on the forewing, primarily in the median area of the wing and on the hindwing in the post-median area. On the forewing, there is a pattern of black dots of varying size, and on the hindwing there is an orange band in the submarginal area similar to that of the males, except that it is much more fully developed and often extends onto the forewing along the outer margin posteriorly. On the underside, the female ground color is similar to the male except of a more yellowish cast. On the underside, both sexes have a pattern of black spots on the forewing, which is more accentuated in the females with larger spots and more of them developed. On the hindwing there is also a pattern of black spots, with the most prominent ones being in the post-median area but in a number of individuals these spots have grayish-tan centers, which in some cases renders virtually the entire spot grayish-tan rather than black, although it still stands out from the background color. The orange banding in the submarginal area of the hindwing is largely confined to the area near the anal angle and is thinner than on the upperside. Included under nominotypical *xanthoides* is the subspecies *luctuosa* Watson and Comstock (1920), which we consider a synonym. In analyzing the characters of a long series

of *L. xanthoides* from the Tehachapi Mountains (the type locality) and other southern California mountain ranges, we are unable to see any consistent differences between these populations and nominotypical *L. xanthoides* from northern California.

- ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 292 (1852).
- TYPE LOCALITY: "Mountains of California". Type locality restricted to Sacramento, California, by Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990). Holotype in U. S. National Museum.
- DISTRIBUTION: This species is widely distributed through the state at low to mid-elevations from San Diego County northward through the foothills and mountains of southern California through the Coast Ranges, Central Valley, and west slope of the Sierra Nevada to the north end of the Sacramento Valley. It is also found in the northern Owens Valley and in several adjacent canyons of the east slope of the Sierra Nevada and the western slope of the White Mountains in extreme southern Mono County and northern Inyo County.
- ELEVATION RANGE: From near sea level to 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES: *L. xanthoides* is usually found in dryish meadows near some sort of water source such as a spring or intermittent stream or permanent stream. It is also found in canyon bottoms and valleylands where there may not be any water on the surface nearby, but where drainage supports a reasonably moist soil for the *Rumex* foodplants of this species that prefer such situations.
- PHENOLOGY: Species is strictly univoltine, with adults recorded from mid-May to mid-July and an apparent peak of flight activity in mid-June.
- FOODPLANTS: For nominotypical *xanthoides*, the following *Rumex* species (Polygonaceae) have been recorded as foodplants: *R. hymenosepalus* Torr., *R. pulcher* L., *R. californicus* Rech. F., *R. crispus* L., and *R. conglomeratus* Murr.

b. *L. x. obsolescens* Emmel and Pratt

- DIAGNOSIS: This isolated desert population of *L. xanthoides* is characterized by an extreme reduction in the size of the black markings on the underside, with many spots disappearing completely in some specimens. Additionally, the males tend to have a paler orange aurora on the submarginal area of the hindwing dorsally, and in the females this orange aurora tends to be expanded from that seen in typical *xanthoides*, as well as having smaller black spots within it than is seen in the typical insect. Females of this subspecies are almost uniformly grayish-brown on the forewing, with only very reduced areas of light orange scaling just distal to the end of the discal cell and near the posterior angle of the forewing.
- ORIGINAL DESCRIPTION: Emmel and Pratt, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990).
- TYPE LOCALITY: Hunter Mountain, at extreme southeastern end of Saline Valley, Inyo County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: So far as is known, this subspecies is confined to the Hunter Mountain area.
- ELEVATION RANGE: 6,000 to 7,000' elevation.

- HABITAT AND PLANT COMMUNITIES:** The butterfly occurs in small, dry meadows, usually near springs or with an intermittent stream source nearby, within an admixture of Pinyon-Juniper Woodland and Sagebrush Scrub plant communities. The periphery of these small meadows and springy areas supports a fairly abundant growth of *Angelica lineariloba* Gray, an important nectar source which comes into full bloom at the time this Copper is flying.
- PHENOLOGY:** Adults begin flying in late June and continue into early August, with the peak abundance during the first half of July.
- FOODPLANTS:** G. Ballmer and G. Pratt (personal communication) found larvae of this subspecies on *Rumex salisifolius* Weinm. (Polygonaceae).

159. *Lycaena editha* (Mead)

- ADULT BEHAVIOR:** Males perch in open spaces on the gravelly or rocky slopes, or small clearings in meadows, or along roadsides or trails, usually in full sun. The species is frequently sympatric with *Lycaena cupreus*, which uses both the same native and introduced *Rumex* species as does *L. editha*; however, they are usually allochronically separated, as *L. editha* overwinters as an egg and the main flight is in late July to early August, whereas *L. cupreus* overwinters as a half-grown larva and completes development more rapidly the following year, usually emerging in June.
- LIFE HISTORY:** The early stages have not previously been described. The eggs are laid on or near the *Rumex* plants; if laid on the plants, they are usually deposited on the stems near the base of the plant. If not laid on the stems, the eggs are usually deposited on vegetative debris or small rocks in the immediate vicinity of the stem of the foodplant. The eggs overwinter and the larvae hatch immediately after snowmelt the following spring.
- The following descriptions of the mature larva and the pupa pertain to material reared from the Mt. Shasta and Dunsmuir areas in Siskiyou County. The larva is apple-green in ground color. Running the length of the mid-dorsal line is a reddish-purple band bordered laterally on either side by a diffuse white area, and then a yellow area that proceeds to blend into the green ground color. The overall effect of the dorsal coloration is to accentuate the red stripe. On the sides, there is a pale yellowish-green or whitish lateral band running below the spiracles the length of the body. The larva is covered with yellow punctae and short yellowish hairs arising independently from the skin. The pupa is a very light tan, with light mottling of darker brown speckles across the entire surface. There is a faintly darker pigmentation, suggesting a dorsal band of brown across the abdomen. Some inter-individual variability occurs in the extent of brown speckling across the tan ground color.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** See discussion under General Remarks in *Lycaena xanthoides* section.
- GEOGRAPHIC AND SEASONAL VARIATION:** As the species is univoltine, there is no seasonal variation. Specimens of this butterfly from the White Mountains tend to have slightly larger spots on the underside than populations at similar elevations in the Sierra Nevada. Specimens from the Manache Meadows area of Tulare County are somewhat lighter above in the females and have a stronger

yellowish or orangish cast to the ground color of the underside. Further investigations of these sets of populations may reveal enough consistent differences that some sort of subspecific delineation is warranted.

GENERAL REMARKS: As noted above under the section on Foodplants, many populations of this butterfly in California feed on an introduced *Rumex* species and do not seem to have a native foodplant in these localities. Thus, it is possible that many of the populations that we are seeing at the low to mid-elevations in the Sierra Nevada and in the Mt. Shasta region are rather recent, perhaps colonized within the last 100 years. Of particular interest to note is the recent discovery by S. Mattoon of a colony of this butterfly in the North Coast Range. [STERLING, PLEASE FILL IN LOCALITY HERE.]. Since there are not previous records for this species in the Coast Range and this newly discovered population appears to be associated with an introduced *Rumex*, we may be witnessing the continued expansion of the range of this species as it follows the weedy *Rumex acetosella* L. into appropriate montane habitats.

SUBSPECIES: This small Copper occurs typically in dry sagebrush amid mixed open conifer situations in California eastward to northwestern Colorado and north into southeastern Washington, Idaho, and Montana. It is essentially a montane species throughout its range. There are two subspecies within our state.

a. *L. e. editha* (Mead)

DIAGNOSIS: This species is similar to *L. xanthoides*, but is noticeably smaller. The ground color of the upperside is usually a slightly lighter shade of brownish-gray than that seen in nomotypical *xanthoides*. Also, the pale orange scalloped aurora in the submarginal area of the hindwing is markedly reduced in the males and even absent in some specimens. On the females, the overall pattern of brownish-gray ground color, dark spots, and patches of yellowish-orange scaling is similar to that seen in *xanthoides*, except that the yellowish areas tend to be more extensive in *editha*. On the underside, *editha* has a rather bold pattern of dark spots on the forewing and very large grayish-brown spots on the hindwing, edged with darker scales. The size of the hindwing spots ventrally is noticeably larger than the post-median curved band of black spots on the forewing, usually at least twice the diameter of these spots, whereas in *xanthoides* the spots on the two wings are approximately equal in size. Also, the ground color of *editha* is darker, more of a grayish-tan on the hindwings in the males with white overscaling; in the females, the white scaling is more extensive on the underside of the hindwing and the forewings tend to have a yellowish flush to the ground color.

ORIGINAL DESCRIPTION: Mead, *Canadian Entomologist*, 10: 198 (1878).

TYPE LOCALITY: Near Carnelian Bay, Lake Tahoe, California. Syntypes in Field Museum of Natural History, Chicago.

DISTRIBUTION: Within California, typical *L. editha* is found in the mid- to higher elevations of the Sierra Nevada, in the higher elevations of the White Mountains, and in the Warner Mountains of Lassen and Modoc counties.

ELEVATION RANGE: 4,000 to 12,000' elevation.

HABITAT AND PLANT COMMUNITIES: Typically found in dry meadows, roadsides, or along trails, sometimes on rocky or gravelly slopes within the Montane Coniferous forest, Sub-Alpine forest, or Arctic Alpine Fellfield communities.

PHENOLOGY: Strictly univoltine, but with a rather long flight period with specimens recorded from late June to mid-September, with one early October record.

FOODPLANTS: For the higher elevation populations in the Sierra Nevada and White Mountains, the foodplant is *Rumex paucifolius* Nutt. ex Watts. (Polygonaceae). We believe records for *Potentilla* and *Horkelia* (Rosaceae) to be erroneous. At the mid-elevation populations, the butterfly is known to use an introduced *Rumex*, *R. acetosella* L.. In many of these mid-elevation populations, this *Rumex* appears to be the only foodplant with no native species being used. This could indicate that many of these populations are of recent introduction following the introduction of the European weedy *Rumex*.

b. *L. e. robusta* Emmel and Pratt

DIAGNOSIS: This is a large, low-elevation subspecies of *L. editha* occurring in the Mt. Shasta region. In addition to its larger size, it is characterized by having reduced size of spots on the underside in comparison to typical higher elevation *editha*. The relationship of the ratio of the size of the hindwing spots being much larger than the post-median black spots of the forewing on the ventral surface is maintained in this set of populations. It also differs from typical *editha* in that the females tend to be darker, with reduction of the yellowish scaling on both forewings and hindwings and a similar reduction in the prominence of the orange aurora on the submarginal area of the hindwing. The larvae of this subspecies are virtually indistinguishable from the larvae of Sierran *L. editha*, and are readily distinguishable from the larvae of *L. xanthoides* (G. Pratt and G. Ballmer, unpublished studies).

ORIGINAL DESCRIPTION: Emmel and Pratt, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990).

TYPE LOCALITY: Railroad Park, Dunsmuir, Shasta County, California. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This subspecies is found in the Mt. Shasta region from northern Shasta County and possibly northwestern Plumas County northward through Siskiyou County to southern Oregon.

ELEVATION RANGE: 3,500 to 5,000' elevation.

HABITAT AND PLANT COMMUNITIES: [S. MATTOON, PLEASE FILL IN.]

PHENOLOGY: This subspecies flies from mid-June to early August, depending on elevation and rainfall pattern for the year.

FOODPLANTS: At the type locality, larvae of this subspecies have been collected on *Rumex acetosella* L. (G. Ballmer, personal communication).

160. *Lycaena hermes* (W. H. Edwards)

One of our most famous endemic butterflies, *Lycaena hermes* has an exceedingly restricted range. Its known distribution in the United States includes only part of San Diego County. It also occurs south of the border almost 100 miles, to a point

18 miles south of Santo Tomas in Baja California. Everywhere, the Hermes Copper colonies are closely associated with and confined to the vicinity of the host plant, which itself has a much broader range throughout the Coast Ranges in California. The use of a rhamnaceous host plant by *hermes* is unique in the genus *Lycaena*, a presumably ancient worldwide genus of relatively few, phenotypically similar species.

DIAGNOSIS: This is one of the two tailed Copper species in our state, the other one being *L. arota*. *Hermes* is rather readily distinguished by the dark dull ground color of the upperside with the extensive bright yellow area in the medial part of the forewing, the yellow bordering in the anal area extending into the tail, and the very distinctive deep lemon-yellow underside ground color. There is sexual dimorphism, but it is not nearly so marked as in all of the other California *Lycaena* species.

ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Ent. Soc.*, 3: 21 (1870).

TYPE LOCALITY: "California", restricted to vicinity of San Diego, San Diego County, California by F. M. Brown, *Transactions American Ent. Soc.*, 95: 165 (1969). Neotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Ent. Soc.*, 95: 166 (1969).

DISTRIBUTION: In California, this species is wholly confined to San Diego County, where it occurs from near the coast to a point about 40 miles inland from the coast and a northernmost point about 50 miles north of the Mexican border. From San Diego County it extends southward into Baja California approximately 100 miles.

ELEVATION RANGE: From near sea level to approximately 3,500' elevation.

HABITAT AND PLANT COMMUNITIES: Mostly in Coastal Sage Scrub or Chaparral plant communities, where *Rhamnus crocea* Nutt. in T. & G. is common.

PHENOLOGY: Records range from May 20 to July 20, with a peak flight for males around June 10 and a peak flight for females about June 20 (Thorne, 1963).

ADULT BEHAVIOR: Males perch on the foodplant, but according to Thorne, are not particularly aggressive. A possible type of cryptic mimicry protecting the adults was first noted by Thorne (1959). Because the Redberry foodplant (*Rhamnus crocea*) is evergreen, its leaves mature singly. During the flight season of *L. hermes*, a mature leaf will appear here and there on the plant as a bright yellow spot against the background of dark green foliage. At a short distance, such a leaf appears to the collector's eye very much like a perched *hermes* in size and color. But the yellow leaves are much more common than the butterfly, and after repeated disappointments they no longer attract the collector. Presumably, potential predators such as birds also are deflected from searching for the butterflies by this cryptic yellow resemblance. Both sexes are avid flower visitors and the nectar source of choice is *Eriogonum fasciculatum* Benth.

LIFE HISTORY: The life history was first described by Comstock and Dammers (1935b), with additional details in Thorne (1963). The eggs are laid on the stems of *Rhamnus crocea* Nutt. in T. & G. and overwinter until the following spring. The white echinoid egg is covered with deep pits created by high irregular ridges. The physical appearance of the egg is very similar to that of *Lycaena gorgon*. The micropyle area is deeply depressed. The mature larva is apple-green in ground color with a mid-dorsal band of darker green bordered with yellowish-green in a broken irregular band. Laterally on each segment, there are two faint and

indistinct yellow diagonal marks, a third faint yellow mark arising from the region around the spiracle, and a fourth one (very indistinct) below that on each segment. The ventral surface is pale green and the spiracles are dark brown. The body is sparingly covered with silvery white dots which, under high magnification, are observed to be pillar-shaped stout projections with rounded ends. The body is also completely covered by minute short brown hairs which are not erect and can only be seen with a strong hand lens. Those on the front of the first segment and on the caudal end are much longer. The head is a dirty yellow color, with the mouth parts brown. The ocelli are white on a black field. The cervical shield is quite distinctive and is shaped like a double barb spear point. The basal color is brown, bisected by a bluish-white bar across the center. The pupa is grass-green in color and has a narrow mid-dorsal yellow stripe extending from the fifth to ninth segments. Subdorsally, a second yellow band runs longitudinally over the thorax and abdomen and bends abruptly at each segmental juncture edging this juncture for some distance laterally. Each abdominal segment is also crossed laterally by three diagonal yellow bars. The spiracles are a soiled orange in color. The entire surface is lightly covered with olive-brown spots of various sizes. Mid-dorsally on the fourth segment, there is a black triangle. On the ninth to the caudal segments in the mid-dorsal line occurs a black quadrate spot on each segment, those placed near the tail shading off to brown. The entire pupa, except for the wing cases, is sparingly covered with minute silvery white processes which appear under magnification as trumpet-shaped projections. The butterfly is single-brooded and overwinters in the egg stage.

FOODPLANTS:	Red Berry, <i>Rhamnus crocea</i> Nutt. in T. & G. (Rhamnaceae), is the only known foodplant.
CHROMOSOME NUMBER:	Unknown.
SIMILAR SPECIES:	This <i>Lycaena</i> species is unique in North America.
GEOGRAPHIC AND SEASONAL VARIATION:	None.
GENERAL REMARKS:	The existing populations are apparently quite stable from year to year, with no wide fluctuation in numbers noted by Thorne (1959, 1963) or later lepidopterists. While there does not seem to be need at this point in time to place the species on an endangered or threatened species list, the situation with potential loss of habitat in populous San Diego County certainly bears continued monitoring.

161. *Lycaena arota* (Boisduval)

ADULT BEHAVIOR:	Males of all three subspecies perch in small clearings in many different situations from sagebrush to gulleys to ridgetops and valleys. They begin perching at about 0715 and actively perch until about 1100 hours (at least in Colorado). Scott (1974) has described the mating behavior. The male darts after a passing female and flies about 14 centimeters off the ground for several meters. Then the female lands on a branch, the male lands behind and then starts flicking his wings and vibrating them. The female remains quiescent, the male then crawls alongside and bends his abdomen either right or left to attempt copulation. Unreceptive females will flap their wings ten or more times a second while sitting. Males in Colorado may move as far as 214 meters in several days, but most individuals of both sexes do not move at all from day to day. In Colorado, males and females live an average of only four days. In northern California, they are believed to be longer-lived (Mattoon, personal communication).

Both sexes feed commonly on flowers and may even be found visiting mud.

LIFE HISTORY: The life history was first described by Comstock (1927b for egg; 1928a for other stages). The turban-shaped egg is off-white in color and has about fourteen heavy vertical ribs that stand up above the surface and have shallow cross-ribbing with no deep depressions like in *hermes* or *gorgon*. The mature larva is green in ground color, somewhat darker at the head end. The surface is covered with minute white granulations. Minute yellowish-white hairs arise from the skin surface but not from the tiny granules. A very faint double light colored line occurs dorsally and there is a fine single yellowish lateral line below the spiracles. The larva of both the typical race and *nubila* are shown in the accompanying figures. The variably colored pupa is brown or mottled yellow-brown. There are minute hairlike processes with flaring trumpet-shaped ends scattered over the surface. The pupa is supported by a silk girdle around the thorax.

CHROMOSOME NUMBER:

SIMILAR SPECIES: This is one of the only two tailed Coppers in our California fauna, the other being the very distinctive *Lycaena hermes*.

GEOGRAPHIC AND SEASONAL VARIATION: Despite the widespread populations of the nomotypical subspecies within our state, and the diverse habitats utilized, there seems to be little if any geographic variation from one area to another.

GENERAL REMARKS: It is curious that this species has not shown up in the mountain ranges of the eastern Mojave Desert, where one of its foodplants, *Ribes velutinum* Greene, is locally common in some of the canyons.

SUBSPECIES: This tailed Copper occurs in montane areas throughout the west, from southern California north to southern Oregon and eastward to the Rocky Mountains of Colorado and central New Mexico. Within our state occur three of the four known subspecies.

a. *L. a. arota* (Boisduval)

DIAGNOSIS: This is the most widespread subspecies in California. In the males the dorsal surface is a dull tan with a purplish sheen. There is a dark border on both forewing and hindwing, and a scalloped orange aurora near the anal angle and the tail. The upperside of the female is pale orange, with extensive dark brown markings and a more extensive orange aurora in the submarginal area of the hindwing. Ventrally, the forewing ground color is a whitish tan-gray with an orangish flush in the post-median area; the ground color of the hindwing ventrally is a dull tannish-gray. A pattern of variously shaped brownish-black markings in the proximal two-thirds of both wings and a pattern of whitish markings in the distal one-third of both wings defines the general wing pattern on both sexes. An irregular reddish to orangish line is found in the submarginal area near the tail and the anal angle of the hindwing.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 293 (1852).

TYPE LOCALITY: "California", restricted to Juba Mountains by W. P. Comstock and Huntington, *Journal New York Entomological Society*, 67: 79 (1959). Re-restricted by Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990) to Lower Feather River Canyon, Butte County, California. Holotype in U. S. National Museum.

- DISTRIBUTION:** This subspecies is widely distributed through cismontane California from San Diego County northward through the San Jacinto Mountains, San Bernardino Mountains, and thence northwestward to the Tehachapi and Tejon Ranges in Kern County. From there it is found northward through the Coast Ranges and the west slope of the Sierra Nevada to the Klamath Mountains Assemblage and the Mt. Shasta region.
- ELEVATION RANGE:** From 250' elevation to 7,600' elevation.
- HABITAT AND PLANT COMMUNITIES:** Found in several different plant communities, depending on elevation, including Montane Coniferous Forest, Chaparral, Foothill Woodland, and Northern Oak Woodland. The butterfly is found on dry slopes and in canyon bottoms, particularly near watercourses.
- PHENOLOGY:** This species is strictly univoltine, with records ranging from late May to mid-September, depending on elevation and other local habitat conditions.
- FOODPLANTS:** Various species of *Ribes* are recorded as foodplants including the following species in California: *R. roezlii* Regel., *R. quercetorum* Greene, *R. californicum* H. & A., *R. aureum* Pursh, and *R. divaricatum* Dougl.

b. *L. a. virginiensis*

- DIAGNOSIS:** This is a weakly differentiated subspecies of the Great Basin which enters our area on the east slope of the Sierra Nevada. In this subspecies the ground color of the underside on the hindwing tends to be more brown and the forewing ventrally on the male has an orange flush. Also, there is a tendency for the white markings in the post-median area of the hindwing and forewing to be slightly larger than in nominotypical *arota*. Additionally, females in these populations tend to be slightly more lightly marked than in typical *arota*.
- ORIGINAL DESCRIPTION:** E. H. Edwards, *Transactions American Ent. Soc.*, 3: 21 (1870).
- TYPE LOCALITY:** Virginia City, Nevada. Neotype in American Museum of Natural History, designated by F. M. Brown, *Transactions American Ent. Soc.*, 95: 164 (1969).
- DISTRIBUTION:** In our area, this subspecies is found along the east side of the Sierra Nevada from Inyo County to Mono County; it is also found in the Sweetwater Mountains of Mono County and in the White Mountains and Inyo Mountains of Mono and Inyo counties. It is also found in the Coso Range and on Hunter Mountain in the western Death Valley region.
- ELEVATION RANGE:** From 6,000 to 9,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** This butterfly typically is found along watercourses in the Pinyon-Juniper Woodland plant community of the western Great Basin. It also occurs within areas of Sagebrush Scrub.
- PHENOLOGY:** Records range from mid-June to early September, with apparent peak of abundance in early to mid-July.
- FOODPLANTS:** For subspecies *virginiensis*, the following *Ribe* species have been documented as foodplants: *R. velutinum* Greene and *R. aureum* Pursh.

c. *L. a. nubila* J. A. Comstock

- DIAGNOSIS: This coastal southern California subspecies is characterized by the generally darker ground color of the dorsal surface and extensive dark markings on the female, and a wider dark marginal band on both sexes. On the underside, it is also a darker brownish-gray than typical *arota*.
- ORIGINAL DESCRIPTION: J. A. Comstock, *Bulletin Southern California Academy Sciences*, 25: 34 (1926).
- TYPE LOCALITY: Griffith Park, Los Angeles, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is found in the Santa Monica Mountains of Ventura and Los Angeles counties, the western foothills of the San Gabriel Mountains, and in the Santa Ana Mountains. There is an apparent blendzone with typical *arota* on the south slope of the San Gabriel Mountains.
- ELEVATION RANGE: From 1,000 to 2,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This butterfly is found in moist coastal canyons, with heavy growth of either Chaparral, or Southern Oak Woodland, or Riparian Woodland. The butterfly is typically found along canyon bottoms where males perch on medium-sized shrubs, usually near small streams or trails.
- PHENOLOGY: We have records from late May to mid-August, with the majority of specimens taken during the latter part of June and the first week in July.
- FOODPLANTS: The recorded foodplant of this subspecies is *Ribes aureum* Pursh ssp. *gracillimum* (Cov. & Britt.) Jeps.

Subfamily **Polyommata** Swainson

162. *Leptotes marina* (Reakirt)

This medium-sized Blue is found throughout the lowlands of southern California, and sporadically in the central and northern portions of the state. In our parks and suburban areas, it often flies abundantly, due to the extensive planting of *Plumbago* perennials as ornamentals.

- DIAGNOSIS: A medium-sized lycaenid, with males having bright blue uppersides and female dorsal surfaces suffused with brown. The underside pattern has a series of apparent rows of brown spots alternating with white bands proceeding outward from the body to the marginal black dots.
- ORIGINAL DESCRIPTION: Reakirt, *Proceedings Academy Natural Sciences of Philadelphia*, 20: 87 (1868).
- TYPE LOCALITY: "Orizaba nr. Vera Cruz, Mexico". The probable syntypes are in the Field Museum of Natural History, Chicago.
- DISTRIBUTION: In southern California this species is found throughout the deserts to the coastal areas, as well as in the Channel Islands on Santa Catalina and Santa Cruz. It becomes more uncommon at middle elevations in the mountains, and as one goes northward in the state. In years of extreme abundance, it may become temporarily established in such areas as the Sacramento Valley or the lower elevations of

Mono County on the east side of the Sierra Nevada, but these populations do not persist. It is unclear which, if any, of the southern California populations are permanently established. It seems likely that populations established on *Plumbago* in the urban and suburban areas of coastal southern California are ongoing populations, in view of the fact that in these areas freezes are rare and the butterfly is likely able to survive the winters. To the east in the desert areas, the butterfly may be only transiently established from the spring months to the fall months, as mid-winter records from these areas are lacking and occasional freezes in most of the habitats in these areas may be lethal to potentially overwintering individuals of this sub-tropical species.

ELEVATION RANGE: The majority of records seem to fall into an elevation range from sea level to approximately 6,000' elevation, but there are records of this species as high as 10,000', such as in the White Mountains of Mono County.

- HABITAT AND PLANT COMMUNITIES:** The butterfly has been taken in the rather wide variety of plant communities and habitats, including urban and suburban gardens, agricultural areas, disturbed weedy waste areas, Coastal Sage Scrub, Chaparral, Oak Woodland, Montane Coniferous Forest, Creosote Bush Scrub, Pinyon-Juniper Woodland, Coastal Strand, and Riparian Woodland.
- PHENOLOGY:** While *Leptotes marina* is multiple-brooded and has been recorded regularly in Los Angeles as a breeding resident in every month of the year, the main flight period in southern California is March to October, with a peak from July into the fall.
- ADULT BEHAVIOR:** This butterfly flies close to the ground in a seemingly weak, irregular flight. This can be deceptive when the butterfly is flying rapidly away from a pursuer. The adults of both sexes hover around Fabaceae foodplants, and frequently alight on stems as well as flowers to feed.
- LIFE HISTORY:** The turban-shaped egg is a delicate light green in ground color, with a raised whitish network. The mature larva is exceedingly variable in color and pattern, with every intergrade between almost pure light green to a rich brown with heavy chocolate-colored bands and diagonal stripes. The genetics of this color and pattern variability would be an exceptionally interesting study. The pupa is pale ochre-brown, with pale grey wingcases and spots of dark brown. It is suspended by a silken girdle and bears short hairs over the surface.
- FOODPLANTS:** Leadwort, *Plumbago* (Plumbaginaceae) and *Wisteria* species (Fabaceae) in urban areas; elsewhere, a variety of Fabaceae are used, e.g., alfalfa (*Medicago*), pea (*Lathyrus*), sweet pea, *Lotus scoparius* (Nutt. in T. & G.) Otteley and *Astragalus* species. It has also been found using *Amorpha californica* Nutt. (False Indigo) in Lone Pine Canyon at the east end of the San Gabriel Mountains (Chris Henne, personal communication). Oviposition has also been recorded on *Adenostoma fasciculatum* (Rosaceae) (J. F. Emmel, unpublished data).
- CHROMOSOME NUMBER:**
- SIMILAR SPECIES:** There are no similar species of *Leptotes* in our area, but either species of *Hemiargus* might be momentarily mistaken for this butterfly. The latter two species in our fauna can be distinguished by their smaller size and by other characters detailed under the discussion of each of those *Hemiargus* species.
- GEOGRAPHIC AND SEASONAL VARIATION:** This butterfly occupies an extensive range outside of California, east to western Illinois and Nebraska and south through Texas to Central America. It cannot overwinter in the more northerly parts of its range such as Kansas and Nebraska, though it may breed there. These northerly colonies are established each year by summer migrants, and this remarkable ability of this small butterfly to move considerable distances explains in large part why little or no significant geographic variation has been described in this species. Likewise, there is no apparent seasonal variation through the year.
- GENERAL REMARKS:** Suprisingly, this butterfly does not occur in the southeastern and eastern states. In southern Florida and southern Texas, it is replaced by a related species, *L. cassius*, which is found south through the northern part of the Caribbean.

163. *Brephidium exilis* (Boisduval)

This is one of the smallest known butterflies in the world, with a forewing length in some males of only 8 mm. Its weak flight and tiny size attract little attention, although it occurs in abundance in the lowlands and deserts of southern California.

- DIAGNOSIS: This species is immediately distinguished by its small size and its distinctive underside pattern. The ground color is greyish white near the body and brown outwardly; the fringes are mostly white. The dorsal surface of the wings is blue basally and brown distally.
- ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 294 (1852).
- TYPE LOCALITY: "California". Restricted by Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990) to . Holotype in U. S. National Museum.
- DISTRIBUTION: This tiny blue occurs commonly in the lowlands and deserts of southern California, and extends northward in the Central Valley to the Sacramento Valley and along the east side of the Sierra Nevada to at least Lassen County in northeastern California. It has been found on Santa Catalina and Santa Cruz Islands offshore, and throughout the mountains of both deserts, as well as at mid-elevations along the east slope of the Sierra Nevada and in the Inyo and White Mountains of Inyo and Mono Counties.
- ELEVATION RANGE: This butterfly ranges from 178' below sea level, at Furnace Creek Ranch in Death Valley to at least 7,000' elevation in the mountains; the higher elevation montane populations may be only transiently established ones. Certainly some of the montane records for this species (such as Donner Pass, 7,000' elevation) represent stray individuals in years of extreme abundance and do not represent on-going established populations. At higher elevations in the Inyo Mountains, the butterfly is associated with a native *Atriplex* species as high as 8,000' elevation and it is possible that these particular populations are permanently established ones.
- HABITAT AND PLANT COMMUNITIES: The butterfly has been found in such diverse habitats and plant communities as Coastal Salt Marsh, Alkali Sink in the deserts, Desert Riparian Woodland, Creosote Bush Scrub, Pinyon-Juniper Woodland, Shadscale Scrub, Sagebrush Shrub, and Joshua Tree Woodland. In agricultural and suburban areas, it is usually found in disturbed areas where weedy plants in the family Chenopodiaceae are found as weedy colonizers.
- PHENOLOGY: This species is multiple brooded and the butterfly has been recorded in every month of the year in the counties of coastal southern California as well as in the Sacramento Valley. Although such a range of records suggests continuous flight and breeding throughout the year, this pattern seems highly dependent on winter temperature and rainfall patterns; in particularly prolonged cold winters the species may spend several months in some sort of diapause.
- LIFE HISTORY: The tuban-shaped egg is a delicate bluish-green with a raised white network across its surface. The mature larva is yellowish-green and is covered with brownish tubercles bearing minute white processes. It usually bears a yellowish-white dorsal line and a bright yellow, narrow lateral line. The pupa is variable in color, but is usually a light yellowish-brown, with scattered brown dots. Minute hairs are present on the abdomen and at a few other points on the pupal surface. Larvae of the Western Pygmy Blue pupate on the host plant and the pupal stage is apparently the diapause state. As many of the host species are tumbleweeds, Shapiro (1973a) has aptly suggested that passive dispersal of pupae on the dried

plants in fall and winter may be a significant factor in the remarkable colonizing ability of the insect.

ADULT BEHAVIOR: This butterfly has a very weak flight, and flies extremely close to the ground. It is usually found just around its foodplant clumps, and visits mallows and other wildflowers for nectar. The tiny proboscis of this species means that the adults often have to go through considerable contortions and probing at the base of a flower to obtain any nectar.

FOODPLANTS: *Chenopodium* (Pigweed) and *Atriplex* (Saltbush) species in the family Chenopodiaceae, especially *Atriplex semibaccata* R. Br. (Australian Saltbush), an introduced plant which is abundant in waste places in southern California. Henne has found larvae on *Atriplex hymenelytra* Wats. at Red Rock Canyon in Kern County. Comstock (1927a) and Downey (in Ehrlich and Ehrlich, 1961) also record *Petunia parviflora* Juss. (Solanaceae) as a host; this may not be a valid recorded foodplant, for as Shapiro (1973a) points out, another species of *Petunia* is toxic to various insect larvae. Host plants in lowland central California listed by Shapiro (1973a) are the following: *Atriplex patula* L. ssp. *hastata* (L.) Hall. & Clem. (probably the principal host in salt marshes throughout the range of *B. exilis*), *Atriplex rosea* L. (the most frequent host throughout the Sacramento Valley), *Atriplex cordulenta* Jeps., *Atriplex semibaccata* R. Br., *Suaeda fruticosa* (L.) Forsk. (= *S. moquini* Greene). On the last host, populations of larvae become so dense at Davis and other sites in Yolo County as to constitute a potentially significant threat to its seed production, at least locally. Shapiro (1973a) suggests that records on *Chenopodium* may well be due to misidentification of *Atriplex rosea*, which resembles that genus strongly. He never found oviposition or larvae on *Chenopodium* plants, even those in close proximity to *Atriplex* or *Suaeda* bearing many larvae.

The butterfly has also been recorded on an introduced species of Aizoaceae, *Sesuvium verrucosum*, by J. Emmel and G. Pratt (unpublished data).

CHROMOSOME NUMBER:

SIMILAR SPECIES: None in our area. A second species occurs from coastal Alabama south into Florida along coastal salt marshes and tidal flats. One stray has been reported from Galveston, Texas.

GEOGRAPHIC AND SEASONAL VARIATION: No geographic or seasonal variation has been noted in this species despite its occurrence in every month of the year and its distribution from California to Texas and south to Venezuela.

GENERAL REMARKS: For such a tiny butterfly with weak flight, the western Pigmy Blue is remarkably widely distributed in the neotropics as well as the southwestern United States. It also strays northward as far as Colorado, Nebraska, Kansas, and Oregon. The delicate wings and small size are no index to this species' evolutionary success as a wide-ranging species.

164. *Everes comyntas comyntas* (Godart)

This is the Eastern Tailed Blue, which occurs predominantly east of the 110th Meridian and extends from Montreal in Canada south to Florida. On the west coast, this species occurs from northern Oregon south through central California in the interior valleys, well isolated from the main distribution of the species which has its western terminus in eastern Colorado.

DIAGNOSIS: This species closely resembles the following species, *E. amyntula*, but in *comyntas* the ventral surface of the hindwing has two orange spots, the black ventral spots are distinct and the dorsal surface of the hindwing often has one orange spot in the males and two in the females.

ORIGINAL DESCRIPTION: Godart, *Enc. Meth.*, 9: 660 [1824].

TYPE LOCALITY: "North America". Holotype in Museum Nationale de Histoire Naturelle, Paris, France.

DISTRIBUTION: In California, this butterfly is found in the lower valleys of the Mt. Shasta region in Siskiyou County southward through the Central Valley to the vicinity of Bakersfield. It is also found in the Owens Valley in Inyo County.

ELEVATION RANGE: From near sea level to approximately 4,000' elevation.

HABITAT AND PLANT COMMUNITIES: Generally, this species is found in riparian habitats in the Central Valley, as well as in disturbed areas where there is agricultural activity, such as along dirt roads, at the edges of cultivated fields, etc. At the foot of the Sierra Nevada foothills, along the eastern edge of the Great Central Valley, populations are sometimes found within the Foothill Woodland plant community where they are associated with disturbed situations where one foodplant, *Lotus purshianus* (Benth.) Clem & Clem., is locally common.

PHENOLOGY: The species is multivoltine, with adults appearing in March of April and a succession of broods continuing into October or November. Overwintering is presumed to be as a full-grown larva as in the closely related *Everes amyntula*.

ADULT BEHAVIOR: Adults are frequently found at flowers and will also visit mud to sip water. Males are frequently seen patrolling throughout the day near the host plant in search of females.

LIFE HISTORY: The eggs are pale green with white ridges and are laid singly on host flowers or on young leaves. The larvae normally feed on the flowers and fruits of the host. The mature larva is dark green in ground color with many pale dots, a dark green or brownish mid-dorsal stripe, obscure brownish oblique sub-dorsal marks, and a whitish lateral line (edged by reddish) in the middle of the body. Less common color forms have ground colors of red-brown (sometimes with green stripes), violet-brown, or yellow-brown. The pupa is either pale or dark green in ground color, with the abdomen yellowish-green or brownish-yellow. There is a mid-dorsal stripe of dark green, edged with black spots, or blackish. Black oblique dashes occur on the side of the abdomen. A less common form of the pupa is whitish dorsally, and whitish on the abdomen. This species hibernates as a nearly mature larva, sometimes within the host pods.

FOODPLANTS: This species uses various herbaceous annual and perennial Fabaceae. In California, the following are verified foodplants: *Melilotus indicus* (L.) (Ken Davenport, personal communication); *Lotus purshianus* (Benth.) Clem. & Clem. (J. F. Emmel, unpublished data). In the Sacramento delta area, the species is sometimes associated with *Lotus scoparius* (Nutt. in T. & G.) Otteley, and this is presumed to serve as a host there (J. F. Emmel, unpublished data).

CHROMOSOME NUMBER:

- SIMILAR SPECIES:** This species closely resembles the Western Tailed Blue, *Everes amyntula*. However, *amyntula* has only one orange ventral spot on the hindwing (a second spot is sometimes present very faintly) and its black underside spots on the hindwing are usually less distinct. *E. amyntula* tends to be somewhat larger in size than *E. comyntas*, particularly in the lower elevation populations of *amyntula*; high elevation populations of *amyntula* tend to be similar in size to *comyntas*. The females of *amyntula* tend to have varying amounts of basal blue scaling on the upperside, often involving at least half of the wing surface, whereas females of *comyntas* tend to be largely uniformly brown. Generally, the Eastern Tailed Blue (*E. comyntas*) is a valley bottomland insect, whereas *E. amyntula* tends to be a foothill or montane species. Additionally, *comyntas* is a multivoltine insect, whereas *amyntula* tends to be univoltine in most of its populations.
- GEOGRAPHIC AND SEASONAL VARIATION:** Seasonal variation has not been noticed among the various broods of *comyntas*, and populations on the east side of the Sierra Nevada do not seem to differ in facies from those of the Great Central Valley.
- GENERAL REMARKS:** It is remarkable that *E. comyntas* and *E. amyntula* are largely allopatric. Even in the Canadian Zone where the ranges of the two species come into contact, this allopatry is pronounced with *amyntula* being the sole occupant of the lower Canadian Zone in the west (*comyntas* is the sole occupant of the lower Canadian Zone in the eastern United States). In the eastern United States, *E. comyntas* occupies habitats which are very similar to those utilized by *Icaricia acmon* in the western United States. These two species also use a similar set of foodplants. It would be of interest to study areas in the Central Valley of California where these two species are sympatric to see if there is significant competition between the two. Another interesting possibility for investigation is that these western populations of "*comyntas*" may represent a third tailed-blue species, perhaps separable by electrophoretic or careful chromosomal studies from its siblings.

165. *Everes amyntula amyntula* (Boisduval)

This tailed lycaenid species is found in numerous populations throughout the foothills and mountains of California, as well as along the immediate coast in southern California and on most of the Channel Islands.

- DIAGNOSIS:** Similar to *E. comyntas* but generally larger, with females having a greater amount of blue scaling and with the black spots on the underside in both sexes generally less distinct than those in *comyntas*.
- ORIGINAL DESCRIPTION:** Boisduval, *Ann. Soc. Ent. France*, (2)10: 294 (1852).
- TYPE LOCALITY:** "California". Restricted by Emmel, Emmel, and Mattoon (1988, *Journal Research Lepidoptera*, :) to

Holotype in U. S. National Museum.
- DISTRIBUTION:** This species is widespread in the state, occurring in scattered populations throughout the cismontane foothills and mid-elevations in the mountains; It is also found on the high east slope of the Sierra Nevada as well as in the higher desert mountains of Mono and Inyo counties. High elevation populations are also known in the northern Sierra Nevada (such as at Donner Pass), and in the Mt. Shasta region (such as Mt. Eddy, etc.).
- ELEVATION RANGE:** From near sea level to nearly 10,000' in the mountains of the Death Valley region.

- HABITAT AND PLANT COMMUNITIES:** This species is found in a variety of habitats within the state. It is found in grassy fields, on open slopes, and gravelly ridge tops, within the following plant communities: Coastal Sage Scrub, Chaparral, Foothill Woodland, Southern Oak Woodland, Montane Coniferous Forest, Subalpine Forest, Sagebrush Scrub, Pinyon-Juniper Woodland, Valley Grassland, and Arctic-Alpine Fellfields.
- PHENOLOGY:** The butterfly may be univoltine in some localities such as the very highest elevations or in all populations in extremely dry years. Otherwise, it appears to be at least partially multivoltine, with records ranging from February to September. The majority of records are from March through June for most of the low to mid-elevation populations within the state.
- ADULT BEHAVIOR:** Like its eastern cousin, this species is frequently observed nectaring on flowers and sipping water at mud flats. It mimics the hairstreaks in its tailed hindwing appearance and distracting "eyespot" of orange located near the base of the tail. No studies have yet been done to ascertain whether these markings and the tail-like structure are effective in deflecting bird or lizard attack from the vulnerable head region to the expendable tailed hindwing portion.
- LIFE HISTORY:** The echinoid eggs are pale green and are deposited singly on the flowers or young seedpods of hosts. The mature larva is highly variable in ground color, ranging from a greenish-straw color with pink and maroon markings, through a yellowish-green with pale mauve markings, to a solid green, with darker mid-dorsal line. The entire body surface is covered with short fine white hairs arising from minute black punctae of various sizes. The species overwinters as fully grown larvae, generally remaining in the *Astragalus* pods, where they have been feeding on the young seeds. The pupa is pale soiled buff, occasionally greenish-grey or olive white, with a dark brown dorsal band and blotches. Long white hairs are scattered over the surface.
- FOODPLANTS:** *Astragalus* species (Fabaceae). Species which have been recorded as used by *amyntula* in California are the following: *A. whitneyi* Gray, *A. lentiginosus* Dougl., *A. douglasii* (T. & G.) Gray, *A. trichopodus* (Nutt.) Gray ssp. *leucopsis* (Torr.) T. & G..
- CHROMOSOME NUMBER:**
- SIMILAR SPECIES:** See discussion above and under *E. comyntas*. In localities where the two species could conceivably be sympatric, such as in the lowest elevations of the west slope Sierra Nevada foothills, *amyntula* may usually be distinguished by the chalky white ground color and the rounded apex of the wing, compared to the grey ground color and pointed apex of the forewing in *comyntas*.
- GEOGRAPHIC AND SEASONAL VARIATION:** No significant seasonal variation has been noted among the various broods of *amyntula*. The high-elevation *amyntula* populations such as at Mt. Eddy, in the Donner Pass region, or in the Inyo-White Mountains, are all consistently smaller than lowland *amyntula* populations. Furthermore, these high-elevation populations seem to be strictly univoltine, suggesting a possible physiological difference from populations in the lower elevations. Further detailed study of these high-elevation populations may lend support to giving them subspecific rank.
- The desert mountain populations have reduced black markings and are paler in general aspect than the Sierran populations.

GENERAL REMARKS: The genitalia of both sexes in these two species are distinct and perhaps provide the only certain way to distinguish between all specimens that one may encounter in the ranges of the two species in California. In *comyntas* males, the end of the male uncus is concave with a point in the middle, when viewed from above. In *amyntula*, the male genitalic uncus is convex with a point. The larvae of the two species bear honey glands and eversible tubes, and are attended by ants in the wild. The pupae are known to stridulate (Downey, in Howe, 1975).

166. *Celastrina argiolus* (Linnaeus)

ADULT BEHAVIOR: Although this butterfly is found over a rather wide geographic area, the species is rather local in occurrence. In the western United States, as in California, adults tend to stay quite close to their host plants. In England, where the same species occurs, T. Shreeve has found that adults move rather extensive distances even between separate patches of forest, averaging 1.7 kilometers for males and 2 kilometers for females. Adults will sip nectar from a number of flowers and also visit dung and mud. Adults often perch and patrol around shrubs on hilltops, in addition to patrolling near their hosts.

LIFE HISTORY: The early stages have been recorded by various authors for the eastern United States subspecies of this butterfly, but not from material in our area until the present work. The turban-shaped egg is pea green and the reticulation observed on other lycaenid eggs is gathered into a series of pale stubby prominences. The mature larva is extremely variable in pattern and color, ranging from nearly pure green to magenta in ground color, with a series of chevron markings to either side of an irregular triangular marked mid-dorsal line. The pupa is brown or light yellowish-brown, often with brown blotches. Hibernation is in the pupal stage.

CHROMOSOME NUMBER:

SIMILAR SPECIES: None in our area.

GEOGRAPHIC AND SEASONAL VARIATION: This butterfly is one of the most variable known geographically as one follows its Holarctic distribution. In North America, various subspecies occur from central Alaska east to Labrador south to the Gainesville area of Florida and on through Mexico to Panama. It is not found in the warmer areas of southern Florida, the Bahamas, or the central parts of our southwestern deserts, but it does occur in most of the higher desert mountain ranges. The subspecies identified in the above section delineate the major geographic variation in our state. Seasonally, the spring examples are usually slightly smaller and more violet tinged above than the later brood, which tends to be more heavily bordered with black in both sexes.

GENERAL REMARKS: This butterfly, *Celastrina argiolus*, is the first named, most numerous, and most widespread of all the component species of the *Lycaenopsis* group of a major tribe of Blues. Species of this general groups are distributed throughout the Holarctic and Oriental Regions, including the Papua New Guinea subregion. Within the Oriental Region, they are more numerous in species than any other group of comparable taxonomic status with the sole exception of one group of genera. *Celastrina argiolus* ranges from Europe and North Africa to the Far East, where it occurs southward to within 15 degrees of the Equator, and in America from Alaska to Panama. While it is not considered a migrant, its powers of dispersal must be considered exceptional. The butterfly is a weak and usually fluttering

sub-montane species, yet it has reached every continental area and has adapted to many climates and foodplants.

A honey gland is present on the seventh abdominal segment and eversible tubercles on the eighth abdominal segment. Ants occasionally tend the larvae, but their presence is by no means essential. It is easy to rear *C. argiolus* without ant assistance. The group has been revised and examined on a worldwide basis in a very fine monograph by Eliot and Kawazoe (1983).

One of the most widespread and phenotypically variable lycaenids in North America, this Blue is distributed from the sub-Arctic in northern Canada to the tropical mountains of Central America. Many geographic races and seasonal forms have been named from across this geographic range. In California, we have three sets of populations that are phenotypically distinct.

a. *C. a. echo* (W. H. Edwards)

DIAGNOSIS: The Echo Blue is the commonest Pacific Coast subspecies and ranges from northern Baja California north through California to Oregon, Washington and British Columbia in Canada. Generally, the wing pattern of this subspecies *echo* is remarkably stable, both geographically and seasonally, and is characterized by its large size and relatively light coloration. At higher elevations, adults are somewhat more heavily bordered with black.

ORIGINAL DESCRIPTION: W. H. Edwards, I, 2: 506-507 (1864).

TYPE LOCALITY: "California", restricted to San Francisco, California by F. M. Brown and Clench, in F. M. Brown, *Transactions American Entomological Society*, 96: 429-431 (1970). Neotype in Carnegie Museum, designated by F. M. Brown and Clench, in F. M. Brown, *Transactions American Entomological Society*, 96: 430-431 (1970).

DISTRIBUTION: This butterfly is widespread in the state, occurring from the higher mountains of southern California and the Channel Islands northward through the Coast Ranges and Sierra Nevada to the Klamath Mountains region, the Mt. Shasta region, and Lassen County.

ELEVATION RANGE: From near sea level to approximately 8,000' on the west slope of the Sierra Nevada.

HABITAT AND PLANT COMMUNITIES: The butterfly is found in a variety of habitats and plant communities but generally prefers riparian woodland situations or open slopes within these communities. The following plant communities have been recorded for this species within California: Coastal Sage Scrub, Chaparral, Montane Coniferous Forest, Southern Oak Woodland, Northern Oak Woodland, Foothill Woodland, and Mixed Evergreen Forests.

PHENOLOGY: This butterfly flies from the early spring to summer (January to July), depending upon elevation. It may be bivoltine in the lowlands and foothills, at least in years of favorable precipitation and host plant condition.

FOODPLANTS: *Ceanothus* species, including *C. cuneatus* (Hook.) Nutt., *C. leucodermis* Greene, and *C. integerrimus* H. & A. (Rhamnaceae), Dogwood, *Cornus* (Cornaceae), *Spiraea* (Rosaceae), *Adenostoma fasciculatum* H. & A. (Rosaceae), *Quercus* species (Fagaceae), and *Holodiscus* species (Rosaceae): several legumes

according to Comstock (1927a). The precise foodplants in California need to be investigated, especially with regard to the frequency that each is used.

b. *C. a. near cinerea* (W. H. Edwards)

- DIAGNOSIS: This race tends to be smaller and rather darker than the more coastal *echo* populations.
- ORIGINAL DESCRIPTION: W. H. Edwards, *Papilio*, 3: 8 (1883).
- TYPE LOCALITY: "Fort Grant, Cochise County in Mt. Graham, Arizona", restricted to Fort Grant, west side of Mt. Graham, Arizona by Clench in F. M. Brown, Transactions American Ent. Soc., 96: 427-428 (1970). Lectotype in Carnegie Museum, designated by Clench in F. M. Brown (1970).
- DISTRIBUTION: Populations referable to this subspecies are found in the mountain ranges of the eastern Mojave Desert and north along the east slope of the Sierra Nevada and in the Panamint, Inyo, and White Mountains. Elsewhere, *cinerea* is the subspecies that is common in Arizona and New Mexico in the southern Rocky Mountains and adjacent plateau areas. It ranges southward into the mountains of Chihuahua, and penetrates northward to central Colorado, Utah, and Nevada. Typically, this is a mountain subspecies throughout its range.
- ELEVATION RANGE: From 4,500' to elevations above 10,500'.
- HABITAT AND PLANT COMMUNITIES: In the desert mountains, the butterfly is usually found in canyon bottoms or on sparsely forested slopes, within the following plant communities: Pinion-Juniper Woodland, Sagebrush Scrub, and Subalpine Forest.
- PHENOLOGY: The subspecies may be univoltine or bivoltine at a given locality, depending on rainfall patterns and foodplant availability. For the eastern Mojave Desert populations, most adults are taken in March and April but at the higher elevations in these mountains, adults can be taken in late May and early June. In the Death Valley region, the first brood is taken from late May to early July, depending on elevation. The subspecies is sporadically taken during the summer and early fall months in these areas, with these emergences possibly triggered by summer rains. The lack of significant numbers of specimens being taken during this latter part of the flight period signifies that the second generation emergences in these areas is an uncommon phenomenon.
- FOODPLANTS: Several species of Rosaceae have been recorded as foodplants for this subspecies within California. These are, *Petrophytum caespitosum* (Nutt.) Rydb. (Rock Spirea), a plant that grows in mats on limestone ledges in the mountain ranges of the eastern Mojave; *Chamaebatiaria millefolium* (Torr.) Maxima. (John Lane, in litt.); also, this subspecies has been noted in close association with *Holodiscus microphyllus* Rydb. ssp. *microphyllus*, which presumably serves as a larval host.

c. *C. a. ssp. (N. Coast redwoods)*

- DIAGNOSIS: This undescribed segregate, which is found along the immediate coast in extreme northern California, is characterized by greatly enlarged dark markings on the undersides of the wings; in other respects, it is superficially similar to the subspecies *echo*.

- DISTRIBUTION:** Thus far, specimens with this phenotype have been taken only at Prairie Creek Redwoods State Park, Humboldt County, California. Whether it is more widely distributed within the Redwood Forest areas of the North Coast remains to be determined.
- ELEVATION RANGE:** From near sea level to approximately 300' elevation.
- HABITAT AND PLANT COMMUNITIES:** This butterfly is found in riparian situations within the Coastal Redwood Forest; in these areas there is frequent fog and a rather high winter rainfall.
- PHENOLOGY:** The specimens known to us have been taken in the month of April; possibly there is a second brood in June or July.
- FOODPLANTS:** Unknown.

167. *Glaucopsyche lygdamus* (Doubleday)

- SPECIES SYNOPSIS:** The *Glaucopsyche lygdamus* complex of blues is extraordinarily diverse in California, with considerable geographic variation as well as differences in biology of these populations. Only the most distinctive populations have been formally named as subspecies to date.
- ADULT BEHAVIOR:** Individuals of *G. lygdamus* tend to be rather sedentary, generally not straying far from their host plants. The males perch on prominent stems or branches of the host plant or nearby shrubs, whereas females spend considerable time standing on the host and walking over it in pre-oviposition behavior.
- LIFE HISTORY:** Described by Comstock (1929a), and Comstock and Dammers (1934), and figured here with photographs from larvae reared by the authors. The echinoid egg is flattened above and below, with a raised white network over the surface. The eggs are laid singly on the tender leaf tips of the *Lotus* host. The mature larva is a normally vivid green, covered with silvery white hairs, although it may vary from pale green or pale coffee color to purplish (Langston, 1969). A broad distinctive mid-dorsal band of dark magenta grades to scarlet at its edges, with a row of yellow triangles (light mauve centers) on either side of this band. A gland in the middle of the tenth segment provides a secretion for which ants tend the larvae (records summarized in Downey and Lange, 1956). Pupation usually occurs on the foodplant, using a silk girdle and button. Sometimes the pupa is formed amid debris (Langston, 1969). The pupa is pale brown, profusely speckled with black dots arranged in groups. A few short white hairs occur on the head and posterior portions of the abdomen.
- CHROMOSOME NUMBER:**
- SIMILAR SPECIES:** None in existence today, although formerly some forms of the extinct *Glaucopsyche xerces* resembled some phenotypes of *lygdamus*.
- GEOGRAPHIC AND SEASONAL VARIATION:** Obviously, the geographic and seasonal variation in this species is considerable, even judging only from the number of named subspecies. The basic differences among the subspecies reside in size of the wings, the grey dusting on the undersides and the intensity of the blue coloration on the dorsal surface, including purplish or greenish tints in some subspecies. Nothing is known of the environmental or genetic components of this variation.

GENERAL REMARKS: There is one report of a pupa of this species having been found in an ant nest, suggesting a strong symbiotic relationship with ants. The larvae are also generally heavily tended by ants in nature, although the relationship is not obligatory for larval development, as evidenced by laboratory rearing studies.

SUBSPECIES: This species is also a widespread Blue, occurring across the northern United States from coast to coast and across all of Canada northward into Alaska. It is absent only from the hottest and southernmost areas of the United States. Within our state, we recognize eight subspecies and related groups of populations.

a. *G. l. australis* F. Grinnell

DIAGNOSIS: The adults of this subspecies are relatively small compared to the other California *lygdamus* subspecies, with the males lustrous blue above and females partly blue and partly dark brown. The black spots on the ventral surface of the secondaries are smaller in both sexes than *incognitus*, the next subspecies to the north. The Southern Blue flies in abundance throughout cismontane southern California, wherever its foodplant, *Lotus scoparius*, grows commonly (especially in disturbed areas such as recent burns, road cuts, and canyon slopes).

ORIGINAL DESCRIPTION: F. Grinnell, *Canadian Entomologist*, 49: 350 (1917).

TYPE LOCALITY: Pasadena, California. Holotype in American Museum of Natural History.

DISTRIBUTION: This subspecies is found from northern Baja California northward to the Monterey County coast, with its stronghold in the cismontane areas of southern California from San Diego County northward to Santa Barbara County. A set of populations is found on Santa Cruz Island which differs slightly from typical *australis*, but here is considered part of that subspecies. The only other Channel Island that *G. lygdamus* is found on is Santa Rosa Island, but the phenotype represented by this segregate differs from typical *australis* and has been described as a separate subspecies, *G. l. pseudoxerces* Emmel and Emmel.

Populations of *G. l. australis* on the El Segundo Sand Dunes in Los Angeles County sometimes show phenotypic tendencies towards *sabulosa*, but are largely most similar to more inland populations of *australis*.

ELEVATION RANGE: From near sea level to approximately 6,000' elevation; the majority of populations seem to occur below 4,000' elevation.

HABITAT AND PLANT COMMUNITIES: The butterfly is typically found in both Coastal Sage Scrub and Chaparral, particularly in areas where there has been a recent fire, allowing the fire-adapted major host of this subspecies, *Lotus scoparius* (Nutt. in T. & G.) Ottley, to grow abundantly. It is also found on Coastal Strand habitats such as the El Segundo Sand Dunes. Other populations are known along the desert slope of the southern California mountains inhabiting such plant communities as Pinyon-Juniper Woodland and Creosote Bush Scrub, particularly where these habitats are close to an area of chaparral. Occasionally, the species is found at the lower edges of the Montane Coniferous Forest community, again often near chaparral.

PHENOLOGY: This subspecies, as with all the other *G. lygdamus* subspecies, is strictly univoltine. Emergence begins in February at the lowest elevations and continues into April or even early May in some of the higher elevation populations.

FOODPLANTS: The following plants in the family Fabaceae have been recorded as foodplants in southern California: the preferred and probably sole foodplant of most populations is *Lotus scoparius* (Nutt.) Ottley; other documented foodplants include *Lupinus formosus* Greene, and *Astragalus filipes* Torr. (J. F. Emmel, unpublished data).

b. *G. l. incognitus* Tilden

DIAGNOSIS: This central California subspecies of *lygdamus* has previously been known as *behrii* in the literature. F. M. Brown (Transactions American Entomological Society, 96: 415-417, 1970) has shown that the name *behrii* Edwards 1862 pertains to *Glaucopsyche xerces* (Boisduval, 1852) and not to *G. lygdamus* (Doubleday, 1842). Thus, Tilden (1974) applied the name *incognitus* to this member of the *lygdamus* complex, which had never been given a name of its own. The name, which is Latin for "unknown," "unrecognized," or "disguised," is given because this insect was called so long by the name of another insect. This subspecies is slightly larger than *australis*, having a forewing length of 14 to 15 millimeters. The males are lustrous blue above with narrow black borders. Beneath, there is normally a row of uniform black spots on a grey ground color. The female is dark brown, rarely having slight basal scaling of blue near the body.

Under this name, in addition to the nomotypical populations in the central California Coast Range area, we include phenotypically similar populations from the Sacramento Valley, from the Sierra Nevada foothills, and the lower elevations of the Klamath Mountains Assemblage.

ORIGINAL DESCRIPTION: Tilden, *Journal of Research on the Lepidoptera*, 12: 213-214 [1974].

TYPE LOCALITY: Alum Rock Park, Santa Clara County, California. Holotype in California Academy of Sciences.

DISTRIBUTION: In its typical form, *incognitus* is found in the Coast Ranges of central California from Monterey and San Benito counties northward to Napa and Sonoma counties. Northward, phenotypically similar populations occur at low to mid-elevations in the North Coast Ranges and Klamath Mountains region. Populations with similar facies are found in the Sacramento Valley and in the Sierra Nevada foothills from approximately Tulare County northward to the Mt. Shasta region.

ELEVATION RANGE: From near sea level to approximately 4,000' elevation.

HABITAT AND PLANT COMMUNITIES: This subspecies is found on flats, slopes, and along canyon bottoms within the following plant communities: North Coastal Scrub, Chaparral, Valley Grassland, Foothill Woodland, Northern Oak Woodland, Riparian Woodland, Coastal Prairie, and Mixed Evergreen Forest.

PHENOLOGY: Dates of capture range from late January to early May, with most records for the months of March and April.

FOODPLANTS: The larvae have been reared on *Lupinus micranthus* Dougl. in Lindl. in Marin County: they are also recorded on *Lotus scoparius* (Nutt. in T. & G.) Ottley, *Astragalus*, and a large yellow lupine, *Lupinus arboreus* Sims (Howe, 1975). Ova have been found on *Lupinus variicolor* Steud. on the east slope of the San Bruno Mountains (J. F. Emmel, unpublished data). The majority of populations appear to be associated with various perennial *Lupinus* species, but information is lacking on the particular species used in most populations.

c. *G. l. palosverdesensis* E. M. Perkins and J. Emmel

This recently described subspecies was first discovered in 1973 in the few remaining undisturbed seaward canyons and marine terraces on the Palos Verdes Peninsula of southern California (Perkins and Emmel, 1978). The butterfly was federally listed as an Endangered Species in 1980. The City of Rancho Palos Verdes then achieved the dubious distinction of being responsible for eradicating the butterfly in 1982-1983, when it developed a baseball field on the last known remaining habitat area. But remarkably this was not the end of the story!

After eleven years of apparent extinction, a small colony was rediscovered by accident on March 10, 1994, at a site on the Los Angeles Harbor side of the Peninsula, at the north end of the city of San Pedro. Preserved since the early part of the 20th century as the Defense Fuel Support Point at San Pedro, with about 30 acres of native plant community fragments, this small site is now the center of an intensive recovery effort headed by Dr. R. H. T. Mattoni and carried out with the full cooperation of the U.S. Navy (Mattoni, 1994). The population count in 1994 was estimated to be less than 300 adults.

DIAGNOSIS: The subspecies *palosverdesensis* is larger than *australis* but smaller than *incognitus*. The mean left forewing length of males in each subspecies is 15.75 millimeters, 15.32 millimeters, and 16.19 millimeters, respectively, whereas females measure 15.93 millimeters, 14.98 millimeters, and 16.43 millimeters, respectively. The upper surface of the males is a darker richer blue color than *australis* and is rather similar to the *incognitus* males further to the north. The dark grey color of *palosverdesensis* females, which is highlighted by blue iridescence, is also distinctive. Unlike *australis* in the surrounding mountains of the Los Angeles Basin, the post-median black spots on the hindwings underneath are larger and better developed in both sexes of *palosverdesensis*. Unlike *incognitus*, whose post-median black spots are also comparably large on both wings, those of *palosverdesensis* are prominently haloed by rings of white. The threat of accelerated residential and commercial development to the continued existence of this subspecies, which was pointed out in the Original Description (Perkins and Emmel, 1978), was unfortunately realized five years later. The type locality population joined the fate of *Glaucopsyche xerces* (Boisduval), another California peninsular endemic from San Francisco, which had been extinct some 35 years at the time *palosverdesensis* was described 400 miles to the south. Fortunately, the 1994 discovery of a surviving colony at a site across the Palos Verde peninsula means this Endangered Species still has a chance to persist.

ORIGINAL DESCRIPTION: E. M. Perkins and J. F. Emmel, *Proceedings Entomological Society Washington*, 79: 468-471 (1978).

TYPE LOCALITY Rancho Palos Verdes, Palos Verdes Peninsula, Los Angeles County, California. Holotype in U. S. National Museum.

DISTRIBUTION: Restricted to the coastal terrace on the southern half of the Palos Verdes Peninsula of southern California, on the cool, fog-shrouded seaward and Los Angeles Harbor sides of the Palos Verdes Hills. This area included the communities of Palos Verdes Estates, Rancho Palos Verdes, Rolling Hills Estates, Rolling Hills, Portugese Bend, and San Pedro. Specimens examined from areas eight miles to the north and to the east of this small distributional range match the phenotype of other populations of *australis*, which inhabit the Los Angeles Basin. Thus, at the time of its discovery and description, this butterfly was one of the world's most restricted taxa.

- ELEVATION RANGE: From almost sea level to 800' elevation.
- HABITAT AND PLANT COMMUNITIES: Coastal Sage Scrub plant community, especially in the vicinity of flowering Rattleweed or Locoweed plants, *Astragalus*.
- PHENOLOGY: All recorded specimens in the type series were collected on dates ranging from February 1st through March 28th. The adults of this subspecies flew much earlier than the great bulk of the other populations of this butterfly in California.
- FOODPLANTS: At the type locality, the sole known foodplant was the milk vetch or rattleweed, *Astragalus trichopodus* (Nutt.) Gray ssp. *Lonchus* (M. E. Jones) Barneby. At the second site (San Pedro) discovered by Mattoni, the butterfly also uses a second host, the widespread *Lotus scoparius* (Nutt. in T. & G.) Ottley.

d. *G. l. deserticola* Austin and Emmel

- DIAGNOSIS: This is a desert subspecies characterized by its relatively large size, relatively broad dark margins dorsally, large ventral spots, and relatively dark females.
- ORIGINAL DESCRIPTION: Austin & Emmel, *Systematics of Western North American Butterflies*, pp. - (1998_),
- TYPE LOCALITY: Cottonwood Pass Road, 0.6-1.8 miles south of Nevada State Route 160, 1340 meters, Spring Mountains, Clark County, Nevada.
- DISTRIBUTION: This subspecies is found from southern Nevada to the higher mountain ranges of the eastern Mojave Desert and the southern Death Valley region.
- ELEVATION RANGE: From 4,000 to 6,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is typically encountered along roadsides, on open flats, along dry desert washes, and sometimes on rocky or gravelly slopes within the following plant communities: Pinyon-Juniper Woodland, Joshua Tree Woodland, Shadscale Scrub, and occasionally at the upper edges of the Creosote Bush Scrub.
- PHENOLOGY: This subspecies flies from late March to mid-May, depending on elevation, with a peak flight in late March and early April.
- FOODPLANTS: All populations of this butterfly thus far have been associated with *Astragalus lentiginosus* Dougl. ssp. *fremontii* (A. Gray) S. Wats. (Fabaceae). Numerous ova and larvae have been found on the flowerbuds and seedbuds of this plant (J. Emmel and G. Pratt, unpublished data).

e. *G. l. near oro* (Scudder)

- DIAGNOSIS: Populations of *G. lygdamus* in the higher mountains of the Death Valley and eastern Owens Valley region seem to be closest to the Rocky Mountain subspecies *oro*; similar populations are found scattered across the Great Basin in the higher mountain ranges of Nevada and Utah. Adults of these populations are characterized by being somewhat smaller, with the males having more silvery blue above with narrower black outer margins. There is sometimes a slight brownish cast to the ventrum, and the spots are much smaller. The females tend

to be much more broadly blue above than in other populations, and have a dark cell-end line on the dorsal forewing.

- ORIGINAL DESCRIPTION: Scudder, *Canadian Entomologist*, 8: 23 (1876).
- TYPE LOCALITY: "Colorado". Type in Museum of Comparative Zoology, Harvard.
- DISTRIBUTION: Populations with this phenotype are found in the White Mountains of Mono and Inyo counties southward through the Inyo Mountains, the Grapevine Mountains, the Panamint Range, and the higher elevations of the Argus Range.
- ELEVATION RANGE: 5,500' to 10,500' elevation.
- HABITAT AND PLANT COMMUNITIES: On open flats, slopes, or along canyon bottoms primarily within the Sagebrush Scrub plant community; populations are also found in the upper edges of the Pinyon-Juniper Woodland and the lower edges of Bristlecone Pine Forest plant communities.
- PHENOLOGY: Dates of capture range from mid-May to early July, depending on elevation and snowpack, with most specimens having been taken in the month of June.
- FOODPLANTS: Most of the California populations of *G. l.* near *oro* are associated with a perennial *Lupinus* species (Fabaceae). Some of the White Mountains populations are associated with *Astragalus* species (also Fabaceae). The following plants have been documented as foodplants of this subspecies within California: *Lupinus alpestris* A. Nels., *L. excubitus* Jones, *Astragalus oophorus* Wats., and *A. fremontii* (Gray) Wats. (J. F. Emmel, unpublished data). Additionally, *Lupinus palmeri* Wats. is suspected to be a possible foodplant in the vicinity of Westgard Pass at the southern end of the White Mountains (J. Emmel and G. Pratt, unpublished data).

f. *G. l.* near *columbia* (Skinner)

- DIAGNOSIS: This Blue is the subspecies found in Oregon, Washington, and in extreme northern California, blending in the east and Great Basin with *oro*. It averages about the same size as *incognitus*, but the underside is paler grey with black spots that are rather smaller in size. Females of *columbia* tend to have less blue and often have an indistinct cell-end-line on the dorsal forewing. We consider the populations of *G. lygdamus* in the sagebrush areas of northeastern California (i.e., in Modoc and Lassen counties) to be closest to the subspecies *columbia*, which was named from the sagebrush country of central Washington. Langston (1969) considered the southern Cascade and Sierra Nevada populations of *G. lygdamus* to fall under this subspecies; we feel that there are sufficient biological differences, as well as phenotypic differences, to consider these montane populations of *lygdamus* to be distinct from the lowland *columbia*.
- ORIGINAL DESCRIPTION: Skinner, *Entomological News*, 28: 213 (1917).
- TYPE LOCALITY: Fort Columbia [=Brewster], Okanogan County, Washington. Holotype in Carnegie Museum.
- DISTRIBUTION: Populations referable to the subspecies *columbia* within California are found in the sagebrush regions of Lassen and Modoc counties in the northeastern corner of California. From here they extend northward through the region east of the Cascades in Oregon and eastern Washington. Apparent intermediate populations

between this subspecies and the subspecies *oro* are found in Idaho, western Montana, and Wyoming.

- ELEVATION RANGE: For the California populations, 4,500' to approximately 6,500' elevation.
- HABITAT AND PLANT COMMUNITIES: Within our state, the butterfly has been taken in both the northern Pinyon-Juniper Woodland plant community and the Sagebrush Scrub plant community.
- PHENOLOGY: This subspecies flies from late April until early June, depending on elevation.
- FOODPLANTS: Unknown for our area, but suspected to be one or more *Astragalus* species.

g. *G. l. pseudoxerces* Emmel and Emmel

- DIAGNOSIS: A single specimen of *G. lygdamus* taken by Scott Miller on Santa Rosa Island appears to represent a distinct geographic segregate. It is characterized by a smaller size, and a lack of black pupils in the spots of the underside, leaving white spots suggestive of the extinct *G. xerces* of San Francisco.
- DISTRIBUTION: Santa Rosa Island, California.
- ELEVATION RANGE: Unknown.
- HABITAT AND PLANT COMMUNITIES: Coastal Sage Scrub.
- PHENOLOGY: The single specimen taken by Miller was taken on April , .
- FOODPLANTS: *Lotus scoparius* (Nutt. in T. & G.) Otteley is strongly suspected for this population, on the basis of its presence on Santa Rosa Island and the widespread use of this particular plant by other *G. lygdamus* populations in southern California. Another possible host on the island is *Astragalus trichopodus* (Nutt.) Gray ssp. *leucopsis* (Torr.) T. & G.

h. *G. l. ssp.* (high elevation, Sierra Nevada)

- DIAGNOSIS: These populations were lumped under the subspecies *columbia* by Langston (1969). However, we feel that there is sufficient distinction, both biologically and phenotypically, to consider these a separate set of populations from the sagebrush-associated *columbia* populations of the eastern Washington and eastern Oregon region. Specimens from these Sierran populations are characterized by generally smaller size and considerable variability in the size of the black spots on the underside. Additionally, the females of these higher-elevation Sierran populations tend to have more blue scaling dorsally in contrast to the somewhat darker *incognitus*-like populations of the Sierra Nevada foothills.
- DISTRIBUTION: These populations are found throughout the higher elevations of the Sierra Nevada and the Klamath Mountains region.
- ELEVATION RANGE: From approximately 4,500' to 10,000' elevation, with most populations in the 6,500' to 9,000' elevation range.

HABITAT AND PLANT COMMUNITIES: These populations are usually found in riparian situations, in boggy meadows, or on vernal moist slopes within the Montane Coniferous Forest plant community.

PHENOLOGY: From late May to late July, depending on elevation and snowpack conditions.

FOODPLANTS: This subspecies uses *Lupinus polyphyllus* Lindl. ssp. *superbus* (Hell.) Munz in the Donner Pass region growing in a seep area on Basin Peak and around Castle Peak (Shapiro, 1977; J. F. Emmel, unpublished data). At Tioga Pass, in the Yosemite region, G. Pratt (personal communication) has taken adults in association with *Lupinus lyallii* Gray, a possible host.

i. *G. l.* ssp. (east slope Sierra Nevada, on *Lotus procumbens*)

DIAGNOSIS:

DISTRIBUTION:

ELEVATION RANGE:

HABITAT AND PLANT COMMUNITIES:

PHENOLOGY: .

FOODPLANTS: This subspecies uses *Lotus procumbens*.

j. *G. l. sabulosa* Emmel, Emmel, and Mattoon

DIAGNOSIS: This subspecies on the coast of Monterey County represents an intermediate both geographically and phenotypically between the San Francisco Bay area subspecies *incognita* and the southern California cismontane subspecies *australis*. Ventrally, it has a spotting pattern most similar to *australis*, but it differs in the more tannish ground color in contrast to the gray of *australis*. Dorsally, the females resemble *incognita* in their uniform brown coloration, in contrast to the females of *australis* which have extensive blue scaling in the basal one-half to two-thirds of the wing. The foodplant is *Lotus scoparius*, the same host used by *australis*. *G. l. incognita* uses other Fabaceous plants, including *Lupinus*, *Vicia*, and *Astragalus*.

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 171-172 (1998j).

TYPE LOCALITY: Sand dunes west of intersection of Palm Avenue and Lake Drive, west of Marina, 60-100' elevation, Monterey County, California. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This subspecies is apparently restricted to the immediate coast in Monterey County and has been taken in the sand dunes west of Marina and at the mouth of Partington Canyon south of Big Sur. Its range may extend southward along the coast to Morro Bay in San Luis Obispo County, and perhaps to the Oso Flaco Sand Dunes in that same county.

ELEVATION RANGE: From near sea level to 100' elevation.

- HABITAT AND PLANT COMMUNITIES: The vegetation on the sand dunes at the type locality is typical Coastal Strand with locally common *Lotus scoparius*, *Eriogonum latifolium*, and *Corethrogyne filaginifolia*. The area is subject to a maritime climate, with mild winters and cool, often foggy summers.
- PHENOLOGY: This subspecies flies in a single brood from early March (perhaps late February in some years) to late April, a flight period similar to that of the populations of *Glaucopsyche xerces* which once flew in the sand dunes of what is now the city of San Francisco.
- FOODPLANTS: The hostplant of the larvae is *Lotus scoparius* (Nutt. in T. & G.) Ottery.

168. *Glaucopsyche xerces* (Boisduval)

- SPECIES SYNOPSIS: The Xerces Blue, a former resident of the sand dunes in San Francisco, was the first butterfly species in North America to have become extinct from human interference. (*Cercyonis sthenele sthenele*, which became extinct around 1880 in the San Francisco sand dunes, was the first subspecies of a wider-ranging species to disappear in historic times.) Today, an international organization devoted to the conservation of invertebrates, The Xerces Society, is named for this diminutive creature, a butterfly which has achieved fame far beyond its size and former restricted geographic distribution. It was one of the most variable butterflies known and would have made a unique tool for research on the effects of population size and geographic distribution on infra- (and intra-) specific variation. As Downey and Lange (1956) point out, "it was so limited in distribution that any individual was geographically within flight range of its contemporaries. In this sense, it could be considered as a species consisting of but one population. Equally important, the wings exhibit extreme continuous and discontinuous variation in macular components." But for its untimely extinction, *G. xerces* would have been an ideal study organism for ecologists and evolutionary biologists. The last known specimens of *xerces* were collected at the Presidio in San Francisco during May 1941 by W. H. Lange (Downey and Lange, 1956) and on March 23, 1943 on the beach side of Sloat Boulevard (Howe, 1975). It has not been collected since 1943 and is presumed to be extinct.
- DIAGNOSIS: This was a large Blue, with its most distinctive characteristics on the ventral surface. Typical *xerces* is the form in which there are a series of large white spots on a background of grey on the underside and the black pupils of these spots are absent. Other forms that occurred in this population at San Francisco have increased amounts of black spotting, including fully pupiled examples that resemble *G. lygdamus incognitus* Tilden. The genitalia of *G. xerces* are very similar to those of *G. lygdamus*, and on the basis of the male genitalia alone, *xerces* would have been assigned subspecific status under *lygdamus*. However, Downey and Lange (1956) pointed out considerable differences between these species in larval stages, adult wing maculation and ecology. Additionally, the two species were once sympatric and hybrids were never detected.
- ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 300 (1852).
- TYPE LOCALITY: "California". Restricted by Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies* (1998a), to San Francisco, San Francisco County, California.
- DISTRIBUTION: All recorded specimens are from San Francisco, and include the area presently covered by the city. Its habitat was sandy areas surrounding a prostrate dune

ecotype of the perennial, *Lotus scoparius* (Nutt.) Ottley. They were associated with ants in these habitats, but were not completely dependent on ants for successful maturation and pupation. The narrow distribution on the San Francisco Peninsula ranged from near Twin Peaks to North Beach, and the Presidio southward to Lake Merced; Lone Mountain, formerly an isolated, sandy hill, was the classical locality for *xerces* in the early 1900's (Langston, 1969). By 1919, the only population found by Lange was flying in a limited area west of the Marine Hospital, Presidio, San Francisco (March 19, 1919). The same area was still inhabited on March 23, 1941. The butterflies were then limited to a small area 65' wide by 140' long in which *Lotus scoparius* (Nutt.) Ottley was found. The last known specimens were collected at the Presidio during May, 1941 (Downey & Lange, 1956).

The *Lotus* occurred in patches in the partial shade of the Monterey Cypress (*Cupressus macrocarpa* Hartw.) in well-drained, sandy soil. *Lupinus arboreus* Sims, which also served the *xerces* females as a host plant for oviposition and larval growth, was widely distributed among *Lotus*, and extended beyond the range of the *Lotus* and the butterflies. In 1956, that same association of plants remained essentially unchanged and also was observed by the authors in 1963-67 in essentially unchanged condition. To the north, similar sandy areas with these *Lotus* and *Lupinus* species occur in Marin County, but the Monterey Cypress does not occur there. It appears that the expansion of the City of San Francisco into the natural sand dune habitat formerly available to *Glaucopsyche xerces* (and the other insects of the region) has destroyed too much of the habitat to continue to support a sustainable population beyond 1943.

- ELEVATION RANGE: From near sea level to approximately 400' elevation.
- HABITAT AND PLANT COMMUNITIES: The coastal sand dunes of the San Francisco Peninsula are part of the classical Coastal Strand Plant Community and this is apparently the only habitat in which *xerces* was found.
- PHENOLOGY: The adults of *xerces* flew in a single brood from about March 10 to April 15th. However, specimens were taken from as early as late February to as late as early June.
- ADULT BEHAVIOR: The flight and mating behavior and oviposition behavior of *xerces* was apparently similar to that of the other *Glaucopsyche* species in California. Downey and Lange (1956) mention that during oviposition on *L. arboreus* Sm., the female alighted, brought the abdomen forward, and placed an egg in the small depression at the base of the leaflet. On *Lotus scoparius* (Nutt. in T. & G.) Ottley, however, the eggs were laid on new growth near the tips of the leaflets or on the dorsal surfaces of the new growth. Wild adults mated in every conceivable combination of spotting types, suggesting there was no selective mating of macular forms.
- LIFE HISTORY: The life history of *xerces* was first described by Williams (1908) and later by Comstock (1927). The egg is echinoid in shape, depressed at the top with the micropyle in a pit. The surface of the egg, which is a delicate pale green ground color, is covered by a raised white network, the meshes quadrilateral and surmounted at each juncture by short rounded process. The mature larva is covered with small piliferous whitish tubercles and a few of a darker shade. The body is pale green in ground color, with a dark green ground color and a broad bordering line of yellowish-green. There are distinct oblique dashes, yellowish-green in color on each segment. There are sub-horizontal and horizontal bands of the same color, but more obscure. The whitish spiracles run along the upper edge of the latter band. A yellowish-white line runs laterally, becoming pale lilac

ventrally and pale yellowish towards the posterior segments. A pale greenish-yellow band occurs on four prolegs. There are a pair of whitish eversible sacs on the eleventh segment, and a secretory gland on the tenth segment, associated with the tending ants. However, as evidenced by successful laboratory rearings in the absence of ants, they are (were) facultative myrmecophiles and are (were) not completely dependent on ants for their welfare (Downey and Lange, 1956). Long hairs occur on each side of the dorsal surface. The whole body is covered with a whitish pile. The color and pattern are variable as in other Blue species. The short, stout pupa has pale greyish-green thoracic and wingcase areas. The abdomen is pale wood-brown, minutely reticulated. A broad rusty brown median line narrows on the mesothorax, where it is nearly black, and expands again on the prothorax. A very fine greenish line runs through the dorsal band of the thorax. A number of additional spots and blotches are variously placed. Considerable variation in the intensity and color of markings occurs, with some pupae being quite pale. Diapause was in the pupal stage, with the length of that stage averaging between ten and eleven months (Downey and Lange, 1956).

FOODPLANTS: Eggs and larvae of *xerces* were found on *Lotus scoparius* and *Lupinus arboreus* Sims, with *Lupinus micranthus* Dougl. as well as *Astragalus menziesii* Gray serving as substitute foodplants for captive larvae. In 1939 Lange found that as many as nine eggs were laid per plant and that the *Lotus* was slightly favored by the females, with an average of 3.4 eggs per plant compared to 2 eggs per plant for the *Lupinus*.

CHROMOSOME NUMBER: Unfortunately, this species became extinct before techniques for chromosome study of butterflies had been worked out.

SIMILAR SPECIES: See discussion under Diagnosis.

GEOGRAPHIC AND SEASONAL VARIATION: An intensive analysis of wing variation in 344 historical specimens has been given by Downey and Lange (1956), from which was derived the typical maculation. The presence or absence of spots appeared to be under genetic control, while the absolute size of the spots may have been environmentally affected. Of the 33.7% showing the "typical" *xerces* pattern, no division was made of the number of individuals having large or small macules, or pupiled or non-pupiled spots. The maculation of the hindwing is more variable than that of the forewing, with missing spots in many cases. The dorsal shade of blue in the males was also quite variable, but in general tended to be of a lighter shade than that found in adjacent races of *G. lygdamus*. Similarly, the brown of the female dorsal surface exhibited continuous variation. In all females, however, there was a basal infusion of blue scales on the dorsal surface. The average wing length of the male forewing was 16.2 millimeters (range of 13.0 to 18.0) and of the female forewing, 15.8 millimeters (14.0 to 17.8 millimeters). No difference in size range was found among the named forms and no shape difference could be detected in the specimens examined.

Downey and Lange were able to compare 56 specimens taken in 1907 and 1909 with 59 specimens taken in 1931 and 1932. "The same range of variability in size of wings, color, frequency of individual macules, and macular combination was shown in both. The only striking difference was percentage of increase of the form *xerces*, from 21% of the individuals taken in the early years to 45% in the latter group. While the authors suggested that selective collecting may have influenced these figures, no environmental feature could be related to this increase.

It is interesting that as early as 1884, *xerces* was believed to be extinct (see Edwards, 1884, p. 303). In 1906, W. G. Wright (p. 222) also reported that *xerces* was "lost for 30 years"; The problem was that both authors considered *xerces* to be distinct from another form, *antiacis*, and made no mention of this latter form being "lost". The form *xerces* was the unpupiled white spotted form and *antiacis* was the heavily pupiled form present in the same area. This suggests that the *xerces* form was in the minority in the population for at least the last two decades prior to 1900. Williams (1910) states that *xerces* was rare in that year, although formerly abundant, and that *antiacis* was more common than *xerces*. Skinner (1914) reported one year, presumably 1913, that an unusual ratio of one-third *antiacis* to two-thirds of *xerces* was observed. Skinner received the information and these specimens from Huguenin, who told Skinner that for the 25 years preceding that time, the reverse ratio had been found. Williams (1908) reared sixteen larvae, all of which emerged as form *antiacis*.

In the large total set of material examined by Downey and Lange (1956), 36% were *xerces* (unpupiled) forms and 63% were pupiled individuals representing the distribution of these forms over a period of many years of collecting.

GENERAL REMARKS:

The exact causes of the extinction of *xerces* in 1943 may be laid ultimately to the expansion of the City of San Francisco through the preceding 60-80 years. Apparently, the population was simply inhabiting too small an area (65' wide by 140' long) to survive at that point in time. In such small populations, a minor change in climate or other environmental factor could prove devastating, especially to a species that flew in a single annual brood and had no options to react; spatial limitations, little time, and a small genetic pool of variability led to extinction in a proximal sense.

This was not the first butterfly to be exterminated by the growth of the City of San Francisco (*Cercyonis sthenele sthenele* being the first), and it undoubtedly will not be the last. In the late 1980's and 1990's developmental ecological pressure on the San Bruno Mountains populations of several remaining endemic butterflies of the San Francisco area became immense and still continue today. For the huge neighboring urban human population, this area is the last natural and undeveloped parcel. Unfortunately, however, the loss of *xerces* may be the most tragic of all these stories of endangered San Francisco endemic species from the viewpoint of science, which could have used this incredibly variable and interesting butterfly to study the very basis of genetic variability in natural populations exposed to extreme selection pressures and perhaps have lent its findings to the salvation of many other species of endangered and threatened wildlife around the world (including, ultimately, mankind).

169. *Glaucopsyche piasus* (Boisduval)

SPECIES SYNOPSIS:

This lovely "Arrowhead Blue" occurs from British Columbia south through the western coastal and Sierra Nevada ranges as well as the Rocky Mountains. The complex of *Glaucopsyche piasus* subspecies across this wide distribution was reviewed in detail by Brown (1971) and a new subspecies (*Toxeuma*). That author described another subspecies, *G. p. nevada* (Brown, 1975), from the Great Basin ranges of central Nevada. Emmel, Emmel, and Mattoon (1998j) studied the phenotypic and biological differences of numerous populations of this species within California, and concluded three distinct sets of populations were undescribed and required new subspecific names. Thus we now find 7 subspecies of *Glaucopsyche piasus* occurring within California.

- ADULT BEHAVIOR:** The adults may be locally abundant in restricted colonies around perennial lupine species, but they stick rather closely to these hosts. Males tend to patrol throughout the day near the host, seeking females.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** The adults are unmistakable. The early stages closely resemble those of *Glaucopsyche lygdamus*, and may be confused with this species in situations where both butterflies are using the same host *Lupinus* species. Larvae of *G. lygdamus* have been found on *Lupinus formosus* Greene and *L. albifrons* Benth. in populations of *G. piasus* using these host plants; in all such instances, the *G. lygdamus* was represented by only a single larva, in contrast to the numerous individuals of *G. piasus* on the same plant. This suggests that the use of *G. piasus* foodplants in such situations by *G. lygdamus* is more-or-less a fortuitous event, and probably does not represent the primary host of *G. lygdamus* in that particular locality.
- GEOGRAPHIC AND SEASONAL VARIATION:** Over the range of this butterfly from the Rocky Mountains to coastal California and north to British Columbia, there is considerable variation in the width of the dark wing margins and the ventral pattern on the hindwings. Each of the subspecies described below, however, is reasonably distinct within its geographic range and little overlap seems to occur. As noted below, there is a potential blend zone area between the subspecies *toxeuma* and typical *piasmus* in the northern tier of counties. Additionally, a possible blend zone exists between the subspecies *piasmus*, *excubitus*, and *nevada* in the higher elevations of the Bishop Creek drainage of Inyo County; unfortunately, only a small number of specimens from this area, suggesting this type of blending, is currently available for study. Specimens of *G. p. sagittigera* from the San Jacinto Mountains of Riverside County occasionally show tendencies of the San Diego County subspecies *umbrosa*.
- LIFE HISTORY:** These were described originally by Comstock and Coolidge (1930). The eggs are placed principally on the ventral side of the host leaves, but may also be deposited on the dorsal surface, and even on the flower stalks. The larvae feed on the contents of the thick, juicy leaves, sometimes burrowing entirely inside. Usually several of the posterior larval segments are left protruding from the leaf surface. The apical portion of the leaves seems to be the preferred part, and even the stalk may be riddled. In molting, the larvae withdraw from the leaves and descend usually to the undersurface. Pupation takes place in debris surrounding the base of the foodplant. The egg has a flattened top and bottom, and is a delicate pea-green color with a raised white network. The mature larva is quite variable in color. The most common form is a reddish ground color, with whitish oblique dorsal lateral stripes and a green ventral surface. Alternatively, the larva may be pale yellow-green or greyish green in ground color, with a red mid-dorsal band and red lateral dashes. The larva may also be greenish-yellow in ground color with bluish-white oblique lateral dashes and a bluish mid-dorsal line. Finally, some larvae are entirely pale yellow in color. Pupation takes place in debris near the base of the food plant. The pupa is an olive green except on the abdomen, where it is wood-brown in color. The species hibernates in the pupal stage.
- GENERAL REMARKS:** The factors governing the spotty distribution and general scarcity of this species remain undetermined. This would be a fruitful area for investigation. The close association of the larvae with ants deserves further study.

There are seven races of this beautiful Blue in the state of California. The arrowhead shaped, bold white markings on the underside of the hindwing give this butterfly its common name of the Arrowhead Blue. All the races are quite local and are rarely abundant.

a. *G. p. piasus* (Boisduval)

- DIAGNOSIS:** The typical subspecies is paler dorsally and ventrally than the other subspecies of *piasus* and is rather lightly marked. It is distinguished by a row of white arrowhead spots on the ventral surface which blend into the pale gray ground color.
- ORIGINAL DESCRIPTION:** Boisduval, *Ann. Soc. Ent. France*, (2)10: 299 (1852).
- TYPE LOCALITY:** "California". Brown (1971) suggested that the type locality was probably the vicinity of San Francisco, but no populations were recorded there. Restricted by Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies* (1998a) to Hwy. 70 at Soda Creek, E. Branch North Fork Feather River Canyon Plumas County, California. Holotype in U. S. National Museum.
- DISTRIBUTION:** The nominotypical subspecies is found on the west slope of the Sierra Nevada, from Kern County northward to Plumas County. Populations in the North Coast Range and southern Klamath Mountains region appear to be closer to nominotypical *piasus* than to any other populations within the state.
- ELEVATION RANGE:** Most of the Sierran west slope populations occur from approximately 2,000' to 5,000' elevation, but higher elevation populations are known up to approximately 7,000' elevation, such as in the Lake Tahoe region or Greenhorn Mountains of Kern County. In the North Coast Ranges and the Klamath Mountains region, most populations seem to be in the 2,000 to 6,000' range.
- HABITAT AND PLANT COMMUNITIES:** This subspecies occurs in rather open montane coniferous forests, in situations where the host *Lupinus* species is locally abundant.
- PHENOLOGY:** This subspecies flies in a single brood from early May to early July, depending on elevation and snowpack.
- FOODPLANTS:** *Lupinus albifrons* Benth. is the host in Lake County in the North Coast Range (J. F. Emmel, unpublished data). This lupine species is also apparently a host on the west slope of the Sierra Nevada, by association. Data are lacking for associated hosts at other populations of the nominotypical subspecies, probably a result of the general scarcity with which collectors encounter this butterfly.

b. *G. p. sagittigera* (C. and R. Felder)

- DIAGNOSIS:** This is the low to mid-elevation southern California subspecies of *G. piasus*. It is distinguished by the much darker contrasting ground color of the underside, as well as a broader border of dark scaling on the upperside of both wings. Additionally, females tend to have variously developed russet spots in the submarginal area of the hindwing on the upperside. Although the most accessible colonies of this butterfly in the immediate vicinity of Los Angeles were exterminated by housing developments in the first half of this century, a fairly large number of populations of the butterfly still exists at widely scattered localities throughout southern California. The subspecies names *catalina* (Reakirt) and *rhaea* (Boisduval) are synonyms (see also Brown, 1971, 1975).

- ORIGINAL DESCRIPTION: C. and R. Felder, Reise... Novara, *Lepid. Rhop.*, 2: 281 (1865).
- TYPE LOCALITY: "Sonora". Restricted by Brown (1971) to the vicinity of Los Angeles, California. Types in British Museum.
- DISTRIBUTION: Populations of this butterfly are found in the low to mid-elevations (below 6,000') of the San Gabriel and San Bernardino Mountains, the San Jacinto Mountains, and the mountains of Santa Barbara, Ventura, and Kern counties. Additionally, a small number of specimens is known from San Luis Obispo and Monterey counties; these are currently lumped here under *sagittigera*. However, additional material may suggest that these represent another subspecies. Note that the subspecies *G. p. gabrielina* is found at 7,000-9,000' above the elevation range of *G. p. sagittigera* in the San Gabriel and San Bernardino Mountains of San Bernardino County. This is an unusual altitudinal separation of two geographically overlapping subspecies.
- ELEVATION RANGE: From approximately 1,000' elevation to 6,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is typically found in open areas where certain *Lupinus* species are abundant, usually on flats or rather broad open canyon bottoms, but sometimes on slopes, within the following plant communities: Coastal Sage Scrub, Chaparral, Southern Oak Woodland, and Montane Coniferous Forests.
- PHENOLOGY: The butterfly flies from mid-March to early May, depending on elevation and flowering time of the host *Lupinus* species.
- FOODPLANTS: The host for most of the populations of this butterfly appears to be *Lupinus formosus* Greene; a number of populations also use *Lupinus excubitus* Jones ssp. *austromontanus* (Heller) C. P. Sm. (J. F. Emmel, unpublished data).

c. *G. p. umbrosa* Emmel, Emmel and Mattoon

- DIAGNOSIS: This recently described subspecies was formerly lumped with *G. p. sagittigera*, but it is distinguished by a dark, suffused, "smoky" ground color of the underside with corresponding reduction of the "arrowhead" marks on the underside. Additionally, females of this species have marked enhancement of the russet spots along the submarginal area of both hindwing and forewing, and this character is frequently present in the males also, at least on the hindwings.
- ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 172-173 (1998j).
- TYPE LOCALITY: Laguna Mountains, slope about 0.2 air mile east of Big Laguna Lake, 5,450' elevation, San Diego County, California.
- DISTRIBUTION: This subspecies is apparently restricted to the higher mountains of San Diego County, from the Laguna and Cuyamaca Mountains northwestward to the Palomar Mountain region and Temecula in extreme southern Riverside County. It is not known from Baja California but may possibly be present in the Sierra San Pedro Martir in northern Baja California, where two potential host *Lupinus* species (including *formosus*) are found in similar habitats. To the north, there are intermediate populations between this subspecies and the Transverse Range subspecies *sagittigera* in the San Jacinto Mountains.

- ELEVATION RANGE: From 4,000 to 6,000' elevation.
- HABITAT AND PLANT COMMUNITY: The typical habitat for this subspecies is a gentle gravelly slope edged by large open meadows below and yellow pine forest above, with locally abundant bushes of *Lupinus formosus*, the foodplant of *umbrosa*.
- PHENOLOGY: These populations fly in a single brood from mid-April to mid-June, depending on elevation.
- FOODPLANTS: The subspecies is known to use *Lupinus formosus* Greene in the Laguna Mountains (J. Emmel and G. Pratt, unpublished data), and *Lupinus excubitus* Jones ssp. *halli* (Abrams) C. P. Sm. in the Mt. Palomar region (J. F. Emmel, unpublished data).

d. *G. p. nevada* F. M. Brown

- DIAGNOSIS: This subspecies, described from material collected in central Nevada, is unusually dark on the upperside with very broad blackish markings. Material from the White Mountains of California adjacent to the south central Nevada border is nearly identical with this subspecies. The subspecies *nevada* is noticeably darker on the dorsal surface and has much wider dark marginal areas than are found on typical specimens of the other subspecies. This is especially true of the females of *nevada*. The subspecies *G. piasus piasus*, from coastal regions of California, has very subdued contrast on the underside of the hindwings. The other Southern California subspecies, *G. piasus sagittigera* and *G. p. umbrosa*, with greater contrast on the ventral surface of the hindwing, have narrower marginal dark zones and are much paler on the upperside, and usually have bold rusty patches in the submarginal areas on the dorsal surface of the females. Such patches are occasionally found on *nevada*, but always are much smaller and usually obsolescent.
- ORIGINAL DESCRIPTION: F. M. Brown, *Proceedings of the Entomological Society in Washington*, 77: 501-504 (1975).
- TYPE LOCALITY: Bob Scott Campground, Toiyabe National Forest, Lander County, Nevada, 7300-7500' above sea level. Holotype in U. S. National Museum.
- DISTRIBUTION: In California, this butterfly is found in the higher elevations of the White Mountains, as well as on several of the high passes or high eastern slope of the Sierra Nevada from the Mammoth Lakes region northward to Sonora Pass; it is probably also present in the Sweetwater Mountains of Mono County just east of the Sonora Pass area, but specific records are lacking.
- ELEVATION RANGE: 8,000 to 11,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is typically found in dwarfed Sagebrush Scrub situations where the host *Lupinus* species are locally abundant among the *Artemisia* plants, usually on gravelly to rocky slopes or in open gullies.
- PHENOLOGY: Adults fly from mid-June to mid-July, depending on elevation and snowpack.
- FOODPLANTS: In the White Mountains, the butterfly is closely associated with *Lupinus argenteus* Pursh var. *tenellus* (Doug. ex Don) D. Dunn.

e. *G. p. excubita* Emmel, Emmel and Mattoon

DIAGNOSIS: This recently described subspecies occurs on the eastern side of the Sierra Nevada, often in association with *Lupinus excubitus* Jones. The name of the foodplant and the butterfly means "guardian"; this is in reference both to the primary host of the butterfly and also in reference to the habit of the adults of perching on prominent parts of the host plant shrubs, i.e., like a "guardian".

While rather similar to nominotypical *pius* of the western slope of the Sierra Nevada, *G. p. excubita* differs in its much greater contrast in light grayish brown ground color ventrally, and smaller size. The ventral "arrowhead" markings are more distinct and smaller, and somewhat shorter than those in typical *pius*. Dorsally, both sexes have a somewhat broader dark marginal border on both forewing and hindwing, though not as much as in the very dark subspecies *nevada* to the north and east, and not to the degree developed in the southern California subspecies *sagittigera* and *umbrosa*. *Excubita* resembles paler specimens of the southern California *sagittigera*, but it lacks the greater development of paler orange marginal scaling seen in that subspecies. Additionally, the dark spotting ventrally is reduced from that seen in subspecies *nevada*.

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American butterflies*, pp. 173-174 (1998j).

TYPE LOCALITY: Bishop Creek [vicinity of Andrews Camp, 8150', south fork of Bishop Creek], Inyo County, California. Currently at this site is a U.S. Forest Service Campground, known as Four Jeffrey Campground (see Emmel, Emmel, and Mattoon, 1998j).

DISTRIBUTION: This subspecies is found along the east slope of the Sierra Nevada from northern Kern County northward to approximately southern Mono County. The northern limit of this subspecies is approximately the area of Grant Lake, just southwest of Mono Lake. To the north, the dark subspecies *nevada* is found from the Virginia Lakes area northwest of Mono Lake northward to Sonora Pass; these *nevada* populations apparently represent a westward extension through the Sweetwater Mountains from *nevada* populations of the western Great Basin, such as in the White Mountains.

ELEVATION RANGE: From 4,000 to 8,000' elevation.

HABITAT AND PLANT COMMUNITIES: Typically found on steep granitic sand canyon slopes within the Joshua Tree Woodland, Sagebrush Scrub, or Pinyon-Juniper plant communities of the east slope of the Sierra Nevada.

PHENOLOGY: The subspecies flies in a single brood from late March to late June, depending on elevation and seasonal rainfall or snowfall conditions.

FOODPLANTS: The primary host for most populations of this subspecies is *Lupinus excubitus* Jones, a plant which is often found in large, showy colonies on the steep granitic sand slopes of the canyons of the eastern slope of the Sierra Nevada. Populations in southern Mono County, which are phenotypically extremely similar to the populations in Inyo County, are closely associated with *Lupinus inyoensis* Heller. On one occasion, two ova were found by J. F. Emmel on the flowerbuds of *Astragalus lentiginosus* Dougl. which was growing adjacent to several plants of *Lupinus excubitus* Jones; although the latter was obviously not the primary host in this particular locality (Ninemile Canyon), the observation does indicate that if

given a choice of oviposition substrate, the females will sometimes choose fabaceous plants growing close to their normal *Lupinus* hosts.

f. *G. p. toxeu*ma F. M. Brown

DIAGNOSIS: This subspecies is closest in appearance to *nevada*, both subspecies having rather similar blue tones on the dorsal surface. However, *toxeuma* has much narrower dark margins than are found on *nevada*. The ventral surfaces of this pair of subspecies are also very similar. On *nevada*, the post-discal series of black spots (at the inner edge of the whitish zone) is complete, though varying in size. On *toxeuma* specimens, this series of spots is incomplete. The set of populations in California which seem closest to this subspecies, namely along the northern border of the state, actually seem to be intermediate in facies between *toxeuma* and typical *pius*us.

ORIGINAL DESCRIPTION: F. M. Brown, *Journal Lepidopterist Society*, 25: 245 (1971).

TYPE LOCALITY: Garnett Valley, Summerland, British Columbia. Holotype in Canadian National Collection.

DISTRIBUTION: This subspecies (named originally from British Columbia and adjacent areas of Washington State and Idaho) penetrates our area of California in the northern half of Siskiyou County and in Modoc County. Further collecting for *G. pius*us in this region of the state should help to determine whether a cline exists between these populations and typical *pius*us to the south.

ELEVATION RANGE: From 3,000 to 6,000' elevation.

HABITAT AND PLANT COMMUNITIES: Open flats or slopes within the lower elevations of Montane Coniferous Forest or within the Sagebrush Scrub plant communities.

PHENOLOGY: Specimens are recorded from early May to late June, depending on elevation.

f. *G. p. gabrielina* Emmel, Emmel, and Mattoon

DIAGNOSIS: This subspecies is most similar to nominotypical *pius*us, but differs primarily in its smaller size, the slightly darker aspect of the ventral surface, and the slightly more developed dark brown borders dorsally in females. It uses *Lupinus elatus* Jtn. and probably *L. andersonii* Wats. as hosts. It occurs only in the higher elevations (above 7,000') of the San Gabriel Mountains and the San Bernardino Mountains.

G. p. gabrielina is separated from the nearest nominotypical *pius*us populations in the Greenhorn Mountains of the southern Sierra Nevada by approximately 75 air line miles. Another subspecies of *G. pius*us, *sagittigera* Felder & Felder (1863), occurs in the San Gabriel Mountains, but the populations of this latter subspecies are found at low to mid elevations and use *Lupinus formosus* Greene as a larval foodplant. *G. P. sagittigera* is readily distinguished from *gabrielina* by its much darker aspect ventrally, and very sharply demarcated white sagittate (arrow-shaped) markings on the ventral hindwing; additionally, males and females have much broader dark brown borders dorsally, and there is more extensive development of the pale pinkish-orange lunules in the submarginal area of the dorsal hindwing in females. The flight period of *sagittigera* is usually one to three months earlier than that of *gabrielina*, depending upon elevation.

- ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 174-175 (1998j).
- TYPE LOCALITY: San Gabriel Mountains, ridge running east from Mt. Islip, west northwest of Windy Gap, 7600-7000' elevation, Los Angeles County, California.
- DISTRIBUTION: This subspecies is found in the higher elevations of the San Gabriel Mountains, above 7000', where it is always associated with *Lupinus elatus* Jtn. A similar set of populations is found at high elevations in the San Bernardino Mountains in the Mt. San Geronimo area, associated with *Lupinus andersonii* Wats.
- ELEVATION RANGE: From 7000' to at least 9000' elevation.
- HABITAT AND PLANT COMMUNITIES: The preferred habitat is an open dry slope within Upper Montane. Coniferous Forest, with locally abundant growth of *Lupinus elatus* Jtn
- PHENOLOGY: This high-altitude subspecies flies in a single brood from early June to early July, depending upon elevation.
- FOODPLANTS: In the higher San Gabriel Mountains populations, *Lupinus elatus* Jtn. serves as the larval host. In the higher San Bernardino Mountains populations, *Lupinus andersonii* Wats. is the suspected host (J. F. Emmel, unpublished).

167. *Philotes sonorensis* (C. and R. Felder)

- SPECIES SYNOPSIS: This distinctively colored blue, with brilliant blue iridescence and prominent red splotches, is unmistakable. It has an extensive range through cismontane southern California, and it also occurs in scattered populations to the north in central California and south into Baja California. Two subspecies are recognized.

a. *P. s. sonorensis* (C. and R. Felder)

- DIAGNOSIS: The males of this subspecies are characterized by a pale blue iridescent ground color on the upperside with reddish-orange splotches in the submarginal area of the forewing, a small black bar at the end of the discal cell, a series of three to four black dots in the subapical area, and a relatively thin black border at the apex of the forewing. The fringe scales of both forewing and hindwing are composed of alternating sets of white and blackish scales, giving a checkered appearance to the edge of the wing. On the underside, the ground color is a dull gray with, on the forewing, a post-median band of black dots, paler orange splotches corresponding to the same location as on the upperside, and a checkered fringe. On the hindwing, there is a series of distinct to indistinct black markings crossing the wing in several irregular bands, giving a variegated appearance.

On the females, the upperside ground color tends to be a darker shade of iridescent blue and there is a marked increase in the amount of black scaling and black markings over that seen in the male. The reddish-orange splotches on the forewing are more expanded than the similar markings on the male, and additionally, the female has two similar splotches on the hindwing in the submarginal area near the anal angle. There is a post-median irregular row of black dots on the forewing and several smaller similarly placed black markings on the hindwing near the end of the cell. The submarginal areas of the forewing are largely filled in with black scaling, and on the hindwing the submarginal area is characterized by a row of prominent black spots. The fringe is checkered as in

the male. On the underside, the markings are much as those seen in the male, with the exception of the ground color being slightly darker.

- ORIGINAL DESCRIPTION: C. and R. Felder, Reise... Novara, Lepid. Rhop., (2): 281 (1865).
- TYPE LOCALITY: "Sonora". The term "Sonora" was both the Felder's and Boisduval's term for the area around Los Angeles in southern California (see Brown, 1967). Type locality restricted by Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies* (1998d), to Los Angeles, California. Lectotype in British Museum.
- DISTRIBUTION: The butterfly is found from the central Coast Ranges of Santa Clara and Stanislaus counties southward through the remaining Coast Ranges to the Transverse Ranges and mountains of western Riverside and San Diego Counties. It is also found on the north slope of the San Emigdio Range and northward through the Sierra Nevada foothills of Kern County to Placer County and Nevada County at its northernmost localities (near Auburn and Lang Crossing on the American River; see Shapiro, 1974) on the west slope of the Sierra Nevada. South of California, it extends into Baja California at least as far as Punta Prieta.
- ELEVATION RANGE: From near sea level to approximately 6,000' elevation (the highest record being the summit of Garnet Peak, Laguna Mountains, San Diego County).
- HABITAT AND PLANT COMMUNITIES: The butterfly is typically found in small rocky canyons, on steep rocky, generally north-facing slopes, and occasionally on boulder-strewn or rocky wash bottoms (Hovanitz, 1967). These habitats are usually found within the Coastal Sage Scrub or Chaparral plant communities, but the butterfly has also been taken within the lower edges of Montane Coniferous Forest, Foothill Woodland, Southern Oak Woodland, Riparian Woodland, and Pinyon-Juniper Woodland along the western edge of the desert.
- PHENOLOGY: *Philotes sonorensis* is an early spring flier, peaking in February and March in most years, but at higher elevations, the adults may fly in May or even June. Complete details of population sites and the general biology of the species are given in excellent publications by Langston (1963, 1965, 1969a), and the information recorded above supplements his details with records found in more recent years.
- ADULT BEHAVIOR: This butterfly is one of the best studied lycaenids because of the classic work (1955-1962) of Mattoni and Seiger (1963), which analyzed the population structure of the species in the Fish Canyon portion of the San Gabriel Canyon Wash near Los Angeles. They found that there was a highly nonrandom pattern of movement and that the butterflies would move as far as 819 meters, but return to the general area of original capture. When adults were moved 40 meters to a new site in a displacement experiment in 1962, a significantly greater proportion of butterflies returned to their initial capture site than was expected on a random basis (Keller, Mattoni, and Seiger, 1966). The authors hypothesized that the butterflies respond to cues such as topographic features, floristic associations, degrees of shadow from rocks and bushes, and gradients of preferred adult nectar sources, to remain in the effective environment to which they are adapted. The populations in the Fish Canyon site were remarkably dense; in 1956, a total of 972 specimens were captured 1226 times in 11 collecting days of a 29 day period in six sampling stations, each 80 meters in diameter. This population set in the San Gabriel wash was later described as a new subspecies, *P. s. extinctus*, after it disappeared in 1967 (Mattoni, 1991).

- FOODPLANTS: *Dudleya lanceolata* (Nutt.) Britt. & Rose, *D. abramsii* Rose, and *D. saxosa* (Jones) Britt. & Rose (Crassulaceae) in southern California. In the northern parts of its range, it is associated with *Dudleya c. cymosa* (Lem.) Britt. & Rose, *Dudleya cymosa* (Lem.) Britt. & Rose *setchellii* (Jeps.) Moran, and *D. c.* (Lem.) Britt. & Rose *minor* (Rose) Moran. These plants are commonly known as Live-forevers.
- CHROMOSOME NUMBER: Highly variable in the populations studied to date, ranging from $n = 17$ to 44. The modal number is 22 in Placer County populations, 23 in El Dorado County, and 19 in Stanislaus County (Emmel, Trew, and Shields, 1973). The chromosomes of southern California populations have not yet been studied.
- SIMILAR SPECIES: This butterfly is unmistakable, due to the prominent red splotches in the center of the wings.
- GEOGRAPHIC AND SEASONAL VARIATION: As the butterfly is univoltine, there is no seasonal variation. An adult form that lacks all black spots except the central forewing spot (form "*comstocki*") is present in fair proportions and in both sexes in certain populations, and is apparently inherited as a genetic mutant.
- Some geographic variation in populations within the state has been noted, but it is rather poorly studied to date. The populations on the west slope of the Sierra Nevada tend to have more males with a small amount of red scaling on the hindwing in the same area as the red spot on the females. Populations in southern California tend to have a higher number of black spots on the male forewing in comparison to populations in the Central Coast Ranges and the Sierra Nevada foothills. Populations on the Monterey County coast, such as at Partington Canyon, tend to have a washed-out appearance with paler dorsal and ventral surfaces. Populations along the desert edge in southern California tend to have less contrast in the shading of the ground color in the discal area versus the submarginal area of the underside of the wing; additionally, these desert-edge populations tend to have a greater uniformity in the size of the black markings on the underside of the hindwing, giving a more evenly checkered or grizzled appearance. Because the butterfly is usually taken in rather small numbers at any given locality, there are few long series of specimens for meaningful comparisons of geographic differences.
- GENERAL REMARKS: This is one of the most interesting blues in our fauna, particularly with reference to the tremendous chromosomal variability which has not been found heretofore in other nearctic butterflies. Lesse (1960, 1969) found great chromosomal variability in populations of species of the lycaenid butterfly genera *Lysandra* and *Agrodiaetus*, but until the discovery of such variability in *Philotes sonorensis*, the nearctic lycaenids that had been surveyed tended to have a modal number of 24 for a haploid set (Maeki and Remington, 1961).

b. *P. s. extincta* Mattoni

- DIAGNOSIS: The principal differences between *extincta* and nominotypical *sonorensis* are both phenotypic and biological (Mattoni, 1991): (1) postmedian macule pattern frequency and dimorphism of a unique form; (2) complex difference in the ventral ground color and maculation pattern; and (3) very high population densities. The dorsal cyanic blue overlay in the males and females is identical, but the melanic marginal band in the females is wider and the macules are up to 30% larger than in other populations, presenting a darker overall aspect. On the ventral surface of the hindwing, both sexes of *extinctus* show a strikingly darker, heavily marked pattern compared to samples of even closely adjacent nominotypical populations higher in the San Gabriel Mountains. The adult form "*comstocki*," with virtually

no black macules, is uniquely present in fair numbers in the *extinctus* population samples which we still have preserved in collections today. The San Gabriel wash population of *extinctus* included tens of thousands of adults annually in the 8-square-kilometer area that the population inhabited; no other known population of the species had or has the potential of such abundance, and this density was not a function of the hostplant density which was unexceptional there. The striking high density of *extinctus* and low densities of nominotypical *sonorensis* populations is viewed as a genetic trait as important as morphological characters in defining taxon differences (Mattoni, 1991).

ORIGINAL DESCRIPTION: Mattoni, R. H. T., *Journal of Research on the Lepidoptera*, 28(4): 297-309 (1991) ("1989").

TYPE LOCALITY: Upper San Gabriel Canyon Wash, Los Angeles County, California. Holotype in Smithsonian Institution.

DISTRIBUTION: This subspecies was confined (1922-1967) to approximately 8 square kilometers of the upper San Gabriel wash in Los Angeles County. It became extinct after the 1967 flight period, when the U.S. Army Corp of Engineers destroyed its entire range in the course of providing a spreading basin for ground water recharge, ironically a project which would be banned today in favor of saving natural riparian habitat.

ELEVATION RANGE: The type locality and only known site lies at 800' elevation.

HABITAT AND PLANT COMMUNITIES: The mount of the San Gabriel river Canyon on the south side of the San Gabriel Mountains formerly supported Chaparral plant community shrubs and *Yucca* plants with a grassy and wildflower-filled understory on its upper banks and a sandy wash bottom with abundant granite boulders along the river itself. Groups of western sycamore trees, live oak, alder and bay trees were typically scattered in the canyon, but these had been repeatedly thinned or temporarily extirpated by human activities, such as the 1854-1861 gold rush on the East Fork of the San Gabriel River, when an estimated \$2 million in gold was recovered (Robinson, 1990), or later gravel mining. The butterfly survived all these vicissitudes until 1967, when its whole habitat was obliterated by man.

PHENOLOGY: This subspecies flew in a single brood from February to April.

FOODPLANTS: The San Gabriel Wash population used *Dudleya lanceolata* (Nutt.) Britt. & Rose as a larval host plant.

c. *P. s.*

DIAGNOSIS:

ORIGINAL DESCRIPTION:

TYPE LOCALITY:

DISTRIBUTION:

ELEVATION RANGE:

HABITAT AND PLANT
COMMUNITIES:

PHENOLOGY:

ADULT BEHAVIOR:

FOODPLANTS:

d. *P. s.*

DIAGNOSIS:

ORIGINAL DESCRIPTION:

TYPE LOCALITY:

DISTRIBUTION:

ELEVATION RANGE:

HABITAT AND PLANT
COMMUNITIES:

PHENOLOGY:

ADULT BEHAVIOR:

FOODPLANTS:

e. *P. s.*

DIAGNOSIS:

ORIGINAL DESCRIPTION:

TYPE LOCALITY:

DISTRIBUTION:

ELEVATION RANGE:

HABITAT AND PLANT
COMMUNITIES:

PHENOLOGY:

ADULT BEHAVIOR:

FOODPLANTS:

f. *P. s.*

DIAGNOSIS:

ORIGINAL DESCRIPTION:

TYPE LOCALITY:

DISTRIBUTION:

ELEVATION RANGE:

HABITAT AND PLANT
COMMUNITIES:

PHENOLOGY:

ADULT BEHAVIOR:

FOODPLANTS:

168. *Philotiella speciosa* (Hy. Edwards)

ADULT BEHAVIOR: This butterfly has a weak and inconspicuous flight, which passes unnoticed by most observers. It hovers within a few inches of the ground, pausing occasionally to rest on vegetation. Often the flight period on the deserts is restricted to the morning hours, before the winds arise around 11:00 a.m. If conditions are calm, males patrol throughout the day, usually in gulches, in search of females. Shields (1987) notes that males at the large colony at Red Mountain in San Bernardino County defend territories, chasing other males and Diptera.

LIFE HISTORY: Described in detail by Comstock and Dammers (1932). The creamy white eggs are laid singly on the foodplant and hatch in eight days. The larva may be fed in the laboratory on a substitute foodplant found in coastal areas, *Chorizanthe californica* (Benth.) Gray (Polygonaceae). On either this plant or *Oxytheca* in the deserts, the larvae feed only on the small fleshy points which arise from the stem around the leaf junctures. When at rest, the protectively colored larvae curl around the stem on the inside of the bracts. The mature larva, somewhat more slender in form than the closely-related *Euphilotes* larvae, is apple-green in ground color and is covered with short white hairs. Most larvae have a mauve or rose-colored mid-dorsal band which expands near the posterior edge of each segment. The caudal segments are slightly tinged with rose. Pupation occurs in a loose silken web on the soil, and the pupa overwinters. The pupa is a chestnut brown in color.

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: Distinct by both its wing shape and small size, as well as wing pattern, from all near-relatives. Originally placed in the genus *Philotes*, this species was assigned to the Old World genus *Zizeeria* by Shields (1974) and then transferred to the new genus *Philotiella* by Mattoni (1977). It is morphologically distinct from the genus *Euphilotes*, which contains most of the species formerly in the *Philotes*.

GEOGRAPHIC AND SEASONAL VARIATION: As the butterfly is univoltine, there is no seasonal variation. The desert populations of this butterfly are remarkably uniform in phenotype from one area to another. Specimens from the scattered localities in the

mountains are so few that meaningful geographic delineation of these populations is not presently possible.

GENERAL REMARKS: The montane populations of this species are particularly puzzling. It remains to be determined whether these are relictual populations or evidence of stray-dispersal from the desert populations. None of these localities seems to produce specimens of this butterfly reliably year after year and most of the records are singleton specimens, suggesting that only small resident populations exist in these areas, if at all. The foodplants of the montane populations are unknown and would be a fruitful area for further research. Shields (1987) emphasizes that ecological requirements for good seed germination and growth of one larval foodplant, *Eriogonum reniforme* Torr. & Frem., are frequently not met. Since the butterfly flies only when the foodplant is in bloom, timing and duration of late fall and early winter rains is apparently critical for both the plant and the butterfly's emergence.

This extremely small species is found principally in California and Nevada, with populations also found in extreme western Arizona and Baja California Norte. Two geographic subspecies have been named; both are found in California.

a. *P. s. speciosa* (Hy. Edwards)

DIAGNOSIS: This small Blue is distinct from all other members of related genera by the complete absence of orange-red spots, its very small size, the uniform brown of the female and the pale lilac-blue of the male.

ORIGINAL DESCRIPTION: Henry Edwards, *Proceedings California Academy Sciences*, 7: 173 (1876).

TYPE LOCALITY: Haviilah, Kern County, California. Holotype in American Museum of Natural History.

DISTRIBUTION: This Blue is found in the western and northeastern Mojave Desert, northward through the Death Valley region to the foothills of the White Mountains and the Sherwin Summit area of the east slope of the Sierra Nevada. Disjunct populations are known in Imperial County at the western edge of the Colorado Desert, at several isolated localities on the west slope of the Sierra Nevada in Kern and southern Tulare Counties, in northeastern Ventura County, and in the western San Gabriel Mountains. From California, the species extends into Nevada where it ranges from Pershing County to Clark County. It is conceivable that the butterfly may be found in Lassen County in California, as Munz (1959) lists Lassen County as part of the range of the foodplant, *Oxytheca perfoliata* T. & G.

ELEVATION RANGE: From 900' elevation to approximately 6,500'.

HABITAT AND PLANT COMMUNITIES: In the Mojave Desert populations, the butterfly is typically found in Creosote Bush Scrub situations, generally on rocky to gravelly slopes, particularly those composed of volcanic substrates. In the Death Valley region, most populations appear to be found within the Shadscale Scrub plant community. In populations taken in the mountains, such as the west slope of the Sierra Nevada, the San Gabriel Mountains or the Quatal Canyon (Ventura County) populations, the dominant plant community appears to be a xeric phase of the lower edge of Montane Coniferous Forest or the upper edges of Chaparral communities.

PHENOLOGY: This subspecies is univoltine, and seems to fly only in years of normal or above normal rainfall; in very dry years, the butterfly is either very scarce or totally absent from given localities. In the deserts, the main flight period appears to be

from mid-April to mid-May, depending on locality and elevation and pattern of rainfall for that season. In the montane populations, specimens have been taken in May and June.

FOODPLANTS: *Oxytheca perfoliata* T. & G. in the Mojave Desert, *O. trilobata* Gray at Little Rock in Los Angeles County, and *Eriogonum reniforme* Torr. & Frem. (Polygonaceae) in both the Mojave and Colorado Deserts (see Thorne, 1961; Shields, 1987). Mature larvae have also been found on the flowers of *Eriogonum pusillum* T. & G. (Langston, in Howe, 1975, p. 330).

b. *P. s. bohartorum* (Tilden)

DIAGNOSIS: The males of this subspecies are characterized by the lavender ground color on the dorsal surface and the wide brown margins on the forewings. The females are solid smoky gray-brown on the dorsal surface.

ORIGINAL DESCRIPTION: J. W. Tilden, *Journal Research Lepidoptera*, 6: 281-283 (1967) [1968].

TYPE LOCALITY: Briceburg, Mariposa County, California. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This subspecies is presently known only from several localities in Mariposa County on the west slope of the Sierra Nevada. A single record of the species, collected by John S. Garth in 1925, from near Hume Lake (1830 m contour line, where it intersects with the Hume Lake road) in Fresno County apparently also pertains to this subspecies.

ELEVATION RANGE: From 1,500 to 2,500' for the Mariposa County populations; approximately 6,000' for the Hume Lake record.

HABITAT AND PLANT COMMUNITIES: At the Briceburg locality, the butterfly is typically found on rather steep gravelly slopes or at damp sand in canyon bottoms, with a sparse Chaparral community on the surrounding slopes.

PHENOLOGY: The Mariposa County records range from April to June, with an apparent peak flight in mid-May. The type specimens were collected at five different locations along the north side of the Merced River at Briceburg on April 23-24, 1966, and other records originally indicated a late-April peak (see Shields, 1987).

FOODPLANTS: Unknown for subspecies *bohartorum*, but *Chorizanthe membranacea* Benth. (Polygonaceae) is suspected by Shields (1974, 1987) as a possible foodplant.

c. *P. s. purissima* Priestaf and J. Emmel

DIAGNOSIS:

ORIGINAL DESCRIPTION:

TYPE LOCALITY:

DISTRIBUTION:

ELEVATION RANGE:

HABITAT AND PLANT
COMMUNITIES:

PHENOLOGY:

FOODPLANTS:

169. *Euphilotes battoides* (Behr)

ADULT BEHAVIOR: Despite the great diversity of subspecies of this butterfly, virtually all subspecies show very similar patterns of adult behavior and the following description should apply to all populations of this species.

In any given locality, emergence of males appears to take place several days to a week or more prior to the emergence of females, on the average. The adults remain very close to the *Eriogonum* foodplants, generally repeatedly landing on the flowers of the plant both for nectar (in the case of both sexes) and for oviposition (in the case of the females). The adult flight period is closely correlated with the early bloom of the *Eriogonum* flowers; at the peak of the adult flight, approximately half of the *Eriogonum* flowerheads will be in bloom, with the other half in a flowerbud stage. The females generally oviposit on the inner surface of a petal of an *Eriogonum* flower, choosing one that has just opened. The males will sometimes perch on nearby vegetation, typically on small shrubs or bushes in the immediate vicinity of the foodplants. At night, both sexes rest on the stems of small shrubs or the *Eriogonum* foodplants with the head downward; this position appears to afford protection from both strong winds and also occasional rain that may fall during the flight of the adults. The males are very strongly attracted to mud or damp sand, particularly around springs or along stream banks; only rarely are females taken at moisture. Arnold (19) noted that in at least one population of *E. b. allyni*, the adults were extremely local, flying an average of only six meters for males and eleven meters for females during their lifespan, which averaged four days for males and five days for females.

CHROMOSOME NUMBER:

SIMILAR SPECIES: These butterflies are often extremely close in phenotype to sympatric *Euphilotes enoptes* ssp. They can only be distinguished with certainty by the structure of the genitalia of the adults. *E. battoides* differs from all other nearctic species in this genus by having a deeply bifurcate valva in the male genitalia. In *E. enoptes*, the valva is entire and subquadrate. The outer distal end has a series of eighteen to twenty-two (usually twenty-one) short spines, giving the end of the valva a saw-tooth appearance (Langston, in Howe, 1975). The female genitalia are also remarkably different (see figure).

In the field, the two species normally can be readily separated simply by their associated *Eriogonum* host, which is usually different for the two butterflies. However, there are some situations where such an assumption could lead to misidentification. For example, in the San Bernardino Mountains, both *E. battoides* and *E. enoptes* use *Eriogonum kennedyi* Porter in Wats., but in different localities. Thus, for certainty of identification an examination of the male genitalia is helpful for separating the two species.

GEOGRAPHIC AND SEASONAL VARIATION: *E. battoides* is strictly univoltine in all of its populations, to our knowledge; this is in contrast to *E. enoptes*, which is often at least partially bivoltine in many of its populations. Thus, there is no seasonal variation in *battoides*. This species reaches its greatest

geographic subspeciation within the state of California, undoubtedly due to the extensive range of ecological situations and variety of available foodplants occupied by the different populations.

LIFE HISTORY: Described in detail for the subspecies *bernardino* from Lee Lake, Riverside County, material by Comstock and Dammers (1934). The echinoid-shaped, bluish-white eggs are laid singly on flowers of *Eriogonum*, and the larvae feed exclusively on the flower parts and young seeds. They are extremely well concealed because of their cryptic coloration. The mature larvae are extraordinarily variable in color and pattern, ranging from a uniform pale blue green, through green with chocolate markings, lemon-yellow with chocolate, pale soiled yellow, to a uniform pink. The entire larva, except the head, is covered with short fine silvery white hairs. It has been suggested (Emmel and Emmel, 1973) that this great variability in ground color is selectively advantageous in matching the variable color changes through which the host flowers progress, and in preventing a predator from "fixing" his larval search image for a particular color morph. The figured larva in the Dammers painting is the form with pale green body color and rich chocolate pattern. Pupation takes place, apparently without any silken attachment, in the desiccating blossoms of the *Eriogonum*. The pupa is pale chestnut in color, with a slight suggestion of green on the wingcases. There are no hairs on any portion of the pupa.

[The larvae of other subspecies will be briefly described here in comparison to the above description for *bernardino*.]

GENERAL REMARKS: The *E. battoides* complex has been studied extensively by Pratt (1988) who has carried out detailed studies of foodplants, immature stages, and isoenzyme variation in numerous populations. The results of these studies indicate that there may be at least two or three species or semi-species groups within the complex. These would be as follows: 1) a group associated with the nominate subspecies, including *glaucon*, *oregonensis*, *intermedia*, *baueri*, *comstocki*, *argocyanea*, *hadrocheilos*, *panamintensis*, *allyni*, and the Coxey Meadow segregate, 2) the *bernardino* group, including subspecies *martini*, *inyomontanus*, and an unnamed segregate from the Vizcaino Desert in Baja California, and 3) a group involving the late summer-flying subspecies *euromojavensis* and *ellisi* from the Colorado Plateau. Hybridization studies between these different groups would be most enlightening in refining the taxonomy of this highly complex species.

The attractive Square-Spotted Blue has diverged into a number of races throughout the western United States, especially in California. Langston (1969a) and Emmel and Emmel (1973) gave important early reviews of the extensive subspeciation in *battoides*. Additional subspecies have been identified in recent years by Oakley Shields and Gordon Pratt, and several other segregates are also listed here in the present account. Thus, there are a total of sixteen geographic segregates in our California fauna for this species.

a. *E. b. battoides* (Behr)

- DIAGNOSIS: The nominotypical subspecies is the high-elevation form in the Sierra Nevada of California. It is recognized by the large black quadrate spots on the ventral surface of both wings. These black spots are considerably heavier and darker than in any other *Euphilotes*. Blackish suffusion occurs between the spots as well.
- ORIGINAL DESCRIPTION: Behr, *Proceedings California Academy Sciences*, 3: 282 (1867).
- TYPE LOCALITY: San Joaquin River, 11,000' elevation, California. Langston (in Howe, 1975) places the type locality at Mineral King in Tulare County; this cannot be correct, as Mineral King is on the Kaweah River and furthermore, an analysis of the route of the California State Geological Survey Party, which took the type specimens (Farquhar, 1966), indicates that the probable type locality was close to Mono Pass in the drainage of the South Fork of the San Joaquin River in northeastern Fresno County. The types, which were in the California Academy of Sciences, were destroyed in the 1906 San Francisco earthquake and fire.
- DISTRIBUTION: This subspecies is found in higher elevations of the Sierra Nevada, from the area around Mineral King in Tulare County northward to the northern Yosemite region. A somewhat disjunct population is also known on the summit of Glass Mountain in Mono County, just east of the Sierra Nevada in the Sherwin Summit region. A small series of specimens in the Carnegie Museum from Gold Lake, Sierra County, California, allegedly representing this subspecies, is a highly disjunct population for typical *battoides* and may either be mislabelled or represent a lower-elevation ecotype of the *E. b. battoides* subspecific phenotype.
- ELEVATION RANGE: From 9,000 to 12,500' elevation; the elevation for the specimens taken at Gold Lake is unknown.
- HABITAT AND PLANT COMMUNITIES: This subspecies is typically found on rather bare, open, gravelly to somewhat rocky ridgetops or slopes within the Arctic-Alpine Fellfields plant community.
- PHENOLOGY: The butterfly is univoltine, as are all the *E. battoides* subspecies. Dates for the single brood range from mid-June to early September, depending on elevation and snowpack in a given year. The majority of records fall in the month of July.
- FOODPLANTS: The following species of *Eriogonum* (Polygonaceae) are used by *E. b. battoides*: *E. lobbii* Torr. & Gray var. *lobbii*; *E. incanum* Torr. & Gray; *E. polypodium* Small (Shields, 1977). Additionally, the butterfly is closely associated with a prostrate *E. umbellatum* Torr. subspecies near Horseshoe Meadow in Inyo County (J. F. Emmel, unpublished data).

b. *E. b. glaucon* (W. H. Edwards)

- DIAGNOSIS: This subspecies is found along the western edge of the Great Basin and in eastern Oregon, eastern Washington, and southwestern Idaho. Ventrally, both sexes have smaller black spots than *battoides battoides*. However, both these black spots and the red-orange band are wider and more extensive than in subspecies *intermedia*. Females have a well-developed submarginal orange band on the dorsal hindwing surface. Females from the type locality have a uniformly brown ground color dorsally, but at the southern end of its range on the east slope of the Sierra Nevada in Inyo County, females have varying amounts of basal blue scaling dorsally.
- ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Ent. Soc.*, 3: 210 (1871).

- TYPE LOCALITY: "Nevada", restricted to Storey County, Nevada by F. M. Brown, *Transactions American Ent. Soc.*, 96: 406 (1970). Lectotype in American Museum of Natural History, designated by F. M. Brown, *Transactions American Ent. Soc.*, 96: 409 (1970).
- DISTRIBUTION: In California, this subspecies is found from the east slope of the Sierra Nevada in Inyo County northward along the east slope to northern Mono County. It then extends through extreme western Nevada and is found again in California in the northeastern corner of the state in Lassen and Modoc counties. It reaches its westernmost limit within the state in the Mt. Shasta region. There are also records along the west side of Lake Tahoe; otherwise, in the Sierra Nevada proper, it seems to be confined to the east slope.
- ELEVATION RANGE: From 5,000' to 8,500' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is typically found in the Sagebrush Scrub plant community of the western edge of the Great Basin. Most populations are found on steep to gentle granitic or volcanic slopes where the growth of the usual foodplant, *Eriogonum umbellatum* Torr., is favored.
- PHENOLOGY: *E. b. glaucon* populations fly from mid-May to late June, depending on elevation and progression of the season in a given year.
- FOODPLANTS: The preferred foodplant of most *glaucon* populations on the east slope of the Sierra Nevada appears to be *Eriogonum umbellatum* Torr. var. *nevadense* Gand. Other *Eriogonum* species with which the butterfly is closely associated include *E. sphaerocephalum* Dougl. ex. Benth. var. *halimoides* (Gand.) S. Stokes (Shields, 1977), and *E. lobbii* T. and G. (J. F. Emmel, unpublished data).

c. *E. b. oregonensis* (Barnes and McDunnough)

- DIAGNOSIS: In this localized subspecies of the southern Cascades and extreme northwestern California, the diagnostic characters include a broad black border on the dorsal surface of the males, and largely brown females bearing an orange aurora on the submarginal area of the hindwing dorsally. Adults have a dusky underside bearing spots that are somewhat intermediate in size between those seen in *E. b. glaucon* and those seen in *E. b. battoides*.
- ORIGINAL DESCRIPTION: Barnes and McDunnough, *Contributions Natural History Lepidoptera North America*, 3: 214 (1917).
- TYPE LOCALITY: Crater Lake, Klamath County, Oregon.
- DISTRIBUTION: This butterfly is apparently confined to Klamath County, Oregon (Shields, 1977) and extreme northwestern California in the mountains of Del Norte County and on the western slopes of the Cascade Range along Highway 97, near Grass Lake Summit, Siskiyou County (S. Mattoon, unpublished data).
- ELEVATION RANGE: From 2,500 to 3,500' for the California populations; 5,000 to 7,500' for the Klamath County, Oregon populations.
- HABITAT AND PLANT COMMUNITIES: The Del Norte County habitat used by what we call *oregonensis* is in rich, weathered, decomposing serpentine rubble rock or sandy ridge crests, where the suspected host plant (by adult association), *Eriogonum ternatum*, sporadically turns up. The surrounding

vegetation type can sometimes be a modified Mixed Evergreen Forest; however, the coniferous forests that are predominant through the rich serpentine uplands habitat in extreme northwestern Del Norte County have been referred to as serpentine pine barrens, in reference to the stunted sparse nature of *Pinus monticola* and *Pinus contorta* that are indicators of it. The western slopes of the Cascades in Siskiyou County produce populations in open *Artemisia* Scrub, which is heavily interspersed with lupine and *Eriogonum* suspected to be *E. marifolium*. These sagebrush ridges are adjacent to Northern Juniper Woodland elements below, and Yellow Pine Forests above.

The Del Norte County populations are generally restricted to habitat that falls along the normal daily fog break area adjacent to and inland from the coast. The populations of *oregonensis* in Siskiyou County are along the Highway 97 route that leads directly north to Klamath Falls and Crater Lake in Oregon. The type locality is in Klamath County, Oregon.

There is one additional *Eriogonum* species growing in a rather pure stand on a rocky ridge crest one mile north of Wimer Springs (on County Road 305) in Del Norte County that has adjacent *E. ternatum* plants. Several males and females of what look like the most typical *oregonensis* taken in Del Norte County came from direct association with this different *Eriogonum*.

PHENOLOGY: This taxon has been taken throughout the month of June, flying until mid-July.

FOODPLANTS: For the Del Norte County populations, the adults are closely associated with *Eriogonum ternatum* Howell, strongly suspected to be the foodplant. In Oregon, the apparent foodplant by adult association is *Eriogonum marifolium* T. & G. (Shields, 1977).

d. *E. b. intermedia* (Barnes and McDunnough)

DIAGNOSIS: This subspecies is found in the northern California mountains and on the west slopes of the Sierra Nevada at low to moderate elevations (Langston, in Howe, 1975). The ventral surfaces of both sexes are distinctive. The small black spots and orange "band" are reduced to a series of lunules. The dorsal surface of most males has rather wide, dark borders and the females have an orange band in the anal area of the hindwing.

ORIGINAL DESCRIPTION: Barnes and McDunnough, *Contributions Natural History Lepidoptera North America*, 3: 214 (1917).

TYPE LOCALITY: Shasta County, California. Holotype in U. S. National Museum.

DISTRIBUTION: This subspecies is found on the west slope of the Sierra Nevada from the southern Lake Tahoe region northward to the Mt. Shasta and eastern Klamath Mountains region within California. There is one record for Morrow County in Oregon.

ELEVATION RANGE: From approximately 1,000' at the north end of the Sacramento Valley to 8,000' in the mountains. Most populations seem to be above 4,500' elevation.

HABITAT AND PLANT COMMUNITIES: Usually on open rocky or gravelly slopes within the Montane Coniferous Forest plant community.

PHENOLOGY: Records range from early June to early August, depending on elevation and progression of the season.

FOODPLANTS: Most populations are associated with *Eriogonum marifolium* Torr. and Gray; Shields (1977) also notes an adult association for at least one population with *E. incanum* Torr. and Gray.

e. *E. b. comstocki* (Shields)

DIAGNOSIS: This is a montane subspecies of the Piute Mountains and Tehachapi Mountains region of Kern County, which is characterized by a relatively thin, dark marginal band on the upperside of the males, brown females with a prominent orange aurora on the dorsal secondaries, and undersides characterized by a very pale ground color and reduction in the size of the black and orange markings.

ORIGINAL DESCRIPTION: O. Shields, *Bulletin Allyn Museum*, 28: 12 (1975).

TYPE LOCALITY: Tehachapi, Kern County, California. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This subspecies is known only from relatively high elevations in the Tehachapi and Piute Mountains of Kern County. It has not been collected in the Tehachapi Mountains since the type series was taken in 1918 by John Adams Comstock. On the basis of what is known about the habitat and foodplant of the butterfly in the Piute Mountains, it is likely that further exploration of the higher elevations of the Tehachapi Mountains during the expected flight period would produce additional specimens of this subspecies from that range.

ELEVATION RANGE: From 6,000 to 8,300 feet elevation.

HABITAT AND PLANT COMMUNITIES: In the Piute Mountains, the butterfly is found around rocky outcroppings within the Montane Coniferous Forest.

PHENOLOGY: The type series was taken on July 22, 1918; recent records from the Piute Mountains show a flight period from early to mid-July.

FOODPLANTS: In the Piute Mountains localities, the butterfly is associated with a subspecies of *Eriogonum umbellatum* Torr., and G. Pratt (personal communication) has collected larvae from the flowerheads of this plant.

f. *E. b. argocyanea* Pratt and J. Emmel

DIAGNOSIS: This is a subspecies of the western Death Valley region which is characterized by a phenotype very similar in appearance to subspecies *baurii*, but with even greater development of the blue areas on the upperside and with somewhat less prominent dark markings on the underside.

ORIGINAL DESCRIPTION:

TYPE LOCALITY: Hunter Mountain, Inyo County, California.

DISTRIBUTION: This butterfly is found at mid-elevations in the mountains of the western Death Valley region from the Nelson Range south to the Argus and Coso Ranges, all in Inyo County.

ELEVATION RANGE: 5,500 to 7,000' elevation.

HABITAT AND PLANT COMMUNITIES: In the type locality, this butterfly is found in a mixed Sagebrush Scrub and Pinyon-Juniper Forest plant community, characteristically on somewhat open granitic sandy or rocky slopes, where the foodplant is locally abundant. In the Coso Range, a population is known from a volcanic plateau within the Shadscale Scrub plant community.

PHENOLOGY: This subspecies flies from mid-May to mid-June, with a peak flight during the last week in May and the first week in June.

FOODPLANTS: The sole host of this subspecies is apparently *Eriogonum umbellatum* Torr. var. *nevadense*.

g. *E. b. hadrocheilos* Pratt

DIAGNOSIS: This is an early summer-flying subspecies known only from the south end of the White Mountains in Inyo County. It is characterized by an extremely broad black border on the upperside of males, with an orange aurora of varying development on the submarginal area of the hindwing. The females have a uniform brown ground color with a prominent orange aurora on the dorsal hindwing; both sexes show a somewhat suffused appearance of the dark spots on the underside of the forewing towards the posterior margin, giving a somewhat smoky appearance as in *Euphilotes enoptes dammersi*.

ORIGINAL DESCRIPTION: G. Pratt, *Journal Research Lepidoptera*, : , 19 .

TYPE LOCALITY: 3.5 road miles south of Westgard Pass, Inyo County, California.

DISTRIBUTION: The butterfly is known from only a few localized populations in the vicinity of Westgard Pass at the south end of the White Mountains in Inyo County.

ELEVATION RANGE: 6,500 to 7,500' elevation.

HABITAT AND PLANT COMMUNITIES: This subspecies occurs in the Pinyon-Juniper Woodland plant community where it is found on rather gentle, gravelly to rocky slopes or in wash bottoms or canyon bottoms where the *Eriogonum* foodplant is locally abundant.

PHENOLOGY: The flight period is from early to mid-July.

FOODPLANTS: The apparent sole host of this subspecies is *Eriogonum umbellatum* Torr. var. *subaridum* (S. Stokes) Munz.

h. *E. b. panamintensis* Pratt

DIAGNOSIS: This is a *glaucon*-like subspecies of the Panamint Range in Inyo County. It is characterized by relatively large size, males with a moderately wide black border on the wing margins of the upperside, and a relatively pale ground color on the underside of both sexes. Females are a uniform brown ground color with a reduced orange aurora in the submarginal area of the hindwing.

ORIGINAL DESCRIPTION: G. Pratt, *Journal Research Lepidoptera*, : (19).

TYPE LOCALITY: Thorndike Camp, Wildrose Canyon, Panamint Range, Inyo County, California.

DISTRIBUTION: This blue is known only from the Panamint Range in Inyo County.

- ELEVATION RANGE: From approximately 6,500 to 9,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This butterfly is found both in Pinyon-Juniper Woodland and Sagebrush Scrub plant communities, where it is typically found on open gravelly to rocky slopes or canyon bottoms.
- PHENOLOGY: This subspecies has a similar phenology to *E. b. hadrocheilos*, previously treated, in that it flies from late June to mid-July, with a peak flight in early July.
- FOODPLANTS: The apparent sole host of this subspecies is *Eriogonum umbellatum* Torr. var. *subaridum* (S. Stokes) Munz.

i. *E. b. allyni* (Shields)

- DIAGNOSIS: This is the well-known El Segundo Blue, a federally listed Endangered Species since 1976. Emmel and Emmel (1973) pointed out that the then undescribed butterfly was unique and in danger of extinction. The populations continued declining during the 1970's and 1980's (Arnold, 1983, 1986). A major conservation study and recovery program was then carried out under the principal direction of R. H. T. Mattoni (see Mattoni (1992) for a fascinating account of this effective program to restore both the dunes habitat and the butterfly). A subspecies of the immediate coast in Los Angeles County, *E. b. allyni* is characterized by enlargement of the dark markings on the underside of both sexes, giving an overall very dark appearance to the underside of the wings. Males have a moderately wide black border dorsally, with a obsolescent to fairly prominent pale orange aurora in the submarginal area of the hindwing. Females are brown above, with an orange aurora on the hindwing that is relatively well-developed.
- ORIGINAL DESCRIPTION: O. Shields, *Bulletin Allyn Museum*, 28: 10-11 (1975).
- TYPE LOCALITY: El Segundo, Los Angeles County, California. Holotype in Allyn Museum of Entomology.
- DISTRIBUTION: Confined to a short narrow band along the immediate coast in Los Angeles County, where it ranges in fragmented relict populations from the El Segundo Sand Dunes southward to the Palos Verdes Peninsula. The El Segundo Blue is currently listed as an Endangered Species and may not be collected except by federal permit.
- ELEVATION RANGE: From near sea level to approximately 300' elevation.
- HABITAT AND PLANT COMMUNITIES: This butterfly is found in the Coastal Strand plant community where it is usually found in stabilized sand dunes, although the Palos Verdes Peninsula populations are found on cliff faces or rocky slopes immediately above the ocean breakers.
- PHENOLOGY: This is a summer-flying subspecies which has a rather long flight period due to the moderating influence of the ocean. Captures range from early July to early September, with a peak flight period in early August.
- FOODPLANTS: *Eriogonum parvifolium* Sm. in Rees. is the host in the El Segundo Sand Dunes. *E. cinereum* Benth. may be occasionally used by the populations on the Palos Verdes Peninsula in situations where this plant is intimately associated with the principal host, *E. parvifolium* Sm. in Rees. (J. Emmel and J. Lane, unpublished data).

j. *E. b. ssp.* (Coxey Meadow)

- DIAGNOSIS:** This is a *baueri*-like subspecies of the San Bernardino Mountains. Although the adult phenotype is extremely similar to that of *E. b. baueri*, it differs from *baueri* by having a slightly more prominent orange aurora on the underside of both sexes, reduction of the black markings on the ventral surface of the forewing from that seen in *baueri* (thus rendering a lighter, less suffused appearance to the surface of the forewing in this subspecies), and somewhat less development of the basal blue scaling on the dorsal surface of the females as well as a more yellowish-orange aurora on the female in contrast to the more pinkish or reddish-orange aurora seen in *baueri*. There are also differences in the isoenzyme frequencies in this species in comparison to the pattern seen in *baueri* (Pratt, 1988). Additionally, the butterfly is adapted to a different *Eriogonum* host plant from that used by *baueri*.
- DISTRIBUTION:** Thus far, this butterfly is known only from the vicinity of Coxey Meadow, in the San Bernardino Mountains. Of particular interest is the fact that this species uses a foodplant which is also used by *Euphilotes enoptes* within the same mountain range but in other localities; to our knowledge, there are no sympatric populations of the two species, *enoptes* and *battoides*, in the San Bernardino Mountains.
- ELEVATION RANGE:** 5,800 to 6,200' elevation.
- HABITAT AND PLANT COMMUNITIES:** This subspecies is found on open gravelly slopes and ridges within a sparse Pinyon forest and Chaparral plant community.
- PHENOLOGY:** This is one of the earliest-flying *battoides* subspecies, particularly in view of the elevation at which it is found. It flies from late April to mid-May.
- FOODPLANTS:** The apparent sole host of this population is *Eriogonum kennedyi* Porter in Wats.

k. *E. b. bernardino* (Barnes and McDunnough)

- DIAGNOSIS:** This small southern race occurs in the upper Sonoran and Transition Zones throughout cismontane southern California. It is the common spring and early summer subspecies that is found most often in lower canyons and dry washes. The adults of this species are among the smallest of the *battoides* subspecies. The spots on the underside are clearly defined on a uniform light grey background and the females have a prominent submarginal orange band on the upper side of the hindwings.
- ORIGINAL DESCRIPTION:**
- TYPE LOCALITY:** Camp Baldy, San Bernardino Mountains, California. Holotype in U. S. National Museum.
- DISTRIBUTION:** This subspecies is found from the Central Coast Ranges of San Benito County and Monterey County southward through the Coast Ranges, the west slope of the extreme southern Sierra Nevada southward through the Transverse Ranges, and the mountains of cismontane southern California. From California it extends southward into Baja California. The precise southern limits of its range in Baja California are undetermined at this time. Along the western edge of the Mojave Desert, particularly around the east end of the San Bernardino Mountains, there begins a blend zone which extends eastward into the desert subspecies *martini*.

There may be a similar blend zone between the subspecies *bernardino* and the subspecies *inyomontanus* on the east slope of the extreme southern Sierra Nevada.

- ELEVATION RANGE: From near sea level to approximately 6,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is typically found in either Chaparral or Coastal Sage Scrub plant communities where the foodplant, *Eriogonum fasciculatum* Benth., is often a dominant subshrub.
- PHENOLOGY: Records range from the end of April to mid-July, depending on elevation and progression of the season in a given locality. Most populations seem to fly in the latter half of May or first two weeks of June.
- FOODPLANTS: *Eriogonum fasciculatum* Benth. ssp. *fasciculatum* Benth., ssp. *polifolium* (Benth.) S. Stokes and ssp. *foliolosum* (Nutt.) S. Stokes (Polygonaceae).

I. *E. b. martini* (Mattoni)

- DIAGNOSIS: This subspecies occurs from western Arizona to the eastern and central Mojave Desert of California. It is known from many isolated desert mountain ranges in eastern California. A small subspecies, *martini* differs from *bernardino* in the lighter blue of the males, and it also has a lighter ventral surface than all other subspecies. There is an exceptionally well-developed orange-red band ventrally, which averages one-eighth of the total wing expanse (Langston, in Howe, 1975). Females often have some blue scaling on the dorsal surface of both forewings and hindwings, in the basal area.
- ORIGINAL DESCRIPTION: R. Mattoni, *Bulletin Southern California Academy Sciences*, 53: 157 [1955].
- TYPE LOCALITY: Oatman, Mohave County, Arizona. Holotype in U. S. National Museum.
- DISTRIBUTION: Within California, this butterfly is most commonly encountered in the mountain ranges of the eastern Mojave Desert, including the Kingston, Clark, New York, Mid Hills, Providence, Granite, and Old Woman Mountains. It is also found in a number of the smaller mountain ranges of the central and southeastern Mojave Desert, including the Chemehuevi Mountains, the Sheep Hole Mountains, the Coxcomb Mountains, and the Little San Bernardino Mountains, and the ranges of the western Mojave Desert.
- ELEVATION RANGE: 3,000 to 6,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This butterfly is found from the upper edges of the Creosote Bush Scrub plant community into the Shadscale Scrub and Pinyon-Juniper Woodland communities; it is typically found on open gravelly to sandy slopes or ridges, in large dry washes, or occasionally on steep bouldery canyon slopes.
- PHENOLOGY: Records for this subspecies range from early April to late June, depending on elevation and progression of the season; in most localities, the peak flight period appears to be late April to mid-May. While it is often common in its flight season, it is not frequently collected because collectors usually do not explore these desert ranges in May, a time too late for most spring species of the desert.
- FOODPLANTS: *Eriogonum fasciculatum* Benth. ssp. *polifolium* (Benth.) S. Stokes.

m. *E. b. inyomontanus* Pratt

DIAGNOSIS: This is a *bernardino*-like subspecies of the mountains of the Death Valley region and east slope of the Sierra Nevada. It is characterized by a small size, often smaller than *bernardino*, a reduction in the width of the black border on the dorsal surface of the males, frequent presence of blue scaling in the basal area of the females dorsally, and a somewhat more prominent orange aurora on the hindwing of the females.

ORIGINAL DESCRIPTION: G. Pratt, *Journal Research Lepidoptera*, : (19).

TYPE LOCALITY:

DISTRIBUTION: This butterfly is found primarily in the mountains of Inyo County (hence, the name *inyomontanus*), from the southern end of the White Mountains and the Sierra Nevada east slope southward to the El Paso Mountains of northern Kern County.

ELEVATION RANGE: 4,000 to 8,000' elevation.

HABITAT AND PLANT COMMUNITIES: Populations are found in the upper edges of Creosote Bush Scrub through both Pinyon-Juniper Woodland and Sagebrush Scrub plant communities, and sparsely in the Shadscale Scrub plant community. Colonies are typically found on sandy, gravelly or rocky slopes or canyon bottoms where the *Eriogonum fasciculatum* Benth. foodplant is often locally common.

PHENOLOGY: This subspecies flies from mid-May to early July, depending on elevation and progression of the season.

FOODPLANTS: The apparent sole host of this subspecies is *Eriogonum fasciculatum* Benth. ssp. *polifolium* (Benth.) S.Stokes.

n. *E. b. euromojavensis* Pratt

DIAGNOSIS: This is a late summer-flying eastern Mojave Desert subspecies characterized by relatively small size, a uniform brown ground color dorsally on the females, with a reduced orange aurora on the hindwing, a very pale ground color on the underside of both sexes (almost whitish in appearance), with the submarginal dark spots on the underside of the forewing forming almost a continuous line, giving a borderlike effect to this area of the wing, and a reduced orange aurora on the underside of the hindwing in both sexes.

ORIGINAL DESCRIPTION: G. Pratt, *Journal Research Lepidoptera*, : (19).

TYPE LOCALITY: Macedonia Canyon, Mid Hills, eastern Mojave Desert, San Bernardino County, California.

DISTRIBUTION: This butterfly is found in the ranges of the eastern Mojave Desert, from the Providence Mountains northward through the Mid Hills and New York Mountains to Clark Mountain and the Kingston Range in northern San Bernardino County and extreme southeastern Inyo County. From here the subspecies ranges eastward into extreme southern Nevada.

ELEVATION RANGE: From 4,500 to 6,500' elevation.

- HABITAT AND PLANT COMMUNITIES:** This subspecies is typically found on open slopes, usually north-facing, on sandy, gravelly, or rocky substrates, within the Pinyon-Juniper Woodland, Sagebrush Scrub, or Shadscale Scrub plant communities. Although the type locality is on a granitic substrate, most of the other localities for this subspecies are on limestone substrates which favor the growth of the foodplant, *Eriogonum heermannii* Dur. & Hilg.
- PHENOLOGY:** This subspecies flies from mid-August to mid-September, with a peak flight period during the last week of August and first week of September.
- FOODPLANTS:** The two foodplants of this subspecies are *Eriogonum heermannii* Dur. & Hilg. and *E. microthecum* Nutt. It is yet to be determined whether both foodplants need to be present in a given locality to ensure the presence of the butterfly; in some localities in the eastern Mojave Desert where only *Eriogonum heermannii* Dur. & Hilg. is present, the butterfly appears to be absent, suggesting that possibly both species of *Eriogonum* need to be present. Perhaps this dependency involves adult nectar-source availability; the larvae can be found on either host.

170. *Euphilotes enoptes* (Boisduval)

- ADULT BEHAVIOR:** The adults of *E. enoptes* behave much like those of *E. battoides* in that much of the adult activity is centered around the *Eriogonum* host plant in a given locality. Adults of both sexes repeatedly land on flowers or stems of the host plant, both for nectar and for perching sites. Adult emergence is closely correlated with the early full bloom of the foodplant; courtship and mating often occurs on the flowers of the host plant. *E. enoptes* is probably a more vagile species than is *E. battoides*. As has been noted above, many populations of *E. enoptes* are at least partially bivoltine and involve 2 separate *Eriogonum* hosts at different times in the season which may have a slightly different micro-distribution within a given habitat. Thus, adults which result from larvae feeding on one host and which emerge at the time of an alternate host being in bloom must be mobile enough to exploit alternative foodplants if the plant on which they fed to maturity is not available at the time of their emergence.

The adults have only rarely been noted at nectar sources other than their *Eriogonum* host plants. Males are attracted to mud or damp sand, particularly along canyon bottoms or near springs. Both sexes roost at night on stems of either the foodplant or nearby small shrubs, in a head-downward position.

- LIFE HISTORY:** The life history of *E. e. dammersi* was described by Comstock and Henne (1965). The echinoid egg is light blue-green in color and the top is deeply depressed. The eggs are laid singly in the buds of blossoms of the host, and larval feeding is confined exclusively to the flower. The mature larva is ivory-white in ground color, with tinges of pink. The mid-dorsal stripe is pinkish-brown, the diagonal lateral markings are brown, and the low lateral line is pinkish. Blotches of pink occur on each segment between this line and the more dorsal slashes. The larva is completely covered by short white hairs, giving the larva a frosted appearance. The pupa is uniform pale chestnut and lacks hairs. It is supported by a silk girdle and caudal silk button.

The life history of *E. e. bayensis* was described by Langston and Comstock (1966); in this subspecies the mature larvae are a nearly uniform rose yellow, with no spots or stripes. Although Langston and Comstock record five larval instars, more recent studies indicate that there are probably only four larval instars in this species (G. Pratt and G. Ballmer, unpublished data). The adult flight period is

remarkably short in duration in this subspecies, although the initiation may vary from late May to early July, with oviposition synchronized to match the late bud or early flower stage of the foodplant. The mature larvae have much reduced pinkish ground color stripes and geometric patterns compared to the other members of the genus that have been studied.

CHROMOSOME NUMBER:

SIMILAR SPECIES: See discussion under *Euphilotes battoides*.

GEOGRAPHIC AND
SEASONAL VARIATION:

In the populations of *E. enoptes* which appear to be at least partially bivoltine, there is no apparent difference in phenotype between the earlier and later-flying adults, although this situation has not been studied in any great detail and certainly bears further study. Because *E. enoptes* tends to be a more vagile species and frequently uses more than one host in a given locality or region, there tends to be more potential in this species complex for blendzones between different geographic subspecies. This is in contrast to *E. battoides* where usually only a single host is used in a given locality and the potential for blendzones between subspecies is correspondingly much less. As has been noted in the discussions above under the various subspecies, there is an apparent rather large blendzone of several geographic subspecific characters in the mountains of Kern County and eastward into the Transverse Ranges of the San Gabriel Mountains and the San Bernardino Mountains. In this region, there seems to be a blending of characters of subspecies *tildeni*, *enoptes*, *langstoni*, and *dammersi*. In the mountains of the Death Valley region, there is a set of populations which here has been lumped under typical *enoptes* but perhaps represents a distinct geographic subspecies; unfortunately, inadequate series of specimens are presently available to assess this situation more thoroughly.

GENERAL REMARKS:

A study by G. Pratt and G. Ballmer (1987) demonstrates the complexity of trying to apply a classical taxonomic approach to the *E. enoptes* complex. In this study, the *E. enoptes* populations in the San Bernardino Mountains were compared to one another and to *E. enoptes* populations in other areas of the state in phenology, host plants, and larval setation patterns. Despite considerable variation in phenology and host plant usage within the San Bernardino Mountains populations, the similarity in larval setation of the populations suggests that they are probably all closely related, and more so to each other than to populations outside of this immediate geographic area. Similar studies of other sets of *E. enoptes* populations would shed considerably more light on this fascinating situation.

SUBSPECIES:

Ten subspecies of this widespread western species fly in California. Often they are separated from sympatric *Euphilotes battoides* populations by differences in flight periods (flying in late summer or fall versus the spring-flying *battoides*), or

by differing foodplant species. The two species are frequently difficult to distinguish phenotypically, even in the laboratory, and a specialist generally uses differences in the male and female genitalia to be certain of identification.

a. *E. e. enoptes* (Boisduval)

DIAGNOSIS: The typical subspecies occurs on both the east and west slopes of the Sierra Nevada, as well as in the mountains of north central and northeastern California. The nominate subspecies has distinctive markings on the ventral surface, where the orange "band" is reduced to a series of lunules, which may be faint or obsolescent in many specimens. The upperside of the male is blue, with wide dark borders. The female is dark brown dorsally, and occasionally has a few faint orange lunules on the hindwings.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 298 (1852).

TYPE LOCALITY: "California". Restricted by Emmel, Emmel, and Mattoon, *Journal Research Lepidoptera*, : (1988), to North Fork at confluence of east branch North Fork Feather River, Plumas County, California. Holotype in U. S. National Museum.

DISTRIBUTION: The nominate subspecies is widespread in the state, ranging from both the western and eastern slopes of the Sierra Nevada northward to the Mt. Shasta and Klamath Mountains region as well as the Warner Mountains. There are also populations in the Panamint Range and Coso Range of Inyo County which are here lumped under typical *enoptes*, although they show some differences both in phenotype and in isoenzyme electrophoresis studies (Pratt, 1988). Populations at the southern end of the Sierra Nevada in Kern County appear to show some blending characteristics towards subspecies *tildeni* of the South Coast Ranges; additionally, populations in the Transverse Ranges of southern California were lumped by Shields (1977) with the nominate subspecies, but in our opinion are closer to subspecies *tildeni*, both biologically and phenotypically. In the extreme northwestern part of California and in the North Coast Ranges, there appears to be a rather broad blendzone between nominate *enoptes* and subspecies *bayensis* which is found in the southern half of the North Coast Ranges and the San Francisco Bay area.

ELEVATION RANGE: From 2,000 to 10,500' elevation, with most populations in the 2,000 to 8,000' range.

HABITAT AND PLANT COMMUNITIES: This subspecies is usually found on dry, open slopes within the Montane Coniferous Forest plant community. However, because of the rather wide ecological tolerance of its foodplant, *Eriogonum nudum* (Dougl. ex Benth.) the butterfly is also sometimes taken within the following plant communities: Chaparral, Foothill Woodland, Northern Oak Woodland, Sagebrush Scrub, and Sub-Alpine Forest.

PHENOLOGY: Records range from early May to early October, with the majority of records during the months of June and July. In some localities, the subspecies is at least partially bivoltine, with a late-spring generation associated with one *Eriogonum* foodplant and a late-summer or early-fall flight associated with another, later-blooming species of *Eriogonum*. Rearing studies by G. Pratt (1988) indicate that offspring of adults of the late-summer flight in some *E. enoptes* populations can produce some pupae which will hatch out in the late spring and some which hold over until late summer the following year, both types resulting from a single late-summer female. Additionally, offspring reared from spring-flying females of some populations will produce pupae which emerge within a short period of time,

indicating that these butterflies are capable of being bivoltine in nature. In the case of *E. battoides*, when a spring-flying and late-summer flying entity occur in the same locality, it appears that these are sympatric but univoltine, biologically differently adapted subspecies rather than two generations of the same population. In contrast, *E. enoptes* appears to be more ecologically flexible and to produce both spring-flying and late summer flying adults from a single population.

FOODPLANTS: Most populations of nominate *enoptes* are associated with various subspecies or varieties of *Eriogonum nudum* Dougl. ex Benth.; these varieties include var. *deductum* (Greene) Jeps., var. *pubiflorum* Benth. in DC., var. *nudum*, and var. *scapigerum* (Eastw.) Jeps. In some localities where late-summer individuals have been taken, the adults are associated with *Eriogonum wrightii* Torr. ex Benth. in DC. (G. Austin, personal communication; J. F. Emmel, unpublished data).

b. *E. e. dammersi* (J. A. Comstock and Henne)

DIAGNOSIS: This late-summer and fall-flying subspecies is characterized by its large size and the underside has an extensive dark suffusion on the forewings, sometimes almost obscuring the large black spots.

ORIGINAL DESCRIPTION: J. A. Comstock and Henne, *Bulletin Southern California Academy Sciences*, 32: 24 (1933).

TYPE LOCALITY: Snow Creek, Riverside County, California. Holotype in U. S. National Museum.

DISTRIBUTION: This subspecies is found along the western edge of the Colorado Desert in Riverside and San Diego counties and along the eastern and northeastern edge of the San Bernardino Mountains at the southern edge of the Mojave Desert. From here it extends eastward into the Little San Bernardino Mountains of Joshua Tree National Monument and northeastward to the mountain ranges of the eastern Mojave Desert, including the Kingston, Clark, New York, Mid-Hills, Providence, and Granite Mountain Ranges of that region. There are a few populations known from the lower elevations of the Santa Ana Mountains and the western base of the San Jacinto Mountains. From California, the subspecies extends eastward into central Arizona and southern Nevada.

ELEVATION RANGE: From 1,800 to 6,500' elevation.

HABITAT AND PLANT COMMUNITIES: Most populations along the western edge of the Colorado Desert occur in transitional habitats which are various admixtures of Chaparral, Pinyon-Juniper Woodland, Creosote Bush Scrub, and Coastal Sage Scrub plant communities. Typically, the subspecies is found on open canyon slopes or in open canyon bottoms where growth of the foodplant is favored.

PHENOLOGY: Records range from late August to mid-October; most of the eastern Mojave populations seem to fly somewhat earlier than the populations along the western edge of the Colorado Desert. In the desert-facing canyons of the San Jacinto Mountains, the main flight occurs in early October.

FOODPLANTS: For the populations along the western edge of the Colorado Desert in Riverside County and at the east end of the San Bernardino Mountains, as well as in the Santa Ana Mountains, *Eriogonum elongatum* Benth. is the foodplant; for populations in the eastern Mojave Desert, the host is *Eriogonum wrightii* Torr. ex Benth. in DC. var. *wrightii*. On the desert slope of the San Diego County Mountains, *E. wrightii* var. *membranaceum* Stokes ex Jeps.; on the desert-facing

slopes of the Santa Rosa Mountains and the southern face of the Little San Bernardino Mountains, *E. wrightii* var. *nodosum* (Small) Munz is the primary host. Occasional adults are taken in association with *E. nudum* Dougl. ex Benth. ssp. *pauciflorum* (Wats.) Munz, but this may be a fortuitous association of adults flying from nearby plants of *E. elongatum* Benth. or *E. wrightii* Torr. ex Benth. in DC.

c. *E. e. bayensis* (Langston)

- DIAGNOSIS: This subspecies is found around the San Francisco Bay area and the North Coast Ranges of California. No other species of *Euphilotes* occur with it. The male is distinguished by the slightly narrower marginal borders on the dorsal surface of the hindwings. The ventral surface on both sexes has a light grey ground color, the small but distinct spots, and a prominent row of sub-marginal red spots on the secondaries (Langston, *in* Howe, 1975).
- ORIGINAL DESCRIPTION: R. Langston, *Journal of the Lepidopterists' Society*, 17: 208-212 [1964].
- TYPE LOCALITY: China Camp, near Point San Pedro, Marin County, California. Holotype in California Academy of Natural Sciences.
- DISTRIBUTION: This butterfly is found in the counties bordering the northern half of San Francisco Bay, namely Contra Costa, Solano, and Marin counties northward through Sonoma County to Mendocino and Humboldt counties in the North Coast Ranges (see also Langston, 1970). There is an apparent possible blend zone with nominotypical *enoptes* at the north end of the North Coast Ranges in the southern Klamath Mountains Assemblage.
- ELEVATION RANGE: From near sea level to approximately 1,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is typically found on steep embankments, bluffs, or road cuts within the northern Coastal Scrub plant community, as well as Foothill Woodland, Chaparral, and Valley and Foothill Grassland.
- PHENOLOGY: This subspecies flies from late May to mid-July, depending on locality and precipitation and temperature pattern for the season. This late spring to early summer flight period is in contrast to the phenology of its nearest relative, *E. e. tildeni*, which flies in two broods, the first in May and the second in late summer.
- FOODPLANTS: *Eriogonum nudum* Dougl. ex Benth. var. *auriculatum* (Benth.) Tracey ex Jeps. near the San Francisco Bay, and *E. nudum* Dougl. ex Benth. var. *nudum* in the North Coast Ranges (Langston, *in* Howe, 1975; Shields, 1977). Both plants come into bloom in late spring to early summer and have white flowers, on which the larvae feed.

d. *E. e. tildeni* (Langston)

- DIAGNOSIS: This subspecies is found along the inner Coast Ranges of central California, inhabiting the hot dry rain shadow area of the foothills bordering the San Joaquin Valley. Individuals occur in very low density in the scattered populations. The males are distinguished by the wide dark borders on the dorsal surface of the wings and the dark coloring in the subcostal area of the hindwing, resulting in a reduced amount of blue. The ventral surfaces of both males and females have slightly suffused forewings with proportionately large black spots, and bear a prominent row of submarginal orange-red spots on the hindwing.

- ORIGINAL DESCRIPTION: Langston, *Journal of the Lepidopterists' Society*, 17: 212-216 [1964].
- TYPE LOCALITY: Del Puerto Canyon, 22 miles west of Patterson, Stanislaus County, California. Holotype in California Academy of Natural Sciences.
- DISTRIBUTION: This subspecies is found in the inner South Coast Ranges from Monterey County and Stanislaus County southward to San Luis Obispo County and western Kern County (see also Langston, 1970). In the Marina Dunes of coastal Monterey County, there is an ecotype associated with *Eriogonum latifolium* which is closest to *tildeni* by isoenzyme studies (Pratt, 1988). Both spring-flying and late summer-flying populations in much of Kern County appear to be referable to *tildeni* or to a *tildeni-dammersi-enoptes* blend; along the north slope of the San Gabriel and San Bernardino Mountains, there appears to be a rather broad blendzone between *tildeni*-like phenotypes and some individuals tending towards subspecies *dammersi*. Populations in the San Bernardino Mountains in particular seem to show a considerable amount of both ecological and phenotypic variation between these 2 subspecies. (See Pratt and Ballmer, 1987, for a detailed discussion of the San Bernardino Mountains populations of *enoptes*.)
- ELEVATION RANGE: For the Coast Range colony populations, 1,000 to 3,600' elevation; for the Kern County, San Gabriel and San Bernardino Mountains populations, 2,000 to 7,500' elevation; for the Marina Dunes ecotype, near sea level.
- HABITAT AND PLANT COMMUNITIES: This subspecies is typically found on open slopes, roadcuts, canyon bottoms, and open gravelly to rocky flats within several plant communities; in the Coast Ranges, it is found within the Foothill Woodland plant community or Chaparral areas. The Kern County, San Gabriel and San Bernardino Mountains populations are found within Montane Coniferous forests, Joshua Tree Woodland, Chaparral, Coastal Sage Scrub, and Southern Oak Woodlands. The Marina Dunes ecotype flies in coastal sand dunes, where *Eriogonum latifolium* is locally abundant in the Coastal Sand Dune plant community.
- PHENOLOGY: This subspecies is apparently at least partly bivoltine with a spring brood flying in May, and another larger, more regular emergence occurring in late summer. Pratt (1988) has shown that larvae collected from flowerheads of the foodplants in late summer (i.e., from the late summer-flying adults) produce pupae which, after refrigeration and upon subsequent warming, will show two peaks of emergence; one, a "spring" cluster of emergences, which would correspond to the May brood, and a "late summer" emergence which would correspond to the individuals flying from August into September. What is unusual about this bivoltinism in a *Euphilotes* species is that the spring and late summer broods use different foodplants, which have a slightly different microdistribution within a given habitat; thus, the adults would have to be somewhat more vagile and opportunistic than other more sedentary members of the genus. The Marina Dunes ecotype is univoltine, flying in June and early July.
- FOODPLANTS: Larval foodplants are late summer and fall-blooming forms of *Eriogonum nudum* (Dougl. ex Benth.) that bear yellow flowers. In different localities the foodplant subspecies that have been determined are *auriculatum* (Benth.) S. Stokes, *indictum*, *nudum* (Dougl. ex Benth.) S. Stokes, and *saxicola* (Langston, in Howe, 1975). Pratt (1987) has also found larvae on *E. roseum* in the Piute Mountains region of Kern County. The *tildeni*-like populations in the Kern County area and on the north slope of the San Bernardino Mountains both use *Eriogonum wrightii* Torr. ex Benth. in several localities. Additionally, the San Gabriel Mountains

populations use *E. nudum* (Dougl. ex Benth.) S. Stokes var. *saxicola*, and the San Bernardino Mountains populations use both *E. kennedyi* Porter in Wats. and *E. elongatum* Benth. The Marina Dunes ecotype uses *Eriogonum latifolium* Sm.

e. *E. e. smithi* (Mattoni)

- DIAGNOSIS: This butterfly is known only from the coastal fog belt of Monterey County in California, where it inhabits the immediate coast of the Big Sur country. The male is distinguished by the broad marginal border of the hindwings. The ventral surface of both males and females has a faint terminal line and a light ground color with large prominent spots.
- ORIGINAL DESCRIPTION: Mattoni, *Bulletin Southern California Academy Sciences*, 53: 160 [1955].
- TYPE LOCALITY: Burns Creek, State Highway 1, Monterey County, California. Holotype in U. S. National Museum.
- DISTRIBUTION: This subspecies is confined to coastal Monterey County from Big Sur southward to several miles north of the San Luis Obispo County line.
- ELEVATION RANGE: From near sea level to approximately 200' elevation.
- HABITAT AND PLANT COMMUNITIES: On cliffs, steep slopes, and roadcuts along the immediate coast, within the northern Coastal Scrub plant community.
- PHENOLOGY: This subspecies flies during a period of mid-August to early September, with an apparent peak in the last two weeks of August.
- FOODPLANTS: The foodplant is *Eriogonum parvifolium* Sm. in Rees. (Pratt and Ballmer, 1987).

f. *E. e. langstoni* (Shields)

- DIAGNOSIS: This is a spring-flying subspecies of the east slope of the Sierra Nevada. In this subspecies, both sexes have an increased amount of blue dorsally, rendering a very narrow dark margin on the males and considerable blue on the females, often being developed extensively in the basal one-half of both forewing and hindwing; ventrally, the ground color is pale with a reduction in size of the black markings.
- ORIGINAL DESCRIPTION: O. Shields, *Bulletin Allyn Museum*, 28: 23-24 (1975).
- TYPE LOCALITY: Six miles south of Sherwin Summit, Mono County, California. Holotype in Allyn Museum of Entomology.
- DISTRIBUTION: This subspecies is found along the east slope of the Sierra Nevada from extreme southern Mono County southward to Inyo County. Populations of *E. enoptes* on the desert slope of the extreme southern Sierra Nevada in Kern County, as well as populations in the El Paso Mountains of Kern County seem to be closest to *langstoni* (G. Pratt, personal communication).
- ELEVATION RANGE: For the Inyo County and Mono County populations, from 5,500 to 6,500' elevation. For the Kern County populations, from 2,000 to 5,500' elevation.
- HABITAT AND PLANT COMMUNITIES: Populations are found on steep slopes, small canyon bottoms, and on open gravelly to rocky flats, within the Sagebrush Scrub plant

community, Joshua Tree Woodland, and the upper edge of Creosote Bush Scrub.

PHENOLOGY: For the Inyo County and Mono County populations, mid-May to early June; for the Kern County populations, late March to late April, depending on slope exposure, temperature and precipitation patterns for the season.

FOODPLANTS: For the Inyo County and Mono County populations, both *Eriogonum nudum* var. *pubiflorum* Benth. and *E. kennedyi* Porter ex Wats. var. *purpusii* (Bdg.) Reveal are used. For the Kern County populations, the foodplant is *E. nudum* var. *pubiflorum*.

g. *E. e. cryptorufies* Pratt

DIAGNOSIS: This is a small subspecies of the Peninsular Ranges of southern California and northern Baja California. It is characterized by marked reduction of the orange-red aurora on the underside, often totally lacking any orange scaling, hence the name *cryptorufies* or "hidden red".

ORIGINAL DESCRIPTION: G. Pratt, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990).

TYPE LOCALITY: Pyramid Peak, San Jacinto Mountains, Riverside County, California.

DISTRIBUTION: This subspecies is known from the southeastern portion of the San Jacinto Mountains, the Santa Rosa Mountains, and the mountains of northern Baja California.

ELEVATION RANGE: For the California populations, from 5,000' to 7,000' elevation.

HABITAT AND PLANT COMMUNITIES: Usually on open gravelly slopes within the upper edges of the Mixed Chaparral community.

PHENOLOGY: Probably univoltine most years, but the butterfly has the capacity to be bivoltine as in laboratory rearing studies some pupae will hatch out immediately. The foodplant, despite being an annual, has a fairly long blooming period and in years of adequate summer rainfall could sustain a second brood in summer. Our records for adults are all during the month of May with an apparent peak flight from mid-May to late May.

FOODPLANTS: Larvae have been collected on a spring-blooming ecotype of *Eriogonum davidsonii* Greene (G. Pratt, 1987). This is a rather widespread annual *Eriogonum* in California, but field investigation of numerous other populations of this plant (most of which are the summer-blooming ecotype) have failed to reveal an associated *E. enoptes* with it.

h. *E. e. ancilla* (Barnes and McDunnough)

DIAGNOSIS: This is the Rocky Mountain subspecies of *enoptes*. It ranges from Colorado west across various scattered locations in the Great Basin. Typical *ancilla* have a well-developed orange-red submarginal band on the underside, with a relatively dark grey ground color and darker suffusion on the primaries (Langston, in Howe, 1975). Dorsally, males have a broad black border and a rather dark blue ground color; females are brown above, with a somewhat reduced orange aurora on the hindwing.

- ORIGINAL DESCRIPTION: Barnes and McDunnough, *Contributions Natural History Lepidoptera North America*, 4: 79 (1918).
- TYPE LOCALITY: Eureka, Juab County, Utah. Holotype in U. S. National Museum.
- DISTRIBUTION: This subspecies barely enters California along the eastern border from the White Mountains of Inyo and Mono counties northwestward to several localities in Mono County, both on the east slope of the Sierra Nevada and on a peak just east of the main Sierra Nevada.
- ELEVATION RANGE: From 6,500' to 10,000' elevation, with most of the populations in our area below 8,000'.
- HABITAT AND PLANT COMMUNITIES: Within the state, the butterfly is found on rocky to gravelly open slopes, usually within the Sagebrush Scrub plant community but also at the upper edge of Pinyon-Juniper Woodland community or within the Montane Coniferous forest community.
- PHENOLOGY: Adults fly from late May to early July, depending on elevation. This subspecies appears to be strictly univoltine in contrast to several of the other *E. enoptes* populations within California.
- FOODPLANTS: This subspecies feeds on *Eriogonum umbellatum* Torr. in all populations known within the state.

i. *E. e. pseudointermedia* Pratt

- DIAGNOSIS: The phenotype of this subspecies has a remarkable resemblance to *E. battoides intermedia*, hence the name *pseudointermedia*. Males have a broad black border dorsally, and females are brown dorsally, with a relatively small aurora on the hindwing. On the underside, there is reduction of the black markings as in *E. b. intermedia*. This subspecies is separated from *intermedia* with certainty only by examining the genitalia.
- ORIGINAL DESCRIPTION: Pratt, *Journal Research Lepidoptera*, : (19).
- TYPE LOCALITY: Castle Peak, Nevada County, California.
- DISTRIBUTION: This subspecies thus far is known only from the vicinity of Donner Pass and Castle Peak, just north of Lake Tahoe. However, further field work in the Lake Tahoe region should turn up additional populations of this butterfly, and possibly show a fairly continuous distribution of populations from the Castle Peak area southward into Mono County where subspecies *ancilla* is found.
- ELEVATION RANGE: 7,000 to 9,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is typically found on open, somewhat wind-swept slopes and ridges within the Subalpine Forest plant community; on these open slopes, *Artemisia tripartita* Nutt. and *A. arbuscula* Nutt. are relatively common along with *Eriogonum umbellatum* Torr. subspecies.
- PHENOLOGY: This subspecies flies from late June to mid-July in a single brood.
- FOODPLANTS: *Eriogonum umbellatum* Torr. subspecies (G. Pratt, personal communication).

j. *E. e. giulianii* Pratt

- DIAGNOSIS: This is a subspecies of the northern Death Valley region which superficially resembles *E. battoides baueri*. It is characterized by a relatively thin black border dorsally on the males, increased blue basal scaling dorsally on the females, and an underside which superficially resembles that of *E. b. baueri*.
- ORIGINAL DESCRIPTION: Pratt, *Journal Research Lepidoptera*, : (19).
- TYPE LOCALITY: Wahguhye Peak, Grapevine Mountain, Esmeralda County, Nevada.
- DISTRIBUTION: This subspecies is found in the Last Chance Range in northern Inyo County and in the Grapevine Mountains of Inyo County, California, and Esmeralda County, Nevada.
- ELEVATION RANGE: 6,000 to 8,300' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is found in the upper portions of the Pinyon-Juniper Woodland plant community, typically on open slopes or open ridgetops.
- PHENOLOGY: This subspecies is strictly univoltine with the single brood flying from late May to early July, depending on elevation.
- FOODPLANTS: Larvae have been taken on *Eriogonum umbellatum* Torr. var. *versicolor* (J. F. Emmel, unpublished data).

171. *Euphilotes mojave* (Watson and W. P. Comstock)

- The Mojave Blue flies in the springtime over the Mojave and Colorado Deserts of southern California, with populations being occasionally encountered on the bordering western mountain slopes. The species is often ecologically sympatric with other spring-flying *Euphilotes* species (*enoptes* near *langstoni*, *battoides bernardino* and *b. martini*, *speciosa*, and *sonorensis*); the phenotypically different but genitally similar *E. enoptes dammersi* flies in the fall in areas where these 2 entities are sympatric.
- DIAGNOSIS: The male is pale lilac blue on the dorsal surface, while the female has extensive blue dorsally, similar to the female of *E. enoptes langstoni*. On the hindwings, this blue overscaling may cover most of the wing, while on the female forewing the blue scaling is restricted to the basal half. A prominent red-orange band occurs on both dorsal and ventral surfaces of the female and on the ventral surface of the male.
- ORIGINAL DESCRIPTION: F. E. Watson and W. P. Comstock, *Bulletin American Museum Natural History*, 42: 455 (1920).
- TYPE LOCALITY: Mojave Desert, California. Holotype in American Museum of Natural History. Collected on April 18, 1914, with an allotype, and a paratype collected on April 18, 1914; all three specimens supplied to W. P. Comstock through a dealer.
- DISTRIBUTION: This species is found from the northern edge of the Colorado Desert northward through the major portion of the Mojave Desert to Inyo County. From here it extends eastward into southern Nevada.

- PHENOLOGY:** This species is probably univoltine in most populations in most seasons, but laboratory rearings indicate that it has the capability of a second generation within a short period of time in that some pupae will eclose within 2 weeks of pupation. Records range from late March to early June, with a peak flight in late April in most localities.
- ADULT BEHAVIOR:** The adult flight period coincides with the spring blooming desert wildflowers and adult nectar-feeding, oviposition and larval feeding takes place on flowers of *Eriogonum pusillum* in most populations. Like the other *Euphilotes* species, *mojave* is a relatively weak flier and stays close to the foodplant and the ground surface.
- LIFE HISTORY:** These have been described in detail with a color plate in Comstock (1966). The echinoid egg is ivory-white in ground color and the top is deeply depressed with a minute micropyle in the center. The usual reticulation of raised walls covers the surface as in other *Euphilotes* eggs. The mature larva is not yellow-green like the earlier instars, but is yellow in ground color, heavily overlaid with bars, dashes, and spots of deep rose, arranged in regular patterns. The larvae have a conspicuous dark red mid-dorsal line. A heavy coating of minute white hairs occurs across the body surface. The larvae of *E. mojave* have far more prominent setae than the larvae of the *E. enoptes* complex (Pratt and Ballmer, 1987). The hairless pupa is brown, with a slight yellow tinge on the abdominal segments.
- FOODPLANTS:** *Eriogonum pusillum* Torrey & Gray is the larval host in most populations of *E. mojave*. Additionally, *E. reniforme* Torr. & Frem. (Polygonaceae) is used by at least several populations.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** *E. mojave* adults may closely resemble the adults of *E. enoptes langstoni*. They may be fairly readily distinguished by their associated hosts: *E. mojave* with *Eriogonum pusillum* Torrey & Gray or *E. reniforme* Torr. & Frem., and *E. enoptes langstoni* with *Eriogonum kennedyi* Porter in Wats. or *E. nudum* (Dougl. ex Benth.) S. Stokes. Other *Euphilotes* which may somewhat superficially resemble *E. mojave* are *E. enoptes giulianii* in the Last Chance Range or Grapevine Mountains, *E. battoides baueri*, and *E. battoides argocyanea*. The *E. battoides* may be readily distinguished from *mojave* by the genitalia. The male valves of *mojave* have the same outline as *enoptes*, but differ in that the characteristic saw-tooth outer edge is reduced to a single terminal spike followed by two small prongs (first noted by Watson & Comstock, 1920). While this character indicates a relationship to *rita* Barnes & McDunnough, the shape of the aedeagus or penis differs, having the narrow-lobed base of *enoptes* and not the broad-lobed base of *rita* (Watson & Comstock, 1920). *E. e. giulianii* may superficially resemble *E. mojave* in that its females often show extensive blue scaling dorsally, but it may be readily distinguished by its close association with *Eriogonum umbellatum* Torr. ssp. *versicolor*.
- GEOGRAPHIC AND SEASONAL VARIATION:** As the species is univoltine, there is no seasonal variation. *E. mojave* populations are remarkably similar in phenotype in various portions of its range and no significant geographic variation within the state has been noted. However, populations in extreme southern Nevada are apparently distinctive enough from the California *mojave* populations to be considered a separate subspecies (G. Austin, unpublished data).
- GENERAL REMARKS:** This species has been lumped by some authorities (Watson & Comstock, 1920; Miller & Brown, 1981) under *enoptes*. We treat it as a separate species for the

following reasons: (1) The larval setation pattern is readily distinguished from the larval setation pattern of *E. enoptes* populations; (2) Isoenzyme electrophoresis studies also suggest a distinction between *mojave* and the remainder of the *E. enoptes* complex (Pratt, 1987); (3) the genitalia differ as described above; (4) *E. mojave* is sympatric and synchronic with *E. enoptes* in several areas along the western edge of the Mojave Desert (e.g., vicinity of Pinyon Mountain, Kern County) with each using a different host and showing other subtle ecological differences within their respective populations (Pratt, unpublished data).

172. *Euphilotes pallescens*

- ADULT BEHAVIOR:** Like other *Euphilotes* species, the adults of *E. pallescens* tend to stay fairly close to their foodplants. Nectaring, mating, perching, and oviposition all largely take place on the stems or flowers of the foodplant. Adults of *E. p. confusa* will also perch on the stems of small shrubs within the vicinity of the foodplant. At night, the adults roost on stems of either the foodplant or on those of small shrubs, with the head oriented downward.
- LIFE HISTORY:** The early stages of the subspecies *elvirae* were described in detail by Comstock and Henne (1967). The echinoid egg is pale green and has a deeply depressed top as well as sloping sides. The usual network of raised white walls is present. The eggs are deposited singly, each being placed deeply in the flower of the buckwheat. The mature larva is ivory-white in ground color, with a slight tinge of green. There is a discontinuous mid-dorsal line of pinkish-brown dashes, and a diagonal dorso-lateral line of brownish-pink on the side of each segment. The body surface is covered with minute white stubby knobs or setae. Pupation occurs among small flat pebbles and dry twigs near the base of the foodplant. The pupa (6 mm. in length) is at first a delicate green and later changes to a uniform orange-yellow. No body hairs were noted on the pupal surface.
- CHROMOSOME NUMBER:** T. C. Emmel and O. Shields (unpublished data) have found that the chromosome number for *E. p. pallescens* is N=34, while that for *E. rita emmeli* has a chromosome number of N=33. Further investigation of chromosome numbers and the *Euphilotes rita-pallescens* complex are clearly indicated.
- SIMILAR SPECIES:** Within California, *E. pallescens* may be sympatric with either *E. battoides* (such as at Butterbrecht Peak, Kern County) or with *E. enoptes* (on the desert slope of the Kern County mountains). In these localities, *pallescens* is distinguished by the very whitish ground color on the underside with quadrate black spots on the underside of the forewing. In the sympatric individuals of *E. enoptes* on the desert slope of the Kern County mountains, the underside ground color tends to be a light brownish-grey and the dark spots on the underside of the forewing tend to be more oval-shaped or irregularly shaped rather than quadrate. The spring-flying *E. battoides* which may be taken in the same localities as the spring-flying *E. pallescens* on the desert slope of the Kern County mountains tends to also have a more greyish ground color on the underside, with some dark scale suffusion on the underside of the forewing in contrast to the much more crisply outlined quadrate spots on the underside of the forewing of *E. pallescens*. Examination of the genitalia is also extremely helpful in determining which species are represented in a given sample of specimens.
- GEOGRAPHIC AND SEASONAL VARIATION:** In localities where there is a long flight period or where both spring and late-summer specimens have been taken, there is no significant difference in the phenotypes represented. The apparent blendzone or cline between the subspecies *elvirae* and *pallescens* along the east slope

of the Sierra Nevada has been described under those 2 subspecies. The population of *E. p. confusa* in the Cottonwood Mountains seems to highly isolated from other *pallascens* populations and no intermediate population between this subspecies and any other *pallascens* subspecies are presently known.

GENERAL REMARKS: The larvae of the three subspecies of this species all seem to be strongly attended by ants. A stronger attractiveness of *E. pallascens* larvae to ants might be a decided selective advantage in this species whose larvae feed on *Eriogonum* species which have relatively small flower clusters and thus less protective cover for the larvae on these plants. Presumably, the ants offer the larvae partial protection against potential predators or parasitoids. It should be noted that some extensive stands of *Eriogonum kearneyi* Tidest. in southern Mono County appear to have no associated *E. pallascens* populations with them; it would be of interest to investigate these areas to see if they lack appropriate ant species, thus preventing the butterfly from successfully establishing itself in these localities.

The taxonomic status of this species in California has changed several times. Through 1975 (Langston, in Howe, 1975), two of the subspecies treated here, namely typical *pallascens* and *elvira*, were considered subspecies of *Euphilotes pallascens*. Subsequently, studies by Oakley Shields and others seem to indicate that *pallascens* and *elvira*, plus another set of populations, were best considered subspecies of *Euphilotes rita* (Barnes and Benjamin). Elsewhere, the typical subspecies *E. r. rita* occurs in Arizona and southwestern New Mexico, and *E. r. coloradensis* Mattoni occurs in eastern Colorado, in gently rolling prairie grassland. As such, the latter subspecies occurs farther east than any other known *Euphilotes* in North America and it flies in late summer. Now, Pratt (1988) has shown that *pallascens* and *rita* are separate species, with our forms best placed again as subspecies of *pallascens*.

a. *E. pallascens pallascens* (Tilden and Downey)

DIAGNOSIS: Described from northwestern Utah in the general vicinity of the Little Granite Mountains, Dugway Proving Grounds, Tooele County, the male of *pallascens* is distinguished by its light blue dorsal coloration, with three to six submarginal spots on the dorsal hindwings. The female of *pallascens* is distinguished by the grey scales near the body on the dorsal forewing surface. Ventrally, both sexes have a very pale ground color and the dark macules are reduced as is the aurora, rendering a very pale appearance.

ORIGINAL DESCRIPTION: Tilden and Downey, *Bulletin Southern California Academy Sciences*, 54: 25 (1955).

TYPE LOCALITY: Little Granite Mountains, Dugway Proving Grounds, Tooele County, Utah. Holotype in California Academy of Sciences.

DISTRIBUTION: This subspecies is found from western Utah across central Nevada to the sagebrush country of the east slope of the Sierra Nevada in Mono County. The California populations referred to this subspecies show some individuals with characters similar to the southern California subspecies *elvira*, and probably represent the beginning of a blendzone with that subspecies.

ELEVATION RANGE: 4,000 to 7,000' elevation with most of the California populations between 6,000 and 7,000'.

- HABITAT AND PLANT COMMUNITIES:** In the Mono Basin, the butterfly occurs within the Sagebrush Scrub plant community in areas where pumice sand favors the abundant growth of one of its foodplants, *Eriogonum kearneyi* Tidestr. On the east slope of the Sierra Nevada, the butterfly is found within a mixture of Sagebrush Scrub and the lower edge of Jeffrey Pine forest on open slopes where the foodplant *Eriogonum microthecum* Nutt. grows. The Mono Basin populations are more similar in their ecological association to topotypical *pallesces* in western Utah, than are the populations associated with *Eriogonum microthecum* Nutt. on the east slope of the Sierra Nevada.
- PHENOLOGY:** Probably largely univoltine, with a possible small second brood in the populations associated with *Eriogonum kearneyi* Tidestr. This *Eriogonum* has a fairly long blooming period in July and August and in at least one Nevada locality, *pallesces* larvae collected on the flowers of this *Eriogonum* produced pupae which emerged within 2 weeks of pupation. The presence of a small second brood may be related to conditions of above normal winter precipitation or possibly also to summer rainfall as well. The populations associated with *Eriogonum microthecum* Nutt. are probably strictly univoltine in view of the shorter blooming period of this particular plant.
- FOODPLANTS:** For the Mono Basin populations, *Eriogonum kearneyi* Tidestr. var. *kearneyi*; for the east slope Sierra Nevada populations, *Eriogonum microthecum* Nutt. var. *ambiguum* (M. E. Jones) Reveal in Munz. At the east base of the Sierra Nevada in Ormsby County, Nevada, *Eriogonum baileyi* S. Wats. var. *divaricatum* (Gandg.) Reveal is used by *E. r. pallescens* populations there.

b. *E. p. elvira* (Mattoni)

- DIAGNOSIS:** This is a subspecies of the western edge of the Mojave Desert and western edge of the Owens Valley which flies in late summer and early fall. *E. p. elvira* most closely resembles *E. p. pallescens*, but it is characterized by the distinctive shape of the hindwing, showing a maximum expanse at vein M₁ instead of M₂ and a rather straight outer margin. Additionally, there is a rather wide ventral marginal band and the underside spots are strongly subquadrate. In various portions of its range, *elvira* is geographically sympatric with four other earlier flying *Euphilotes* species (Langston, 1969a).
- ORIGINAL DESCRIPTION:** Mattoni, *Journal of Research Lepidoptera*, 4: 94-99 [1966].
- TYPE LOCALITY:** 3.5 miles west of Pearblossom, Los Angeles County, California. Holotype in Los Angeles County Museum. The type locality is a desert wash at 3,400' elevation, about 3.5 miles southwest of Pearblossom.
- DISTRIBUTION:** This subspecies is found along the western edge of the Mojave Desert from the north slope of the Little San Bernardino Mountains in Joshua Tree National Monument and Morongo Valley just west of the Monument westward along the north base of the San Bernardino and San Gabriel Mountains, and thence northward along the east slope of the mountains of Kern County and the east slope of the Sierra Nevada to approximately the Inyo-Mono County line. As noted under subspecies *pallesces*, the east slope Sierra Nevada populations represent somewhat of a broad blendzone between these two subspecies (*elvira* and *pallesces*).
- ELEVATION RANGE:** 3,000 to 6,500' elevation.

HABITAT AND PLANT COMMUNITIES: The populations associated with *Eriogonum plumatella* are typically found in broad open dry desert washes within the Joshua Tree Woodland plant community. Along the east slope of the Sierra Nevada, the populations associated with *Eriogonum microthecum* Nutt. occur within the Sagebrush Scrub plant community.

PHENOLOGY: Records for this subspecies range from mid-May to late September. It is probably univoltine in most localities in most years, but laboratory rearing studies by G. Pratt indicate that a second brood is possible within the flowering period of the foodplant, at least in the case of *Eriogonum plumatella* Dur. & Hilg. Most of the *E. plumatella*-associated populations fly from late July to mid-September, with a peak flight in late August and early September. Those populations on the east slope of the Sierra Nevada associated with *Eriogonum microthecum* Nutt. fly from late July to late August or early September, depending on seasonal precipitation and temperature patterns. Specimens have been taken in mid-May at Butterbrecht Peak in Kern County, apparently associated with the annual *Eriogonum davidsonii* Greene. There is also a late August-early September flight in this same region associated with *Eriogonum wrightii* Torr. ex Benth. and *E. plumatella* Dur. & Hilg.; whether these 2 different flights represent different broods of the same population or sympatric but allochronic univoltine populations remains to be determined.

FOODPLANTS: *Eriogonum plumatella* Dur. & Hilg. (Polygonaceae) is the foodplant for the populations along the southwestern edge of the Mojave Desert. Along the east side of the Sierra Nevada, the foodplant is *Eriogonum microthecum* Nutt. var. *ambiguum* (M. E. Jones) Reveal in Munz. On the desert slope of the Kern County mountains, in addition to *E. plumatella* Dur. & Hilg., *Eriogonum wrightii* Torr. ex Benth. and *E. davidsonii* (Greene) Jeps. are both suspected (J. F. Emmel and G. Pratt, unpublished data).

c. *E. p. confusa* Pratt

DIAGNOSIS: A subspecies of the western Death Valley region, in which the males are characterized by a terminal band of moderate width on the upperside, while the females are uniformly dark brown in ground color with a small orange aurora on the submarginal area of the hindwing dorsally. On the underside, the ground color is whitish with reduced size of spots on the hindwing but somewhat enlarged or suffused spots on the underside of the forewing, often with considerable dark suffusion in the posterior half of the forewing, rendering an appearance somewhat similar to that of *E. enoptes dammersi* in this particular character.

ORIGINAL DESCRIPTION: Pratt, *Journal Research Lepidoptera*, : (19).

TYPE LOCALITY: Rest Spring, Cottonwood Mountains, Inyo County, California.

DISTRIBUTION: This subspecies is known only from the vicinity of the type locality in the Cottonwood Mountains of the western Death Valley region.

ELEVATION RANGE: 6,000 to 7,000' elevation.

HABITAT AND PLANT COMMUNITIES: This butterfly is found within a rather depauperate phase of the Shadscale Scrub plant community of the Death Valley region. Within the area of type locality, the butterfly is found on rolling hills, slopes, and in small ravines within an area of rather poor soil supporting sparse plant cover.

- PHENOLOGY:** This subspecies is probably largely univoltine, with adults flying from late June to early August, depending on seasonal temperature and precipitation patterns. The foodplant goes through a long enough blooming period to allow a second brood from early-emerging adults. Laboratory rearing studies should help to determine whether a second brood is possible as it is in *E. p. pallescens* populations.
- FOODPLANTS:** Larvae have been collected on the flowers of *Eriogonum deflexum* Torr. (G. Pratt and J. F. Emmel, unpublished data) and this apparently represents the sole foodplant within the type locality. *Eriogonum heermannii* Dur. & Hilg. is also present in the area where the adults fly, and blooms in mid-summer, but is apparently not used by this species. Numerous individuals of *E. heermannii* Dur. & Hilg. were beaten for larvae by G. Pratt and J. Emmel, but failed to produce any *E. pallescens* larvae, whereas plants of *E. deflexum* readily yielded larvae. The use of *E. deflexum* by this subspecies of *E. pallescens* is particularly interesting in that it is an annual *Eriogonum* and only one other set of *E. pallescens* populations is known which exclusively uses an annual *Eriogonum* as foodplant: namely, those along the eastern base of the Carson Range, Nevada, on *E. baileyi*.

173. *Agriades podarce* (C. & R. Felder)

- ADULT BEHAVIOR:** Adults of both sexes usually remain in close association with their *Dodecatheon* foodplants within the wet meadows. Males patrol the wet meadows and perch on low shrubs or grasses within the habitat, while females tend to be more sedentary and spend more time landing on and crawling over the foodplant in ovipositional behavior.

- LIFE HISTORY:** The eggs are deposited on the leaves of the foodplant. The young larvae bore into the succulent *Dodecatheon* leaves and can be seen through transparent "windows" within the foodplant leaves, much like the larvae of *Philotes sonorensis*. This species overwinters as a half-grown larva, but the site of diapause in nature is unknown. The mature larva is

[TCE to describe)

The pupa is

- CHROMOSOME NUMBER:** Counted from Colorado material as $n=$ (Emmel, Eliazar, and Harris, 19).
- SIMILAR SPECIES:** In flight, this butterfly may be confused with *Icaricia saepiolus*, which is a frequent wet meadow associate of *A. glandon*. *I. saepiolus* tends to have a more vigorous flight and can readily be distinguished from *A. glandon* in color pattern once captured.
- GEOGRAPHIC AND SEASONAL VARIATION:** No blendzone between the Klamath Mountains segregate and subspecies *podarce* of the northern Sierra Nevada is presently known. Similarly, typical *podarce* does not seem to blend with the higher elevation populations of the central and southern Sierra Nevada

segregate. Further study of geographic variation of this species complex is clearly indicated.

GENERAL REMARKS:

The taxonomy of the North American *Agriades* has yet to be satisfactorily addressed. Our material has variously been referred to as subspecies of *A. glandon*, *A. aquilo*, and *A. franklini*. European *A. glandon* feeds on the genera *Androsace* and *Soldanella* (Primulaceae); *A. aquilo* in Norway, feeds on *Astragalus alpinus* (F. M. Brown, personal communication); and *A. franklini* in the American Arctic and Greenland feeds on *Saxifraga oppositifolia* (F. M. Brown, personal communication). The subspecies *podarce*, *bryanti* (Alaska), the central and southern Sierra Nevada segregate, and the Klamath Mountains segregate all feed on *Dodecatheon* (Primulaceae). The Rocky Mountain *Agriades* feed on *Androsace septentrionalis* (J. F. Emmel et al, 1971). This suggests that the Pacific Coast populations from Alaska to California and the Rocky Mountain populations are most closely related to the European *A. glandon*, at least in foodplant usage, while the Arctic American *A. franklini* and the Scandinavian *A. aquilo* constitute two other species complexes which are very closely related. Foodplant acceptance experiments by Gordon Pratt (unpublished data) indicate that larvae from the Colorado populations of *Agriades* accept *Dodecatheon* rather reluctantly, suggesting still a further specific separation between the Rocky Mountain and the Pacific Coast Mountain entities. Additionally, there are morphologic differences in the first instar larvae of these two sets of populations (Pratt and Ballmer, unpublished data). A study of the North American *Agriades*, including microecological requirements, studies of immature stages, foodplant choice, hybridization studies, and isoenzyme electrophoresis, is particularly needed in order to clarify relationships.

The species in this genus, *Agriades*, are often grouped with species of the following three genera, *Lycaeides*, *Icaricia*, and *Plebulina*, in the single genus *Plebejus* (Langson, in Howe, 1975; Scott, 1986). We use the subgeneric names in parentheses here to help show additional groupings of the taxa involved. Detailed studies of the larvae of these butterflies by Ballmer and Pratt (1988) support the division into four subgenera.

This distinctive species, *Agriades glandon*, occurs across the Arctic areas of the world (e.g., Nekrutenko, 1975) from Scandinavia east to Siberia and into the North American Arctic, south into California on the west coast and central New Mexico in the Rocky Mountain area. We have three subspecies in California.

a. *A. p. podarce* (C. and R. Felder)

DIAGNOSIS: The males on the dorsal surface have a pale iridescent blue ground color with fairly broad but indistinct dark brown terminal bands on the forewings with varying development of round dark brown spots in the submarginal area of the hindwing. Superimposed on this are patches of white scaling in the submarginal areas which are indistinctly developed on the forewings and more extensively developed to varying degrees in the submarginal area of the hindwing. Females are largely dull brown dorsally, with indistinct darker terminal band markings on both wings. Ventrally, the whitish scaling is markedly developed, covering most of the distal half of both forewing and hindwing. In the proximal half of both wings ventrally, there is pale brown ground color upon which are superimposed several patches or spots of white scaling. Superimposed on the entire underwing pattern is a pattern of small to indistinct black spots, generally haloed by white scaling.

ORIGINAL DESCRIPTION: C. and R. Felder, Reise....Novara, *Lepid. Rhop.*, 2: 282 [1865].

- TYPE LOCALITY: "California". Restricted by Emmel, Emmel, and Mattoon, Journal Research Lepidoptera, : (1988) to Donner Pass, Placer County, California. Lectotype in British Museum.
- DISTRIBUTION: This subspecies is found in the mid- to higher elevations of the Sierra Nevada from the vicinity of Carson Pass northward to the Gold Lake region in Sierra County.
- ELEVATION RANGE: 6,200 to 9,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is typically found in boggy meadows within the Montane Coniferous Forest or Subalpine Forest plant communities.
- PHENOLOGY: Strictly univoltine with most populations flying during the month of July, but with records ranging from mid-June to early August, depending on elevation and seasonal temperature and precipitation patterns.
- FOODPLANTS: In California, Alpine *Dodecatheon* species are used, including *D. jeffreyi* Van Houtte and *D. alpinum* (Gray) Greene (J. F. Emmel, G. Ballmer, and G. Pratt, unpublished data) (Primulaceae). The record for *Vaccinium nivictum* Camp. (Downey in Howe, 1975), is probably in error.

b. *A. p. ssp.* (high elevation Sierra Nevada populations)

- DIAGNOSIS: These are populations of the southern and central Sierra Nevada which are more boldly marked ventrally than typical *podarce*. The whitish scaling which is extensive on the ventral surface of *podarce* is reduced in these populations, and the dark spots are much larger. Even within this set of populations, there is considerable variation, with the populations at the highest elevation having specimens that show the most boldly marked pattern.
- DISTRIBUTION: Higher elevations of the Sierra Nevada, from Sonora Pass southward to southern Tulare County. An isolated population is present at Sawmill Meadow on Glass Mountain in Mono County, east of the Sierra Nevada.
- ELEVATION RANGE: 9,000 - 11,000' elevation.
- HABITAT AND PLANT COMMUNITIES: Wet meadows to vernal moist gravelly slopes within the Subalpine Forest or Arctic-Alpine Cushion Plant communities.
- PHENOLOGY: Records range from late June to late August, depending on elevation and snowpack.
- FOODPLANTS: Both *Dodecatheon alpinum* and *D. jeffreyi* are suspected for these populations (J. F. Emmel, unpublished data).

c. *A. p. ssp.* (Klamath Mountains)

- DIAGNOSIS: This distinctive segregate of the Klamath Mountains region and southern Cascades is characterized by larger size than typical *podarce*, somewhat darker ground color of blue on the upperside in males and a darker brown ground color on the upperside of females, while ventrally it is characterized by much bolder black spotting and greater contrast between the brown and white patches of scales ventrally.

- DISTRIBUTION: This subspecies is found in scattered localities within the Klamath Mountains region, the Mt. Shasta and northern Mt. Lassen region, northward into the Cascades of extreme southern Oregon.
- ELEVATION RANGE: From 5,000 to 8,000' elevation.
- HABITAT AND PLANT COMMUNITIES: As with subspecies *podarce*, this segregate is usually found in open boggy meadows within the Montane Coniferous Forest plant community.
- PHENOLOGY: Records range from mid-June to early September, with the flight period dependent on snowpack, and seasonal temperature and precipitation patterns, and elevation.
- FOODPLANTS: *Dodecatheon jeffreyi* (Shapiro, 1981).

174. *Lycaeides idas* Linnaeus

This blue species shows extraordinary geographic variation in North America, with 12 named subspecies recognized by Miller and Brown (1981). With the recently described *L. i. azureus* Emmel, Emmel and Mattoon (1998j), we have 4 subspecies found within California.

- SPECIES SYNOPSIS: Our two species of blues in the genus *Lycaeides* include *idas* and *melissa*. Well-studied by the novelist and lepidopterist Vladimir Nabokov (1943, 1944, 1949; see also Masters, 1972), *L. idas* was formerly known as *L. argyrognomon* Bergstrasser in many publications, and was considered a holarctic species. The confusing taxonomic changes in this species name have been summarized by Scott (1986): "Since V. Nabokov studied the taxonomy of [*L.*] *idas* (which he called *argyrognomon*), *P. melissa*, and their relatives using a detailed examination of wing pattern and male abdominal structures, name changes in Europe arising from the study of type specimens mean that Nabokov's "*argyrognomon*" is *idas*, and his "*ismenias*" is *argyrognomon*, which occurs only in Eurasia." As a result of these changes, *argyrognomon* does not occur in North America, although as noted, it has been used widely as the species name for *idas* populations in major reference works (e.g., Howe, 1975).

Within California, then, we have four subspecies of *idas*. However, because of the great interpopulation diversity, these named races do not necessarily adequately describe the extent of variation in this extraordinarily variable species.

- ADULT BEHAVIOR: The adults tend to stay fairly close to areas where the foodplant grows, generally flying over boggy meadows or on the open slopes where the more xeric habitat associated populations occur. Females tend to be somewhat more sedentary than males, often alighting on the foodplant and walking over it for considerable periods of time.

- LIFE HISTORY: [T.C. Emmel, please fill in.]

The species overwinters as an egg (G. Pratt, G. Ballmer, and J. F. Emmel, unpublished data).

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: This butterfly can be extremely similar to *Lycaeides melissa* with which it is occasionally sympatric in the more eastern parts of its range within California. Generally, *L. idas* tends to be found in more mesic habitats west of the Sierran Cascade crest, while *L. melissa* is generally found east of that mountain axis and in more xeric or lowland habitats, although several high-elevation ecotypes are known. In general, *L. melissa* tends to have a more boldly patterned underside with greater development of the orange scaling in the submarginal areas. The females of *melissa* frequently have at least some blue scaling in the basal area of both forewing and hindwing dorsally; the exception to this, of course, is the subspecies *L. idas azureus* which has extensive blue scaling in females, although this blue scaling is of a much paler shade than that seen in *melissa* females. Additionally, the male genitalia of the two species differ in respect to the relative length of the falcial arms as shown in Figure --.

GEOGRAPHIC AND SEASONAL VARIATION: As the species is univoltine, there is no seasonal variation. With respect to geographic variation, there is a broad blendzone in northern California in the Klamath Mountains and Mt. Shasta region eastward to the Warner Mountains between the Cascadian subspecies *ricei* and the Sierra Nevada *anna*. Within this region, populations may be found which seem to be pure *ricei*, pure *anna*, or varying combinations of the two phenotypes, as well as intermediate phenotypes within a given population. Reference to Map 174 will give some indication of the extent of this blendzone.

GENERAL REMARKS: The North Coastal subspecies, *L. i. lotis*, has been placed on the Endangered Species List by the U. S. Government and the State of California. Its current status is undetermined, and it may prove to be extinct at the time of this writing. Efforts are still being made to preserve the habitat of this subspecies and hopefully ensure its continued existence.

a. *L. i. anna* (W. H. Edwards)

DIAGNOSIS: This is the subspecies of the west slope of the Sierra Nevada. It has noticeably reduced maculation on the ventral side of the hindwings, but not to the degree seen in subspecies *ricei*. The ground color on the ventral surface is powdery white with a tendency towards a yellowish cast in the female. Females lack blue scaling on the dorsal surface. The orange areas on the female dorsal surface vary considerably and may be reduced to a narrow line arched in each cell to a bar-like shape that is heavily suffused with brown scaling. While these orange areas are distinct on the hindwing, they may be blurred or faintly marked on the forewing.

ORIGINAL DESCRIPTION: W. H. Edwards, *Proceedings Academy Natural Sciences*, Philadelphia, 13: 163 (1861).

TYPE LOCALITY: "California", restricted to vicinity of Truckee, Nevada County, California by F. M. Brown, *Transactions American Ent. Soc.*, 96: 366-367 (1970). Neotype in Carnegie Museum, designated by Nabokov, *Bulletin Museum Comparative Zoology*, 101: 486 (1949).

- DISTRIBUTION:** On the west slope of the Sierra Nevada at mid-elevations, from Tulare County northward to approximately the Mt. Lassen region. From here it blends northward with the subspecies *ricei* in the Warner Mountains of the northeastern part of the state and in the southern Mt. Shasta region.
- ELEVATION RANGE:** From 4,500' to 8,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** Found in open and boggy meadows to vernal moist meadowy slopes within the Montane Coniferous forest plant community.
- PHENOLOGY:** Univoltine, with records ranging from late June to early September, with the majority of records during the latter half of July.
- FOODPLANTS:** Oviposition has been observed on *Lupinus andersonii* at Donner Pass, California (J. F. Emmel, and O. Shields, unpublished data). Additionally, Sierran populations are frequently associated with *Lotus oblongifolius*, and undoubtedly use this as a foodplant. Probably other Fabaceous plants are used in the Sierra Nevada populations, but remain to be recorded.

b. *L. i. ricei* (Cross)

- DIAGNOSIS:** This subspecies of the Cascade Range is characterized by a marked reduction in the underside markings resulting in some specimens which are almost immaculate beneath. Usually only the post-median band of dark spots ventrally is consistently present. On the upperside, males are a lilac blue with a very narrow black marginal line and females tend to be brown dorsally, with marked reduction of the orange aurora on the hindwing, often leaving only small orange crescents around the black submarginal spots.
- ORIGINAL DESCRIPTION:** Cross, *Pan-Pacific Entomologist*, 13: 88 (1937).
- TYPE LOCALITY:** Big Cultus Lake, Deschutes County, Oregon. Holotype in Denver Museum of Natural History.
- DISTRIBUTION:** In the Cascade Range, from northern California in the Mt. Shasta region and Klamath Mountains region northward to British Columbia.
- ELEVATION RANGE:** From 2,500' to 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** Within California, there seem to be 2 subsets of populations as far as their particular ecological requirements. One group of populations is found in boggy meadows and is associated with *Lotus oblongifolius*; a second group of Subalpine populations are found on somewhat dryish gravelly, rocky slopes and are associated with either *Astragalus whitneyi* (Shapiro *et al.*, 1981) or a prostrate *Lupinus* species (J. F. Emmel and S. O. Mattoon, unpublished data). The boggy meadow populations are found within the Montane Coniferous forest plant community while the more xeric site populations occur within open areas in the Montane Coniferous Forest or Subalpine Forest plant communities.
- PHENOLOGY:** Univoltine, with records ranging from mid-June to late September, depending on snowpack, seasonal temperature and precipitation patterns and slope exposure.
- FOODPLANTS:** For the California populations of this subspecies, most appear to use *Lotus oblongifolius* (Shapiro *et al.*, 1981; J. F. Emmel, unpublished data). Additionally,

populations are associated with *Astragalus whitneyi* (Shapiro *et al.*, 1981), and a prostrate *Lupinus* species in the Siskiyou Mountains (J. F. Emmel and S. O. Mattoon, unpublished data). In southern Oregon, the butterfly is known to utilize *Lathyrus torreyi* and *Vicia exigua* (Shields *et al.*, 1970).

c. *L. i. lotis* (Lintner)

- DIAGNOSIS:** This subspecies is confined to the immediate coast in northern California and is similar to subspecies *anna*, but tends to have a slightly darker ground color ventrally, as well as enhancement of the dark markings on the underside. The orange scaling in the submarginal area of the ventral hindwing is generally minimally developed, as in *anna*.
- ORIGINAL DESCRIPTION:** Lintner, *30th Report New York State Museum Natural History*, [1876]: 169 (1878).
- TYPE LOCALITY:** Mendocino County, California. Holotype in New York State Museum.
- DISTRIBUTION:** This subspecies is one of the most restricted in distribution in the state, being known only from a single habitat, a sphagnum bog under a Pacific Gas & Electric Company powerline near the town of Mendocino in Mendocino County. There are old records for the subspecies at Point Arena in Mendocino County, but it has not been taken there in recent years. Even the status of the last known population within the town of Mendocino itself is not currently known. Only 2 adults were observed in 28 days of field searching during April-July of 1977, 1978, and 1979 by Arnold (1983). Those adults were found near the bog in association with *Lotus formosissimus* Greene (Fabaceae). These low population levels might have been due to the bog desiccating in the drought of 1976 and 1977, because in 1980 and 1981, Arnold observed 14 adults at the type locality.
- ELEVATION RANGE:** From sea level to approximately 100' elevation.
- HABITAT AND PLANT COMMUNITIES:** The Mendocino locality is a sphagnum bog surrounded by a closed-cone pine forest which is dominated by *Pinus muricata* (R. Arnold, 1983). Typical bog plants found here include sphagnum moss, *Drosera* sundews, and *Coreus* (dogwoods).
- PHENOLOGY:** Dates of capture or observation range from late May to late June, with an apparent peak flight in mid-June.
- FOODPLANTS:** Although no actual oviposition has been observed, the probable foodplant is *Lotus formosissimus* Greene (Fabaceae). This supposition is based on an observation by J. F. Emmel (unpublished) in 1970 in which a female *lotis* was observed to land repeatedly on a patch of this *Lotus* species and probe several times with her abdomen into the foliage of the plant. Another legume present in the Mendocino bogs where *lotis* flies is *Lathyrus vestitus bolanderi* (Wars.) C. L. Hitchc., and this species could also conceivably serve as a host.

d. *L. i. azureus* Emmel, Emmel, and Mattoon

- DIAGNOSIS:** This is a subspecies occurring in the North Coast Ranges in Trinity County, immediately characterized by females which have a considerable development of blue scaling on the upperside, often involving the entire proximal three-quarters of the forewing and most of the hindwing. Additionally, on the underside the black markings in the proximal two-thirds of the wings are prominently

developed, in contrast to the other subspecies of *L. idas* in California which tend to have diminution of these markings. In *ricei*, the ventral surface is almost devoid of black markings and the submarginal series of metallic spots is virtually absent. In subspecies *anna* of the west slope of the Sierra Nevada, the ventral markings are developed to a greater extent than that seen in *ricei*, but they are still relatively lightly marked in contrast to *azureus*. The coastal subspecies *lotis* is somewhat similar in ventral markings to *azureus*, but has uniformly brown females in all the known population collections.

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 175-176 (1998j).

TYPE LOCALITY: White Rock, Forest Service Guard Station, 10 miles south of Wildwood, Trinity County, California. Holotype in natural History Museum of Los Angeles County.

DISTRIBUTION: Thus far, this subspecies is known from the type locality near the crest of the extreme southern Trinity Mountains. White Rock Guard Station is located on the south-facing slopes of the drainage divide that gives rise to the headwaters of the East fork of the South Fork Trinity River which drains northwest to the coast, and Cottonwood Creek which draws northeast to the Sacramento Valley. White Rock faces south across the canyon at North Yolla Bolly Mountain in the Coast Range mountains. The distribution is so far poorly known, but appears to be associated with South Fork Mountain, a major northeast-running ridgeline that bounds the South Fork Trinity River on the west and extends eastward almost to Highway 299 at Berry Summit. Other known *azureus* populations are several miles north of the type locality at Regan Meadows in Shasta County, and several colonies at the north end of South Fork Mountain in eastern Humboldt County from Horse Mountain Ski Area and Grouse Mountain, and a location in between these points. The phenotype may be more widespread, as unconfirmed reports indicate captures to the northeast in the Whiskeytown Lake area. Further east into the Cascade Range, at Latour State Forest east of Redding, an *anna* colony produces a very low incidence of blue females.

ELEVATION RANGE: All known populations range from 4,300' to 5,500'.

HABITAT AND PLANT COMMUNITIES: *Azureus* breeding areas presently known are all located within the lower limits of Red and White Fir Forests, with many elements of Mixed Evergreen or Yellow Pine Forest intruding. Indicators of the wet meadow habitat are the larval host (by observed oviposition) *Lotus oblongifolius* (Benth.) Green var. *nevadensis* (Gray), and indicator plants such as *Helenium bigelovii* Gray, and *Heracleum (Lanatum) maximum* Bartr. Lupine species are also abundant in the drier areas, while in the boggy spots, *Equisetum arvense* L., *Carex amplifolia* Boott, and *Habenaria dilatata* (Pursh) Hook are common.

PHENOLOGY: The type series was taken on July 4, 1979 and consists of worn to fresh individuals, suggesting a flight period from mid-June to late July.

FOODPLANTS: The butterfly is associated with *Lotus oblongifolius* (Benth.) Greene, and this represents the probable foodplant.

175. *Lycaeides melissa* (W. H. Edwards)

SPECIES SYNOPSIS:

- ADULT BEHAVIOR:** Comstock (1929) was the first to note that "the female of the species spends a lot of time in a pretense of laying -- walking up and down the plant, and even on the ground at its base, before ovipositing. Though she seems very particular about choosing a site, the eggs may finally be laid on any portion of the plant, or even on dead leaves, sticks, or pebbles in proximity to it." Adults may be frequently found sipping flower nectar and visiting mudflats. Males patrol most of the day around the host plant seeking females.
- LIFE HISTORY:** The eggs are pale green with white ridges, turning white with maturation. The larvae feed on both leaves and flowers of the host. The mature larva is green or whitish-green in ground color and covered with white hairs, with a cream lateral stripe. Honey glands and tentacles are present and the larvae are heavily tended by ants. The pupa is yellow-green in ground color with the wing covers sometimes straw in color and the abdomen sometimes whitish. This species apparently hibernates in the egg stage.
- CHROMOSOME NUMBER:** $n = 24$ in Colorado material of this species (Emmel and Eliazar, 1989).
- SIMILAR SPECIES:** See discussion under *L. idas*.
- GEOGRAPHIC AND SEASONAL VARIATION:** In the multivoltine populations, no significant seasonal variation has been noted. Geographically, there appears to be a north-south cline within the state in regards to the amount of blue scaling dorsally on females. In the southern California mountains, a much higher percentage of females have blue scaling dorsally, and this percentage seems to steadily decrease as one goes north in the state. Unfortunately, large samples of females from any given locality are not presently available, so we can only allude to this apparent phenomenon at present.
- GENERAL REMARKS:** This species is apparently much more vagile and colonizing than is *L. idas*. This probably accounts for the much wider distribution of this species and its occurrence in disturbed habitats, as well as natural ones. Further study of the alpine populations of this butterfly is indicated to determine their relationship to the lower elevation populations: are these a biologically different entity, or are they simply the results of colonization from lower elevation populations?
- SUBSPECIES:** There are two subspecies of the Orange Margined Blue in our state. This attractive lycaenid has a wider range of distribution than *L. idas*, not only occurring over much of the southern part of the latter's territory but extending through much of the southwestern United States and northern Mexico.

a. *L. m. paradoxa* (F. H. Chermock)

- DIAGNOSIS:** This low to mid-elevation subspecies is characterized by a whitish ground color beneath, and a prominent development of orange scaling in the submarginal areas ventrally. The females range from individuals with nearly all brown ground color dorsally to some which have very extensive development of blue scaling in the proximal half to two-thirds of both forewing and hindwing. Even within a single population there can be considerable variation in the amount of blue scaling present on the females. The southern California populations tend to have a greater percentage of "blue" females in any given population, with the highest percentage of these occurring in the mountains of San Diego County. Although we are lumping all low to mid-elevation populations of *L. melissa* in the state under this subspecies, there may be more than one segregate involved here.

- ORIGINAL DESCRIPTION: F. H. Chermock, *Canadian Entomologist*, 76: 214 [1945].
- TYPE LOCALITY: Tehachapi Mountains, California. Location of type not known but believed to be Canadian National Collection.
- DISTRIBUTION: This is the butterfly that was previously known in various popular books as subspecies *inyoensis* Gunder or *inyoensis* Nabokov. Gunder used the name as a transition form, which had no nomenclatural validity. Nabokov elevated this name to a subspecific name to cover the southern California *melissa*, in 1949, but this was four years after Chermock had named the southern California populations with the subspecific name *paradoxa*. Thus, the correct name to apply is *paradoxa* Chermock. It ranges from the mountains of San Diego County northward in the Inner Coast Range to Monterey County, and along the east slope of the Sierra Nevada to Siskiyou and Modoc counties.
- HABITAT AND PLANT COMMUNITIES: This subspecies is typically found in open wet to dry meadows, commonly along streams or in mountain valleys, or on flats in large valley basins such as in the Owens Valley or Salinas Valley. The usual surrounding plant communities include Montane Coniferous Forest for most of the southern California populations, Joshua Tree Woodland along the east flank of the extreme southern Sierra Nevada, Pinyon-Juniper Woodland and Sagebrush Scrub in the Owens Valley region, and Valley Grassland in the Salinas Valley.
- PHENOLOGY: Most of the California populations of this butterfly appear to be at least bivoltine, with perhaps three or four broods in some of the southern California populations in very wet years or years of abundant summer rainfall. Records range from April to mid-November for the southern California populations, and June through September for the northern California populations.
- FOODPLANTS: Wild licorice, *Glycyrrhiza lepidota* Pursh. (Leguminosae) was first recorded by Comstock (1929) as the foodplant in southern California; this plant is also used in the Owens Valley (J. F. Emmel, unpublished data) and even in the Texas Panhandle (by *L. melissa melissa* (Edwards); Rickard and Vernon, 1975). In Ventura and Kern counties, the adults are associated with *Lupinus formosus* Greene; in the San Jacinto Mountains, the adults are closely associated with *Astragalus douglasii* (T. & G.) Gray, *Lupinus latifolius* J. G. Agardh., and *Lotus purshianus* (Benth.) Clem. & Clem. (J. F. Emmel, unpublished data). Larvae in the lab can be reared on Wisteria. In the Great Basin fringe and Modoc Plateau areas of northern California, it is commonly found in close association with Alfalfa, *Medicago sativa* L., which is frequently established in waste places or grown as a cultivated crop. The rather high population density developed in such association by the fall months strongly suggests alfalfa may be a foodplant as well as nectar source.

b. *L. m. fridayi* (F. H. Chermock)

- DIAGNOSIS: We apply this name to high-elevation populations of *L. melissa* in California; two or three ecotypes comprise these high-elevation populations, and further study may indicate that more than one subspecies is involved here. Adults of this subspecies are much like those of *paradoxa*, with the exception of the males having a slightly wider terminal black band superiorly along the edges of the wings, as well as slight reduction of the orange markings both dorsally and ventrally in comparison to those on *paradoxa*. The dorsal ground color of females of these high-elevation populations tends to be uniform brown with a much

smaller percentage of individuals showing basal blue scaling than is seen in *paradoxa* populations.

- ORIGINAL DESCRIPTION: F. H. Chermock, *Canadian Entomologist*, 76: 215 [1945].
- TYPE LOCALITY: Mammoth, California. Location of type not known but presumably Canadian National Collection.
- DISTRIBUTION: These high-elevation populations are known from the White Mountains in Inyo and Mono counties, in the Sierra Nevada from the Mammoth Lakes region northward to Sonora Pass, as well as on Mt. Eddy in the Klamath Mountains Assemblage. Some *Lycaeides* populations in the Warner Mountains of Modoc and Lassen counties may also represent this entity, although genitalic examination of males from these areas to date indicate that all are *idas*, even those marked like *melissa*.
- ELEVATION RANGE: 8,500' to 11,000' elevation.
- HABITAT AND PLANT COMMUNITIES: In the White Mountains, populations are found on open slopes within a Dwarfed Sagebrush Scrub plant community. In the Sierra Nevada, populations are found on open gravelly to rocky slopes within the Subalpine Forest plant community. On Mt. Eddy, the butterfly is taken on open gravelly slopes and ridges within the Subalpine Forest plant community.
- PHENOLOGY: These high-elevation populations all appear to be univoltine, with adults flying from early July to mid-August.
- FOODPLANTS: In the White Mountains, populations are closely associated with *Lupinus argenteus*; in the Sierra Nevada the butterfly is associated with *Astragalus whitneyi* Gray (Shapiro *et al.*, 1981).

176. *Plebejus saepiolus* (Boisduval)

- SPECIES SYNOPSIS: This species is widespread in the boreal regions of North America and ranges southward both in the Rocky Mountain region to Arizona and New Mexico, and in California in the higher mountains and along the northern coast. Within its immediate habitat, it is often the most abundant butterfly, sometimes fairly swarming over its foodplant. There are six subspecies in our state.
- ADULT BEHAVIOR: Adults tend to be very local near the host plants in wet meadows. The *Trifolium* larval host plants are by far the most important nectar source for adult *saepiolus*. The males patrol constantly through the clover patches, seeking females; the females remain on the foodplants for long periods of time, crawling over the *Trifolium* flowerheads in pre-ovipositional behavior. In the case of subspecies *albamontana*, the adults tend to be more generally distributed over dryish slopes in the habitat, nectaring at the flowers of the host plant. In mark-release-recapture studies in subalpine Colorado, Sharp and Parks (1973) found *Plebejus saepiolus* to be quite sedentary and to show a striking degree of correlation with the micro-distribution of its oviposition host *Trifolium*, which itself has a patchy distribution. Those authors suggested that this distribution pattern represents one strategy available to a small, weakly-flying butterfly in a seasonally unpredictable subalpine environment. "By maintaining sedentary populations closely associated with the perennial plant which provides both larval food and nectar for the adults, *Plebejus saepiolus* can minimize uncertainties in finding a source of food" (Sharp and Parks, 1973).

- LIFE HISTORY:** The greenish-white eggs are laid on the flower heads of clover (*Trifolium* species), usually on the outer edges of the flower buds within the flower head. The pre-diapause larvae apparently feed exclusively on the flowers and fruits, while the post-diapause larvae feed exclusively on the leaves of the host. In subspecies *hilda*, the ground color of the larva is yellowish-green, with a lateral pale yellow line. There is a mid-dorsal, somewhat indistinct dark green line. The pupa is pale tan with pale grayish to greenish-tan wingcases and thoracic areas; it is sometimes slightly mottled with black. The second instar larvae hibernate, probably within the drying flower heads of the host (J. F. Emmel, G. Pratt, and G. Ballmer, unpublished data).
- CHROMOSOME NUMBER:** n = 24 in Colorado *saepiolus* populations (Emmel and Eliazar, 1989).
- SIMILAR SPECIES:** In flight, this species may be confused with *Agriades glandon*, which sometimes flies in the same habitats. Reference to the color plates for distinguishing the color patterns of the two species will allow ready separation.
- GEOGRAPHIC AND SEASONAL VARIATION:** As the species is univoltine, there is no seasonal variation. Within a given population, there is considerable variation among individuals, with the females showing a greater degree of variation than the males. In subspecies in which the orange aurora on the dorsal hindwing of the female is present, there are varying degrees of development of this orange scaling in different individuals. In the case of nominotypical *saepiolus* and in subspecies *albamontana*, where the females have blue basal scaling dorsally, there is some variation in the extent of this blue scaling. Within the populations that we lump under subspecies *aehaja*, from the Klamath Mountains Assemblage southward to the southern Sierra Nevada, there is a north-south cline in the amount of orange scaling dorsally on the females, with the darkest females present in the northwestern part of the Klamath Mountains Assemblage, some of which have no orange scaling at all on the upperside, with an increase of the amount of orange scaling as one goes southward in the Sierra Nevada. Thus, there is somewhat of a cline towards subspecies *austrosierra* at the extreme southern end of the Sierra Nevada and in the mountains of Kern County. Populations assigned to subspecies *hilda* in the San Jacinto Mountains and the mountains of San Diego County are somewhat atypical, generally having a darker orange on the submarginal area of the hindwing dorsally in the females than do the nominotypical populations in the San Bernardino mountains. On the extreme north coast, populations of *aehaja* are found within eight air miles from those of *insulanus*, with no evidence of blending or contact.
- GENERAL REMARKS:** Studies of the immature stages of this species by G. Ballmer and G. Pratt (1988) indicate that this species probably belongs in the same genus as *Icaricia icarioides*; therefore, we have not used the genus *Plebejus* as used by Miller and Brown (1981).

SUBSPECIES:

a. *P. s. saepiolus* (Boisduval)

- DIAGNOSIS:** Typical *saepiolus* is found along the northern California coast from Sonoma County to Mendocino County. Although the nominotypical name has heretofore been applied to the populations in the Sierra Nevada, examination of Boisduval's types in the U. S National Museum, as well as his description of this insect,

indicate that the original type material came from the coastal area of northern California, probably Sonoma County. The males are metallic blue dorsally, with a fairly broad dark terminal band on both forewing and hindwing, and a white fringe. Ventrally, on the males the ground color is a light gray with a pattern of medium-sized black dots on both forewing and hindwing. The females of this subspecies have a dull brown ground color dorsally, with fairly well-developed basal metallic blue scaling on both forewing and hindwing; additionally, there is faint development of a pale orange aurora in the submarginal area near the anal angle. Ventrally, the female pattern is similar to that of the male except that the ground color is a brownish to tannish gray. Individuals of this subspecies average slightly larger in size than those of other *saepiolus* populations in the state, with the exception of the *insulanus* populations along the extreme northern coast.

- ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 296 (1852).
- TYPE LOCALITY: "Mountains of California". Restricted by Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies* (1998a) to Bear Valley, near Olema, Marin County, California. Lectotype in U. S. National Museum.
- DISTRIBUTION: This nominotypical subspecies occurs long the immediate coast in Mendocino and Sonoma counties, as well as a few miles inland in Sonoma County.
- ELEVATION RANGE: From sea level to approximately 1,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This blue is usually found in wet meadows within the Closed Cone Pine Forest plant community, or adjacent to serpentine Chaparral.
- PHENOLOGY: The butterfly is univoltine, with adults flying from late May to early July.
- FOODPLANTS: The host is unknown for the nominotypical populations, but *Trifolium wormsjoldii* Lehm. is strongly suspected, as the adults are usually associated with this plant.

b. *P. s. littoralis* Emmel, Emmel, and Mattoon

- DIAGNOSIS: This subspecies is found in scattered pockets along the coast of extreme northern California. It is distinguished from typical *saepiolus* by a larger size, a reduction in the size of the black markings on the underside, and somewhat less blue basal scaling on the females dorsally.
- ORIGINAL DESCRIPTION:
- TYPE LOCALITY:
- DISTRIBUTION: Within California, this butterfly has been found only at the Fort Dick sand dunes in Del Norte County in the extreme northwestern part of the state. From here it is likely that it extends northward along the Oregon coast in Curry and Lincoln counties as shown by Dornfeld (1980) on his range map for *P. s. saepiolus*. In British Columbia, *P. s. insulanus* was described from Vancouver Island (Blackmore, 1919, *Proc. Ent. Soc. British Columbia*, (14): 8); it is not known if it penetrates south on the Washington coast, a state in which it is recorded only as an inland species in state faunal treatments to date (Pyle, 1974; Christensen, 1981).
- ELEVATION RANGE: From near sea level to approximately 50' elevation.

HABITAT AND PLANT COMMUNITIES: This butterfly inhabits a narrow band of coastal sand dunes that extends from the Oregon state line south along the immediate Del Norte County coast to Crescent City, California. The area is bordered on the inland side by a narrow band of Shore Pine, *Pinus contorta*. The pines and understory of shrubs such as *Baccharis pilularis* ssp. *consanguinea*. Wolf are draped in moss and interspersed with fern. Marsh and wetland grasses and reeds grow in the areas where the water table just surfaces, and presumed *Trifolium* foodplant of this subspecies is found along the perennially moist to damp borders of these marshy pockets.

PHENOLOGY: This subspecies flies from late May to early July in a single brood.

FOODPLANTS: Unknown, but *Trifolium wormskjoldii* Lehm. is strongly suspected.

c. *P. s. hilda* (J. and F. Grinnell)

DIAGNOSIS: This butterfly is found in certain southern California mountain ranges. It is distinguished from the typical subspecies to the north by the brighter blue of the males, the distinct and extensive orange band on the hindwings and forewings in the female, and the larger spots on the clear bluish-white (in males) to brownish-white (in females) ventral surface.

ORIGINAL DESCRIPTION: J. and F. Grinnell, *Journal New York Entomological Society*, 15: 46 (1907).

TYPE LOCALITY: Upper cienega at head of South Fork, Santa Ana River, California. Holotype in American Museum of Natural History.

DISTRIBUTION: This butterfly is found from the San Bernardino Mountains southward to the mountains of San Diego County. The San Diego County populations on Palomar Mountain, the Laguna Mountains, and the Cuyamaca Mountains may all be extinct at this time. Large populations are still found in the higher meadows of the San Bernardino and San Jacinto Mountain ranges.

ELEVATION RANGE: From 5,000 to 9,000' elevation.

HABITAT AND PLANT COMMUNITIES: The butterfly is typically found in open wet meadows within the Montane Wet Meadow plant community.

PHENOLOGY: Captures are recorded for early June through early August, with a peak flight in late June and early July.

FOODPLANTS: For this subspecies, the following clovers are used: *Trifolium wormskjoldii* Lehm., *T. monanthum* Gray, and *T. longipes* Nutt. var. *atrorubens* (Greene) Jeps. (Leguminosae) (J. F. Emmel, unpublished data).

d. *P. s. aureolus* Emmel, Emmel, and Mattoon

DIAGNOSIS: This subspecies of the San Gabriel Mountains is characterized by very extensive development of pale orange scaling dorsally on the females, with enlargement of the black spots ventrally in both sexes.

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Systematics of Western North American Butterflies*, pp. 178-179 (1998j).

TYPE LOCALITY: Big Pines, San Gabriel Mountains, Los Angeles County, California. Holotype in Los Angeles County Museum of Natural History.

DISTRIBUTION: This butterfly is known from a single wet meadow near Big Pines in the San Gabriel Mountains. Most other similar meadows in the area have had their water supply tapped for domestic use and are altered to the extent that they probably could no longer serve as habitat, if indeed they once did. In fact, in recent years a deep well has been put in service at the head of the type locality meadow. Specimens of this subspecies were last observed in the field in 1985 (by S. O. Mattoon). The current status of the butterfly is uncertain, and it is certainly an appropriate candidate for listing under the federal Endangered Species Act.

ELEVATION RANGE: From 6,800 to 6,900' elevation.

HABITAT AND PLANT COMMUNITIES: This rare subspecies flies in a large wet meadow within the Montane Coniferous Forest plant community.

PHENOLOGY: The adults fly in a single brood from early June to late July, depending on seasonal snowfall and temperature patterns.

FOODPLANTS: Oviposition has been recorded on *Trifolium wormskjoldii* Lehm. (J. F. Emmel, unpublished data).

e. *P. s. austrosierra* Emmel, Emmel, and Mattoon

DIAGNOSIS: This is a subspecies of the Piute Mountains region of Kern County and the extreme southern Sierra Nevada and Tulare County, characterized by females having somewhat of an intermediate appearance between subspecies *hilda* and subspecies *aehaja* of the main bulk of the Sierra Nevada to the north. Females have an orangish-brown ground color dorsally, with a fairly well-developed but somewhat ill-defined pale orange aurora in the submarginal area of the hindwing, extending onto the forewing at least in the posterior half of the submarginal area. Ventrally, the ground color is paler in both sexes than in subspecies *aehaja*, and the black markings are slightly more developed. Additionally, it tends to average slightly larger in size than more northern Sierra Nevada material.

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1989).

TYPE LOCALITY: Big Meadow, near Cannell Peak, Tulare County, California. Holotype in Los Angeles County Museum of Natural History.

DISTRIBUTION: This subspecies is found from the higher elevations of the Piute Mountains in Kern County northward to the Sierra Nevada of southeastern Tulare County.

ELEVATION RANGE: From 5,500' to 9,000' elevation.

HABITAT AND PLANT COMMUNITIES: Wet meadows within the Montane Coniferous Forest plant community.

PHENOLOGY: This subspecies flies from early June to mid-July.

FOODPLANTS: Unknown for this subspecies.

f. *P. s. aehaja* (Behr)

- DIAGNOSIS: This name is applied to montane populations in central and northern California which in previous publications have been considered to represent typical *saepiolus*. Males are metallic blue dorsally, with a medium width terminal band. Females are brown dorsally, and lack basal blue scaling; there is only weak development of a pale orange aurora in the submarginal area of the hindwing.
- ORIGINAL DESCRIPTION: Behr, *Proceedings California Academy Natural Sciences*, 3: 280 (1867).
- TYPE LOCALITY: "Alpine headwaters Tuolumne River, California". Type destroyed in 1906 San Francisco earthquake and fire.
- DISTRIBUTION: This is a widespread subspecies of the Sierra Nevada, Klamath Mountains Assemblage, and the Warner Mountains. From here it extends northward into the Cascades of Oregon, Washington, and southern British Columbia. Eastward, populations of *saepiolus* range to the Rocky Mountains where the subspecies *whitmeri* is found; the pattern of geographic subspeciation between the Sierran Cascade Range and the Rocky Mountains remains to be worked out.
- ELEVATION RANGE: 3,600 to 10,600' elevation.
- HABITAT AND PLANT COMMUNITIES: This subspecies is found in Montane Wet Meadow habitats, usually surrounded by Upper Montane Coniferous Forest, Great Basin Sagebrush Scrub, or Subalpine Forest, but some populations occur in meadows within the Arctic-Alpine Cushion Plant community.
- PHENOLOGY: Captures are recorded from late May to early September, with a peak flight in late June to early July in most localities. The highest elevation populations may not begin flying until late July or early August in some years.
- FOODPLANTS: This subspecies has been associated with the following species of *Trifolium*: *T. longipes* Nutt., *T. wormsjoldii* Lehm., and *T. productum* Greene (Shapiro *et al.*, 1981). In the Warner Mountains, Mattoon (unpublished data) records *T. tridentatum* Lindl. var. *tridentatum*.

f.

g. *P. (l.) s. albamontana* Austin and Emmel

- DIAGNOSIS: An alpine subspecies of the White Mountains of California and Nevada, characterized by small size, and considerable development of blue scaling on the females dorsally. In most females, there is blue scaling covering at least the proximal one-third of both forewing and hindwing, and in many cases this extends to the submarginal area. There is slight development of the orange aurora in the submarginal area of the hindwing with some orange scaling usually present in the vicinity of the anal angle. The underside ground color tends to be darker in both sexes, with enlargement of the black markings compared with that seen in the other subspecies.
- ORIGINAL DESCRIPTION: Austin and Emmel, *Natural History Museum of Los Angeles County Contributions in Science*, : (1989).
- TYPE LOCALITY: McAfee Meadow, White Mountains, Mono County, California. Holotype in Los Angeles County Museum of Natural History.

- DISTRIBUTION:** This subspecies is confined in distribution to the White Mountains of Inyo and Mono counties, California, and adjacent Esmeralda County, Nevada.
- ELEVATION RANGE:** From 7,000 to 13,000', but mostly above 10,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** This subspecies is found in two types of habitat in the White Mountains. The majority of populations seem to be on open, treeless, gravelly slopes in the Arctic Alpine Cushion Plant community where the major foodplant, *Trifolium andersonii* Gray ssp. *mononense* (Greene) J. Gillett is abundant. Additionally, the butterfly is found in moister habitats, such as along stream banks and within wet meadows in the Great Basin Coniferous Forest and the Mountain Sagebrush Scrub plant communities.
- PHENOLOGY:** Adults fly from late June to late August, depending on elevation, and progression of the season. The major flight of the higher alpine populations seems to be in mid to late July.
- FOODPLANTS:** *Trifolium andersonii* Gray ssp. *monoense* (Greene) J. Gillett *mononense* is by far the most commonly used host of this subspecies; this *Trifolium* species, which is adapted to somewhat dryish open slopes in the Arctic-Alpine Zone of the White Mountains, is one of the most abundant plants in this zone of the range. Additionally, *Trifolium monanthum* Gray, *T. wormskjoldii* Lehm., and *T. longipes* Nutt are all probably used as well in the moister meadow habitats of the subspecies.

h. *P. s. albamontana* Austin and Emmel

i. *P. s. bishopi* Emmel, Emmel, and Mattoon

j. *P. s. near maculosis* Austin

k. *P. s. norte* Emmel, Emmel, and Mattoon

l. *P. s. palomara* Emmel, Emmel, and Mattoon

177. *Plebejus icarioides* (Boisduval)

- ADULT BEHAVIOR:** Adults of both sexes are closely associated with the *Lupinus* foodplants, and frequently alight on them. Males tend to perch on plants that are located in small ravines or washes to await passing females. The females are more sedentary, often spending much of their time landed on or walking over the *Lupinus* foodplants. Males are frequently attracted to moist sand or mud; nectar sources for this species are poorly documented, but include several *Eriogonum* and composite species.
- LIFE HISTORY:** The life history of subspecies *evius* was described by Comstock and Dammers (1935a). The echinoid eggs are a delicate greenish-white and are covered with projecting white papillae. They are laid singly on the foodplant, usually on the upper surfaces of the leaves, and hatch in five to eight days. The mature larva is green with three indistinct white diagonal bars on the sides of each segment. The body is covered with very short white hairs. They feed for about a month,

exclusively on the leaf epidermis in our experience, and then go into hibernation as half-grown larvae until the following spring. The post-diapause larvae feed on the new growth of the *Lupinus* species, and in the case of herbaceous perennials, often bore into the succulent stems of the newest growth. The larvae are frequently attended by ants. Pupation occurs at the base of the foodplant, using a silk button and girdle. The pupa is green on the wingcases, head, and thorax, and a chestnut red with blotches of green on the abdomen. Short chestnut red hairs are scattered over the surface, except on the wingcases. The pupal stage lasts about three weeks.

CHROMOSOME NUMBER:

SIMILAR SPECIES:

There are three other species of blues which may be confused with *icarioides*. Small specimens of *icarioides* may resemble *I. saepiolus* or *I. shasta*. In the case of *I. saepiolus*, the more metallic blue dorsally in the males, the smaller size, and association with a wet meadow habitat will usually serve to readily distinguish this species. *I. shasta* males are usually readily distinguished from *I. icarioides* males by their broader dark borders dorsally, but occasionally the females may be similar, particularly in worn specimens. Examination of the submarginal area ventrally on the hindwing will show the presence of metallic scales around the black spots, whereas in *icarioides* these metallic spots are absent; additionally, *shasta* adults are much smaller. A third species which may be confused with *icarioides* is *Glaucopsyche lygdamus*. *G. lygdamus* may be distinguished by the more metallic quality of the blue scaling dorsally, the thinner terminal dark line in the males, and the lack of any orange aurora in the submarginal area of the hindwing dorsally in the females. Also, *lygdamus* tends to have few to absent black markings in the submarginal area of both wings ventrally.

GEOGRAPHIC AND SEASONAL VARIATION:

As the species is univoltine, there is no seasonal variation. As indicated by the long list of subspecies of *I. icarioides* in California alone, this species shows considerable geographic variation. Even within the segregates that we have delineated above, there is some variation from population to population and further refinements in this treatment would be an appropriate subject of study. Even within a given population, there is considerable variation among individuals.

GENERAL REMARKS:

This species may be involved in a mimicry complex with a moth, several species of blues, a copper, and a hairstreak. Downey (1965) describes the possible mimicry complex between *I. icarioides* and the Noctuid moth, *Caenurgina caerulea* Grote. Both species feed on Lupine, the moth may be partially diurnal, the moth is blue in contrast to its near relatives which tend to be brownish or dark colored, and the moth has a similar flight behavior to *icarioides*. As *Lupinus* plants contain alkaloids (Robinson, 1968), both the moth and *icarioides* may be potentially poisonous to predators, indicating a case of Mullerian mimicry. As noted under the Similar Species section above, there are at least three other Blues which resemble *I. icarioides*; in the case of *G. lygdamus*, there is a fairly close resemblance in both size and color pattern when these two species are sympatric. In some localities both species use the same species of lupine as a host, and thus may again represent a case of Mullerian mimicry. The copper species, *Lycaena heteronea*, superficially resembles *I. icarioides* with which it may be sympatric. This copper feeds on *Eriogonum* species and may or may not be poisonous or distasteful (Austin, 1972). Lastly, adults of the hairstreak, *Satyrrium fuliginosum*, often resemble dark females of *I. icarioides*, and show a somewhat similar flight pattern and perching behavior. In a given locality where the two species are sympatric, *S. fuliginosum* may use the same *Lupinus* species as does *I. icarioides*, again suggesting a possible Mullerian mimicry complex.

This butterfly occurs across western North America west of the Great Plains. It ranges from northern Baja California and Arizona north to Alaska, usually occurring in discrete populations in close association with the lupine foodplants. Populations may be found from sea level to over 12,000'. It is one of the most variable butterflies in our fauna, and laboratory rearings (Downey, in Howe, 1975) have shown that most of the color differences that are used to describe subspecies are markedly affected by environmental conditions. Thus, Downey has suggested that most of these subspecies in western North America should be "considered on the basis of general locality, and not on any hard and fast morphological criteria." In this spirit, then, and acknowledging the wide variability of this species even within single populations, we divide the California *icarioides* into twelve subspecific groupings.

a. *P. i. icarioides* (Boisduval)

DIAGNOSIS: We apply the nominotypical subspecies name to populations on the west slope of the Sierra Nevada northwestward to the Klamath Mountains assemblage and North Coast Ranges. In these populations, both sexes tend to be fairly large. The males are mostly blue dorsally, with a medium-width brown terminal line on the forewing and a thin brown terminal line on the hindwing with varying development of a brown spot within the submarginal area of each cell. Ventrally, the males have a very pale grayish-tan ground color upon which are superimposed a pattern of dark brown to blackish spots; on the hindwing in the post-median area of the wing, these spots are relatively small and are usually encircled by a vague halo of white scales. The females have varying degrees of blue scaling basally on the dorsal surface, with a brown terminal band occupying approximately two-fifths of the distal portion of the forewing and the anterior one-third of the hindwing. In the submarginal area of the hindwing, the orange aurora which is present on some subspecies tends to be indistinct to absent in this subspecies, and is replaced by a pattern of obsolescent brown spots. Ventrally, the pattern on the female is similar to that in the male except that the ground color tends to be a slightly darker shade of tannish-gray.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Ent. Soc. France*, (2)10: 297 (1852).

TYPE LOCALITY: "Mountains of California". Hovanitz (1937) fixed the type locality of the nominotypical subspecies as between 2,000 and 4,000' in El Dorado and Nevada counties, California (see Downey, in Howe, 1975, p. 344). Re-restricted by Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1990), to 0.5 roadmiles west of Paxton, Feather River Canyon, 2,500', Plumas County, California. Holotype in U.S. National Museum.

DISTRIBUTION: This is the most widely distributed subspecies within the state, occurring from the west slope of the Sierra Nevada in Tulare County northward through the Sierra Nevada-Cascade Range foothills and mid-elevations to the Mt. Shasta region, the Klamath Mountains assemblage, and the North Coast Ranges. We consider the subspecies *helios* (W. H. Edwards) (type locality: Fawn Lodge, Trinity County, California) to be synonymous with nominotypical *icarioides*. With additional study of the North Coast Range and Klamath Mountains populations, particularly with emphasis on foodplants and biological characters, there may be sufficient grounds to identify segregates within this area that are separable from nominotypical *icarioides*.

ELEVATION RANGE: From 1,000' to 9,200' elevation.

- HABITAT AND PLANT COMMUNITIES:** Most typically, the butterfly is found on open slopes within the Lower and Upper Montane Coniferous Forest plant communities where perennial *Lupinus* species, the foodplants, are locally abundant. At the higher elevations, some of these populations may be within the Subalpine Forest plant community, whereas at the lower elevations, they may be present in Foothill Woodland or Northern Oak Woodland plant communities.
- PHENOLOGY:** The species is strictly univoltine. Records range from late April to early September, with most records in the period late May through mid-July, depending on elevation.
- FOODPLANTS:** The following species of *Lupinus* have been documented as foodplants of the nominotypical subspecies: *L. andersonii* S. Wats.; *L. arbustus silvicola* (Heller) Dunn; *L. fulcratus* Greene; *L. latifolius* J. G. Agardh.; and *L. meionanthus* Gray (Downey and Fuller, 1961).

b. *P. i. fulla* (W. H. Edwards)

- DIAGNOSIS:** This is the subspecies name applied to populations of the east slope of the Sierra Nevada from extreme northern Inyo County northward. In this subspecies, the males are similar to nominate *icarioides* dorsally, but ventrally there is marked reduction of the black spotting, particularly on the hindwing, leaving often only a few somewhat indistinct whitish patches where the spots would normally be in the post-median area of the wing. In the females, the brown scaling is much more extensive dorsally, often covering the distal half of the forewing and the distal two-thirds of the hindwing. Ventrally, the females are similar to the males. We consider the name *ardea* (W. H. Edwards) (type locality, Virginia City, Storey County, Nevada) to be synonymous with *fulla*.
- ORIGINAL DESCRIPTION:** W. H. Edwards, *Transactions American Ent. Soc.*, 3: 194-195 (1870).
- TYPE LOCALITY:** "California", restricted to Sonora Pass, Mono County, California by Downey, in F. M. Brown, *Transactions American Ent. Soc.*, 96: 384-387 (1970). Neotype in Carnegie Museum, designated by Downey, in F. M. Brown, *Transactions American Ent. Soc.*, 96: 386-387 (1970).
- DISTRIBUTION:** This subspecies is widespread on the east slope of the Sierra Nevada from extreme northern Inyo County northward to the east slope of the Carson Range in extreme western Nevada; from here, it extends eastward to the Wassuk Range, on the west side of Walker Lake, Nevada. Populations with similar phenotypes occur northward to Lassen County where gradual blending takes place with populations nearest in facies to subspecies *pembina*. In the northeastern corner of the state, many populations have individuals which show varying degrees of blending among the nominate *icarioides* of the west slope of the Sierra Nevada, subspecies *fulla* and subspecies *pembina*. Longer series of specimens from localities in Lassen and Modoc counties are needed to assess this situation more accurately.
- ELEVATION RANGE:** From 5,000 to 10,500' elevation.
- HABITAT AND PLANT COMMUNITIES:** This subspecies is typically found on open slopes within the Great Basin Sagebrush Scrub plant community where its *Lupinus* foodplants are common. At the higher elevations, this butterfly is found in ecotones where Great Basin Sagebrush Scrub blends into Upper Montane Coniferous Forest and Subalpine Forest.

PHENOLOGY: Records range from early June to mid August, with a peak flight for most populations in mid to late July.

FOODPLANTS: In the type locality at Sonora Pass, the foodplant is *Lupinus meionanthus* Gray; additionally, the subspecies uses *L. caudatus* Kell., *L. arbustus silvicola* (Heller) Dunn, and *L. argenteus* var. *tenellus* (Dougl. ex G. Don) Dunn. (Downey and Fuller, 1961). Also, the butterfly is associated with *L. inyoensis* Heller (J. F. Emmel, unpublished data).

c. *P. i. pardalis* (Behr)

DIAGNOSIS: In this subspecies of the San Francisco Bay region, the most prominent feature is the enlarged black spots on the underside of both sexes. Additionally, females of this subspecies tend to be largely or entirely brown above, with little or no basal blue scaling.

ORIGINAL DESCRIPTION: Behr, *Proceedings California Academy Natural Sciences*, 3: 279 (1867).

TYPE LOCALITY: Contra Costa Range, vicinity San Antonio, California. Type lost in 1906 San Francisco earthquake and fire.

DISTRIBUTION: This subspecies is found in the central Coast Ranges from Monterey and San Benito counties on the south, northward to Marin, Sonoma, and Napa counties. In general, it tends to occur in inland localities away from the immediate coast, although it is found rather close to San Francisco Bay in Alameda and Santa Clara counties. In Monterey and San Luis Obispo counties to the south, there are populations of *icarioides* which appear to be intermediate between *pardalis* and the southern California subspecies *evius*. At the northern edge of the distribution of *pardalis*, there does not appear to be a similar blendzone with the *icarioides* populations in the North Coast Ranges which are most closely related to nominotypical *icarioides*.

ELEVATION RANGE: From near sea level to 4,300' elevation.

HABITAT AND PLANT COMMUNITIES: Some populations are found in grassy fields (Foothill and Valley Grassland plant community) such as at Stanford, while others are found on grassy to brushy slopes within Northern Coastal Scrub, Mixed Chaparral, Foothill Woodland, or Northern Oak Woodland.

PHENOLOGY: Records range from early April to mid-June, with the majority of populations flying during May.

FOODPLANTS: The following *Lupinus* species have been documented as foodplants of this subspecies: *L. albifrons* Benth. (Downey and Fuller, 1961); and *L. formosus* Greene (J. F. Emmel, unpublished data). In general, the valley bottom grassland populations are associated with *L. formosus* Greene and the slope populations are associated with *L. albifrons* Benth.

d. *P. i. pheres* (Boisduval)

DIAGNOSIS: The most distinctive features of this subspecies are in the female. That sex is characterized by a light brown dorsal surface and the presence of a prominent white discal spot on the forewing (females from other locations usually lack such a spot). In *pheres*, the whitish halo surrounding this spot is particularly notable.

Because of the reduced black spotting elsewhere on the underside in both sexes, particularly on the hindwings, the white halos around the very reduced or absent pupils are particularly apparent and give a white-spotted appearance to the ventral surface.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. France*, (2)10: 297 (1852).

TYPE LOCALITY: San Francisco, California. Holotype in U. S. National Museum.

DISTRIBUTION: Named from the city of San Francisco, whose populations are extinct. A very similar phenotype occurs in populations associated with sand dunes at Point Reyes in Marin County. Barnes and McDunnough (1919) noted that *P. i. blackmorei*, named by those authors from the local and very distinctive populations on the southern portion of Vancouver Island in British Columbia, was extremely similar to *pheres* Bdv. from the San Francisco region except for *blackmorei*'s brilliant silvery-blue dorsal surface in the male, as contrasted to the lilac-blue of *pheres*. Its ventral spots are broadly encircled with white, as in *pheres*, and are only faintly dotted in the center with black scales.

ELEVATION RANGE: From sea level to approximately 200' elevation.

HABITAT AND PLANT COMMUNITIES: This butterfly is (was) found within the Coastal Dune Sand Plant community where three types of bush lupine are usually present: *L. chamissonis* Eschs., *L. arboreus* Sims, and *L. variicolor* Steud.

PHENOLOGY: Records for the San Francisco populations range from early April to mid June; in the Point Reyes area, records range from mid April to early July. Because of the proximity to the coast and frequent fogs during the flight period, the flight period in any given locality is rather extended, often lasting two months.

FOODPLANTS: The principal host of the San Francisco populations was *Lupinus chamissonis* Eschs. In the Point Reyes area, the butterfly is closely associated with *L. variicolor* Steud.

e. *P. i. missionensis* (Hovanitz)

DIAGNOSIS: This subspecies is found on the hills of the San Francisco peninsula from Twin Peaks southward to the San Bruno Mountains of extreme northern San Mateo County. Additionally, populations which are phenotypically extremely similar occur on the hills of Marin County in the immediate vicinity of the Golden Gate. *P. i. missionensis* is similar to *pheres* dorsally, but ventrally it tends to have a darker ground color and black spots instead of white spots. These black spots are approximately half the size of those seen in the geographically proximate subspecies *pardalis*.

ORIGINAL DESCRIPTION: Hovanitz, *Pan-Pacific Entomologist*, 13: 187 (1937).

TYPE LOCALITY: Twin Peaks, San Francisco, California. Holotype in California Academy of Sciences.

DISTRIBUTION: From the San Bruno Mountains and extreme northern San Mateo County northward to Twin Peaks in San Francisco. In southern Marin County, this subspecies is found on the hills just west and southwest of Sausalito.

ELEVATION RANGE: From near sea level to approximately 1,400' elevation.

- HABITAT AND PLANT COMMUNITIES:** The butterfly is found in three different types of habitats in the San Bruno Mountains, depending on which of the three *Lupinus* species foodplants is present. In the areas where it is associated with *L. albifrons* Benth., the plant tends to grow in rocky to gravelly open ridges or slopes, or on roadcuts, within the Northern Coastal Scrub plant community. In the populations associated with *L. variicolor* Steud., it is usually in grassland on open slopes. In the populations associated with *L. formosus* Greene, the habitat is within grassland along an open creek bottom.
- PHENOLOGY:** Populations on southern exposures show a flight period from late March through mid-April, whereas populations on ridgetops and more northern exposures fly from late April to early June. In the populations associated with *L. formosus* Greene in the canyon bottoms at the east base of the San Bruno Mountains, the flight period is from mid-May to mid-June.
- FOODPLANTS:** The following *Lupinus* species have been documented as larval foodplants of *missionensis*: *L. albifrons* Benth. ex Lindley, *L. formosus* Greene, and *L. variicolor* Steudel. (Arnold, 1983; J. F. Emmel, unpublished data).

f. *P. i. moroensis* (Sternitzky)

- DIAGNOSIS:** This coastal population in the vicinity of Morro Bay in San Luis Obispo County has a silvery cast to the dorsal surface of the male, due to an infusion of white scaling along with the blue, particularly along wing veins. The female dorsal pattern is similar to that seen in subspecies *pheres*, except that the brown areas are duskier, and there is a suggestion of an orange aurora in the submarginal area of the hindwing. Ventrally, both sexes show reduction of the black spotting on the hindwing, leaving white spots with very faintly pupiled centers: the ventral ground color is slightly darker than that seen in subspecies *pheres*.
- ORIGINAL DESCRIPTION:** Sternitzky, *Pan-Pacific Entomologist*, 7: 93 (1930).
- TYPE LOCALITY:** Morro Beach, San Luis Obispo County, California. Holotype in California Academy of Sciences.
- DISTRIBUTION:** The Morro Blue flies only along the immediate coast in San Luis Obispo and western Santa Barbara counties. This distinctive subspecies may soon become extinct in its present range as increasing development and use of "dune-buggies" destroy the butterflies' sand dune habitats. The dune vegetation is in many places being torn to shreds by these vehicles and even collecting in these areas has become dangerous due to the off-road vehicle traffic. The type locality at Morro Bay has been disturbed, in part, by the nuclear power plant there. The strongest remaining population seems to be at Oso Flaco Dunes in San Luis Obispo County. This race also occurs at Pismo Beach and in scattered localities inland in San Luis Obispo County (Emmel and Emmel, 1973; Downey in Howe, 1975).
- ELEVATION RANGE:** From near sea level to approximately 300' elevation.
- HABITAT AND PLANT COMMUNITIES:** This butterfly is found within the Coastal Dune Sand Plant community, where it is found on stabilized sand dunes where the *Lupinus* foodplant is locally abundant.
- PHENOLOGY:** Records range from mid-April to late June, with the main flight occurring during the month of May. Because of the proximity to the ocean and the fairly frequent

fogs which occur during the flight period of this species, the flight period may last for one to two months.

FOODPLANTS: The butterfly is closely associated with *Lupinus chamissonis* Eschs., and this is undoubtedly the foodplant.

g. *I. i. evius* (Boisduval)

DIAGNOSIS: In this subspecies of the southern California mountains, both sexes have an expansion of the dorsal blue scaling. In the males, there is a narrow dark terminal line dorsally; in the females, there is considerable expansion of the blue scaling to involve the basal two-thirds of the wing to sometimes almost the entire wing. In the dorsal submarginal area of the hindwing in the females, there is frequently varying development of a pale orange aurora. Ventrally, both sexes show varying development of the black markings which ranges from that seen in typical *icarioides* to fairly boldly marked specimens.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Ent. Soc. Ent. Belgique*, 12: 49 (1869).

TYPE LOCALITY: "Southern California". Restricted by Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1989) to vicinity of Los Angeles, Los Angeles County, California. Holotype in U. S. National Museum.

DISTRIBUTION: This subspecies is rather widespread through the higher mountains of southern California from the Laguna Mountains in San Diego County northward through the San Jacinto Mountains to the San Bernardino, San Gabriel, and Tehachapi ranges. From here it extends westward into the mountains of Ventura and Santa Barbara counties. In Kern County, north of the Tehachapi Range, fairly typical *evius* populations are found in the Piute Mountains and the Greenhorn Mountains. Northward, there is an apparent blendzone with typical *icarioides* on the west slope of the Sierra Nevada, and with subspecies *eosierra* on the east slope of the Sierra Nevada. In San Luis Obispo County, there is an apparent blendzone with subspecies *pardalis* of the central Coast Ranges. Populations in the Santa Ana Mountains of Orange County are somewhat atypical with reduced spotting ventrally and are perhaps deserving of subspecific recognition, but here are lumped with subspecies *evius*.

ELEVATION RANGE: From 1,000 to approximately 9,000' elevation, with most populations below 7,000'.

HABITAT AND PLANT COMMUNITIES: Most populations are associated with dense stands of *Lupinus* within the Lower and Upper Montane Coniferous Forest plant communities in the mountains. Other populations are associated with open areas within Mixed Chaparral, particularly in broad open canyon bottoms or on flats within this plant community.

PHENOLOGY: Records range from early April to late July, depending on elevation and progression of the season. Most populations fly during the month of May or June.

FOODPLANTS: The following *Lupinus* species have been documented as foodplants of subspecies *evius*: *L. formosus* Greene, *L. excubitus* Jones ssp. *austromontanus* (Heller) C. P. Sm., *L. elatus* Jtn., and *L. andersonii* Wats. We believe the record for an annual Lupine, *L. densiflorus* Benth. var. *glareosus* (Elmer) C. P. Sm., an observation by J. C. Montgomery reported by Downey and Fuller (1961) to be an error in

identification; in our experience, the populations at Frazier Park, Kern County, are associated with *L. formosus* Greene or *L. excubitus* Jones.

h. *P. i. argusmontana* Emmel, Emmel, and Mattoon

- DIAGNOSIS:** This subspecies of the western Death Valley region is characterized by its smaller size and reduction of the dark markings, both dorsally and ventrally. Dorsally, males have a very thin terminal dark line, and the females have considerable expansion of the blue areas. Ventrally, the black spotting is greatly reduced on both forewing and hindwing. On the forewing, only the spots in the post-median area of the wing remain in most specimens. On the hindwing the black spots are greatly reduced or absent.
- ORIGINAL DESCRIPTION:** Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1989).
- TYPE LOCALITY:** Mountain Springs Canyon, Argus Mountains, Inyo County, California. Holotype in Los Angeles County Museum.
- DISTRIBUTION:** This subspecies is confined to the Argus Mountains and the Nelson Range in Inyo County.
- ELEVATION RANGE:** From 5,000' to 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** Open slopes or canyon bottoms within the Pinyon-Juniper Woodland or Great Basin Sagebrush Scrub plant communities.
- PHENOLOGY:** This subspecies flies from early May to early June.
- FOODPLANTS:** In the Argus Range, the butterfly is associated with *Lupinus excubitus*, and this is assumed to be the foodplant. In the Nelson Range, it uses two species of lupine: *L. alpestris* A. Nels., and *L. excubitus* Jones (J. F. Emmel, unpublished data).

i. *P. i. panamintinus* Emmel, Emmel, and Mattoon

- DIAGNOSIS:** In this subspecies of the western Death Valley region, the adults tend to be larger than those of subspecies *argusmontana* but smaller than typical *icarioides*. In the males, the terminal line dorsally is moderately wide, and the blue ground color is of a darker shade than is seen in subspecies *argusmontana*. In the females, there is less development of the blue scaling with light brown scaling occupying approximately the distal half of the forewing. On the hindwing dorsally, there is faint development of a pale orange aurora in the submarginal area. Ventrally, this subspecies is characterized by a much greater development of the black spotting, with the spots in the post-median area of both forewing and hindwing often encircled by white halos, making these spots stand out even more boldly from the pale grayish-tan ground color.
- ORIGINAL DESCRIPTION:** Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1989).
- TYPE LOCALITY:** Wildrose Canyon, in a small side canyon 1.5 airmiles SSW of Wildrose Peak, 6,600 to 6,900' elevation, Panamint Range, Inyo County, California.

- DISTRIBUTION:** This subspecies in its typical form is found in the Panamint Range; populations with an extremely similar phenotype and only minor differences occur in the Inyo Mountains of Inyo County and are here lumped under subspecies *panamintinus*.
- ELEVATION RANGE:** From 5,000' to 9,000' elevation, with most populations in the 6,000' to 7,500' range.
- HABITAT AND PLANT COMMUNITIES:** Typically found on open, gravelly to somewhat sandy slopes, or occasionally on talus slopes, or in canyon bottoms, within the Pinyon-Juniper Woodland, Great Basin Sagebrush Scrub, or Mountain Sagebrush Scrub plant communities; a few populations occur within the lower edges of the Great Basin Coniferous Forest in both the Inyo and Panamint Mountains.
- PHENOLOGY:** This subspecies flies from early May to early July, depending on elevation and seasonal temperature and precipitation patterns.
- FOODPLANTS:** This subspecies utilizes at least two *Lupinus* species: *L. excubitus* Jones and *L. alpestris* A. Nels. (J. F. Emmel, unpublished data).

j. *P. i. albihalos* Emmel, Emmel, and Mattoon

- DIAGNOSIS:** This is a subspecies of the California-Nevada border region, with a distribution centering in the White Mountains. It is characterized by a relatively large size, a medium-width terminal band dorsally in the males, females which are largely brown but with some degree of basal blue scaling in most specimens, and an underside ground color which is much darker than in other California subspecies of *icarioides*. This ground color is a dull brownish-gray, and the white and black spotting pattern which is superimposed upon it consequently shows considerably more contrast than that seen in the other subspecies. On the forewing, the black spots in the post-median area ventrally are ringed with white scaling and stand out boldly from the dark background. On the hindwing, the black spots in the post-median area are reduced in size but usually present, at least to some degree, and are widely ringed with white scaling, giving somewhat of an eyespot aspect to these markings.
- ORIGINAL DESCRIPTION:** Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1989).
- TYPE LOCALITY:**
- DISTRIBUTION:** This subspecies is found throughout the White Mountains of the California-Nevada border region, as well as in the extreme north end of the Inyo Mountains, and in the Silver Peak Range in Esmeralda County, Nevada.
- ELEVATION RANGE:** 7,000 to 11,500' elevation.
- HABITAT AND PLANT COMMUNITIES:** Populations of this butterfly are typically found within the Mountain Sagebrush Scrub plant community where the *Lupinus* foodplants are locally abundant on open, gravelly slopes. The dominant vegetation in these localities is a dwarf sagebrush scrub (*Artemisia arbuscula* Nutt.).
- PHENOLOGY:** This subspecies flies from early July to mid-August, depending on elevation and seasonal temperature and precipitation patterns. The peak flight seems to be in mid- to late July in most areas.

FOODPLANTS: The butterfly is closely associated with *Lupinus argenteus* Pursh. var. *tenellus* (Dougl. ex Don) D. Dunn, and this is presumed to be the foodplant (J. F. Emmel, unpublished data).

k. *P. i. eosierra* Emmel, Emmel, and Mattoon

DIAGNOSIS: This is a subspecies of the southern part of the east slope of the Sierra Nevada, characterized by smaller size, pale blue ground color dorsally in the males, with a relatively thin terminal band, expansion of the blue areas dorsally on the females, with this blue being a relatively pale shade, and an underside characterized by a marked reduction of the black spotting, often being absent in the spots on the hindwing. This subspecies is distinguished from subspecies *fulla* to the north by the much greater extent of brown scaling dorsally on the females in *fulla*, the larger size of *fulla*, and the more washed out underside ground color and spotting on *fulla* in comparison to this subspecies. It also somewhat resembles the southern California subspecies *evius*, but differs again in the smaller size, the greater reduction of black markings ventrally, particularly on the hindwing, and the usual absence of an orange aurora in the submarginal area of the dorsal hindwing in the female.

ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Natural History Museum of Los Angeles County Contributions in Science*, : (1989).

TYPE LOCALITY:

DISTRIBUTION: This subspecies is found on the east slope of the Sierra Nevada from approximately the Kern-Inyo County line northward to the Inyo-Mono County line.

ELEVATION RANGE: From 5,000 to 10,500' elevation, with most populations below 8,000'.

HABITAT AND PLANT COMMUNITIES: This butterfly is typically found on open, sandy to gravelly slopes, particularly sandy granitic talus slopes where *Lupinus excubitus* Jones is abundant. These slopes may occur within the Joshua Tree Woodland, Pinyon-Juniper Woodland, or Great Basin Sagebrush Scrub plant communities. In the case of populations where the foodplant is a *Lupinus* species other than *L. excubitus* Jones, the usual plant association is Great Basin Sagebrush Scrub.

PHENOLOGY: For the lower elevation populations, adults fly from early April to mid-May, with a peak flight in late April and early May; in the higher elevation populations, the flight period extends from early June to late July, depending on elevation.

FOODPLANTS: The principal foodplant for most populations is *Lupinus excubitus* Jones; at the northern edge of its range, *L. montigenus* Heller and *L. inyoensis* Heller are both associated lupines.

l. *P. i. nr. pembina* (W. H. Edwards)

DIAGNOSIS: Populations in the northeastern corner of California are closest to this subspecies of the northwestern Rocky Mountain region. Adults are characterized by the following characters: On the males, the terminal band dorsally tends to be reduced in width and is quite thin on the hindwing with a series of submarginal black spots. The females tend to have extensive brown scaling dorsally, occupying the outer

two-thirds of the wings. Ventrally, this subspecies has the white spots on the hindwing pupiled with small black spots; these black spots are somewhat intermediate in size between those seen in nominotypical *icarioides* and the absent or obsolescent spots in subspecies *fulla*.

ORIGINAL DESCRIPTION: W. H. Edwards, 1862, *Proceedings of the Academy of Natural Sciences*, Philadelphia, 14: 224, "April 1862".

TYPE LOCALITY: "Lake Winnipeg". Restricted to Lost Horse Road, Ravalli County, Montana, in the Bitterroot Mountains, by F. M. Brown, 1970, *Transactions of the American Entomological Society*, 96: 353-433.

DISTRIBUTION: Populations of this phenotype in California are found in Modoc and Lassen counties, from the east flank of the Sierra Nevada in Lassen County northward to the Warner Mountains region.

ELEVATION RANGE: 5,000' to 8,000' elevation.

HABITAT AND PLANT COMMUNITIES: This subspecies is found in the more mesic portion of the Great Basin Sagebrush Scrub and Pinyon-Juniper Woodland, extending from the basin valley floors and sinks as "fingers" upward through coniferous forests to the very summits of the local mountain ranges. These relatively mesic areas characteristically support an abundance of perennial lupines, sunflowers, and other spring and early summer wildflowers. Due to the abundance of the host lupine, this butterfly becomes one of the most commonly encountered blues in the Great Basin. The habitat often is adjacent to either permanent or springtime meadows, fed by small intermittent streams or rivulets. Like many other *icarioides* populations, this subspecies is attracted to wet sand or mud in these moist places and will often congregate in great numbers. Several species of *Eriogonum* and sunflowers are especially attractive nectar sources.

PHENOLOGY: Adults fly from late June to early August, depending on elevation and progression of the season.

FOODPLANTS: Unknown for the California populations, but presumably at least one host is *Lupinus argenteus* Pursh., with which several populations are associated.

178. *Plebejus (Icaricia) shasta* (W. H. Edwards)

This medium-sized Blue species is distributed throughout the mountain regions of western North America. While the wing pattern is somewhat similar to that of *I. acmon* of lower elevations, the ventral post-median spots are brown (not black like those of the ventral forewing) and black dashes usually occur in the middle of the dorsal forewing and hindwing pattern. While adults fly for only a short time, they may be very numerous in favored population areas.

ADULT BEHAVIOR: The adults stay in close proximity to the foodplants and usually fly only a few inches above the ground. A fair amount of time is spent by both sexes landed either on the foodplants, nearby vegetation, or the ground, as the open ridgetop and open slope habitats of this species lend themselves to frequent winds. The females, before ovipositing, hover about and land repeatedly on the foodplant, and then walk over the plant for several seconds to minutes before ovipositing. Nectar sources have not been recorded for this species.

LIFE HISTORY: This was recorded in part by Emmel and Shields (1980). The ova may be placed on leaf surfaces, petioles, stems, and seedpods. Occasionally, ova are deposited on ground litter near the base of the foodplant. Although diapause was thought to occur as a partly grown larva in the paper by Emmel and Shields, recent studies by G. Pratt and J. Emmel indicate that the ova hibernate. The ova then hatch soon after snowmelt in early spring. The larvae feed both on the new vegetative growth of the foodplant, as well as on the flowers and young fruit. While not feeding, the larvae rest in ground litter near the base of the foodplant. The ground color of the mature larva is a dirty white or cream, with prominent dark brown chevrons when viewed dorsally. The pupa is a light tan to pale greenish-tan with pale green wingcases.

At least four species of ants have been noted to "tend" the larvae (Emmel and Shields, 1980). The significance of myrmecophily in our North American lycaenids has been little studied in comparison to thorough research on the association between lycaenid larvae and ants in Africa, Australia, Asia, and Europe (e.g., see reviews by Clark and Dickson, 1956; Malicky, 1970; Henning, 1983). Likewise, the significance of sound production by lycaenid pupae needs to be studied at length in natural situations, such as with both symbiotic ants and predaceous ants (Downey, 1966).

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: See discussion under *I. icarioides*. *I. shasta* is sometimes sympatric with an alpine subspecies of *I. lupini*. It may be distinguished from this species by the lack of a prominent orange aurora in the submarginal area of the *I. shasta* males, and a similar marked reduction or absence of the orange aurora in the submarginal area of the *I. shasta* females.

GEOGRAPHIC AND SEASONAL VARIATION: As the species is univoltine, there is no seasonal variation. The complex geographic variation of this species over its greater range is discussed by Emmel and Shields (1980). Further study of the Great Basin populations would be an area of fruitful research.

The populations in the Sierra Nevada included under nominate *shasta* are somewhat variable, with lower elevation specimens being slightly larger and having expansion of the dark areas dorsally in both sexes. C. L. Fox (1924) named these darker populations *comstocki*, but Comstock (1927) illustrates both "typical" *shasta* and topotypical *comstocki* from the same locality; thus, it is our opinion that the name *comstocki* is a synonym of nomotypical *shasta*, but could be retained as a form name for the darker phenotype of this subspecies.

GENERAL REMARKS: For additional details on the biology and foodplants of this species, the reader is referred to the paper by Emmel and Shields (1980).

a. *P. (I.) s. shasta* (W. H. Edwards)

DIAGNOSIS: The males of this subspecies have wide, dark borders on the dorsal surface of the forewing, and the underside of the forewing usually has a black post-basal spot present. The nominotypical subspecies of *I. shasta* is confined to the Sierra Nevada of California and the Carson Range in extreme western Nevada.

ORIGINAL DESCRIPTION: W. H. Edwards, *Proceedings Academy Natural Sciences*, Philadelphia, 14: 224-225 (1862).

- TYPE LOCALITY: "California", restricted to south of Kings-Kern Divide, Tulare County, California by F. M. Brown, *Transactions American Ent. Soc.*, 96: 403 (1970). Neotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Ent. Soc.*, 96: 404 (1970).
- DISTRIBUTION: This subspecies is found in the Sierra Nevada in mountains at mid- to higher elevations from Tulare County northward to Nevada County. Populations in eastern Plumas County and western Lassen County along the east flank of the Sierra Nevada appear to be phenotypically closer to the western Great Basin populations. The record of this species occurring in Siskiyou County in northern California reported by Emmel and Shields (1980) is apparently erroneous.
- ELEVATION RANGE: From 7,000 to 11,300' elevation.
- HABITAT AND PLANT COMMUNITIES: This species typically occurs on open, exposed, sunny, gravelly-soiled and well-drained flats, slopes, hilltops, or ridges. These areas are usually within the Upper Montane Coniferous Forest plant community, Subalpine Forest, or Arctic Alpine Cushion Plant communities. The associated vegetation in these habitats is usually scrubby, low-growing, and relatively sparse.
- PHENOLOGY: From mid-July to late August, depending on elevation and snowpack. Most populations seem to have their peak flight in late July to early August.
- FOODPLANTS: For the Sierra Nevada populations, the following species of Fabaceae are used: *Astragalus purshii* Dougl.; *A. whitneyi* Gray; *Lupinus breweri* Gray var. *bryoides* C. P. Sm. in Jeps.; *L. lyallii* Gray. A single instance of the species using *Lupinus arbustus* Dougl. has been reported; this is apparently not a regularly used foodplant (All records in Emmel and Shields, 1980).

b. *P. (I.) s. pallidus* Austin

- DIAGNOSIS: These *I. shasta* populations of the western Great Basin differ from nomotypical *shasta* in the following characters: specimens tend to be slightly smaller; dorsally, the males have a thinner terminal dark band on the forewing, and on the hindwing the black spotting in the submarginal area tends to be reduced and less shaded with dark scaling; on the females, dorsally, there is expansion of the blue scaling on both forewing and hindwing, often covering three-quarters of the wing; ventrally, the spotting pattern is somewhat bolder with greater contrast between the areas of dark brown and black scaling and white scaling, rendering a more variegated pattern to the wing.
- DISTRIBUTION: Populations with this phenotype are widely scattered over the western Great Basin and eastern Oregon; in California, they are found in the White Mountains of Inyo and Mono County, and in the Warner Mountains in the northeastern corner of the state; populations with a similar phenotype are found in Plumas and Lassen County on the east flank of the Sierra Nevada.
- ELEVATION RANGE: 7,000 to 12,500' elevation.
- HABITAT AND PLANT COMMUNITIES: The typical habitat is similar to that described for the nomotypical subspecies. Most *pallidus* populations occur in the Subalpine Forest or Mountain Sagebrush Scrub plant community and are associated with a dominant growth of dwarfed, scrubby *Artemisia* species.

PHENOLOGY: These populations fly from early July to mid-August, depending on elevation and snowpack.

FOODPLANTS: The following species of Fabaceae have been recorded as foodplants of *pallidus* populations within California: *Astragalus kentrophyta* Gray var. *implexus* (Canby) Barneby; *A. purshii* Dougl.; and *Trifolium andersonii* Gray ssp. *monoense* (Greene) J. Gillett. Other hosts for populations in Nevada and Utah, as well as documentation of these California foodplants, are listed in Emmel and Shields (1980).

179. *Plebejus (Icaricia) acmon* (Westwood and Hewitson)

ADULT BEHAVIOR: Adults of *I. acmon* fly close to the ground and have somewhat of a "jerky" flight pattern. They are usually found in proximity to the foodplants, and frequently perch on them or on adjacent vegetation. The males and occasionally the females are attracted to mud or damp sand. Nectar sources are poorly documented for this species, but presumably would include some of its *Eriogonum* host plants if they happen to be in bloom at the time the adults are flying.

LIFE HISTORY: The life history has been recorded for the nominotypical subspecies. The echinoid egg is a delicate pale green. Eggs hatch about seven days after oviposition and the mean time of larval development is approximately 32 days at 67°F. This may be decreased to as short as fifteen days at 84°F. The mature larva is soiled yellow to green with variable dorso-lateral markings, and is covered with short downy white hairs. A narrow dorsal stripe is greenish. The pupa is greenish on the abdomen and brown elsewhere. Pupae hatch in about 10-15 days in nature. Goodpasture (1973c) states that diapause is facultative in all three species of the *P. acmon* group; larval diapause in the second or third instar may be prevented easily by rearing freshly laid eggs to adult under long day regime (16 hours light, 8 hours darkness) or continuous illumination. There are four larval instars. The overwintering site in nature is apparently in leaf litter at the base of the foodplant. When leaf litter is swept away by winter flooding, as occasionally happens at Putah Creek near Davis, overwintering larvae for the spring brood of adults is lost and the species is re-established later in the year by colonizing adults of this very vagile butterfly (Shapiro, 1974c). Larval diapause is believed to be terminated in the wild between 30 and 60 days prior to the first seasonal appearance of the adults.

CHROMOSOME NUMBER: n = 24, from material taken at Davis in Yolo County and at Monticello Dam in Napa County, California (Goodpasture, 1973b).

SIMILAR SPECIES: The characteristics that differentiate the three species in the *Plebejus acmon-lupini-neurona* complex are given by Goodpasture (1973a). In our area, *acmon* and the *Dedeckera*-associated segregate may be differentiated by the pink submarginal band on the hindwing of the males in contrast to the orange color of *a. texana* and *lupini*. *Plebejus acmon* is also almost always smaller than *P. lupini*.

For more certain separation of the species *acmon* and *lupini*, examination of both male and female genitalia is helpful. In the males, the uncus in dorsal view is sharply pointed in *acmon*, but blunt in *lupini*; in *P. a. texana* it is intermediate. In the female genitalia, when viewed dorsally, the shape of the sterigma is tubular in *P. acmon*, whereas in *P. lupini* it is heart to spade-shaped apically; in *P. a. texana*, it is apically bulbous, and sharply pointed.

GEOGRAPHIC AND
SEASONAL VARIATION:

In many populations of typical *acmon*, considerable seasonal variation in extent of cyanic blue scaling on the upper wing surface occurs in the females. Also, early spring females with extensive blue scaling (form "cottlei," named by Fordyce Grinnell (1916) from San Francisco) differ markedly from the usually concolorous brown summer phenotype. This intense violet-blue condition tends to be particularly pronounced in females of coastal and low elevation populations that have extended, early spring to late summer flight periods (Goodpasture, 1973c). Goodpasture has tested the progeny of females taken at Monticello Dam and has found that the earliest females produce progeny that are progressively less blue than their mothers, and that by June all female progeny essentially lack blue scaling. In another named aberration, form "labecula" (Watson & Comstock, 1920), the male and female differ from typical *acmon* in that the extradiscal rows of spots on the ventral surface of the wings are obsolete to absent. The male and female types of "labecula" came from the vicinity of San Francisco and Nevada, respectively.

GENERAL REMARKS:

The biology and systematics of this species and the two closely related species which follow are reviewed in detail by Goodpasture (1973c). Goodpasture's morphological and biological study showed that in California, reproductive isolation among the three species appeared to be complete or nearly so; genitalic intermediacy between *P. lupini* and *P. acmon* or *P. neurona* was not observed. However, intermediacy and convergence in most characters of wing color and pattern occurs at numerous southern California localities. Whether this is the result of convergence, hybridization, or a combination of both these factors remains to be determined.

This common butterfly occurs throughout western North America, from southern Canada southward into northern Baja California and central mainland Mexico. The type of the species is from California, and within our state we have three subspecies or segregates represented.

a. *P. (I.) a. acmon* (Westwood and Hewitson)

DIAGNOSIS:

In the male, the dorsal wing surface is a light purplish-blue of high saturation and brilliance. The submarginal band on the hindwing is pink, while the marginal band on the forewing is reduced to a thin terminal line. Females tend to lack good diagnostic characters (in this species and the next two species, *lupini* and *neurona*; see Goodpasture, 1973c). Dorsally, the female is largely brown, although varying degrees of basal blue scaling occur. There is a prominent orange aurora in the submarginal area of the hindwing. Ventrally, the two sexes are similar.

ORIGINAL DESCRIPTION:

Westwood and Hewitson, *Gen. diurn. Lepid.*, 2: pl. 76, fig. 2 [1852].

TYPE LOCALITY:

"California". Holotype in British Museum.

DISTRIBUTION:

This nominotypical subspecies is widely distributed throughout California, and from our state extends into northern Baja California, eastward into Nevada and northward to Oregon. The northern and eastern limits of its range are uncertain due to an apparent broad blend zone with the subspecies *lutzi* (see Goodpasture, 1973). Because this is a vagile and colonizing species, it occurs in numerous habitats and has been taken in virtually every county of the state. Its occurrence in the deserts is much more sporadic, often being recorded there only in years of above normal rainfall. Likewise, it is not regularly found at the higher elevations, and the only permanent breeding populations may be in the lowlands.

- ELEVATION RANGE: From sea level to 10,000', with most captures recorded below 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is found in numerous habitats and plant communities, but most commonly in either disturbed or weedy areas, or open meadows or fields within the following plant communities: Coastal Dune Sand Plant, Southern Coastal Sage Scrub, Inland Sage Scrub, Northern Coastal Scrub, Mixed Chaparral, Foothill Woodland, Valley and Foothill Grassland, Southern and Northern Oak Woodland, Lower and Upper Montane Coniferous Forest, Great Basin Sagebrush Scrub, Pinyon-Juniper Woodland, and Subalpine Forest.
- PHENOLOGY: The butterfly is multivoltine, with a succession of broods from early spring to late fall. The earliest spring records are for late January and the latest fall records are for late November. Considerable variation in the outer limits of the flight period occur from year to year, depending on seasonal rainfall and temperature patterns.
- FOODPLANTS: *Plebejus acmon* is usually associated with certain perennial species of *Eriogonum* or certain annual and perennial legumes, at least in California where extensive sympatry with *Plebejus lupini* and *P. neuona* occurs. Goodpasture (1974) found that *P. acmon acmon* feeds on more species of plants than any other member of this group of blues, and that it is the only subspecies to utilize legumes as well as Polygonaceae. This butterfly has been observed to use more than one plant family at three sites (in Napa County, Kern County, and San Diego County), but normally it apparently uses only one plant species in a given population. Host species used include *Lotus* and *Astragalus* (Family Leguminosae), especially *L. scoparius* (Nutt.) Ottley, the primary host in southern California (Emmel and Emmel, 1973). In the Polygonaceae, Goodpasture (1974) lists the following records: *Polygonum aviculae* L., *Eriogonum elongatum* Benth., *E. latifolium* Sm., *E. nudum* (Dougl. ex Benth.) S. Stokes, *E. parvifolium* Sm. in Rees., and *E. plumatella* Dur. & Hilg. G. Pratt and J. F. Emmel (unpublished data) have observed a close association of *acmon* and *Eriogonum kennedyi* at Doble in the San Bernardino Mountains, where it is sympatric with *P. neuona*. The butterfly is not known to use *Eriogonum fasciculatum* Benth., a puzzling situation since this *Eriogonum* species is widespread in southern California and is frequently found in the same habitats as *P. acmon*. Possibly, this is the result of competitive displacement by the closely related *P. lupini monticola* which uses this *Eriogonum* species extensively in the mountains of southern California.

b. *P. (l.) a. texana* (Goodpasture)

- DIAGNOSIS: This subspecies closely resembles *Plebejus lupini lupini* in the dorsal wing color, forewing marginal band, color of the hindwings of the marginal band, and the presence of a dark border next to the hindwing submarginal band. These two entities (*lupini* and *texana*) differ in external phenotype primarily in intensity of expression of characters. The male of *texana* has a dorsal wing color of purplish-blue with low saturation and brilliance; the submarginal band on the hindwing is orange, the marginal band on the forewing is broad to very broad, and dark scaling at the apex of the discal cell is prominent. The female is largely brown dorsally, with only about the basal one-fifth of the wing with cyanic blue overlay scaling; it has a prominent orange aurora in the submarginal area of the hindwing. Primarily a southwestern subspecies from Mexico, Arizona, New Mexico, and Texas, it barely enters our area in southeastern California.
- ORIGINAL DESCRIPTION: Goodpasture, *Pan-Pacific Entomologist*, 49: 149-159 (1973).

- TYPE LOCALITY: One mile south of Hillside, Yavapai County, Arizona. Holotype in Los Angeles County Museum.
- DISTRIBUTION: This subspecies is found across Arizona, New Mexico, western Texas, west central Mexico, and scattered parts of Colorado, Utah, Nevada, and extreme southeastern California, occurring most commonly in mountains below about 9,000'. In California, it is known from the Kingston Range, the New York Mountains, the Providence Mountains, and the Granite Mountains north of Amboy, all in San Bernardino County.
- ELEVATION RANGE: In our area, between 4,400' and 7,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This subspecies is found in the canyons of our higher desert mountain ranges in the eastern Mojave Desert, within Pinyon-Juniper Woodland and Great Basin Sagebrush Scrub.
- PHENOLOGY: In the eastern Mojave mountain ranges, the subspecies flies from mid-April to as late as the end of June and again in late August through mid-October, depending on summer rains (Goodpasture, 1973a).
- FOODPLANTS: Host plants for the species outside of California (Goodpasture, 1974) are *Eriogonum effusum* (= *microthecum* Nutt.), *E. racemosum* Nutt., and *E. wrightii* Torr. ex Benth. The host plants in the eastern Mojave Desert are unknown, but *Eriogonum wrightii* is strongly suspected on the basis of adult association.

c. *P. (I.) a. ssp. (Dedeckera-associated populations)*

- DIAGNOSIS: This is a large subspecies associated with the polygonaceous shrub *Dedeckera eurekaensis* in Inyo and Mono counties. Males are similar to *P. a. acmon* but tend to be larger. The females, also larger than typical *acmon*, have extensive blue scaling dorsally, often extending over the basal two-thirds of the forewing and hindwing. Ventrally, it is similar to typical *acmon*.
- DISTRIBUTION: This segregate is known only from Coldwater Canyon on the west slope of the White Mountains, Mono County, and at the extreme southern end of the Last Chance Range in Inyo County.
- ELEVATION RANGE:
- HABITAT AND PLANT COMMUNITIES: The *Dedeckera* colonies grow on rocky talus slopes within the Shadscale Scrub plant community.
- PHENOLOGY: This segregate is apparently univoltine, flying from mid-May to late June.
- FOODPLANTS: Intimately associated with *Dedeckera eurekaensis* (Polygonaceae), the butterfly is presumed to use this species as its foodplant.

180. *Euphilotes baueri baueri* (Shields)

SPECIES SYNOPSIS:

- DIAGNOSIS: This is a spring-flying species in the western Great Basin. It is characterized by reduction of the black border on the male's dorsal surface, extensive blue basal scaling sometimes involving the basal two-thirds of the dorsal wing surface in

females, and dark markings on the underside of both sexes which are somewhat more prominent than those seen in *E. b. glaucon*.

- ORIGINAL DESCRIPTION: O. Shields, *Bulletin Allyn Museum of Entomology*, 28: 15-16 (1975).
- TYPE LOCALITY: West side of Gilbert Pass, Inyo County, California. Holotype in Allyn Museum of Entomology.
- DISTRIBUTION: Within California, this species is found at mid-elevations in the Inyo Mountains and Grapevine Mountains of Inyo County northward through the mid-elevations of the White Mountains to the Adobe Hills region east of Mono Lake in Mono County. From here it extends eastward into western Nevada.
- ELEVATION RANGE: From 4,300 to 6,500' elevation.
- HABITAT AND PLANT COMMUNITIES: This species is typically found on gravelly to sandy slopes and flats within the Pinyon-Juniper Woodland or Sagebrush Scrub plant communities.
- PHENOLOGY: This is an early-flying species, with some adults on the wing as early as the first week of May. The flight period extends into early to mid-June.
- FOODPLANTS: The California populations are all associated with two varieties of *Eriogonum ovalifolium* Nutt.; these are variety *ovalifolium* Nutt. and var. *multiscapum* Gand. (Shields, 1975; J. F. Emmel, unpublished data).

***Plebejus (Icaricia) lupini* (Boisduval)**

- ADULT BEHAVIOR: Adults of both sexes remain in close proximity to the *Eriogonum* foodplants. Males perch on the highest parts of the foodplant or on adjacent vegetation. The females spend a considerable amount of time landed on the foodplant, or walking over it. In populations where the foodplant happens to bloom during the flight period, the adults will visit the *Eriogonum* flowers for nectar. Males are strongly attracted to mud or damp sand for moisture. At night, the adults roost on stems of the host or nearby vegetation with the head pointed downward.
- LIFE HISTORY: [T.C. Emmel, please fill in on basis of kodachrome slides.]
- CHROMOSOME NUMBER: n = 24 for *P. l. lupini* collected at Echo Lake at 8,000' in El Dorado County, and *P. l. monticola* from San Diego County and Los Angeles County (Goodpasture, 1973b).
- SIMILAR SPECIES: See discussion under *Plebejus acmon*.
- GEOGRAPHIC AND SEASONAL VARIATION: In the populations where there has been an apparent second brood, the phenotypes of the two broods do not seem to differ significantly. There is considerable geographic variability in this species, particularly in the southern California populations (Goodpasture, 1973). Within populations of *P. l. monticola*, there is considerable variation in the

females, with some showing extensive cyanic blue scaling dorsally, while others may lack this almost entirely and be largely brown. In the higher elevations of the San Bernardino Mountains, for example, the majority of *monticola* females seem to be of the largely brown form. Populations of subspecies *argentata* seem to be much more homogenous in phenotype in contrast to those of *monticola*. There is an apparent blend zone between subspecies *argentata* and subspecies *lupini* along the east slope of the Sierra Nevada from northern Inyo County into southern Mono County. Populations of *P. lupini* in the North Coast Ranges are slightly atypical, usually showing some basal blue scaling in the females.

GENERAL REMARKS: The reader is referred to the papers by Goodpasture (1973a, 1973b, 1974) for more detailed discussion of this extremely complex species. Laboratory hybridization studies of the species and *P. acmon* or *P. neurona* would be of considerable interest in sorting out the genetic relationships of these butterflies.

This species is genitally distinct from *P. acmon* and is remarkably homogeneous in genitalic form throughout its range from Baja California north to Washington and east to southwestern Utah. However, considerable divergence has occurred in wing color and pattern (Goodpasture, 1973c). We recognize four subspecies as occurring within the state of California.

a. *P. (I.) I. lupini* (Boisduval)

DIAGNOSIS: This subspecies is characterized by its relatively large size, a darker purplish-blue ground color dorsally in the males, with broad marginal bands on the forewings and an orange aurora in the submarginal area of the hindwing which is heavily bordered by dark scaling. The dorsal ground color in the females is largely brown with varying degrees of (usually poorly) developed cyanic overscaling in the basal areas of the wings; the orange aurora in the submarginal area of the hindwing is usually well-developed. Ventrally, both sexes are marked much like *P. acmon*, except that the black markings tend to be slightly reduced in size from that seen in *acmon*.

ORIGINAL DESCRIPTION: Boisduval, *Ann. Soc. Ent. Belgique*, 12: 46 (1869).

TYPE LOCALITY: "Southern California". Restricted by Emmel, Emmel, and Mattoon, *Journal Research Lepidoptera*, : (1988) to Gold Lake, Sierra County, California. Holotype in U.S. National Museum.

DISTRIBUTION: This subspecies is widely distributed in the Sierra Nevada from Tulare County northward to the Warner Mountains, the Mt. Shasta region, the Klamath Mountains Assemblage, and the North Coast Ranges. It is also found in the higher elevations of the White Mountains. From California it ranges northward into the Cascades of Oregon and eastward into the mountains of central Nevada. In the northern and eastern parts of its range outside of California, it seems to form a blendzone of sorts with *P. acmon lutzii* (see Goodpasture, 1973). The populations outside of the Sierra Nevada in northern California are subtly atypical from the Sierran *lupini*, but are lumped here with nominotypical *lupini* until these populations can be studied more completely.

ELEVATION RANGE: From 5,000 to approximately 12,000' elevation.

HABITAT AND PLANT COMMUNITIES: Usually on open gravelly or rocky slopes within the Upper Montane Coniferous Forest or Subalpine Forest plant communities, where its

usual foodplant, *Eriogonum umbellatum* Torr., is locally common. A higher elevation ecotype in the Sierra Nevada and White Mountains is found on open slopes in the Arctic-Alpine Cushion Plant community.

PHENOLOGY: Univoltine, with records ranging from mid-June to mid-August, with a peak flight period in mid- to late July.

FOODPLANTS: The major host in the Sierra Nevada and the Klamath Mountains region is *Eriogonum umbellatum* Torr. (J. F. Emmel, unpublished data; Shapiro et al, 1981). The higher-elevation populations are closely associated with *Eriogonum ovalifolium* Nutt. var. *nivale* (Canby) Jones (J. F. Emmel and G. Pratt, unpublished data).

b. *P. (I.) I. monticola* (Clemence)

DIAGNOSIS: In this subspecies of the southern California mountains, the males are characterized by a silvery blue ground color, moderately wide terminal band on the forewings, and well-developed submarginal spots bordered by pinkish-orange scaling in the submarginal area of the hindwing. The females have extensive blue scaling dorsally over the proximal two-thirds to three-quarters of the forewing and proximal two-thirds of the hindwing; a dark terminal band occupies the distal one-fourth to one-third of the forewing; on the hindwing, the orange to orange-red aurora is well developed and contains a series of well developed black submarginal spots. Ventrally, both sexes are similar to *P. acmon*, except that the dark spots are more boldly developed. Clemence (1909) contrasted the silvery-blue ground color of *monticola* against the violet-blue of typical *acmon*, and emphasized the heavy pronounced ventral markings, including the red crescents on the hindwing, found in *monticola*.

ORIGINAL DESCRIPTION: Clemence, *Canadian Entomologist*, 41: 38 (1909).

TYPE LOCALITY: Although not stated in the original description, the type locality is Upper Arroyo Seco, [San Gabriel Mountains], Los Angeles County, California. This is based on Comstock's (1927) figures of the types which list this as the type locality of the specimens illustrated. Holotype in Natural History Museum of Los Angeles County.

DISTRIBUTION: This subspecies is found at the mid- to higher elevations of the southern California mountains, from San Diego County northward through the Santa Ana and San Jacinto ranges, through the San Gabriel and San Bernardino Mountains northwestward to the higher mountains of Ventura and Santa Barbara County, and northward into the South Coast Ranges of San Luis Obispo and Monterey counties. It is also found in northern Baja California. In the area between the San Emigdio Range and the Tehachapi Mountains in extreme southern Kern County, there is a blend zone with subspecies *chlorina*.

ELEVATION RANGE: From 1,000 to 9,000' elevation, with most populations between 3,000 and 7,000' elevation.

HABITAT AND PLANT COMMUNITIES: The butterfly typically occurs on open flats or open slopes where *Eriogonum fasciculatum* Benth. is locally abundant; this may be within Lower or Upper Montane Coniferous Forests, Mixed Chaparral, Southern Mixed Evergreen Forest, or Great Basin Sagebrush Scrub.

PHENOLOGY: Most populations seem to be univoltine, although a second brood is possible as indicated by laboratory rearings in which larvae fail to enter diapause. The flight period extends from mid-April to early July, depending on elevation.

FOODPLANTS: The sole host for most populations is *Eriogonum fasciculatum* Benth. In San Diego County, females have also been observed to oviposit on *E. wrightii* var. *membranaceum* (S. Stokes) S. Stokes as well as on *E. fasciculatum* var. *polifolium* (Benth.) (Goodpasture, 1974). This subspecies has also been observed to fly in close association with *Eriogonum wrightii* Torr. ex Benth. in the San Jacinto Mountains (J. F. Emmel, unpublished data).

c. *P. (I.) I. chlorina* (Skinner)

DIAGNOSIS: In the Tehachapi Mountains of southern California one finds some populations with the males lacking the cyanic blue color and having a distinctively greenish cast. The females of these populations are brown, much like *P. acmon* females, generally lacking any basal blue scaling. When the females do show blue scaling in the dorsal-basal area, it also has a greenish cast similar to that seen in the males. Skinner (1893) described the ground color of the female as a fawn brown, with an overlying iridescent, very light green. Ventrally, the adults are much like *P. I. monticola*. There is a marginal border of orange on the hindwings. Although this taxon has previously gone under the form name "chlorina", we consider it a true subspecies for this restricted geographic area. It was originally described as a separate species by Skinner (1892).

ORIGINAL DESCRIPTION: Skinner, *Entomological News*, 3(1): 15 (1892).

TYPE LOCALITY: Tehachapi, [Kern County], California. Holotype in Carnegie Museum.

DISTRIBUTION: This subspecies is restricted to the northern and eastern slopes of the Tehachapi Mountains.

ELEVATION RANGE: 3,500 to 6,000' elevation.

HABITAT AND PLANT COMMUNITIES: As with *monticola*, this subspecies is associated with stands of *Eriogonum fasciculatum* Benth. within the following plant communities: Mixed Chaparral, Southern Oak Woodland, Southern Mixed Evergreen Forest, and Great Basin Sagebrush Scrub.

PHENOLOGY: Records range from early May to late July, suggesting the possibility of two broods. The type was taken on July 6th.

FOODPLANTS: The presumed foodplant of this subspecies is *Eriogonum fasciculatum* Benth., with which it is closely associated.

d. *P. (I.) I. argentata* Emmel, Emmel, and Mattoon

DIAGNOSIS: This is a subspecies of the California desert regions from the northern Mojave Desert through the southern and central Death Valley region to the southern Sierra Nevada at low to mid-elevations. It is characterized by a much paler light silvery blue in the males, with reduction of the width of the terminal dark band on the forewing and reduction in the dark spots in the submarginal area of the hindwing. On the females, there is reduction of the dark spots on the submarginal area of the hindwing dorsally, as well as a generally paler orange aurora in the submarginal area; as in the males, the silvery blue scaling dorsally tends to be paler than that

seen in subspecies *monticola*. Ventrally, the dark markings are reduced in size from that seen in *monticola*.

- ORIGINAL DESCRIPTION: Emmel, Emmel, and Mattoon, *Journal Research Lepidoptera*, : (1988).
- TYPE LOCALITY: Slope 0.2 airmile west of junction Saline Valley Road and Hunter Mountain Road, 5,950-6,100' elevation, east end of Nelson Range, Inyo County, California. Holotype in Natural History Museum of Los Angeles County.
- DISTRIBUTION: This subspecies is found in the Panamint, Argus, and Coso Ranges in southern Inyo County; from here, it ranges eastward to the Kingston Range of the eastern Mojave Desert and westward to the east slope of the Sierra Nevada from approximately Owens Lake south to the Piute Mountains region of Kern County. Specimens from the Grapevine Mountains on the California-Nevada border seem closest to this subspecies.
- ELEVATION RANGE: From 3,000 to 9,000' elevation.
- HABITAT AND PLANT COMMUNITIES: In the type locality, the butterfly is found in an admixture of Great Basin Sagebrush Scrub and Pinyon-Juniper Woodland plant communities, on a rocky to gravelly slope where the foodplant, *Eriogonum umbellatum* Torr., is common. The butterfly occupies similar habitats in much of the remainder of its range; in the higher elevations of the Piute Mountains, it is found in Lower and Upper Montane Coniferous Forest plant communities. On the lower elevations of the west slope of the Piute Mountains, the butterfly is found in a sparse Mixed Chaparral or Foothill Woodland association.
- PHENOLOGY: Mostly univoltine, but an occasional mid- to late summer capture indicates a partial second brood in some seasons. The main flight period extends from early May to mid-July, depending on elevation and seasonal temperature and precipitation patterns.
- FOODPLANTS: In the type locality, the butterflies are closely associated with *Eriogonum umbellatum* Torr. var. *nevadense* Gand. and var. *chlorothamnus* Reveal, both of which likely serve as foodplants. In the Panamint Range, the butterfly is associated with *E. umbellatum* var. *subaridum* S. Stokes. In the Kingston Range of extreme northeastern San Bernardino County, the butterfly has been observed to oviposit on *E. umbellatum* var. *ferrisii* (A. Nels.) Stokes. On the southern east slope of the Sierra Nevada, the subspecies is associated with *E. umbellatum* var. *nevadense* and var. *chlorothamnus*. In the higher elevations of the Piute Mountains, it is associated with *Eriogonum umbellatum*, variety undetermined at this time. Some populations at lower elevations in the Piute Mountains region are associated with *Eriogonum fasciculatum* Benth. var. *polifolium* (Benth.) S. Stokes. The Grapevine Mountains populations are associated with *Eriogonum umbellatum* var. *versicolor* S. Stokes.

181. *Plebejus (Icaricia) neurona* (Skinner)

- DIAGNOSIS: This is a relatively local "blue" of the southern Sierra Nevada-Transverse Range axis and it is particularly remarkable in that it is the only *Icaricia* that is *dark brown* in *both* sexes on the dorsal surface. The forewing veins are outlined with orange scaling extending from the margins inward towards the body. Ventrally, it is similar to *P. acmon* except that the ground color tends to have a light brownish cast to it. The genital morphology is almost identical to that of *P. acmon acmon* (Goodpasture, 1973c). However, females of *P. lupini*, which are sometimes

phenotypically identical to females of *P. neurona*, may be distinguished by their apically expanded copulatory organ.

- ORIGINAL DESCRIPTION: Skinner, *Entomological News*, 13: 15 (1902).
- TYPE LOCALITY: Doble, [San Bernardino Mountains], San Bernardino County, California. Holotype in Carnegie Museum.
- DISTRIBUTION: The highly localized colonies have a discontinuous distribution along the southern Sierra Nevada and Transverse Range Axis from southern Tulare County through Kern County into northeastern Ventura County. Scattered colonies then extend southeastward through montane Los Angeles County into western San Bernardino County.
- ELEVATION RANGE: From 4,000' to 8,500' elevation.
- HABITAT AND PLANT COMMUNITIES: Typically found on open gravelly to sandy flats and slopes, usually within Lower and Upper Montane Coniferous Forests, but also in Great Basin Sagebrush Scrub and Pinyon-Juniper Woodland.
- PHENOLOGY: This species is bivoltine, with the first brood flying in May and June and the second brood from early August to mid-September. In very dry years, only the first brood may fly in significant numbers.
- ADULT BEHAVIOR: The adults remain in close proximity to their hostplants, flying only a few inches above the ground and over the foodplants which grow prostrate in mats. Nectar sources have not been documented except in the case of the population at the type locality where flowers of *Eriogonum kennedyi* Porter in Wats. are visited for nectar (J. F. Emmel, unpublished data). The males are attracted to moisture.
- LIFE HISTORY: The echinoid egg is a delicate greyish-green and is covered with a fine whitish reticulation of low raised walls. The eggs hatch about nine days after oviposition (Comstock and Dammers, 1933). The mature larva has an apple-green body surface, with profuse white hairs, giving the suggestion of a grey overcast. There are broad white diagonal lateral bands on the segments, and a faint dark mid-dorsal line. The larva does not taper anteriorly and posteriorly to the same extent as with most other species in this group. Pupation occurs on the foodplant (after about 40 days in the laboratory). A silken girdle and silk button for the cremasteric attachment are used. The front of the pupa is vivid green, with a yellow-green abdomen and bluish-grey wingcases. The body is almost free of hairs. Adults emerge for the second brood only nine days after pupation. The larvae apparently overwinter facultatively in the second or third instar.
- FOODPLANTS: *Eriogonum wrightii* Torr. ex Benth. var. *subscaposum* Wats. and var. *trachygynum* (Torr.) S. Stokes (Polygonaceae) (Goodpasture, 1974). In the type locality, the butterfly uses *Eriogonum kennedyi* Porter ex Wats. (J. F. Emmel and G. Pratt, unpublished data).
- CHROMOSOME NUMBER: $n = 24$ in material from Chuchupate Ranger Station, in Ventura County (Goodpasture, 1973b).
- SIMILAR SPECIES: While this species is similar to *acmon* and *lupini*, it may be distinguished by the dorsal brown wing color in the males and the usual brown wing color combined with orange scaling along the wing veins in the females. Some females of *P. lupini monticola* from the Tejon and Tehachapi Mountains in northern Los Angeles to southern Kern counties, do have forewings that have various degrees

of orange scaling near the apex margin, as in *P. neurona* (see Goodpasture, 1973c). These females may be unequivocally separated by the apically expanded copulatory organ in *lupini*. Rarely, an individual will be found in *I. a. acmon* populations with orange scaling along the wing veins as at the sand dunes at Antioch, Contra Costa County (S. O. Mattoon, unpublished data). Goodpasture has noted that populations of *P. neurona* and *P. lupini monticola*, which are convergent in wing pigmentation phenotype, are parapatric and synchronous in period of adult flight activity.

GEOGRAPHIC AND
SEASONAL VARIATION:

There is no apparent seasonal variation between the two broods. On the west slope of the Piute Mountains in Kern County, adults are consistently larger than those of higher elevation populations. Otherwise, the species does not show any notable geographic variation over its range.

GENERAL REMARKS:

The absence of this species from apparently suitable habitats within its known range is puzzling. It is possible that the presence of certain species of larvae-tending ants is a pre-requisite for the successful survival of any given population, as may be the case in other *Plebejus* species.

182. *Plebulina emigdionis* (F. Grinnell)

DIAGNOSIS:

This rather local species of southern California is sexually dimorphic. Dorsally the males are pale blue with broad brownish marginal bands and a submarginal row of black dots on the hindwing. Ventrally, the coloration is whitish, with a pattern of black dots similar to that of *Plebejus acmon*, and a faintly marked orange submarginal band of spots on the secondaries. The female is a light brown dorsally, overlaid with blue scaling in the basal area of both wings, and has an orange submarginal band on the forewing and hindwing with orange scaling suffusing the surrounding area. Ventrally, it is similar to the male.

ORIGINAL DESCRIPTION:

F. Grinnell, *Entomological News*, 16: 115 (1905).

TYPE LOCALITY:

San Emigdio Canyon, Kern County, California. Holotype in American Museum of Natural History.

DISTRIBUTION:

The type locality is located at the extreme southern end of the San Joaquin Valley. From here it extends southwestward into northern Ventura County and eastward to the southern Owens Valley and along the southwestern border of the Antelope Valley in scattered populations, to its eastern limit along the Mojave River near Victorville.

ELEVATION RANGE:

From 1,000 to 4,500' elevation.

HABITAT AND PLANT
COMMUNITIES:

In the foothill populations, the butterfly is typically found in broad open valley bottoms, usually near an intermittent stream, where the foodplant, *Atriplex canescens* (Pursh) Nutt. is locally common, usually within a Great Basin Sagebrush Scrub or sparse Mixed Chaparral plant community. Along the Mojave River, the butterfly is found on sandy flats where the *Atriplex* is locally abundant, adjacent to extensive stands of cottonwood trees (*Populus fremontii* Wats.), in a Desert Riparian Woodland community. In the southern Owens Valley, the butterfly is associated with stands of *Atriplex* in Alkali Sink Scrub or Shadscale Scrub on sandy flats near the valley bottom, in a more xeric environment than that of the other populations of this butterfly.

- PHENOLOGY:** Several generations occur per year. The first brood flies in late April to May, the second brood in late June and early July, and the third brood in August to early September. The size of the summer broods probably depends in part on summer rainfall. The butterfly was formerly thought to be single-brooded.
- ADULT BEHAVIOR:** The adults stay in close proximity to their *Atriplex* foodplant, and frequently perch on it. Tapping the plants while collecting will often stir up resting adults. No nectar sources have been observed.
- LIFE HISTORY:** The echinoid eggs are deposited singly on the leaves of the host by confined females and hatch in eight to ten days (Comstock and Dammers, 1932). In the wild, ova have been found on the more woody stems of the *Atriplex* host, particularly near the base of the plants (G. Pratt, G. Ballmer, and J. F. Emmel, unpublished data). The mature larva is extremely variable in color and ranges from a greenish through blue-green and grey to a brown ground color. All color morphs are spotted and blotched with black, and have short white hairs over the body. On the eleventh segment of the body are large retractile glands that are protruded when the larva is touched. These organs are highly attractive to ants, as evidenced by numerous field observations. The larvae are able to crawl much more rapidly than other lycaenid larvae, and can move up and down the *Atriplex* stems in a very short time period. Their feeding activity seems to be largely nocturnal in both laboratory and field observations (G. Pratt, G. Ballmer, and J. Emmel, unpublished data). Diapause normally occurs in a late larval instar. The pupa is apple-green or a straw color. It is usually attached to the foodplant by a silk button and girdle.
- FOODPLANTS:** Saltbush, *Atriplex canescens* (Pursh) Nutt. (Chenopodiaceae).
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** While somewhat similar to *Plebejus acmon*, *lupini*, or *neurona*, this species may be readily distinguished by comparison of the figures on the color plates.
- GEOGRAPHIC AND SEASONAL VARIATION:** There is no apparent seasonal variation among the various broods. Geographically, specimens from the northern Ventura County region tend to be larger than those of other populations; specimens from the southern Owens Valley tend to be slightly smaller than those of other populations.
- GENERAL REMARKS:** A most unusual feature is the extraordinary foodplant choice of this butterfly, which was once placed in the same genus *Plebejus* as the species now in the subgenus *Icaricia*. Additionally, the limited known distribution of the butterfly is puzzling in view of the fact that the foodplant is widespread throughout the western United States. It is possible that the butterfly has complex ecological requirements in addition to presence of the proper *Atriplex* foodplant. The very close relationship of the larvae of this species with certain ants suggests that the presence of the proper ant species may be one such specific requirement for the butterfly in a given locality. A study of the specific ecological requirements of this species is clearly needed.

183. *Hemiargus isola alce* (W. H. Edwards)

- DIAGNOSIS:** This butterfly and the following species are both similar in appearance. The male is blue dorsally, with an indistinct blackish terminal band on the forewing and two black dots in the submarginal area of the hindwing near the anal angle. The females are largely brown dorsally, with blue basal scaling on the forewings, and

two distinct black spots in the submarginal area of the hindwing near the anal angle. Ventrally the two sexes are similar, with a gray ground color upon which is superimposed a pattern of black and brown spots, encircled with white scaling. On the forewing, there is a very prominent row of black spots encircled with white in the post-median area of the wing; this row of black spots is greatly suppressed on the following species (*H. gyas*), and this character can be used to readily distinguish the two species.

ORIGINAL DESCRIPTION: W. H. Edwards, *Transactions American Entomological Society*, 3: 272-273 (1871).

TYPE LOCALITY: "Colorado", restricted to Turkey Creek, Jefferson County, Colorado by F. M. Brown, *Transactions American Ent. Soc.*, 96: 362-363 (1970). Neotype in Carnegie Museum, designated by F. M. Brown, *Transactions American Ent. Soc.*, 96: 365 (1970).

DISTRIBUTION: This is a vagile, colonizing species which periodically invades the state. In years of above normal winter rainfall in the deserts, the species often becomes very widespread and abundant in the southern half of the state, and can be taken in a number of habitats. In very dry years, the species is either absent or found in only very small numbers. It seems doubtful that it is a resident in any locality within the state. In addition to numerous localities scattered in the deserts, the butterfly has also been taken at various points in the mountains to as far north as the Yosemite region in the Sierra Nevada and the Sacramento Valley where its presence was noted in 1973. A single adult is known from the Donner Pass region of the Sierra Nevada. It also penetrates westward to the coast, having been taken in the Santa Monica Mountains region and in coastal San Diego County.

ELEVATION RANGE: From sea level to over 10,000' elevation.

HABITAT AND PLANT COMMUNITIES: The butterfly has been taken in numerous habitats and plant communities within the state, but most records seem to be from the Creosote Bush Scrub, Mixed Desert Scrub, Pinyon-Juniper Woodland, Mixed Chaparral, or Lower Montane Coniferous Forest plant communities.

PHENOLOGY: The species is multivoltine with records in our area ranging from April to November.

ADULT BEHAVIOR: The adults have a nervous, jerky flight, and frequently perch on medium-sized shrubs. The males are attracted to mud or damp sand.

LIFE HISTORY: [G. Pratt and G. Ballmer have data on this; to be filled in.]

FOODPLANTS: This butterfly feeds on a variety of plants in the family Fabaceae. In California, documented foodplants include the following species: *Dalea searlesiae* ; *Acacia greggii* [data from Pratt & Ballmer list to be added here].

CHROMOSOME NUMBER: Unknown.

- SIMILAR SPECIES:** The species may be confused with *H. gyas*. The presence of prominent black spots ringed with white on the ventral forewing of *H. isola* will serve to immediately distinguish it from *H. gyas*, which lacks these spots.
- GEOGRAPHIC AND SEASONAL VARIATION:** No variation has been noted in the various generations of this species in a given year. Geographically, adults from all points in the state have a similar facies.
- GENERAL REMARKS:** The ability of this small blue to rapidly colonize large portions of the state in years of exceptional winter precipitation is remarkable. In such seasons, finding this subtropical species in the arctic alpine zone of the Sierra Nevada (such as Tioga Pass), is seemingly incongruous.

184. *Hemiargus ceraunus gyas* (W. H. Edwards)

- DIAGNOSIS:** Dorsally this species is similar to *H. isola*, but the male has an extremely thin terminal black line dorsally, and the black spotting on the hindwing is usually absent; in the female, there is usually more blue dorsally, and only one black spot is present in the submarginal area of the hindwing. Ventrally, the forewings lack the bold black spots of *H. isola* and the overall appearance is more that of a "checkered" pattern.
- ORIGINAL DESCRIPTION:** W. H. Edwards, *Transactions American Ent. Soc.*, 3: 210-211 (1871).
- TYPE LOCALITY:** Tucson, Pima County, Arizona, designated by F. M. Brown and Clench, in F. M. Brown, *Transactions American Ent. Soc.*, 96: 360-362 (1970). Neotype in Carnegie Museum, designated by F. M. Brown and Clench, in F. M. Brown (1970).
- DISTRIBUTION:** Like *H. isola*, this species is also a vagile, colonizing insect. However, it tends to be more confined to the desert regions in years of abundance in contrast to *H. isola* which is found in an overall larger distribution. There are records from numerous localities in the deserts, with a few specimens having been taken in the southern California mountains, such as the Laguna Mountains, the San Bernardino Mountains, the San Jacinto Mountains, and the Santa Monica Mountains. Northward, it has been taken as far as the northern edge of Inyo County.
- ELEVATION RANGE:** From sea level to approximately 8,000' elevation. Most records are below 5,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** This butterfly is found in many ecological situations within the following plant communities: Creosote Bush Scrub, Alkali Sink Scrub, Mixed Desert Scrub, Pinyon-Juniper Woodland, Shadscale Scrub, Mixed Chaparral, Inland Sage Scrub, Foothill and Valley Grassland, Great Basin Sagebrush Scrub, and Lower Montane Coniferous Forest.
- PHENOLOGY:** This species is multivoltine, with records ranging from January to November; in general, it tends to be more abundant in late summer and early fall.
- ADULT BEHAVIOR:** This species also has a jerky flight, and frequently alights on vegetation. The males are strongly attracted to damp sand or mud. They can often be found along the sandy bottoms of desert washes. Adults have been observed to nectar at the flowers of *Eriogonum elongatum* in western Riverside County (J. F. Emmel, unpublished data).

- LIFE HISTORY:** The early stages were first described by Comstock and Dammers (1934). The delicate light green egg is turban-shaped with a depressed top. The surface is covered with small stout nodules, arranged in more or less regular diagonal lines, as with *Brephidium exilis*. The mature larvae (only 0.8 mm. in length) vary widely in body color and pattern. Some are a solid pale green in ground color. Others show green with a mauve subspiracular fold. Still others have a mauve mid-dorsal band added to the last described combination. In others, the body is deep green, light yellow, or even dark yellow. Many of the forms bear two darker diagonal bands of green laterally on each segment. The entire body is covered with short silvery white hairs. The larvae feed on the tips of the young host shoots as well as. Pupation occurs on the foodplant, using a fine silken girdle. The pupa is bright translucent green, with a dark mid-dorsal line.
- FOODPLANTS:** Various species in the family Fabaceae are used, but also several species of *Eriogonum* (Polygonaceae). Comstock and Dammers (1934) recorded *Prosopis* (Mesquite) and *Medicago* (Alfalfa); other fabaceous hosts used in California include: *Lotus scoparius* (Nutt.) Ottley; *Robinia neomexicana* (J. F. Emmel, unpublished data);
- Eriogonum* species recorded for this butterfly include *E. reniforme* Torr. & Frem., (Ballmer and Pratt, unpublished data).
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** See this section under *Hemiargus isola alce*.
- GEOGRAPHIC AND SEASONAL VARIATION:** There have been no differences noted in the phenotype of the various broods of this species. No significant geographic variation occurs within the state.
- GENERAL REMARKS:** This species may be a permanent resident in some areas of the California deserts, particularly in the Colorado Desert. Even in dry years, it tends to be taken in desert localities, although usually very sparingly in these years. Further study of the overwintering ability of this species within the state is indicated.

Superfamily Hesperioidea Latreille

H E S P E R I I D A E

The family Hesperidae, or Skippers, is a member of a different superfamily of Lepidoptera from the rest of the true butterflies. A rough estimate of the total number of species of skippers is approximately 3,500 worldwide. The Giant Skippers are commonly split off as a separate family, the Megathymidae, rather than a subfamily as here. They are differentiated from the rest of the skippers by having a head only half the width of the thorax, palpi noticeably small, large wings with proportionately narrow and pointed forewings, and a boring larva with a body much larger than the head and a whitish ground color with no ornamentation. In addition to the Giant Skippers, the following subfamilies of skippers are found in our fauna: Subfamily Heteroperinae, Subfamily Hesperinae, and the Subfamily Pyrginae. All the skippers are characterized by having: (1) six fully developed legs, with the inner side of the front legs tibia bearing the epiphysis, a moveable lobe in the middle of the distal half, and largely covered with scales; (2) a normal five-segmented foot, with a single pair of terminal claws at the tip; (3) antennae that are strongly curved or hooked at the tip in the true Skippers, or clubbed and not hooked in the Giant Skippers; (4) A head that is almost as wide as the thorax palpi, not noticeably small, in the true Skippers, or the head only half the width of the thorax and the palpi noticeably small in the Giant Skippers; (5) Wings that are relatively small and narrow in relation to body size in the true Skippers, with proportionately narrow and hard pointed forewings and enlarged wings overall in the Giant Skippers; (6) all veins arising from the center "cell" of the forewing are straight and unbranched; (7) larvae that are usually dull-colored, black spines and other ornaments, and having a very slender thorax portion behind the head that looks like a neck. Comparatively little studied in relation to the rest of the butterfly groups, the Skippers have a fascinating diversity of life history habits and behaviors as well as a remarkable species diversity in our state (69 species being recorded to date).

* * * * *

Subfamily Megathyminae J. H. and A. Comstock

The members of this subfamily are known as Giant Skippers. They are found throughout the deserts of our southern California region and also in the coastal areas of San Diego County. To the east, they occur throughout the southwestern United States and into the arid regions of northern and central Mexico, where the greatest speciation has occurred. In the latest systematic review of the family, Freeman (1969) recognized 49 species and 15 subspecies in this exclusively New World skipper family.

The adults are characterized by having a large robust body, a small head (usually half the width of the thorax), prominently clubbed antennae, a wing expanse of usually over 50 mm, and extremely fast and powerful flight. The larval stages bore in the stems or leaves of *Yucca*, *Agave*, or *Manfreda* plants. *Megathymus* larvae pupate in the stems and the pupae have the remarkable ability to move up and down in the larval tunnel. All known species are single-brooded. Of the two genera in California, *Megathymus* uses *Yucca* and is a spring flier, while the *Agathymus* species use *Agave* as hosts and are fall fliers. They are best collected as resting adults in the evening by flashlight, or in the larval stages by careful searching of the hosts, rather than by swinging the net.

188. *Megathymus yuccae* C. V. Riley

Three subspecies of this broadly distributed Giant Skipper fly in different areas of southern California. To the east, more than 30 recognizable local population groups occur on both sides of the Mississippi River, all the way to the East Coast states of North Carolina south to Florida.

CHROMOSOME NUMBER: The chromosome numbers of these three subspecies are unknown, although chromosome numbers of other subspecies to the east are 26 or 27 (Freeman, 1969).

- SIMILAR SPECIES:** No other species of *Megathymus* are known to occur within California.
- GEOGRAPHIC AND SEASONAL VARIATION:** As the species is univoltine, there is no seasonal variation. There is considerable minor geographic variation among the California populations of this species, as there is throughout its range. Only limited samples of most of the California populations are currently available, making it difficult to describe anything other than the broader geographic distribution of the three major subspecies types within California.
- GENERAL REMARKS:** A similar subspecies, *M. y. navajo* Skinner, is sometimes credited to our area based on the phenotype of a population in the Little San Bernardino Mountains. However, the actual range of *navajo* is further to the east in Arizona and New Mexico. This subspecies and the other subspecies of *yuccae* listed here are sometimes credited to the name *coloradensis* as the specific name.

a. *M. y. martini* D. Stallings and Turner

- DIAGNOSIS:** This subspecies is smaller than nominotypical *yuccae*, as are all the western subspecies of this *Megathymus* species. Both sexes are dark brown above and have a prominent band of submarginal buff-colored spots of varying width and shape. In subspecies *martini*, these spots tend to be intermediate in size or width between the subspecies *maudae* of the eastern Mojave Desert and those of the San Diego County subspecies. Ventrally, the ground color is a grayish-brown and the light colored spots are less distinct than they are on the dorsal surface.
- ORIGINAL DESCRIPTION:** D. Stallings and Turner, *Bulletin Southern California Academy Sciences*, 55: 150 (1956).
- TYPE LOCALITY:** Little Rock, Los Angeles County, California. Holotype believed to be in Peabody Museum, Yale University, New Haven, Connecticut.
- DISTRIBUTION:** Martin's Giant Skipper is distributed along the western and southern edges of the Mojave Desert, and south along the western edge of the Colorado Desert in Riverside County. It also extends northward in Inyo County to approximately the southern end of the White Mountains.
- ELEVATION RANGE:** 3,000 to 8,400' elevation.
- HABITAT AND PLANT COMMUNITIES:** The western Mojave Desert and Death Valley region populations are all associated with Joshua Tree Woodland, named for the principle host of this subspecies (*Yucca brevifolia*). Within this community, typical habitats are sandy slopes, flats, or desert washes.
- PHENOLOGY:** The flight period is March to April, with occasional flights as early as January and February.
- FOODPLANTS:** Two hosts have been recorded for *Megathymus yuccae martini*. *Yucca brevifolia* Englem. in Wats. (the Joshua Tree), is used in the western and northern Mojave Desert and Death Valley region. *Yucca schidegera* Roetzl. ex Ortgies is used along the western edge of the Colorado Desert in Riverside County and in the western Mojave Desert. Both *Yucca* species are in the family Agavaceae.

b. *M. y. maudae* D. Stallings, Turner, and J. Stallings

- DIAGNOSIS:** This subspecies is very similar to *martini* and is considered essentially a synonym of it by Roever (Roever *in* Howe, 1975). However, the phenotype of populations of the eastern Mojave Desert populations do show some minor differences from *martini*. The buff-colored markings are somewhat enlarged from that seen in *martini* and are thus somewhat intermediate between subspecies *martini* and subspecies *arizonensis* of Arizona, in which the buff markings are much more prominent.
- ORIGINAL DESCRIPTION:** D. Stallings, Turner, and J. Stallings, *Journal Lepidopterists' Society*, 20: 169-170 (1966).
- TYPE LOCALITY:** 21 miles north of Essex, San Bernardino County, California. Holotype in Peabody Museum, Yale University, New Haven, Connecticut.
- DISTRIBUTION:** Maude's Giant Skipper is found in the eastern Mojave Desert. occurring in the Providence, New York, Clark, and Kingston Mountain Ranges. From here it ranges south to the Turtle Mountains of eastern San Bernardino County.
- ELEVATION RANGE:** From 2,000 to 6,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** Populations of this subspecies are found in a wider variety of habitats than is subspecies *martini*. Populations are found in desert canyons, washes, on flats, and on mountain slopes, within the following plant communities: Pinyon-Juniper Woodland, Joshua Tree Woodland, Great Basin Sagebrush Scrub, Shadscale Scrub, Blackbush Scrub, Mixed Desert Scrub, Calcicolous Desert Scrub, and Creosote Bush Scrub.
- PHENOLOGY:** This subspecies flies in March and April.
- FOODPLANTS:** *Yucca baccata* Torr., *Y. brevifolia* Engelm. *in* Wats., and *Y. schidigera* Roetzl. ex Ortgies (Agavaceae). *Yucca baccata* seems to be the preferred host over the latter two species.

c. *M. y. ssp.* (San Diego County populations)

- DIAGNOSIS:** This set of populations is characterized by greatly reduced size of the buff-colored markings on both sexes.
- DISTRIBUTION:** This subspecies is rather widely distributed in San Diego County from the coastal areas around San Diego north to approximately Del Mar, inland to the western edge of the Colorado Desert. Populations which are somewhat intermediate between this subspecies and subspecies *martini* of the southwestern Mojave Desert are found in western Riverside County in the San Geronio Pass region.
- ELEVATION RANGE:** From near sea level to approximately 3,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** This subspecies is typically found on brushy to sparsely vegetated slopes within the following plant communities: Southern Coastal Sage Scrub, Inland Sage Scrub, Mixed Chaparral, and Desert Transition Chaparral.
- PHENOLOGY:** Adults fly in March.
- FOODPLANTS:** *Yucca schidigera* Roetzl. ex Ortgies (Agavaceae).

ADULT BEHAVIOR: The adults are not known to feed at nectar or moisture. Males typically perch in desert washes, either on low vegetation or on the ground, often patrolling a large area up and down the wash but usually returning to the same perch. Females apparently spend most of their time in ovipositional and foodplant search behavior, seeking out young "suckers" of the foodplants.

LIFE HISTORY: The life history of the California populations was first described for subspecies *martini* by Comstock and Dammers (1934); this description applies to all California populations of this species, as there are virtually no differences between the larvae or pupae of these different populations. The eggs are laid on suckers or new shoots of the *Yucca* plants. The newly hatched larvae then begin feeding in the first instar near the leaf apex, residing in a silken shelter. Sometimes they enter the terminal growth without attempting to feed on the leaf surface. By the end of the second instar, however, they enter the caudex stem and begin to burrow and tunnel for two feet or more through *Yuccas* with trunks or long underground stems. In plant species with a short massive root system, feeding is confined to a smaller chamber of larger diameter. The silken tents normally project from the terminal growth of the plant and usually contain larval frass as well as silk. After overwintering as a larva, pupation occurs in the early spring without further feeding. In these late winter or early spring months, pupae are able to move up and down the burrows inside the *Yucca* plant, apparently moving up into the tower for warmth during the day and down at night into better insulated quarters. They are capable of quite rapid downward movement into the former larval burrows when disturbed. This species is the only member of the genus which, after overwintering as a larva, pupates in the spring without further feeding (Roever, in Howe, 1975). The mature larva is white in color, with no pattern elements and resembles a large beetle grub or larva more than that of a butterfly. The pupa likewise is concolorous (dark brown) and devoid of any notable markings (see figures).

186. *Agathymus stephensi* (Skinner)

This *Agathymus* species is the only Giant Skipper that is reasonably common in California collections. It is found along the western edge of the Colorado Desert.

DIAGNOSIS: On the upper side, this *Agathymus* species is rather dull brown with a pattern of cream-colored spots which are somewhat reduced in size in comparison to the other California *Agathymus* species. On the underside, there is a rather prominent pattern of cream-colored spots on the hindwing.

ORIGINAL DESCRIPTION: Skinner, *Entomological News*, 23: 126 (1912).

TYPE LOCALITY: Mason Valley (La Puerta), San Diego County, California. Holotype in Carnegie Museum.

DISTRIBUTION: Stephens' Skipper is found along the western edge of the Colorado Desert, from the Palms-to-Pine Highway in Riverside County south to northern Baja California. The area of greatest abundance for the species seems to be the western portion of Anza-Borrego Desert State Park, especially near Scissors Crossing, in San Diego County.

ELEVATION RANGE: 1,000 to 4,000' elevation.

HABITAT AND PLANT COMMUNITIES: This species is typically found on rocky slopes or along desert canyon bottoms or washes where the foodplant is locally abundant. These habitats may be found within the following plant communities:

Pinyon-Juniper Woodland, Desert Transition Chaparral, Creosote Bush Scrub, and Semi-Succulent Scrub. The *Agave deserti* foodplant of this species is most abundant in the Semi-Succulent Scrub community, often forming almost pure stands on the desert slopes.

PHENOLOGY: The flight period is September to October. In any given locality, adult emergence seems to take place over a 3-4 week period.

ADULT BEHAVIOR: The adults can be collected much more easily at night than during the daytime. They roost on shrubs and small trees such as junipers, and stand out with the aid of a flashlight or latern. During the daytime, males exhibit perching behavior and perhaps territoriality around *Agave* plants; they apparently wait for newly emerging females at these points. The oviposition behavior of the females is extraordinary, in that the eggs are "flipped" by the female in flight into the leaf bases of the plant.

LIFE HISTORY: The life history was first described by Comstock and Dammers (1934). Further detailed observations on the bionomics of the genus *Agathymus* are given by Roever (1964). The eggs are deposited singly by the female flipping them into the basal portions of the leaf rosette of the *Agave* plant. When the egg hatches, the larva bores into an *Agave* leaf, possibly near the apex of the leaf. The preferred location of the early instar larvae of *A. stephensi* within the *Agave* leaf is apparently unrecorded in the literature. Presumably this species makes an apical gallery similar to other species of the genus, but repeated searches of *Agave* plants in which mature larvae or pupae have been located has failed to reveal such apical galleries (J. F. Emmel, unpublished observations). At some point, the larva makes a gallery near the base of an *Agave* leaf with an opening through the outer surface of the leaf, usually on the upper side. The chamber made by a *stephensi* larva tends to be more bulbous than that of other *Agathymus* species. The larva eventually makes a "trapdoor" at the entrance to the chamber at the surface of the *Agave* leaf and then pupates within the chamber. In the last instar, the larvae show considerable color variation, depending on whether they are actively feeding, or quiescent, or immediately pre-pupal. When the adult emerges from the pupa, it pushes out the "trapdoor" and crawls up the *Agave* leaf and expands its wings. (See accompanying photographs for illustration.)

CHROMOSOME NUMBER: Unknown (Freeman, 1969).

SIMILAR SPECIES: This California *Agathymus* is quite distinctive from the other two species, which have greatly enlarged light markings on the upper sides. Also, no other *Agathymus* species are sympatric with *stephensi*.

GEOGRAPHIC AND SEASONAL VARIATION: There is no seasonal variation in this univoltine species. No significant geographic variation has been noted within the California populations of this butterfly.

GENERAL REMARKS: The problems involved in working out the life history of such an insect as the Giant Skipper are dramatically related in the saga recorded by John Adams Comstock (1956).

187. *Agathymus alliae* ssp.

DIAGNOSIS: The typical form of this skipper was described in 1957 from near Cameron along the Little Colorado River in Arizona. A new subspecies was subsequently found in southeastern California in the eastern Mojave Desert and southern Nevada and was named by Kilian Roever in 1989. Its distinguishing features are a dull brown

ground color on the upper side with extensive yellowish-orange scaling in the basal area of both wings and prominent yellow-orange spots in the post-median area of the wings. Ventrally, the wings are dull brown with a grayish overscaling and a rather indistinct spotting pattern on the hindwing. In comparison to the nominotypical subspecies, the Mojave Desert subspecies has smaller spots.

ORIGINAL DESCRIPTION: Roever, *Journal Research Lepidoptera*, : (1988).

TYPE LOCALITY:

DISTRIBUTION: In California, this Giant Skipper flies in the Ivanpah, Clark, Kingston and Nopah ranges of the eastern Mojave Desert.

ELEVATION RANGE: 4,000 to 6,000' elevation.

HABITAT AND PLANT COMMUNITIES: The butterfly is typically found on limestone slopes or small limestone ridges where the *Agave utahensis* foodplants are locally abundant, in the Calicicolous Desert Scrub community.

PHENOLOGY: The flight period is September to October.

ADULT BEHAVIOR: The males perch on the *Agave* plants or on prominent rocks adjacent to the foodplants. Most of the perching behavior of the males occurs during the morning hours, and by early afternoon most males seem to become rather sedentary, resting in the shade of plants or rocks. Roever (1964) has described the ovipositional behavior of *Agathymus* females. Females land on the *Agave* plants or on nearby substrates such as rocks or branches and curve their abdomen until the tip comes in contact with the substrate, after which the abdomen is returned to its normal position. Expulsion of the egg takes place during this withdrawal of the abdomen from the substrate and, since it lacks an adhesive, falls either into the plant lodging at the base of the leaf or onto the ground. The nocturnal resting site of the adults is not known. No observations of this species coming to moisture have been made; however, it is possible that if suitable sources of water are nearby, this species may show such behavior as is seen in other *Agathymus* species.

LIFE HISTORY: [TCE: Describe briefly from slides]

Undescribed, although photographed (see figures). Stallings and Turner report that in Arizona the females select medium-sized plants for oviposition and that the larval trap-door, which is paper-white, is placed on the underside of the leaf.

FOODPLANTS: *Agave utahensis* Engelm. var. *nevadensis* Engelm. ex Greene. & Roush., and var. *eborispina* (Hester) Breitung (Agavaceae).

CHROMOSOME NUMBER: The only known chromosome count for *Agathymus alliae alliae*, from 15 miles west of Cameron, Arizona is N = 38 (Freeman, 1969).

SIMILAR SPECIES: The other *Agathymus* species of the eastern Mojave Desert, *A. baueri*, is similar, but has more greatly expanded orange areas on the upper side and a more distinctive spotting pattern on the underside of the hindwing. Also, the ranges of the two species do not overlap, with *A. baueri* being found only in the Providence Mountains and the Granite Mountains north of Amboy.

GEOGRAPHIC AND SEASONAL VARIATION: None in the California populations of this species.

GENERAL REMARKS: It is remarkable that the presence of this *Agathymus* species in the eastern Mojave Desert was not appreciated until it was first collected by Kilian Roever in the 1950's. Within its unique habitat, the adults can be fairly common at the peak of their season, much like populations of *A. stephensi*.

188. *Agathymus* species Roever (Providence Mountains and Granite Mountains north of Amboy)

- DIAGNOSIS: This recently described species of the eastern Mojave Desert is characterized by a dull brown ground color dorsally with rather extensive tannish-orange markings on both forewing and hindwing. Ventrally, it has an appearance superficially similar to that of *A. alliae*, except that the spotting pattern on the hindwing is more distinctive and the tannish-orange areas on the forewing are more extensive.
- ORIGINAL DESCRIPTION: Roever, *Journal Research Lepidoptera*, : (1988).
- TYPE LOCALITY: (Providence Mountains)
- DISTRIBUTION: This species is confined in distribution to the Providence Mountains and the Granite Mountains north of Amboy, in the eastern Mojave Desert.
- ELEVATION RANGE: 3,800 to 6,000' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is typically found on rocky limestone or granite slopes, within the following plant communities: Calicolous Desert Scrub, Creosote Bush Scrub, and Pinyon-Juniper Woodland.
- PHENOLOGY: This species flies from mid-September to mid-October.
- ADULT BEHAVIOR: This is similar to that of *A. alliae*. Adults have not been observed at moisture to date.
- LIFE HISTORY: [TCE: Please fill in, at least briefly on the basis of the kodachrome slides.]. The "trapdoor" is usually located on the underside of the leaf.
- FOODPLANTS: The sole host is *Agave deserti* Engelm. (Agavaceae).
- CHROMOSOME NUMBER: (TCE: Contact Killian Roever)
- SIMILAR SPECIES: See discussion under *Agathymus alliae*.
- GEOGRAPHIC AND SEASONAL VARIATION: No differences have been noted between the populations in the Granite Mountains and those in the Providence Mountains.
- GENERAL REMARKS: Because the *Agave deserti* foodplant of this species is rather sparsely scattered over the slopes of the desert mountain ranges in which it occurs, in contrast to the high density of these *Agave* populations along the western edge of the Colorado Desert, the butterfly tends to be rather scarce in nature. Thus a single isolated *Agave* plant may contain several larvae in a given season, in contrast to populations of *A. stephensi*, where many plants may have no larvae at all and frequently plants that do contain immatures will have only a single larva.

Subfamily Heteropterinae Aurivillius

192. *Carterocephalus palaemon* (Pallas)

- LIFE HISTORY:** The early stages of the northeastern U.S. populations have been described in part (see MacNeill, 1975). The pale greenish white egg is hemispherical and about 0.8 mm in diameter. The mature larva is bluish green to uniform cream in ground color, with a darker green mid-dorsal stripe and a whitish or pale yellow stripe on each side; a row of blackish spots is placed below the lateral stripe. Through the fourth instar, the larvae make shelters; thereafter, they lie on the upper surface of the grass blade.
- CHROMOSOME NUMBER:** Unknown.
- SIMILAR SPECIES:** None in North America.
- GEOGRAPHIC AND SEASONAL VARIATION:** As *palaemon* is single-brooded, there is no seasonal variation in either subspecies. The widely distributed subspecies *skada* is uniform in size and coloration throughout northern California.
- GENERAL REMARKS:** It is interesting to note that this skipper species also occurs in Asia, along with 12 other Asian species in the genus *Carterocephalus*. Two of the Asian species also occur in Europe (MacNeill, 1975). All are small to medium-sized skippers that are brown or blackish dorsally, with large orange, yellow or white spots.
- This rather variable but distinctive skipper should not be confused with any other North American species. About equal amounts of orange and black comprise the large spotted pattern of the dorsal forewings and hindwings. It typically inhabits forest glades in boreal areas. There are two subspecies in California.

a. *C. p. skada* (W. H. Edwards)

- DIAGNOSIS:** This medium-sized subspecies has reduced but distinct dorsal orange spotting. The submarginal spot row on the hindwing is usually completed by a spot opposite the cell. The more extensive background color gives a dark appearance to the adults.
- ORIGINAL DESCRIPTION:** W. H. Edwards, *Transactions American Entomological Society*, 3: 196 (1870).
- TYPE LOCALITY:** "Kodiak," Alaska. Neotype in Carnegie Museum, designated by F. M. Brown and L. P. Miller, *Transactions American Entomological Society*, 103: 263-264 (1977).
- DISTRIBUTION:** This subspecies ranges from the Yukon Territory through Alaska and Canada southward in the Rocky Mountain system to Wyoming, and in the West, southward down the Cascade Range to California. In our state, *skada* extends from the central Sierra Nevada northward along the Sierra-Cascade Range axis to Oregon. It is also found in scattered populations throughout the Klamath Mountains Assemblage, with the most southwestern extent south of Highway 299 at Berry Summit in central Humboldt County.
- ELEVATION RANGE:** From 2,000' to 6,000' in the Cascade Range and Klamath Assemblage, and from 3,400' to about 5,000' in the Sierra Nevada.
- HABITAT AND PLANT COMMUNITIES:** In California, *skada* is primarily an inhabitant of grassy openings and glades under or adjacent to a heavily forested canopy in a Coniferous Forest setting. Such habitat is usually found in the Lower and Upper

Montane Coniferous Forest in California and northward, but in this state, it is often also found within Douglas Fir forests adjacent to a stream. An indicator plant that is regularly found in the habitat where *skada* flies is the pea-like vine, *Lathyrus polyphyllus*.

PHENOLOGY: A single-brooded subspecies, *skada* flies in northern California from mid May to early July, with a peak flight in the month of June.

FOODPLANTS: Unknown for this subspecies. In confinement, females of *C. palaemon* will oviposit on Kentucky Bluegrass (*Poa pratensis*), and larvae can be reared on it.

b. *C. p. magnus* Mattoon and Tilden

DIAGNOSIS: This is the largest of the *palaemon* subspecies in North America, and it also bears the clearest and brightest pattern. The dorsal ground color is black, and the dorsal orange spots are large, with the exception of the submarginal row. The latter is composed of small spots and the row is complete on the forewings but incomplete on the secondaries, where a spot opposite the cell is usually lacking.

ORIGINAL DESCRIPTION: Mattoon and Tilden, *Natural History Museum of Los Angeles County Contributions in Science*, : (1989).

TYPE LOCALITY: Plantation, Sonoma County, California.

DISTRIBUTION: To date, this subspecies is known from only two locations along or near the immediate coast north of San Francisco Bay at Guerneville and Plantation in Sonoma County. There is a report of a specimen taken in coastal Mendocino County, but we have not seen material from there.

ELEVATION RANGE: From approximately 50' at Guerneville to near 100' at Plantation.

HABITAT AND PLANT COMMUNITIES: The general habitat in the known population sites is Northern Mixed Evergreen Forest blending into North Coastal Coniferous Forest.

PHENOLOGY: The *magnus* populations are single-brooded, with emergence starting in mid May and a flight period extending until late June. However, this season is variable, depending upon weather conditions along the coast in any given year.

FOODPLANTS:

190. *Piruna pirus* (W. H. Edwards)

See Appendix.

Subfamily Hesperinae Latreille

194. *Nastra julia* (H. A. Freeman)

This butterfly was described from southern Texas, where it is widely distributed. It ranges westward to western Arizona and southeastern California, as well as southward into Mexico.

DIAGNOSIS: This drab skipper formerly was placed in the genus *Lerodea*, as congeneric with *L. eufala* (species number 217 in our list). Phenotypically, it differs by the lighter

yellowish cast on the dorsal surface and a more ochreous overscaling on the ventral surface. However, the genitalia provide the only reliable characters for distinguishing the several species of *Nastra* in the Southwest.

- ORIGINAL DESCRIPTION: H. A. Freeman, *Entomological News*, 56: 204-205 (1945).
- TYPE LOCALITY: Pharr, Texas. Holotype in American Museum of Natural History.
- DISTRIBUTION: In southern California, this species has been taken in the low-lying agricultural valleys of eastern Riverside County and Imperial County. There is also a single record for the vicinity of Bakersfield in Kern County. It is uncertain whether these colonies in the southeastern part of the state are permanently established, or are only transiently established and die out each winter only to be re-established the following year by migrants from the south or east.
- ELEVATION RANGE: From 100' below sea level to approximately 400' above sea level.
- HABITAT AND PLANT COMMUNITIES: The butterfly is typically found in disturbed areas, or at the edges of cultivated fields, particularly where Bermuda Grass is locally common.
- PHENOLOGY: Records for our state are for the months of September and October. Due to the limited amount of collecting which is done in the areas where *N. julia* has been taken, undoubtedly records for other months and hence a longer flight period within the state will be shown.
- ADULT BEHAVIOR: The adult butterflies have been taken at the flowers of *Heliotropium curassavicum*. Otherwise little is known about the adult habits of this species.
- LIFE HISTORY: Undescribed.
- FOODPLANTS: Unknown, although Kendall has reared larvae on Saint Augustine grass (*Stenotaphrum secundatum*) in the San Antonio area of Texas. Bermuda Grass (*Cynodon dactylon* (L.) Pers.) is suspected in California.
- CHROMOSOME NUMBER: Unknown.
- SIMILAR SPECIES: This butterfly may be confused with *Lerodea eufala*, which not only flies in the same habitat, but is generally much more common. In fact, the scant number of records that we have for *N. julia* may be due to the fact that most collectors assume that all small brown skippers that they encounter in the areas where *N. julia* flies are *L. eufala* and neglect to collect them. *N. julia* tends to have a yellowish overscaling on both upper side and underside in fresh specimens, but particularly on the underside, in comparison to *L. eufala* which tends to have a more grayish overscaling ventrally.
- GEOGRAPHIC AND SEASONAL VARIATION: None known.
- GENERAL REMARKS: Collectors are urged to take larger samples of brown skippers when collecting in the agricultural areas of eastern Riverside County and Imperial County in order to hopefully generate more records for this seldom-collected species.

192. *Nastra neamathla* (Skinner and R. C. Williams).

See Appendix.

193. *Oarisma garita* (Reakirt).

See **Appendix**.

194. *Copaeodes aurantiaca* (Hewitson)

This small, pure yellow skipper is found across the American Southwest in arid grassland and open woodland. In our state, it occurs primarily in the Colorado and Mojave Deserts, generally in canyons or washes and in chaparral areas bordering the deserts. This species is often overlooked because of its small size.

DIAGNOSIS: A small, pure yellow skipper with a very fast flight, usually encountered in our desert regions.

ORIGINAL DESCRIPTION: Hewitson, Descr. one-hundred new spp. Hesp., (2): 45 [1868].

TYPE LOCALITY: Type locality not stated in the original description. Holotype in British Museum.

DISTRIBUTION: This skipper is widely distributed in the mountains of both the Colorado and Mojave Deserts, from which it ranges northward to the Death Valley region and westward to the desert slope of the mountains at the western border of our deserts. At least some populations along the western and northern borders of its range do not seem to be consistently present year after year, and may represent periodic reintroductions and temporary establishment.

ELEVATION RANGE: Most records of this species tend to be at fairly low elevations, ranging from sea level to approximately 4,000' elevation; some records in the higher mountains are as high as 7,300' elevation.

HABITAT AND PLANT COMMUNITIES: This butterfly is typically found in small canyons and washes in the desert mountains, usually within the Creosote Bush Scrub or Mixed Desert Scrub plant communities; however, it is also found in other desert plant communities, including Joshua Tree Woodland, Pinyon-Juniper Woodland, and semi-Succulent Scrub. Some of the populations along the desert edge are found in Desert Transition Chaparral.

PHENOLOGY: Records range from the months of February to December, with the majority of records clustering around the months of March and April and again in the late summer and early fall months, from early September to mid-October.

ADULT BEHAVIOR: Males often exhibit perching behavior along canyon bottoms and washes. Despite the small size, both males and females have a very fast flight.

LIFE HISTORY: The early stages were first recorded in detail by Comstock (1929b). The egg is cream and has a slow and glistening texture; the shape is that of a flattened hemisphere. The mature larva is green with a pale mid-dorsal line edged by wide purple bands that become red on each of the two pointed tails. There are two wide, dark green bands on each side. The head is conoidal, with two points projecting dorsally. The face of the head is crossed by two vertical bands of pink, with a large purplish area on each side. The pupa is light straw-yellow, with a sharp, elongated "beak" (the palpal case) projecting forward from the head. Several dark brown mid-dorsal and lateral lines and dots appear as shown in the

figure. There are also two white sub-dorsal lines on each side, the lower line being edged with pink.

- FOODPLANTS: One native host of this butterfly is *Hilaria rigida* (Thurb.) Benth. ex Scribn. (Poaceae) (J. F. Emmel, unpublished data). Additionally, ova and larvae have been collected on cultivated Bermuda Grass (*Cynodon dactylon* (L.) Pers.) in Hemet, California (J. F. Emmel, unpublished data). Undoubtedly, other native grass species are used in the desert mountains, but remain to be determined. The larvae will feed readily on Bermuda Grass in the laboratory.
- CHROMOSOME NUMBER: Unknown.
- SIMILAR SPECIES: This butterfly may be possibly confused with *Pseudocopaeodes eunus*, a larger butterfly associated with salt grass meadow habitats. *P. eunus* may be readily distinguished by its larger size, striated underside markings, and usual association with a salt grass meadow.
- GEOGRAPHIC AND SEASONAL VARIATION: None has been noted to date. Some females have black veins near the margin on the dorsal surface.
- GENERAL REMARKS: This species occasionally turns up in unusual localities such as Mineral King in Tulare County, or the higher elevations of the southern California mountains. Undoubtedly these records represent only transiently established populations, as they do not seem to persist from year to year.

195. *Hylephila phyleus muertovalle* Scott

The Fiery Skipper is an extremely abundant insect throughout the urbanized lowlands of southern California. It is a familiar sight on lawns and flowers used as ornamentals. Our subspecies was recently described by James Scott as distinct from the nominotypical subspecies.

- DIAGNOSIS: The sexes show considerable dimorphism in pattern and coloration with a great range of variability in females. In either sex this species can be identified by the short antennae and the yellow ventral coloration of the hindwing, with dark spots. The males have yellow dorsal marginal veins and narrow jagged dorsal hindwing borders. Females are usually dark brownish on the dorsal surface, with orange bands, but in the California and Arizona populations they are much lighter orange-yellow, and this characteristic led to the naming of the subspecies *muertovalle* by Scott.
- ORIGINAL DESCRIPTION: Scott, *Papilio New Species*, #1, 11 (1981).
- TYPE LOCALITY: Furnace Creek date grove, Death Valley, Inyo County, California.
- DISTRIBUTION: This species is common in urbanized areas of California, particularly the southern half of the state, but it ranges northward to the San Francisco Bay region and throughout the Central Valley. It is also sporadically taken in the desert areas, such as along the Mojave River, in the Panamint Mountains, or in Death Valley. From California the species ranges to the south as far as Argentina in South America, and eastward to Florida.
- ELEVATION RANGE: From sea level to approximately 5,000' elevation, with the majority of records below 3,000'.

- HABITAT AND PLANT COMMUNITIES:** The favored habitat of this species are the Bermuda Grass lawns of southern California; however, lawns composed of other grass species are also populated by this skipper. In the deserts where the butterfly has been taken the locality is generally in a wet meadow habitat or desert riparian situation.
- PHENOLOGY:** Captures for this species are recorded for every month of the year, but the main flight period is from April and May into early December.
- ADULT BEHAVIOR:** The adults are especially attracted to *Lantana* flowers, and are very abundant on lawn grasses. A. Shapiro (Scott, 1986) has shown that adults move an average of about 100 meters between captures in Davis, California, but apparently considerable dispersal out of the area can occur. Males will frequently perch in grassy swales and on lawns or on shrubs to await females. Passing females are pursued by the male and when she lands, he lands beside her, thrusts his head and antennae onto her abdomen and wings, and then flutters and crawls parallel to her, with ensuing mating. Unreceptive females either raise the abdomen, flutter the wings, or fly away (Scott, 1986).
- LIFE HISTORY:** The early stages have been described by Comstock (1927a, 1933). The egg is hemispherical, sharply flattened at the base. The surface is smooth and is a pale bluish-green. The mature larva is a dirty yellowish brown or grey-brown, with dorsal and dorso-lateral brown stripes. The head and collar are black. The pupa is yellowish brown and bears a prominent black dorsal line. The pupa is thickly covered with sharp hairs, arising from low reddish-brown tubercles.
- FOODPLANTS:** Bermuda Grass, *Cynodon dactylon* (L.) Pers. (Gramineae). In addition to the favored Bermuda Grass, females have been observed to oviposit on both *Festuca* species and *Poa pratensis* in lawns where this skipper species is abundant (J. F. Emmel, unpublished data). In the type locality of this subspecies, at Death Valley, the skippers feed on Bermuda Grass in the understory of the date grove.
- CHROMOSOME NUMBER:**
- SIMILAR SPECIES:** None in our area for the males. Some females may be confused with those of *Atalopedes campestris*, but the latter species generally has a large spot below the end of the forewing cell, partly translucent, and the antennae are much longer than in *phyleus*.
- GEOGRAPHIC AND SEASONAL VARIATION:** Several subspecies are found in South America, but until Scott named the population from Death Valley (and by implication, the remainder of southern California), only one subspecies was found north of Panama, *H. phyleus phyleus*. Within the state, there seems to be no significant geographic or seasonal variation.
- GENERAL REMARKS:** One wonders whether or not this species was present at all in the state before civilization arrived, since it seems so scarce in any undisturbed habitats. It is one of the few species in our fauna which thrives in the artificially created human habitats.

196. *Yvretta carus carus* (W. H. Edwards)

This drab, dark brownish skipper is found along the Colorado River in Riverside County. It is uncertain whether this butterfly is permanently established in the irrigated portions of our deserts, or whether our records for it simply represent

periodic reintroductions. It was first collected in California at Fertilla in Riverside County by Rindge in 1939. The Carus Skipper is more widespread in Arizona.

- DIAGNOSIS: This skipper is small to medium-sized and the ground color is a grey-brown with pale yellow, almost whitish spots on the dorsal surface. The ventral surface of the hindwings is yellow, lightly dusted with scattered blackish scales, and the veins tend to be pale tan like the spots of the macular band. The band is somewhat variable and may be on both wings or scarcely present on solely the forewings.
- ORIGINAL DESCRIPTION: W. H. Edwards, *Canadian Entomologist*, 15: 34 (1883).
- TYPE LOCALITY: "West Texas", restricted to Archer County by F. M. Brown and L. Miller, *Transactions American Ent. Soc.*, 103: 276-277 (1977). Lectotype in Carnegie Museum, designated by F. M. Brown and L. Miller (1977).
- DISTRIBUTION: Thus far, this skipper has been taken only in the vicinity of Blythe in Riverside County.
- ELEVATION RANGE: The populations at Blythe occur between 200 and 300' elevation.
- HABITAT AND PLANT COMMUNITIES: The butterfly is found in habitats similar to that of *Nastra julia* and *Lerodea eufala*, such as grassy roadsides or moist areas along irrigation canals.
- PHENOLOGY: Our records are for the months of July and August; undoubtedly further collecting will show a longer flight period for this species. Outside of California, records indicate a flight period from April to September
- ADULT BEHAVIOR: Observations on this have not been recorded.
- LIFE HISTORY: [TCE: Please fill in this section based on the kodachrome slides.]
- FOODPLANTS: Unknown, but feeds readily on both Bermuda Grass (*Cynodon dactylon*) and *Bouteloua gracilis* in the laboratory.
- CHROMOSOME NUMBER: Unknown.
- SIMILAR SPECIES: None in our area.
- GEOGRAPHIC AND SEASONAL VARIATION: The typical subspecies ranges from Texas across New Mexico and Arizona into extreme southeastern California and northern Mexico. A second subspecies, *Y. c. subreticulata* ranges from Panama north through Mexico to west Texas. No seasonal variation has been noted in either subspecies.
- GENERAL REMARKS: Presumably this species will eventually be taken in the Imperial Valley and Coachella Valley, both of which have habitats similar to the Blythe area. Collectors are urged to sample all skippers when collecting in these areas in hopes of producing more records for this species.

197. *Pseudocopaeodes eunus* (W. H. Edwards)

- CHROMOSOME NUMBER: Unknown.
- SIMILAR SPECIES: See discussion above under *Copaeodes aurantiaca*.

GEOGRAPHIC AND
SEASONAL VARIATION:

As noted above, there is variation between the spring brood and later summer broods of the nominotypical subspecies; spring brood specimens tend to be more heavily marked with black above, and the pattern of lines on the undersurface is either more bold or distinct in these specimens, in comparison to the summer brood specimens. For subspecies *flavus*, the earlier broods are similar in markings to those of later broods, but tend to be smaller. Spring brood specimens of subspecies *alinea* seem to be slightly more darkly marked than the late summer brood specimens of this subspecies, but there appears to be no obvious size difference between spring and late summer brood specimens. The subspecies *obscurus* is apparently univoltine. There is a possible blendzone between subspecies *flavus* and *obscurus* in extreme southern Mono County in the Adobe Hills area and also possibly at Round Valley near the Inyo-Mono County line; specimens from these populations sometimes show characters intermediate between these two subspecies.

GENERAL REMARKS:

The first northern California population of this insect was discovered by S. O. Mattoon as a result of searching appropriate habitats adjacent to hot springs. This population occurs along the east side of Honey Lake, 4 miles south of the town of Wendel, in Lassen County, where it flies on heavily grazed alkali flats around a series of hot springs. A search of adjacent Modoc County along the east side of the Warner Mountains, where alkali flats along alkali lakes are abundantly dotted with hot springs, has so far yielded no records of *eunus* despite seemingly ideal salt grass meadow habitats.

These butterflies resemble *Copaeodes aurantiaca* in having almost unmarked orange wings, but the male's stigma, female border and size all differ from the other genus. We have four subspecies recognized within our state: all are generally associated with salt grass meadows in valley bottom habitats.

a. *P. e. eunus* (W. H. Edwards)

DIAGNOSIS: The nominotypical subspecies is characterized by the following combination of features: the ground color of the upper side of both sexes is orange to slightly reddish-orange, with a relatively narrow black border at the outer margins of the wings; ventrally, the ground color is whitish-yellow with a superimposed pattern of indistinct brownish to blackish striations radiating out from the basal areas of the wings. In spring brood specimens of this subspecies, these striations tend to be much more boldly marked, whereas the summer brood specimens tend to have a "washed-out" appearance.

ORIGINAL DESCRIPTION: W. H. Edwards, *Papilio*, 1: 47 (1881).

TYPE LOCALITY: Bottoms of Kern River, near Bakersfield, Kern County, California. Holotype in Carnegie Museum.

DISTRIBUTION: This subspecies is found in disjunct populations from Kern County, along the Kern River, southeastward to the Victorville area along the Mojave River, and southward to San Diego County where it is found in the vicinity of Scissors Crossing and at Jacumba. Dammers (unpublished notes, L. A. County Museum) recorded the species at Panama in the southern San Joaquin Valley in Kern County; it is apparently extinct at this location (Ken Davenport, personal communication). There is also a single record for the species at Porterville in Tulare County (J. W. Tilden).

- ELEVATION RANGE: 400' to 3,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This species is typically found in alkali meadow habitats where salt grass (*Distichlis spicata* var. *stricta*) is locally abundant.
- PHENOLOGY: The nominotypical subspecies is at least bivoltine and possibly multivoltine as captures are recorded from April through early October with peak abundances noted both in the spring at the end of April and in early May and then again in the latter part of September.
- FOODPLANTS: This skipper undoubtedly feeds on Salt Grass (*Distichlis spicata* (L.) Greene), as it is invariably associated with this plant.

b. *P. e. flavus* Austin & Emmel

- DIAGNOSIS: The dorsal ground color of this subspecies is more yellowish-orange than that of nominate *P. eunus*. Spring brood specimens of this subspecies resemble the summer brood in markings, tending to have a rather pale, washed-out appearance, but vary by averaging smaller in size than the later brood. This is in contrast to nominant *P. eunus* which is biphenic in both size and in heaviness of the dark markings.
- ORIGINAL DESCRIPTION:
- TYPE LOCALITY: Loop Road, Stillwater National Wildlife Refuge, Churchill County, Nevada. Holotype in
- DISTRIBUTION: This subspecies ranges from Owens Valley in Inyo and southern Mono counties, north into Nevada through Yerington and Fernley (Lyon County) and the lower Truckee River Valley (Storey and Washoe counties) and east to the Reese River (Lander County) and Big Smokey Valley (Nye County) of central Nevada.
- ELEVATION RANGE: 3,500' to 5,500' elevation.
- HABITAT AND PLANT COMMUNITIES: This subspecies, like the nominotypical subspecies, is found in Alkali Meadow habitats where Salt Grass is abundant.
- PHENOLOGY: This subspecies flies in two broods from early June to mid-July and late July to late September.
- FOODPLANTS: This subspecies has been observed to oviposit on *Distichlis spicata* var. *stricta* near Lone Pine, Inyo County (J. F. Emmel, unpublished data).

c. *P. e. alinea* Scott

- DIAGNOSIS: This subspecies differs from typical *eunus* in being more uniform bright fulvous in color, both dorsally and ventrally. The dark veins near the margins are nearly absent on both surfaces, the brown patches on the dorsal forewing reduced in extent, and the ventral hindwing brown and white streaks are reduced and often nearly absent.
- ORIGINAL DESCRIPTION: Scott, *Papilio New Series*, #1: 12 (1981).
- TYPE LOCALITY: Afton, San Bernardino County, California.

- DISTRIBUTION:** This subspecies is found along the lower Mojave River from Yermo to Afton in San Bernardino County; it is also found in the Ash Meadows area of Nevada and undoubtedly will ultimately be taken in the area around Shoshone in extreme southeastern Inyo County, close to the Ash Meadows area.
- ELEVATION RANGE:** For the Mojave River populations, 1,400 to 2,000' elevation; for the Ash Meadows populations, 2,200 to 3,000' elevation.
- HABITAT AND PLANT COMMUNITIES:** As with the two preceding subspecies, *P. e. alinea* is found in salt grass meadows in the Alkali Meadow plant community.
- PHENOLOGY:** This subspecies is apparently multivoltine as there are records ranging from April to late September with peak abundance is both in April and again in September.
- FOODPLANTS:** This subspecies is also associated with Salt Grass, *Distichlis sticata* var. *stricta*, which is undoubtedly the host.

d. *P. e. obscurus* Austin and Emmel

- DIAGNOSIS:** This subspecies is distinguished by a combination of its browner, less intensely orange, dorsal surface and the heavier black scaling along the veins, outer margin and basally on both surfaces. It is also apparently univoltine in contrast to the other subspecies in this complex.
- ORIGINAL DESCRIPTION:** Austin and Emmel,
- TYPE LOCALITY:** Lompa Lane at Airport Road, Eagle Valley, Carson City, Nevada. Holotype in .
- DISTRIBUTION:** This butterfly is found from southern Mono County at Hot Springs, Hot Creek, northwest of Lake Crowley, northward through the Mono Basin to Carson Valley in extreme western Nevada. A population is also known at Honey Lake, Lassen County, California.
- ELEVATION RANGE:** 4,000 to 6,500' elevation.
- HABITAT AND PLANT COMMUNITIES:** This subspecies is typically found in salt grass meadows or on alkaline flats where salt grass is locally abundant within the Alkali Meadow plant community.
- PHENOLOGY:** In contrast to the other three subspecies of this butterfly, this subspecies is apparently univoltine with a single brood flying from early June to early July.
- ADULT BEHAVIOR:** This species tends to select for perching an open alkali-covered spot surrounded by the host plant grasses. The very wary males fly from spot to spot to challenge any skipper species in their habitat (such as *Hesperia juba* and *Polites sabuleti*). Due to the frequent encounters with the males of these species, *eunus* is constantly changing its perching location within its chosen habitat. Occasionally it visits blooming plants for nectar, such as *Heliotropium curavassicum*. Adults do not appear to wander far from the alkali flat-salt grass meadow habitat.
- LIFE HISTORY:** The egg has been described by Comstock (1931). It is cream, and sub-conoidal in form with a fine surface reticulation of slightly raised walls.
[TCE: Please fill in description of larva and pupa here, from Kodachrome slides.]

198. *Hesperia uncas* W. H. Edwards

CHROMOSOME NUMBER: Unknown.

SIMILAR SPECIES: This species may be confused with both *Hesperia nevada* and *H. miriamae*. These species can be readily distinguished by examination of the undersurface of the hindwing: in *H. uncas*, the white spot in cell CuA₂ is broadly connected to the post-median band; in *H. nevada*, this spot is only narrowly connected to the post-median band. *H. miriamae* has a different ground color than *H. uncas* or *H. nevada*; it is either gray or pale yellowish-gray; in *H. uncas* and *H. nevada*, the underside is more greenish.

GEOGRAPHIC AND SEASONAL VARIATION: As the species is univoltine in California, there is no seasonal variation. With regard to geographic variation, this species is rather variable over its range in the western United States and Mexico and the reader is referred to MacNeill's monograph for treatment of the other subspecies in this complex. Within California, there is phenotypic variation in populations of both the low-elevation subspecies *giulianii* and the high-elevation subspecies *macswaini*, and populations at intermediate elevations are postulated which could prove to have intermediate characters between these two extremes.

GENERAL REMARKS: The subspecies *macswaini* is one of the earliest butterflies to fly at the higher elevations in the White Mountains. Although the species can be locally common, it is often overlooked by collectors. It is likely that this species will eventually be collected in the Modoc Plateau area in northeastern California where habitats very similar to the southern Mono County Great Basin Sagebrush habitats are found; collectors are urged to look for this species during the latter part of May when collecting in that area.

The genus *Hesperia* is one of the most diverse skipper genera in the western United States. The similar appearance of many of the species of *Hesperia* has led to great confusion in the past literature as to which species were actually present in southern California. The outstanding monographic treatment of the genus by MacNeill (1964) cleared up many of the taxonomic and identification problems that had previously caused lepidopterists to shun these attractive skippers.

H. uncas occurs from the Sierra Nevada of California to the western Great Plains and from Saskatchewan to south of Mexico City. Two of the four U.S. subspecies occur in California.

a. *H. u. macswaini* MacNeill

DIAGNOSIS: This subspecies is smaller and more brightly orange above than the typical subspecies from the Rocky Mountains. It resembles *Hesperia nevada* in this respect. Ventrally, the hindwings are greyish-green with the white spots in the males commonly not extended along the veins and with the black patches also commonly missing. The normal shape of the band will separate *macswaini* from *nevada*, and the very slender forewing stigma of the males and more blunt forewings will distinguish *macswaini* from nearby *Hesperia comma* populations (MacNeill, in Howe, 1975).

- ORIGINAL DESCRIPTION: MacNeill, *University California Publications Entomology*, 35: 85-87 (1964).
- TYPE LOCALITY: Blancos Corral, White Mountains, Mono County, California. Holotype in California Academy of Sciences.
- DISTRIBUTION: This subspecies is found in the higher elevations of the White Mountains along the California-Nevada border; it is also found on Waucoba Mountain at the north end of the Inyo Mountains of Inyo County. Additionally, populations along the higher elevations of the eastern face of the Sierra Nevada as well as on Glass Mountain in Mono County just east of the Sierra Nevada crest, are closest to this subspecies.
- ELEVATION RANGE: 8,000 to 12,500' elevation, with most of the White Mountains populations above 10,000'.
- HABITAT AND PLANT COMMUNITIES: This subspecies is typically found on open gravelly flats and slopes within the Mountain Sagebrush Scrub plant community of the White Mountains; it flies in similar habitats along the east side of the Sierra Nevada at higher elevations.
- PHENOLOGY: This subspecies is univoltine, with adults flying from early June to early July.
- FOODPLANTS: The larval foodplant is Needle Grass, *Stipa nevadensis* B. L. Jones (Poaceae) (MacNeill, in Howe, 1975).

b. *H. u. guilianii* McGuire

- DIAGNOSIS: This is a lower elevation subspecies of *Hesperia uncas* found in the Great Basin sagebrush country of Mono County. It is characterized by larger size, a lighter and brighter orange ground color on the upper side and a lighter underside with enlargement of the white markings.
- ORIGINAL DESCRIPTION: McGuire, *Journal Research Lepidoptera*, : (1988).
- TYPE LOCALITY:
- DISTRIBUTION: This subspecies is found in southern Mono County at lower elevations than is *H. u. macswaini*, from the Adobe Hills area northward to the southern Mono Basin region. Its eastern range limits are unknown at this time.
- ELEVATION RANGE: 7,000 to 9,000' elevation.
- HABITAT AND PLANT COMMUNITIES: This subspecies is typically found on open sandy flats, particularly those derived from pumice sand, within the Great Basin Sagebrush plant community, often associated with a sparse *Pinus monophylla* woodland.
- PHENOLOGY: This subspecies is also univoltine, with adults flying from the middle of May to the middle of June.
- FOODPLANTS: A female of this subspecies has been observed to oviposit on a *Stipa* species (Poaceae) in the Adobe Hills type locality (J. F. Emmel, unpublished data).
- ADULT BEHAVIOR: Males of both subspecies exhibit perching behavior usually along roads or in openings within the sagebrush scrub. Females are less commonly observed, and

apparently spend most of their time flying amongst the bunches of the host grass foodplant, pausing to oviposit for only very brief periods of time. Nectar sources have not been recorded for the adults of this species in California.

LIFE HISTORY: The egg is large (about 1.5 mm in diameter) and is greenish-white in color. The shape is smoothly hemispherical, and without evident reticulation except under high magnification (MacNeill, in Howe, 1975). The larva and pupa are undescribed.

199. *Hesperia juba* (Scudder)

Probably the most remarkable statement one can make about this rather large, boldly marked species of the West is that no subspecific differentiation has been described. Yet it is found from British Columbia to Baja California and eastward from the Pacific Coast through the Great Basin to Montana, Wyoming, and Colorado!

DIAGNOSIS: The dorsal ground color is characteristically orange, with a sharply defined tooth-like dark border. The male stigma is slender with the anterior portions being thickly packed with androconia. On the underside of fresh specimens the hindwing is greenish with an irregular macular band. The antennal club of this species is much shorter and more globose, with a very short apiculus, than is characteristic of other species of *Hesperia*. The wingspread is 26 to 38 mm. (MacNeill, in Howe, 1975).

ORIGINAL DESCRIPTION: Scudder, *4th Report Ann. Rept. Peabody Acad. Sci.*, [1871]: 77 (1872).

TYPE LOCALITY: "California, Nevada". Syntypes are supposed to be in the Museum of Comparative Zoology at Harvard University.

DISTRIBUTION: This species is widespread in the state, from the Klamath Mountains assemblage and Warner Mountains in the north southward through the Coast Ranges and the Sierra Nevada to the higher mountains of southern California. It is found in the mountains of the Death Valley region, such as the Argus Range, the Panamint Range, and the Inyo-White Mountains; however, it is absent from the Mojave Desert south of here despite the existence of seemingly suitable habitats in the eastern Mojave Desert. It is found along the desert fringe such as along the north slope of the Transverse Ranges or along the east slope of the Peninsular Ranges. There is one record for the Granite Mountains northeast of Victorville in the central Mojave Desert (J. F. Emmel and G. Pratt, unpublished data).

ELEVATION RANGE: From 1,000 to 8,000' elevation.

HABITAT AND PLANT COMMUNITIES: This *Hesperia* species seems to be the most tolerant of a rather wide variety of ecological conditions and habitats, in contrast to the other *Hesperia* species within the state. It is usually taken either along canyon bottoms, in washes, along streams, or near springs, within the following plant communities: Joshua Tree Woodland, Pinyon-Juniper Woodland, Great Basin Sagebrush Scrub, Lower Montane Coniferous Forest, Upper Montane Coniferous Forest, Subalpine Forest, Mixed Chaparral and Desert Transition Chaparral. *H. juba* is also occasionally taken in other plant communities within the state.

PHENOLOGY: This species is at least bivoltine in the state, with early records ranging from April to July depending on elevation as well as summer and fall records ranging from July through October, suggesting a second or even third brood. The overwintering

stage of this species is unknown; Shapiro (19) has suggested that this species may overwinter as an adult, in view of the fact that at high elevations in the Sierra Nevada, fresh adults can be taken in early fall, and then again in the spring in the same localities. Adults that are taken tend to be somewhat worn, suggesting that they spend the winter as adults. Conceivably, though, these early fall-flying adults could lay eggs which then overwinter or produce first-instar larvae which overwinter. In Colorado, Scott (in litt.) has found that *H. juba* overwinters as a partly-grown larva. Certainly this situation bears much further investigation to determine the diapause stage in California.

ADULT BEHAVIOR: Both sexes of this species, like so many of the other skippers, are avid flower-visitors, particularly in the fall when Rabbit Brush (*Chrysothamnus*) is in full-bloom. The males have been observed to hilltop, although in many of the hilltopping situations the necessary host plants and nectar sources that are attractive are also adjacent. In extreme northwestern California, in the serpentine pine barrens of Del Norte County, Mattoon has observed *juba* under relatively cool environmental conditions in the spring. There they perch, sun themselves by settling on the serpentine rubble rock, and females oviposit by crawling down into the bunch grasses that grow out of the rich serpentine soil. This same host plant is used by *Hesperia comma mattooni* and by *Polites mardon* which both fly sympatrically in the pine barrens. In the Great Basin area, *juba* is quite often found sitting in open gravelly flats where it will fly out to encounter invaders of its habitat. Another commonly utilized perching and territorial area in the desert regions is along a small intermittent or dry watercourse, where the insect will occupy patches of bare sand and challenge all invaders.

LIFE HISTORY: The early stages have been described in detail by MacNeill (1964). The egg is smaller than the other members of the genus, scarcely over 1 mm in diameter. It is smoothly hemispherical in shape. It is initially shining cream-white and soon becomes pinkish and then dull white with a gray cast. The mature (fifth-instar) larva is cream-colored and has short hairs scattered over the surface. The head is black with two short vertical streaks on the upper part of the face. The pupa is dark brown, with darker patches on the head and thorax, and is covered with a waxy bloom. There is a double transverse row of dash-like dark spots on the abdominal segments. The hairs on the head and thorax are hooked. The tongue-case is short, barely protruding beyond the wing pads.

FOODPLANTS: Undetermined in California. J. Scott (in litt.) has recorded the following Poaceae as foodplants in Colorado: *Bouteloua gracilis*, *Bromus tectorum*, and *Poa secunda* var. *sandbergi*.

CHROMOSOME NUMBER:

SIMILAR SPECIES: *Hesperia juba* is commonly found flying with *Hesperia comma* subspecies and occasionally will be taken with *Hesperia nevada* or other similarly colored skipper species. It is probably the largest of all the skipper species that are sympatric in its habitat in northern California and has more pointed forewings, as well as a well-defined marginal border above. The dark, well-defined double spot below the cell on the dorsal forewing surface of *juba* will usually distinguish females from those of *H. comma harpalus*. Likewise the antennal club of *juba* is much shorter than those of the other species.

GEOGRAPHIC AND SEASONAL VARIATION: No significant geographic or seasonal variation has been noted in the California populations of this species.

GENERAL REMARKS: MacNeill (1964) suggests that *H. juba* is a vagile, ecologically versatile species which may be presently rapidly expanding its range. This insect may have been a monotypic species of the Great Basin region which has only recently occupied the extensive geographic and ecologically varied areas which now comprise its range. This would help to explain the lack of any phenotypic divergence in this species.

[illegible]

LITERATURE CITED

If no literature is cited in the text account of a life history, this means that the life history of the species is generally known and is already well described in several generally available books. Also, specific earlier literature citations may be found in major butterfly bibliographies (e.g., Davenport and Dethier 1937, and Tietz 1972).

Abbott, Charles H. 1950. Twenty-five years of migration of the Painted Lady butterfly, *Vanessa cardui*, in southern California. *Pan-Pac. Ent.*, 26(4): 161-172.

Abbott, Charles H. 1951. A quantitative study of the migration of the Painted Lady butterfly, *Vanessa cardui*, in southern California. *Ecology*, 32(2): 155-171.

Abbott, Charles H. 1959. The 1958 migration of the Painted Lady butterfly, *Vanessa cardui* (Linnaeus), in California. *Pan-Pacific Entomologist*, 35(2): 83-94.

Abbott, W. 1959. Local autecology and behavior in *Pieris protodice* Boisduval and Leconte with some comparisons to *Colias eurytheme* Boisduval. *Wasmann J. Biology*, 17(2): 279-298.

Ae, S. A. 1958. Comparative studies of developmental rates, hibernation, and food plants in North American *Colias* (Lepidoptera, Pieridae). *American Midland Naturalist*, 60(1): 84-96.

Aiello, A. 1984. *Adelpha* (Nymphalidae): deception on the wing. *Psyche*, 91(1-2): 1-45.

- Alcock, John. 1983. Hilltopping territoriality by males of the great purple hairstreak, *Atlides halesus* (Lepidoptera: Lycaenidae): Convergent evolution with a pompilid wasp. *Behavioral Ecology and Sociobiology*, 13: 57-62.
- Alcock, John. 1985. *Sonoran Desert Spring*. University of Chicago Press, Chicago. 194 pp.
- Allyn, Arthur C., and John C. Downey. 1976. Diffraction structures in the wing scales of *Callophrys (Mitoura) siva siva* (Lycaenidae). *Bull. Allyn Mus.*, 40: 1-6.
- Anonymous. 1867. California Academy of Natural Sciences, Regular Meeting, April 1st, 1867. *The Mining and Scientific Press* (San Francisco), April 6, 1867: p. 217.
- Anonymous. 1885. Obituary note [H. K. Morrison]. *Entomologica Americana*, 1(5): 100.
- Anonymous. 1904. Dr. Hans Herman Behr. *Entomological News*, 15: 142-144.
- Anonymous. 1909. William H. Edwards. *Entomological News*, 20(5): 193-194.
- Anonymous. 1914. Southwest Museum opening. *Bulletin Brooklyn Entomological Society*, 9(5): 109.
- Anonymous. 1916. The Lorquin Natural History Club. *Lorquinia*, 1(2): 12-14.
- Anonymous. 1962. Burdick Collection to University of Colorado. *J. Lepid. Soc.*, 16(4): 246.
- Anonymous. 1967. Seasons Summary, 1966. [*Vanessa cardui* migration.] *News Lepid. Soc.*, No. 3, 15 April 1967: pp. 4,10.
- Anonymous. 1969. Seasons Summary, 1968. [*Vanessa cardui* migration.] *News Lepid. Soc.*, No. 3, 15 April 1969: pp. 1,5,13.

- Anonymous. 1974. Seasons Summary, 1973. [*Vanessa cardui* migration.] *News Lepid. Soc.*, No. 2, 25 June 1974: pp. 1-2.
- Anthony, George Scott. 1970. Field work on the population structure of *Oeneis melissa semidea* (Satyridae) from the Presidential Range, New Hampshire. *J. Res. Lepid.*, 7(3): 133-148. ("1968").
- Arnaud, Paul H., Jr. 1970. List of the scientific publications and insect taxa described by Francis Xavier Williams (1882-1967). *Occasional Papers California Academy of Sciences*, No. 80: 1-33.
- Arnaud, Paul H., Jr. 1977. Robert Grant Wind (1912-1975). *Pan-Pacific Entomologist*, 53(1): 74-77.
- Arnaud, Paul H., Jr., and Thomas W. Davies. 1976. Obituary: Robert Grant Wind (1912-1975). *J. Lepid. Soc.*, 30(3): 239-244.
- Arnold, Richard A. 1981. A review of endangered species legislation in the U.S.A. and preliminary research on 6 endangered California butterflies (Lepidoptera, Lycaenidae). *Beih. Veroff. Naturschutz Landschaftspflege Bad.-Württ. Karlsruhe*, 21: 79-96.
- Arnold, Richard A. 1983a. *Speyeria callippe* (Lepidoptera: Nymphalidae): application of information - theoretical and graph-clustering techniques to analysis of geographic variation and evaluation of classifications. *Annals Entomological Society of America*, 76(6): 929-941.
- Arnold, Richard A. 1983b. Ecological studies of six endangered butterflies (Lepidoptera, Lycaenidae): island biogeography, patch dynamics, and the design of habitat preserves. *Univ. Calif. Publications Entomology*, 99: 1-161.

- Arnold, Richard A. 1986. Private and government funded conservation programs for endangered insects in California. *Natural Areas Journal*, 5:28-39.
- Arnold, Richard A. 1991. Biological studies of the endangered Lotis Blue butterfly for PG&E's Elk-Fort Bragg 60-kV transmission line. Pacific Gas and Electric Company, Technical and Ecological Services, 3400 Crow Canyon Road, San Ramon, California. 45 pp.
- Austin, George T. 1972. A possible case of mimicry between lycaenid butterflies (Lycaenidae). *J. Lepid. Soc.*, 26(1): 63-64.
- Austin, George T. 1983. A new subspecies of *Speyeria atlantis* (Edwards) (Nymphalidae) from the Great Basin of Nevada. *J. Lepid. Soc.*, 37: 244-248.
- Austin, George T. 1986a. *Pyrgus communis* and *P. albescens* (Hesperiidae) in Nevada. *J. Lepid. Soc.*, 40: 55-58.
- Austin, George T. 1986. A review of the satyrine genus *Neominois*, with descriptions of three new subspecies. *Bulletin Allyn Museum*, No. 107: 1-27.
- Austin, George T. 1986b. A review of the satyrine genus *Neominois*, with descriptions of three new subspecies. *Bulletin Allyn Museum*, No. 107: 1-27.
- Austin, George T. 1987. Nevada populations of *Polites sabuleti* and the descriptions of five new subspecies. *Bull. Allyn Museum*, 109: 1-24.
- Austin, George T. 1991. *Cercyonis pegala* (Fabricius) (Nymphalidae: Satyrinae) in the Great Basin: new subspecies and biogeography. *Bulletin of the Allyn Museum*, No. 135: 1- .

- Austin, George T. 1998a. New Subspecies of HesperIIDae (Lepidoptera) from Nevada and California. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 523-532.
- Austin, George T. 1998b. New Subspecies of Pieridae (Lepidoptera) from Nevada. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 533-538.
- Austin, George T. 1998c. New Subspecies of Lycaenidae (Lepidoptera) from Nevada and Arizona. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 539-572.
- Austin, George T. 1998d. New Subspecies of Nymphalidae (Lepidoptera) from Nevada and Arizona. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 573-586.
- Austin, George T. 1998e. *Callophrys* (Lepidoptera: Lycaenidae) in Nevada, with Description of a New Subspecies of *C. comstocki*. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 619-628.
- Austin, George T. 1998f. Type Data for Butterflies Described from Nevada. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 629-640.
- Austin, George T. 1998g. Variation of *Phyciodes pulchellus* (Boisduval) (Lepidoptera: Nymphalidae) in the Great Basin of Nevada. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 737-748.
- Austin, George T. 1998h. The Correct Name of the *Danaus gilippus* (Cramer) (Lepidoptera: Nymphalidae) in the Southwestern United States. *Systematics of*

Western North American Butterflies. Mariposa Press, Gainesville, Florida. Pp. 749-750.

Austin, George T. 1998i. *Limenitis archippus* (Cramer) (Lepidoptera: Nymphalidae) in Western United States with Special Reference to Its Biogeography in the Great Basin. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 751-762.

Austin, George T. 1998j. A New Subspecies of *Euphilotes pallescens* (Lepidoptera: Lycaenidae) from the Northern Great Basin of Nevada. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 815-818.

Austin, George T. 1998k. Checklist of Nevada Butterflies. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 837-844.

Austin, George T. 1998l. Notes on *Plebejus saepiolus* (Boisduval) (Lepidoptera: Lycaenidae: Polyommatainae) in Nevada, with Description of a New Subspecies. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 819-824.

Austin, George T., and Anna T. Austin. 1981. Butterflies of Clark County, Nevada. *J. Res. Lepid.*, 19(1): 1-63. ("1980")

Austin, George T., and John F. Emmel. 1998a. New Subspecies of Butterflies (Lepidoptera) from Nevada and California. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 501-522.

Austin, George T., and John F. Emmel. 1998b. A Review of *Papilio multicaudatus* Kirby (Lepidoptera: Papilionidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 691-700.

- Austin, George T., and Richard E. Gray. 1998. The *Coenonympha tullia* (Müller) Complex (Lepidoptera: Nymphalidae: Satyrinae) of the Great Basin Region. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 587-612.
- Austin, George T., and William W. McGuire. 1998a. Description of a New Subspecies of *Hesperia comma* (Linnaeus) (Lepidoptera: HesperIIDae) from Nevada. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 481-486.
- Austin, George T., and William W. McGuire. 1998b. *Hesperia uncas* W. H. Edwards (Lepidoptera: HesperIIDae) in the Great Basin Region, with Descriptions of New Subspecies. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 775-794.
- Austin, George T., and Dennis D. Murphy. 1998a. *Euphydryas editha* of the Great Basin, with Descriptions of Three New Subspecies (Lepidoptera: Nymphalidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 407-418.
- Austin, George T., and Dennis D. Murphy. 1998b. Patterns of Phenotypic Variation in the *Euphydryas chalcedona* Complex (Lepidoptera: Nymphalidae) of the Southern Intermountain Region. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 419-432.
- Austin, George T., and Patrick J. Savage. 1998. A New Subspecies of *Satyrrium saepium* (Lepidoptera: Lycaenidae) from the Southeastern Intermountain Region.

Systematics of Western North American Butterflies. Mariposa Press, Gainesville, Florida. Pp. 613-618.

Austin, George T., and Michael J. Smith. 1998a. Revision of the *Thessalia leanira* Complex (Lepidoptera: Nymphalidae: Melitaeinae): *Thessalia leanira* (C. & R. Felder), with Descriptions of Four New Subspecies. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 327-332.

Austin, George T., and Michael J. Smith. 1998b. Revision of the *Thessalia theona* Complex (Lepidoptera: Nymphalidae: Melitaeinae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 333-358.

Austin, George T., John F. Emmel, and Thomas C. Emmel. 1998. A New Neotype and a Rerestriction of the Type Locality for *Lycaena shasta* W. H. Edwards (Lepidoptera: Lycaenidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 115-116.

Austin, George T., John F. Emmel, Thomas C. Emmel, and Sterling O. Mattoon. 1998. A New Subspecies Name for the Western Segregate of *Hesperia nevada* (Lepidoptera: Hesperiidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 487-490.

Axelrod, Daniel I. 1977. Outline history of California vegetation. Pp. 139-193. In Barbour, Michael G., and Jack Major, eds. 1977. *Terrestrial Vegetation of California*. John Wiley & Sons, New York. 1002 pp.

Axelrod, D. J. 1958. Evolution of Madro-tertiary geoflora. *Botanical Review*, 24: 433-509.

- Bailowitz, Richard A. 1988. Systematics of *Ascia (Ganyra)* (Pieridae) populations in the Sonoran Desert. *J. Res. Lepid.*, 26(1-4): 73-81.
- Bakker, E. 1984. An Island Called California. Second Edition. University of California Press, Berkeley. 484 pp.
- Ballmer, Gregory R., and Gordon F. Pratt. 1989a. Instar number and larval development in *Lycaena phlaeus hypophlaeas* (Boisduval) (Lycaenidae). *J. Lepid. Soc.*, 43(1): 59-65.
- Ballmer, Gregory R., and Gordon F. Pratt. 1989b. A survey of the last instar larvae of the Lycaenidae (Lepidoptera) of California. *J. Res. Lepid.*, 27: 1-81. ("1988")
- Barnaby, Rupert C. 1989. Fabales. In Cronquist, Arthur, et al., editors. Intermountain Flora: Vascular Plants of the Intermountain West, U.S.A. Volume Three, Part B. New York Botanical Garden, Bronx, New York.. 279 pp.
- Barnes, William, and J. McDunnough. 1919. A new race of *Plebejus icarioides* from Vancouver Island. *Canadian Entomologist*, 51: 92-93.
- Basinger, A. J. 1926. *Thanaos clitus* (Lepid.: Hesperiiidae) in California. *Entomological News*, 37: 301.
- Bauer, David L. 1955. Notes on the *Papilio machaon* complex in Arizona. *Lepidopterists' News*, 9(1): 7-10.
- Bauer, David L. 1959. A new subspecies of *Microtia dymas* (Nymphalidae) from southern California. *Lepid. News*, 12: 97-100. ("1958")
- Bauer, David L. 1975. Genus *Euphydryas* Scudder. In W. H. Howe, edit., *The Butterflies of North America*. Doubleday, New York. Pp. 174-195.

- Baughman, John F., and Dennis D. Murphy. 1998. Differentiation in a Widely Distributed, Polytypic Butterfly Genus: Five New Subspecies of California *Euphydryas* (Lepidoptera: Nymphalidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 397-406.
- Behr, H. H. 1862. On certain butterflies of California. *Proceedings California Academy of Natural Sciences*, 2(11): 167-169.
- Berger, T. A., and R. C. Lederhouse. 1985. Puddling by single male and female tiger swallowtails, *Papilio glaucus* L. (Papilionidae). *J. Lepid. Soc.*, 39(4): 339-340.
- Bethune, C. J. S. 1909. William Henry Edwards. *Canadian Entomologist*, 41(8): 245-248.
- Birnie, Deborah, and James Dale Smith. 1972. Bibliography of John Adams Comstock, 1883-1970. *Bulletin Southern Academy of Sciences*, 71(2): 60-68.
- Bitzer, Royce J., and Kenneth C. Shaw. 1980. Territorial behavior of the Red Admiral, *Vanessa atalanta* (L.) (Lepidoptera: Nymphalidae). *J. Res. Lep.*, 18(1): 36-49. (1979).
- Bitzer, Royce J., and Kenneth C. Shaw. 1983. Territorial behavior of *Nymphalis antiopa* and *Polygonia comma* (Nymphalidae). *J. Lepid. Soc.*, 37(1): 1-13.
- Blest, A. D. 1957. The function of eyespot patterns in the Lepidoptera. *Behavior*, 11: 209-256.
- Blevins, T. B., and H. M. Blevins. 1944. Some butterflies of Sequoia National Park. *Bull. So. Calif. Acad. Sci.*, 43(3): 122-123.
- Boisduval, J. A. 1873. Note necrologique sur Lorquin, naturaliste-voyageur. *Annals de la Societe Entomologique de France*, 3: 5-10.

- Boisduval, J. A. 1952. Lepidopteres de la Californie. *Ann. Soc. Ent. France*, 2nd Series, 10: 275-324.
- Bower, H. N. 1911. Early stages of *Lycaena lygdamus* Doubleday. *Entomological News*, 22(8): 359-363.
- Breedlove, D. E., and P. R. Ehrlich. 1968. Plant-herbivore coevolution: Lupens and Lycaenids. *Science*, 162: 671-672.
- Breedlove, D. E., and P. R. Ehrlich. 1972. Coevolution: patterns of legume predation by Lycaenid butterflies. *Oecologia* (Berlin), 10: 99-104.
- Brittnacher, John G., Steven R. Sims, and Francisco J. Ayala. 1978. Genetic differentiation between species of the genus *Speyeria* (Lepidoptera: Nymphalidae). *Evolution*, 32: 199-210.
- Brower, Jane V. Z. 1958. Experimental studies of mimicry in some North American butterflies. II. *Battus philenor* and *Papilio troilus*, *P. polyxenes* and *P. glaucus*. *Evolution*, 12: 123-136.
- Brower, Lincoln P. 1958a. Peale's *Lepidoptera Americana* and the correct name for *Papilio multicaudatus*. *Lepid. News*, 12(3-4): 101-102.
- Brower, Lincoln P. 1958b. Larval foodplant specificity in butterflies of the *Papilio glaucus* group. *Lepid. News*, 12: 103-114.
- Brower, Lincoln P. 1959a. Speciation in butterflies of the *Papilio glaucus* group. I. Morphological relationships and hybridization. *Evolution*, 13: 40-63.
- Brower, Lincoln P. 1959b. Speciation in butterflies of the *Papilio glaucus* group. II. Ecological relationships and inter-specific sexual behavior. *Evolution*, 13: 212-228.

- Brower, Lincoln P. 1985. The yearly flight of the Monarch butterfly. *Pacific Discovery*, 38(1): 4-15.
- Brower, Lincoln P., Jane V. Z. Brower, and F. P. Cranston. 1965. Courtship behavior of the queen butterfly, *Danaus gilippus berenice* (Cramer). *Zoologica*, 50: 1-39.
- Brower, Lincoln P., J. N. Seiber, C. J. Nelson, S. P. Lynch, and P. M. Tuskes. 1982. Plant-determined variation in the cardenolide content, thin-layer chromatography profiles, and emetic potency of monarch butterflies, *Danaus plexippus*, reared on the milkweed, *Asclepias eriocarpa* in California. *J. Chemical Ecology*, 8: 579-633.
- Brown, F. Martin. 1934. The localities of T. L. Mead's collection of butterflies from Colorado in 1871. *Journal New York Entomological Society*, 42: 155-162.
- Brown, F. Martin. 1955. The Wheeler Expeditions to the southwestern United States. *Lepidopterists' News*, 9(4-5): 124-126.
- Brown, F. Martin. 1955. Itineraries of the Wheeler Survey naturalists 1871-- Theodore L. Mead. *Lepidopterists' News*, 9(6): 185-190.
- Brown, F. Martin. 1957. Itineraries of the Wheeler Survey naturalists. 1871 -- Ferdinand Bischoff. *Journal New York Entomological Society*, 65: 219-234.
- Brown, F. M. 1957. The type locality for *Ochlodes yuma*. *Lepidopterists' News*, 11(4-5): 153-154.
- Brown, F. Martin. 1958. Itineraries of the Wheeler Survey naturalists. 1871-Ferdinand Bischoff. *Journ. New York Ent. Soc.*, 65: 219-234 [1957].
- Brown, F. Martin. 1958. The correspondence between William Henry Edwards and Spencer Fullerton Baird. Part I. *Proceedings New York Entomological Society*, 66: 191-227.

- Brown, F. Martin. 1959. The correspondence between William Henry Edwards and Spencer Fullerton Baird. Part II. *Journal of the New York Entomological Society*, 67: 107-123.
- Brown, F. Martin. 1961. A note about *Lycaena nivalis browni* (Lycaenidae). *J. Lepid. Soc.*, 15(2): 107-108.
- Brown, F. Martin. 1964. The types of satyrid butterflies described by William Henry Edwards. *Transactions American Entomological Society*, 90: 323-413.
- Brown, F. Martin. 1964. W. H. Edwards' life histories of North American *Coenonympha*. *J. Res. Lepid.*, 3(2): 121-128.
- Brown, F. Martin. 1964. Tyron Reakirt (1844-?). *J. Lepid. Soc.*, 18(4): 211-214.
- Brown, F. Martin. 1965. Oscar Theodor Baron (1847-1926). *J. Lepid. Soc.*, 19(1): 35-46.
- Brown, F. Martin. 1965. Comments on the genus *Cercyonis* Scudder with figures of types (Satyridae). *J. Res. Lepid.*, 4(2): 131-148.
- Brown, F. Martin. 1967. Dr. Edward Palmer's collecting localities in southern Utah and northwestern Arizona. *J. Lepid. Soc.*, 21(2): 129-134.
- Brown, F. Martin. 1967. Lorquin's localities "Sonora" and "Utah." *J. Lepid. Soc.*, 21: 271-274.
- Brown, F. Martin. 1971. The "Arrowhead Blue," *Glaucopsyche piasus* Boisduval (Lycaenidae: Plebejinae). *J. Lepid. Soc.*, 25: 240-246.
- Brown, F. Martin. 1971. *Pseudophilotes* Beuret, 1958. *J. Lepid. Soc.*, 26: 111.

- Brown, F. Martin. 1975. A new subspecies of *Glaucopsyche (Phaedrotes) piasus* from Nevada (Lepidoptera: Lycaenidae). *Proc. Entomol. Soc. Washington*, 77(4): 501-504.
- Brown, F. Martin. 1983. The type of *Argynnis apacheana* Skinner. *J. Lepid. Soc.*, 37(1): 79-80.
- Brown, F. Martin, and Harry K. Clench. 1969. *Thecla viridis* Edwards, 1862 (Insecta, Lepidoptera): proposal to place on the official list. Z. N. (S.) 1857. *Bull. Zool. Nomencl.*, 25(4/5): 188-189.
- Brown, I. L., and P. R. Ehrlich. 1984. Population biology of the Checkerspot butterfly, *Euphydryas chalcedona*. I. Structure of the Jasper Ridge colony. *Oecologia* (Berlin), 47: 239-251.
- Brown, John. 1978. Observations on *Phoebis sennae* (Pieridae). *J. Res. Lepid.*, 17(3): 168-169. (1980).
- Brown, John W. 1981. Notes on the life history and Baja California distribution of *Chlorostymon simaethis sarita* (Skinner) (Lepidoptera: Lycaenidae). *J. Res. Lepid.*, 20(4): 207-213. (1983).
- Brown, John W. 1984. Host records for *Paratrytone melane* (Edwards) (Hesperiidae). *J. Lepid. Soc.*, 38(2): 138.
- Brown, John W. 1990. Urban biology of *Leptodes marina* (Reakirt) (Lycaenidae). *J. Lepid. Soc.*, 44(3): 200-201.
- Brown, John W., and William W. McGuire. 1983. A new subspecies of *Euphyes vestris* (Boisduval) from southern California (Lepidoptera: Hesperiidae). *Transactions San Diego Society Natural History*, 20(3): 57-68.

- Brown, Richard M. 1969a. A new subspecies of *Callophrys fotis* from the San Francisco Bay area (Lycaenidae). *J. Lepid. Soc.*, 23(2): 95-96.
- Brown, Richard M. 1969b. Larva and habitat of *Callophrys fotis bayensis* (Lycaenidae). *J. Res. Lepid.*, 8(2): 49-50. ("1970").
- Brown, Richard M., and Paul A. Opler. 1967. Biological observations on *Callophrys viridis* (Lycaenidae). *J. Lepid. Soc.*, 21(2): 113-114.
- Browning, Peter. 1986. *Place Names of the Sierra Nevada. From Abbot to Zumwalt*. Berkeley: Wilderness Press. 253 pp.
- Browning, Peter. 1988. *Yosemite Place Names. The Historic Background of Geographic Names in Yosemite National Park*. Lafayette, California: Great West Books. 241 pp.
- Brussard, P. F., P. R. Ehrlich, and M. C. Singer. 1974. Adult movements and population structure in *Euphydryas editha*. *Evolution*, 28: 408-415.
- Bryson, C. T. 1985. A new foodplant record for *Atalopedes campestris* (Boisduval) (Hesperiidae). *J. Lepid. Soc.*, 39(4): 335.
- Burdick, W. N. 1939. Comments of a field worker on the new race *Euphydryas chalcedona klotsi* - dos P. (Lepid.-Rhopalocera). *Bull. So. Calif. Acad. Sci.*, 38(1): 36-38.
- Burns, J. M. 1964. Evolution in the skipper butterflies of the genus *Erynnis*. *Univ. Calif. Publ. Entomol.*, 37: 1-214.
- Butler, Arthur G. 1882. On the butterflies collected by Lord Walsingham in California. *Journal of the Linnean Society-Zoology*, 16: 462-474.

- Butler, G. D. 1961. Two parasites of *Hylephila phyleus* Drury in Arizona (Lepidoptera: Hesperiiidae). *Pan-Pacific Entomologist*, 37(4): 202.
- Byers, George W. 1971. A migration of *Kricogonia castalia* (Pieridae) in northern Mexico. *J. Lepid. Soc.*, 25(2): 124-125.
- Callaghan, Curtis J. 1970. Note on *Callophrys* (*Callophrys*) *comstocki* Henne in Nevada. *J. Lepid. Soc.*, 24(3): 228.
- Carpenter, G. D. Hale, and B. M. Hobby. 1944. On *Limenitis bredowii* Geyer (Lep., Nymphalidae) with description of a new subspecies and revival of another. A study in geographical distribution and speciation. *Trans. R. Ent. Soc. Lond.*, 94(2): 311-346.
- Chambers, Donald S. 1963. A preliminary study of foodplant preferences in the *Lycaena helloides* complex (Lycaenidae) in Colorado. *J. Lepid. Soc.*, 17(1): 24-26.
- Champlin, S. B., and P. H. Wells. 1982. Energy reserves and metabolic expenditures of Monarch butterflies overwintering in southern California. *Ecological Entomology*, 7: 249-256.
- Chang, V. C. S. 1963. Quantitative analysis of certain wing and genitalia characters of *Pieris* in western North America. *J. Res. Lepid.* 2: 97-125.
- Chermock, F. H., and R. L. Chermock. 1937. Two new forms of *Papilio rudkini*. *Bull. So. Calif. Acad. Sci.*, 36(1): 8-10.
- Chermock, R. L. 1950. Subspeciation in *Neophasia menapia* Behr. *Proc. Ent. Soc. Wash.*, 52: 44-45.
- Christensen, James R. 1981. *A Field Guide to the Butterflies of the Pacific Northwest*. University Press of Idaho, Moscow, Idaho. 116 pp., 48 pls.

- Clark, Gowan C., and C. G. C. Dickson. 1956. The honey gland and tubercles of larvae of the Lycaenidae. *Lepid. News*, 10(1-2): 37-43.
- Clark, J. F. Gates. 1973. Recent Smithsonian Lepidoptera accessions: the Wilbur S. McAlpine Collection, the E. J. Newcomer Collection. *J. Lepid. Soc.*, 27(3): 240-241.
- Clarke, J. F. Gates. 1973. Recent Smithsonian Lepidoptera accessions. *J. Lepid. Soc.*, 27(3): 240-241.
- Clarke, W. C. 1952. The vegetation cover of the San Francisco Bay Region in the early Spanish period. M. A. Thesis, University of California, Berkeley. 220 pp.
- Clausen, Robert T. 1975. *Sedum of North America North of the Mexican Plateau*. Cornell University Press, Ithaca, New York. 742 pp.
- Clemence, Victor L. 1909. Notes on the forms of *Rusticus acmon* (Db.-Hew.) Scudder, occurring in the vicinity of Pasadena, Calif. *Canadian Entomologist*, 41(1): 38-39.
- Clench, Harry K. 1957. [Book Review] Colorado Butterflies. Part III. Libytheidae, Riodinidae, and Lycaenidae. By F. Martin Brown, assisted by Donald Eff and Bernard Rotger. *Lepid. News*, 11(1-3): 57-60.
- Clench, Harry K. 1961. Subgenus *Incisalia* Scudder. Pp. 201-204. In Ehrlich, Paul R., and Annett Ehrlich, *How to Know the Butterflies*, Wm. C. Brown Co., Dubuque, Iowa. 262 pp.
- Clench, Harry K. 1963. *Callophrys* (Lycaenidae) from the Pacific Northwest. *J. Res. Lepid.*, 2(2): 151-160.
- Clench, Harry K. 1968. Butterflies from Coahuila, Mexico. *J. Lepid. Soc.*, 22(4): 227-231.

- Clench, Harry K. 1970a. A new subspecies of *Brephidium exilis* from Yucatan (Lepidoptera: Lycaenidae). *J. Lepid. Soc.*, 24(1): 3-6.
- Clench, Harry K. 1970b. Communal roosting in *Colias* and *Phoebis* (Pieridae). *J. Lepid. Soc.*, 24(2): 117-120.
- Clench, Harry K. 1976. *Nathalis iole* (Pieridae) in the southeastern United States and the Bahamas. *J. Lepid. Soc.*, 30(2): 121-126.
- Clench, Harry K. 1981. New *Callophrys* (Lycaenidae) from North and Middle America. *Bull. Allyn Museum*, 64: 1-31.
- Comstock, John A. 1920. Butterflies of California. Preliminary announcement. *Bull. So. Calif. Acad. Sci.*, 19(3): 48.
- Comstock, John A. 1920. A new species or race of *Argynnis* from California. *Southwest Science Bulletin* (Southwest Museum), No. 1: 4-5.
- Comstock, John A. 1920. *Argynnis tehachapina*, var. nov. *Southwest Science Bulletin* (Southwest Museum), No. 1: 6-8.
- Comstock, John A. 1924. A new record for California. *Bull. So. Calif. Acad. Sci.*, 23(5): 157.
- Comstock, John A. 1926a. Studies in Pacific Slope Lepidoptera. *Bull. So. Calif. Acad. Sci.*, 25(1): 29-34.
- Comstock, John A. 1926b. Butterflies of California. *Bull. So. Calif. Acad. Sci.*, 25(2): 62-65.
- Comstock, John A. 1926c. Butterflies of California (continued). *Bull. So. Calif. Acad. Sci.*, 25(3): 84-87.

- Comstock, John A. 1927a. Studies in Pacific Coast Lepidoptera. *Bull. So. Calif. Acad. Sci.*, 26(3): 67-70.
- Comstock, John A. 1927b. *Butterflies of California*. Privately published, Los Angeles, California. 334 pp., 63 pls.
- Comstock, John A. 1928a. Studies in Pacific Coast Lepidoptera. *Bull. So. Calif. Acad. Sci.*, 27(2): 63-68.
- Comstock, John A. 1928b. Studies in Pacific Coast Lepidoptera. *Bull. So. Calif. Acad. Sci.*, 27(3): 80-89.
- Comstock, John A. 1929a. The egg of *Glaucopsyche lygdamus australis* Grinnell. *Bull. So. Calif. Acad. Sci.*, 28(1): 6,11.
- Comstock, John A. 1929b. Studies in Pacific Coast Lepidoptera. *Bull. So. Calif. Acad. Sci.*, 28(2): 22-32.
- Comstock, John A. 1929c. Studies in Pacific Coast Lepidoptera. *Bull. So. Calif. Acad. Sci.*, 28(3): 50-58.
- Comstock, John A. 1930a. Studies in Pacific Coast Lepidoptera. *Bull. So. Calif. Acad. Sci.*, 29(1): 21-31.
- Comstock, John A. 1930b. Studies in Pacific Coast Lepidoptera. *Bull. So. Calif. Acad. Sci.*, 29(3): 135-142.
- Comstock, John A. 1931a. Studies in Pacific Coast Lepidoptera. *Bull. So. Calif. Acad. Sci.*, 30(1): 15-19.
- Comstock, John A. 1931b. Studies in Pacific Coast Lepidoptera. *Bull. So. Calif. Acad. Sci.*, 30(3): 87-92.

- Comstock, John A. 1932. Studies in Pacific Coast Lepidoptera. *Bull. So. Calif. Acad. Sci.*, 31(1): 16-18.
- Comstock, John A. 1933. Studies in Pacific Coast Lepidoptera. *Bull. So. Calif. Acad. Sci.*, 32(3): 113-120.
- Comstock, John A. 1934. Studies in Pacific Coast Lepidoptera. *Bull. So. Calif. Acad. Sci.*, 33(1): 34-38.
- Comstock, John A. 1935. Miscellaneous notes on western Lepidoptera. *Bull. So. Calif. Acad. Sci.*, 34(2): 142-154.
- Comstock, John A. 1937. Miscellaneous notes on western Lepidoptera. *Bull. So. Calif. Acad. Sci.*, 36(1): 19-23.
- Comstock, John A. 1938. A new *Apodemia* from California (Lepidopt.). *Bull. So. Calif. Acad. Sci.*, 37(3): 129-132.
- Comstock, John A. 1940a. Argynnid notes. *Bull. So. Calif. Acad. Sci.*, 39(1): 75-77.
- Comstock, John A. 1940b. Notes on the early stages of *Euphydryas gilletti* Barnes. *Bull. So. Calif. Acad. Sci.*, 39(2): 111-113.
- Comstock, John A. 1943. In memoriam: Fordyce Grinnell, Jr., 1882-1943. *Bulletin Southern California Academy of Sciences*, 42(3): 136-137.
- Comstock, John A. 1953a. Collecting butterflies in the coastal area of Mexico near Manzanillo, Colima, with notes on the life history of a rare skipper. *Bull. So. Calif. Acad. Sci.*, 52(2): 43-45.
- Comstock, John A. 1953b. Life history notes on four southern Arizona butterflies. *Bull. So. Calif. Acad. Sci.*, 52(3): 127-136.

- Comstock, John A. 1955. A partial life history of a California butterfly. *Bull. So. Calif. Acad. Sci.*, 54(2): 57-60.
- Comstock, John A. 1956a. Notes on metamorphoses of the giant skippers (Lepidoptera; Megathymidae) and the life history of an Arizona species. *Bull. So. Calif. Acad. Sci.*, 55(1): 19-27.
- Comstock, John A. 1956b. Notes on the life history of two southern Arizona butterflies. *Bull. So. Calif. Acad. Sci.*, 55(3): 171-179.
- Comstock, John A. 1957. Commander Charles Montagu Dammers, 1878-1956. *Bulletin Southern California Academy Sciences*, 56(1): 50.
- Comstock, John A. 1965. Edwin Ray Hulbirt (1886-1965). *J. Lepid. Soc.*, 19(4): 243-244.
- Comstock, John A. 1966. Life history of *Philotes mojave* (Lepidoptera: Lycaeninae). *Trans. San Diego Soc. Nat. Hist.* 14: 133-136.
- Comstock, John A. 1975. Early work on the Megathymidae. *J. Res. Lepid.*, 14(2): 98-99.
- Comstock, John A. 1976a. Old Timers: Enrico Piazza, Fordyce Grinnell, Jr., William Sherman Wright, William Greenwood Wright. *J. Res. Lepid.*, 14(2): 90-92.
- Comstock, John A. 1976b. Early work on the Megathymidae. *J. Res. Lepid.*, 14(2): 98-99. ("1975").
- Comstock, John A., and Carl Coolidge. 1930. The life history of *Philotes sonorensis* Felder. *Bull. So. Calif. Acad. Sci.*, 29(1): 16-21.
- Comstock, John A., and Charles M. Dammers. 1931a. Notes on life history of *Poanes melane* Edw. (Lepid). *Bull. So. Calif. Acad. Sci.*, 30(1): 20-22.

- Comstock, John A., and Charles M. Dammers. 1931b. Notes on the early stages of four California argynnids (Lepid.). *Bull. So. Calif. Acad. Sci.*, 30(2): 4-44.
- Comstock, John A., and Charles M. Dammers. 1931c. The metamorphosis of *Heterochroa bredowii californica*. *Bull. So. Calif. Acad. Sci.*, 30(3): 83-87.
- Comstock, John A., and Charles M. Dammers. 1932a. Early stages of *Melitaea leanira wrightii* Edw. and *Calephelis nemesis* Edw. (Lepidoptera). *Bull. So. Calif. Acad. Sci.*, 31(1): 9-15.
- Comstock, John A., and Charles M. Dammers. 1932b. Metamorphoses of five California diurnals (Lepidoptera). *Bull. So. Calif. Acad. Sci.*, 31(2): 33-45.
- Comstock, John A., and Charles M. Dammers. 1932c. The metamorphoses of six California Lepidoptera. *Bull. So. Calif. Acad. Sci.*, 31(3): 88-100.
- Comstock, John A., and Charles M. Dammers. 1933a. Notes on the life histories of two California lepidopterous insects. *Bull. So. Calif. Acad. Sci.*, 32(1): 27-37.
- Comstock, John A., and Charles M. Dammers. 1933b. Notes on the life histories of four Californian lepidopterous insects. *Bull. So. Calif. Acad. Sci.*, 32(2): 77-83.
- Comstock, John A., and Charles M. Dammers. 1933c. Early stages of three California diurnals (Lepidoptera). *Bull. So. Calif. Acad. Sci.*, 32(3): 105-113.
- Comstock, John A., and Charles M. Dammers. 1934a. Additional notes on the early stages of California Lepidoptera. *Bull. So. Calif. Acad. Sci.*, 33(1): 25-34.
- Comstock, John A., and Charles M. Dammers. 1934b. The metamorphoses of three California diurnals. *Bull. So. Calif. Acad. Sci.*, 33(2): 79-92.

- Comstock, John A., and Charles M. Dammers. 1934c. Notes on the early stages of three butterflies and five moths from California. *Bull. So. Calif. Acad. Sci.*, 33(3): 136-151.
- Comstock, John A., and Charles M. Dammers. 1935a. Notes on the early stages of two butterflies and one moth. *Bull. So. Calif. Acad. Sci.*, 34(1): 81-87.
- Comstock, John A., and Charles M. Dammers. 1935b. Notes on the early stages of three butterflies and six moths from California. *Bull. So. Calif. Acad. Sci.*, 34(2): 120-142.
- Comstock, John A., and Charles M. Dammers. 1935c. Notes on the life histories of three butterflies and three moths from California. *Bull. So. Calif. Acad. Sci.*, 34(3): 211-225.
- Comstock, John A., and Charles M. Dammers. 1936. Metamorphosis of *Strymon leda* Edw. (Lepid. Rhopal.). *Bull. So. Calif. Acad. Sci.*, 35(1): 6-8.
- Comstock, John A., and Charles M. Dammers. 1937. Life history of *Papilio rudkini* Comst. *Bull. So. Calif. Acad. Sci.*, 36(1): 13-18.
- Comstock, John A., and Charles M. Dammers. 1938. Notes on the metamorphosis of *Mitoura spinetorum* Hew. (Lepidoptera, Theclinae). *Bull. So. Calif. Acad. Sci.*, 37(1): 30-32.
- Comstock, John A., and Florence M. Grimshawe. 1935. Early stages of *Papilio polydamus* Pucayus R. & J. *Bull. So. Calif. Acad. Sci.*, 34(1): 76-80.
- Comstock, John A., and Christopher Henne. 1933. A new lycaenid from southern California. *Bull. So. Calif. Acad. Sci.*, 32(1): 23-26.

- Comstock, John A., and Christopher Henne. 1965. Notes on the life history of *Philotes enoptes dammersi*. *Bull. So. Calif. Acad. Sci.*, 64(3): 153-156.
- Comstock, John A., and Christopher Henne. 1967. Notes on the life history of *Philotes rita elvirae* (Lepidoptera; Lycaenidae). *Bull. So. Calif. Acad. Sci.*, 66(2): 99-102.
- Comstock, John A., and Lloyd M. Martin. 1955. A new *Papilio* from California. *Bull. So. Calif. Acad. Sci.*, 54(3): 142-150.
- Comstock, John A., Grace H. Sperry, and John L. Sperry. 1933. Notes on the life histories of two Arizona butterflies. *Bull. So. Calif. Acad. Sci.*, 32(3): 99-104.
- Comstock, John A., John L. Sperry, and Grace H. Sperry. 1936. Notes on the life history of *Oeneis daura* Stkr. (Lepidoptera). *Bull. So. Calif. Acad. Sci.*, 35(3): 165-169.
- *Coolidge, Karl R. 1908a. The Rhopalocera of Santa Clara County, California. *Canadian Entomologist*, 40: 425-431.
- Coolidge, Karl R. 1908b. The life history of *Euchloe ausonides* Boisd. *Entomological News*, 19(5): 204-211.
- Coolidge, Karl R. 1909. Further notes on the Rhopalocera of Santa Clara County. *Canadian Entomologist*, 41: 187-188.
- Coolidge, Karl R. 1910a. Butterfly notes. *Canadian Entomologist*, 42: 315-316.
- Coolidge, Karl R. 1910b. On *Argynnis atossa* Edwards. *J. Ent. Zool.*, 2(3): 282.
- Coolidge, Karl R. 1910c. Notes on the genus *Thecla*. *Canadian Entomologist*, 42(11): 374-375.
- Coolidge, Karl R. 1911. A day with *Euchloe cethura*. *Ent. News*, 22(1): 11-13.
- Coolidge, Karl R. 1911b. Western Lepidoptera IV. *Psyche*, 18: 32-34.

- Collidge, Karl R. 1922. The life history of *Lerodea eufala* Edwards (Lepidoptera, Hesperiiidae). *Ent. News*, 33: 305-309.
- Coolidge, Karl R. 1923. The life history of *Thanaos funeralis* Scud. & Burg. (Lepidoptera; Hesperiiidae). *J. New York Entomological Socety*, 31(4): 175-181.
- Coolidge, Karl R. 1923b. The life history of *Hesperia ericetorum* Boisd. (Lepid.: Hesperiiidae). *Entomological News*, 34(5): 140-146.
- Coolidge, Karl R. 1924a. The life history of *Mitoura loki* Skinner (Lepid.: Lycaenidae). *Ent. News.*, 35: 199-204.
- Coolidge, Karl R. 1924b. Life history of *Heodes helloides* Bdv. (Lepidoptera, Lycaenidae). *Ent. News*, 35(9): 306-312.
- Coolidge, Karl R. 1924c. Life history studies of some Californian Rhopalocera (Lepidoptera). The life history of *Hylephila phylaeus* Drury (Hesperiiidae). *Transactions American Ent. Soc.*, 50(4): 319-324.
- Coolidge, Karl R. 1924d. Life history studies of some Californian Rhopalocera (Lepidoptera). The life history of *Callophrys dumetorum* Boisduval (Lycaenidae). *Transactions American Ent. Soc.*, 50(4): 329-335.
- Coolidge, Karl R., and E. J. Newcomer. 1908. The life history of *Euchloe ausonides* Boisd. *Ent. News*, 19(5): 204-211.
- Coolidge, Karl R., and H. H. Newcomb. 1920. Richard H. Stretch --- an appreciation. *Entomological News*, 31(7): 181-185.
- Cottle, J. E. 1931. Where some rare butterflies fly. *Pan-Pacific Entomologist*, VIII(1): 1-4.

- Crowe, Charles R. 1965. The climatological tool in Lepidoptera research. *J. Res. Lepid.*, 4(1): 23-36.
- Crowe, Charles R. 1970. A possible new hybrid copper. *J. Res. Lepid.*, 8(2): 51-52. ("1969").
- Dammers, Charles M. 1937. A remarkable instance of foodplant selection by a butterfly. *Bull. So. Calif. Acad. Sci.*, 36(1): 23-24.
- Dammers, Charles M. 1940. *Euphydryas chalcedona*. Dbldy. & Hew. *Bull. So. Calif. Acad. Sci.*, 39(2): 123-125.
- Davenport, D., and V. G. Dethier. 1937. Bibliography of the described life-histories of the Rhopalocera of America north of Mexico 1889-1937. *Entomol. Amer.*, 17: 155-194.
- Davenport, K. 1983. Geographic distribution and checklist of the butterflies of Kern County, California. *J. Lepid. Soc.*, 37(1): 46-69.
- Davenport, K. 1988. New distribution records and a probable new larval host plant for *Philotes sonorensis* (Lycaenidae) in Kern and Tulare counties, California. *J. Lepid. Soc.*, 42(4): 291-292.
- Dethier, V. G. 1939. The life history of *Polites peckius* Kby. *Bull. So. Calif. Acad. Sci.*, 38(3): 188-190.
- Dethier, V. G. 1940. The final stages of *Polites mystic* Scud. *Bull. So. Calif. Acad. Sci.*, 39(2): 108-110.
- Dethier, V. G. 1940. Life histories of Cuban Lepidoptera. *Psyche*, 47: 14-25.
- Dethier, V. G. 1942. Notes on the larva and chrysalis of *Polites thermistocles* Latr. *Bull. So. Calif. Acad. Sci.*, 41(1): 41-43.

- Dethier, V.G. 1942. Metamorphoses of common Cuban Pyrginae. *Psyche*, 49: 4-7.
- Dethier, V. G. 1943. The life history of *Polites sabuleti* Bdv. *Bull. So. Calif. Acad. Sci.*, 42(3): 128-131.
- Dethier, V. G. 1944. Notes on the immature stages of *Urbanus tessellata occidentalis* Skin. *Bull. So. Calif. Acad. Sci.*, 43(1): 30-32.
- Dethier, V. G. 1948. Life history of *Hesperia leonardus* Harr. *Bull. So. Calif. Acad. Sci.*, 47(1): 1-2.
- Dethier, V. G. 1954. Chemical factors determining the choice of food plants by *Papilio* larvae. *American Naturalist*, 75: 61-73.
- Dethier, V. G. 1959. Food-plant distribution and density and larval dispersal as factors affecting insect populations. *Canadian Entomologist*, 91: 581-596.
- Dimock, Thomas E. 1972. Type locality and habitat - *Cynthia annabella*. *J. Res. Lepid.*, 10(4): 265-266.
- Dimock, Thomas E. 1973. Three natural hybrids of *Vanessa atalanta rubria* x *Cynthia annabella* (Nymphalidae). *J. Lepid. Soc.*, 27: 274-278.
- Dimock, Thomas E. 1975. Corrections to two articles on aberrant *Cynthia* (Nymphalidae). *J. Lepid. Soc.*, 29(2): 84.
- Dimock, Thomas E. 1978. Notes on the life cycle and natural history of *Vanessa annabella* (Nymphalidae). *J. Lepid. Soc.*, 32(2): 88-96.
- Dixey, F. A. 1915. New species and subspecies of Pierinae. *Trans. Entomol. Soc. London*, Part I: 9-17.
- Dod, F. H. W. 1907. Notes on *Chrysophanus hypophlaeas* and its allies, with description of a new species. *Canadian Entomologist*, 39: 169-171.

- Donahue, Julian P. 1975. Recent donations of Lepidoptera to the Natural History Museum of Los Angeles County. *J. Lepid. Soc.*, 29(2): 130.
- Donahue, Julian P. 1985. Monarch watch. *Western Tanager*, 52(5): 7.
- Dornfeld, E. J. 1959. *Mitoura johsoni* in Oregon and California. *J. Lepid. Soc.*, 13(3): 183.
- Dornfeld, E. J. 1967. On the yellow forms of *Coenonympha tullia* (Satyridae) in Oregon. *Journal of the Lepidopterists' Society*, 21(1): 1-7.
- Dornfeld, E. J. 1980. *The Butterflies of Oregon*. Timber Press, Forest Grove, Oregon. 276 pp.
- dos Passos, Cyril F. 1938. Some new subspecies of North American Lycaenidae (Lepid.). *Canadian Entomologist*, 70(3): 45-48.
- dos Passos, Cyril F. 1951. The entomological reminiscences of William Henry Edwards. *Journal of the New York Entomological Society*, 59(3): 129-186.
- dos Passos, Cyril F. 1960. Taxonomic notes on some nearctic Rhopalocera. 1. Hesperioidea. *J. Lepid. Soc.*, 14(1): 24-36.
- dos Passos, Cyril F. 1964. *A Synonymic List of the Nearctic Rhopalocera*. The Lepidopterists' Society, Memoir No. 1. 145 pp.
- dos Passos, Cyril F. 1981. Some little-known U. S. publications on Lepidoptera II. *J. Res. Lepid.*, 20(2): 111-122. (1982).
- dos Passos, Cyril F., and L. P. Grey. 1947. Systematic catalogue of *Speyeria* (Lepidoptera, Nymphalidae) with designations of types and fixations of type localities. *American Museum Novitates*, No. 1370: 1-30.

Doubleday, Edward, and John O. Westwood. 1848. The Genera of Diurnal Lepidoptera.

Volume I. Longman, Brown, Green, and Longmans, London. Page 180.

Douglas, Matthew M., and J. W. Grula. 1977. Thermoregulatory adaptations allowing ecological range expansion by the pierid butterfly *Nathalis iole* Boisduval.

Evolution, 32: 776-783.

Doudoroff, N. 1935. Notes on two local butterflies. *Pan-Pacific Entomologist*, XI(3): 144.

Douglas, M. M., and J. W. Grula. 1978. Thermoregulatory adaptations allowing ecological range expansion by the Pierid butterfly, *Nathalis iole* Boisduval.

Evolution, 32(4): 776-783.

Downey, John C. 1957. Intraspecific variation in evolution in populations of *Plebejus icarioides* (Bdv.). Ph.D. Dissertation, University of California, Davis. 120 pp.

Downey, John C. 1962. Myrmecophily in *Plebejus (Icaricia) icarioides* (Lepid.: Lycaenidae). *Entomological News*, 73(3): 57-66.

Downey, John C. 1965. Mimicry and distribution of *Caenurgina caerulea* Grt. (Noctuidae). *J. Lepid. Soc.*, 19(3): 165-170.

Downey, John C. 1966. Sound production in pupae of Lycaenidae. *J. Lepid. Soc.*, 20(1): 129-155.

Downey, John C., and D. B. Dunn. 1964. Variation in the Lycaenid butterfly *Plebejus icarioides* (Lycaenidae). III. Additional data on foodplant specificity. *Ecology*, 45(1): 172-178.

Downey, John C., and Woodson C. Fuller. 1961. Variation in *Plebejus icarioides* (Lycaenidae). I. Foodplant specificity. *J. Lepid. Soc.*, 15(1): 34-42.

- Downey, John C., and W. H. Lange, Jr. 1956. Analysis of variation in a recently extinct polymorphic lycaenid butterfly, *Glaucopsyche xerces* (Bdv.), with notes on its biology and taxonomy. *Bull. So. Calif. Acad. Sci.*, 55(3): 153-170.
- Drummond, Boyce A. 1986. Breaking the rules: courtship and mating in *Parnassius* butterflies. Paper presented to Annual Meeting of the Lepidopterists' Society, Ottawa, Canada, May 1986.
- Drummond, Boyce A., Guy L. Bush, and Thomas C. Emmel. 1968. The genetics of larval polymorphism in *Chlosyne lacinia*. *Bull. Ent. Soc. America*, 14: 205.
- Drummond, Boyce A., Guy L. Bush, and Thomas C. Emmel. 1970. The biology and laboratory culture of *Chlosyne lacinia* Geyer (Nymphalidae). *J. Lepid. Soc.*, 24(3): 135-142.
- Dyar, Harrison G. 1891a. Descriptions of some butterfly larvae from Yosemite.--I. *Canadian Entomologist*, 23(8): 172-174.
- Dyar, Harrison G. 1891b. Descriptions of some butterfly larvae from Yosemite.--III. *Canadian Entomologist*, 23(10): 203-209.
- Dyar, Harrison G. 1893a. Life-history of *Papilio eurymedon* Boisd. *Entomological News*, 4: 243-245.
- Dyar, Harrison G. 1893b. Descriptions of Certain Lepidopterous Larvae [*Colias behrii*]. *Canadian Entomologist*, 25(6): 158-160.
- Edwards, Henry. 1881. On some apparently new forms of diurnal Lepidoptera. *Papilio*, 1(4): 50-55.
- Edwards, Henry. 1889. Bibliographical catalogue of the described transformations of the North American Lepidoptera. *Bull. U. S. Nat. Mus.*, 35: 1-37.

- Edwards, William H. 1864. Notes on the Argynnnides of California. *Proc. Entomol. Soc. Phil.*, 3: 434-436.
- Edwards, William H. 1883. Willow as a foodplant of *Papilio rutulus*. *Papilio*, 3: 65.
- Edwards, William H. 1884a. *Butterflies of North America*. Second Series. Houghton-Mifflin & Co., Boston.
- Edwards, William H. 1884b. Description of a preparatory stages of *Phyciodes camillus*, Edw. *Papilio*, 4: 128-134.
- Edwards, William H. 1887. Description of preparatory stages of *Coenonympha ampelos*, Edw. *Canadian Entomologist*, 19(3): 41-44.
- Edwards, William H. 1895. Description of the preparatory stages of *Pholisora catullus*, Fabricius. *Canadian Entomologist*, 17: 245-248.
- Eff, Donald. 1955. The foodplant of *Erynnis pascuvius*. *Lepidopterists' News*, 9: 15.
- Ehrlich, Paul R. 1961. Intrinsic barriers to dispersal in checkerspot butterfly. *Science*, 134: 108-109.
- Ehrlich, Paul R. 1975. Checkerspot butterflies: a historical perspective. *Science*, 188: 221-228.
- Ehrlich, Paul R., and Larry G. Mason. 1966. The population biology of the butterfly *Euphydryas editha*. III. Selection and the phenetics of the Jasper Ridge colony. *Evolution*, 20: 165-173.
- Ehrlich, Paul R., and Dennis D. Murphy. 1981. Butterfly nomenclature: A critique. *J. Res. Lepid.*, 20(1): 1-11. (1982).
- Ehrlich, Paul R., and Dennis D. Murphy. 1982. Nomenclature, taxonomy and evolution. *J. Res. Lepid.*, 20(4): 199-204. (1983).

- Ehrlich, Paul R., and Peter H. Raven. 1964. Butterflies on plants: a study in coevolution. *Evolution*, 18: 586-608.
- Eitschberger, Ulf. 1981. Die nordamerikanischen Arten aus der *Pieris napibryoniae*-Gruppe (Lep., Pieridae). *Atalanta* (Münnerstadt), 11: 366-371.
- Ellis, Scott L. 1974. Field observations on *Colias alexandra* Edwards (Pieridae). *J. Lepid. Soc.*, 28(2): 114-125.
- Emmel, John F. 1981. Two new subspecies of the *Papilio indra* complex from California (Papilionidae). *J. Lepid. Soc.*, 35: 297-302.
- Emmel, John F., and Thomas C. Emmel. 1963a. Field observations on the rare argynnid, *Speyeria egleis tehachapina*. *J. Lepid. Soc.*, 17(4): 243-244.
- Emmel, John F., and Thomas C. Emmel. 1963b. Larval foodplant records for six western *Papilios*. *J. Res. Lepid.*, 1(3): 191-193.
- Emmel, John F., and Thomas C. Emmel. 1963c. Composition and relative abundance in a temperate zone butterfly fauna. *J. Res. Lepid.*, 1(2): 97-108.
- Emmel, John F., and Thomas C. Emmel. 1964. Genetic relationships of *Papilio indra* and *Papilio polyxenes*. *J. Res. Lepid.*, 3(3): 157-158.
- Emmel, John F., and Thomas C. Emmel. 1966. A new *Papilio* from the Mojave Desert of California (Lepidoptera, Papilionidae). *Entomological News*, 77: 57-63.
- Emmel, John F., and Thomas C. Emmel. 1968. Life history notes on *Satyrium sylvinus dryope* Edwards (Lycaenidae: Theclinae). *J. Res. Lepid.*, 7(2): 123-125.
- Emmel, John F., and Thomas C. Emmel. 1968. The population biology and life history of *Papilio indra martini*. *J. Lepid. Soc.*, 22: 46-52.

- Emmel, John F., and Thomas C. Emmel. 1974. Ecological studies of Rhopalocera in a Sierra Nevadan community -- Donner Pass, California. V. Faunal additions and foodplant records since 1962. *J. Lepid. Soc.*, 28: 344-348.
- Emmel, John F., and Thomas C. Emmel. 1979. Christopher Henne (1905-1977). *J. Lepid. Soc.*, 33: 72-75.
- Emmel, John F., and Thomas C. Emmel. 1998a. A New *Euphilotes pallescens* Subspecies (Lepidoptera: Lycaenidae) from the Northern California-Nevada Border Region. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 277-282.
- Emmel, John F., and Thomas C. Emmel. 1998b. A New Species of *Agriades* (Lepidoptera: Lycaenidae) from the Sierra Nevada and Trinity Alps of California, and the Biology and Geographic Variation of *Agriades podarce* in California. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 287-302.
- Emmel, John F., and Thomas C. Emmel. 1998c. A New Subspecies of *Everes amyntula* (Lepidoptera: Lycaenidae) from the California Channel Islands. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 303-306.
- Emmel, John F., and Thomas C. Emmel. 1998d. A New Subspecies of *Ochlodes sylvanoides* (Lepidoptera: HesperIIDae) from Santa Catalina Island in the Southern Channel Islands of California. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 313-316.

- Emmel, John F., and Thomas C. Emmel. 1998e. A New Subspecies of *Polites sabuleti* (Lepidoptera: HesperIIDae) from Santa Rosa Island, California. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 317-320.
- Emmel, John F., and Thomas C. Emmel. 1998f. A Review of the *Speyeria egleis* Complex in California, with the Description of Two New Subspecies (Lepidoptera: Nymphalidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 437-442.
- Emmel, John F., and Thomas C. Emmel. 1998g. A Previously Unrecognized Subspecies of *Speyeria zerene* (Lepidoptera: Nymphalidae) from Coastal Northern California. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 451-454.
- Emmel, John F., and Thomas C. Emmel. 1998h. A New Subspecies of *Papilio indra* (Lepidoptera: Papilionidae) from Northwestern California. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 701-706.
- Emmel, John F., and Thomas C. Emmel. 1998i. A New Subspecies of the Giant Skipper *Megathymus yuccae* from San Diego County, California (Lepidoptera: HesperIIDae: Megathyminae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 763-767.
- Emmel, John F., and Thomas C. Emmel. 1998j. Two New Geographically Restricted Subspecies of *Apodemia mormo* (Lepidoptera: Riodinidae) from the Vicinity of San Bernardino, California. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 795-800.

- Emmel, John F., Thomas C. Emmel, and Bruce M. Griffin. 1998. A New Dwarfed Subspecies of *Papilio indra* (Lepidoptera: Papilionidae) from the Dead Mountains of Southeastern California. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 711-716.
- Emmel, John F., Thomas C. Emmel, and Sterling O. Mattoon. 1975. Check List of the Butterflies and Skippers of California. University of Florida, Gainesville. 5 pp.
- Emmel, John F., Thomas C. Emmel, and Sterling O. Mattoon. 1998a. The Types of California Butterflies Named by Jean Alphonse Boisduval: Designation of Lectotypes and a Neotype, and Fixation of Type Localities. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 3-78.
- Emmel, John F., Thomas C. Emmel, and Sterling O. Mattoon. 1998b. The Types of California Butterflies Named By Pierre Hippolyte Lucas: Designation of Lectotypes and Fixation of Type Localities. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 79-84.
- Emmel, John F., Thomas C. Emmel, and Sterling O. Mattoon. 1998c. Fixation of a Type Locality for *Thecla spinetorum* Hewitson (Lepidoptera: Lycaenidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 85-86.
- Emmel, John F., Thomas C. Emmel, and Sterling O. Mattoon. 1998d. The Types of California Butterflies Named By Cajetan Von Felder and Rudolph Felder: Designation of Lectotypes and Fixation of Type Localities. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 87-94.

- Emmel, John F., Thomas C. Emmel, and Sterling O. Mattoon. 1998e. The Types of California Butterflies Named by Herman Behr: Designation of Neotypes and Fixation of Type Localities. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 95-114.
- Emmel, John F., Thomas C. Emmel, and Sterling O. Mattoon. 1998f. Designation of a Lectotype and Fixation of a Type Locality for *Lemonias edithana* Strand (Lepidoptera: Nymphalidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 123-126.
- Emmel, John F., Thomas C. Emmel, and Sterling O. Mattoon. 1998g. New Subspecies of Pieridae (Lepidoptera) from California, Nevada, and Baja California.. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 127-138.
- Emmel, John F., Thomas C. Emmel, and Sterling O. Mattoon. 1998h. New Subspecies of Nymphalidae from California and a Neotype Designation for *Argynnis rupestris* Behr (Lepidoptera: Nymphalidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 139-158.
- Emmel, John F., Thomas C. Emmel, and Sterling O. Mattoon. 1998i. New Theclinae Subspecies of Lycaenidae from California, Separation of *Incisalia mossii* and *Incisalia fotis*, and Seven Species Groups of the Subgenus *Callophrys* (Lepidoptera: Lycaenidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 159-170.
- Emmel, John F., Thomas C. Emmel, and Sterling O. Mattoon. 1998j. New Polyommata Subspecies of Lycaenidae (Lepidoptera) from California.

Systematics of Western North American Butterflies. Mariposa Press, Gainesville, Florida. Pp. 171-200.

Emmel, John F., Thomas C. Emmel, and Sterling O. Mattoon. 1998k. New Subspecies of HesperIIDae (Lepidoptera) from California. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 201-206.

Emmel, John F., Thomas C. Emmel, and Sterling O. Mattoon. 1998l. A New Subspecies of *Speyeria zerene* (Lepidoptera: Nymphalidae) from the San Francisco Bay Area of California. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 455-460.

Emmel, John F., Thomas C. Emmel, and Sterling O. Mattoon. 1998m. Three New Subspecies of *Hesperia lindseyi* (Lepidoptera: HesperIIDae) in California and Northwestern Nevada. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 475-480.

Emmel, John F., Thomas C. Emmel, and Sterling O. Mattoon. 1998n. *Incisalia polia*: A New Species Record for California, with Description of a New Maritime Subspecies (Lepidoptera: Lycaenidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 811-814.

Emmel, John F., Thomas C. Emmel, and Sterling O. Mattoon. 1998o. A Checklist of the Butterflies and Skippers of California. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 825-836.

Emmel, John F., Thomas C. Emmel, Sterling O. Mattoon, and George T. Austin. 1998. Introduction to New Descriptions and Synonymies of Butterflies from Western

- North America. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 1-2.
- Emmel, John F., Thomas C. Emmel, and Gordon F. Pratt. 1998. Five New Subspecies of *Apodemia mormo* (Lepidoptera: Riodinidae) from Southern California. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 801-810.
- Emmel, John F., Thomas C. Emmel, and Jon H. Shepard. 1967. Range extension of *Callophrys comstocki* (Lycaenidae). *J. Lepid. Soc.*, 21(2): 114.
- Emmel, John F., and Clifford D. Ferris. 1972. The biology of *Callophrys (Incisalia) fotis bayensis* (Lycaenidae). *J. Lepid. Soc.*, 26(4): 237-244.
- Emmel, John F., and Bruce M. Griffin. 1998. A New *Papilio indra* Subspecies (Lepidoptera: Papilionidae) from the Muddy Mountains of Southern Nevada. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 707-710.
- Emmel, John F., and Rudolf H. T. Mattoni. 1990. A new subspecies of *Satyrrium auretteorum* (Lycaenidae) from the Santa Monica Mountains of southern California. *J. Res. Lepid.*, 28(1-2): 100-104. ("1989")
- Emmel, John F., and Godron F. Pratt. 1998. New Subspecies of Lycaeninae from California and a Type Locality Restriction for *Chrysophanus cupreus* W. H. Edwards (Lepidoptera: Lycaenidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 661-680.

- Emmel, John F., and Oakley Shields. 1979. Larval foodplant records for *Papilio zelicaon* in the western United States, and further evidence for the conspecificity of *P. zelicaon* and *P. gothica*. *J. Res. Lepid.*, 17: 56-67.
- Emmel, John F., and Oakley Shields. 1980. The biology of *Plebejus (Icaricia) shasta* in the western United States (Lycaenidae). *J. Res. Lepid.*, 17(2): 129-140. ("1978")
- Emmel, John F., Oakley Shields, and Dennis Breedlove. 1971. Larval foodplant records for North American Rhopalocera. Part 2. *J. Res. Lepid.*, 9(): 233-242. ("1970").
- Emmel, Thomas C. 1967a. Genetic and phenetic differentiation in two complexes of western American butterflies. Ph.D. dissertation, Stanford University, California. 101 pp.
- Emmel, Thomas C. 1967b. Check list of the butterflies of southern California. University of Florida, Gainesville. 10 pp.
- Emmel, Thomas C. 1969a. Methods for studying the chromosomes of Lepidoptera. *J. Res. Lepid.*, 7: 23-28.
- Emmel, Thomas C. 1969b. Taxonomy, distribution and biology of the genus *Cercyonis* (Satyridae). I. Characteristics of the genus. *J. Lepid. Soc.*, 23: 165-175.
- Emmel, Thomas C. 1970. Estimation of natural mutation rates for albinism in two species of the satyrid genus *Cercyonis*. *J. Res. Lepid.*, 8: 65-68.
- Emmel, Thomas C. 1972. A preliminary check list of the butterflies of southern California. *Mid-Continent Lepidoptera Series*, Vol. 4(No. 55): 1-4.
- Emmel, Thomas C. 1973. Dispersal in a cosmopolitan butterfly species (*Pieris rapae*) having open population structure. *J. Res. Lepid.*, 11(2): 95-98. ("1972")

- Emmel, Thomas C. 1975. Genus *Ministrymon* Clench. In Howe, William A., edit., *The Butterflies of North America*. Doubleday, New York. Pp. 298-299.
- Emmel, Thomas C. 1987. The John Adams Comstock Award, 1987: The man we honor, John S. Garth. *News Lepid. Soc.*, 1987(6): 77-80.
- Emmel, Thomas C., and George T. Austin. 1998. What is *Argynnis carolae*? The Cytotaxonomy and Systematic Position of a *Speyeria* Relic Species from Nevada (Lepidoptera: Nymphalidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 443-450.
- Emmel, Thomas C., and John F. Emmel. 1962a. Ecological studies of Rhopalocera in a High Sierran community -- Donner Pass, California. I. Butterfly associations and distributional factors. *J. Lepid. Soc.*, 16: 23-44.
- Emmel, Thomas C., and John F. Emmel. 1962b. Note regarding habitats and Rhopalocera of Donner Pass, California. *J. Lepid. Soc.*, 16: 136.
- Emmel, Thomas C., and John F. Emmel. 1963a. Composition and relative abundance in a temperate zone butterfly fauna. *J. Res. Lepid.*, 1: 97-108.
- Emmel, Thomas C., and John F. Emmel. 1963b. Ecological studies of Rhopalocera in a High Sierran community -- Donner Pass, California. II. Meteorologic influence on flight activity. *J. Lepid. Soc.*, 17: 7-20.
- Emmel, Thomas C., and John F. Emmel. 1968. Life history notes on *Satyrium sylvinus dryope* Edwards (Lycaenidae: Theclinae). *J. Res. Lepid.*, 7: 123-125.
- Emmel, Thomas C., and John F. Emmel. 1969. Selection and host plant overlap in two desert *Papilio* butterflies. *Ecology*, 50: 158-159.

- Emmel, Thomas C., and John F. Emmel. 1971a. An extraordinary new subspecies of *Cercyonis oetus* from central Nevada. *Pan-Pacific Entomologist*, 47: 155-157.
- Emmel, Thomas C., and John F. Emmel. 1971b. A new subspecies of *Papilio indra* from central Nevada (Lepidoptera: Papilionidae). *Pan-Pacific Entomologist*, 47: 220-223.
- Emmel, Thomas C., and John F. Emmel. 1973a. *The Butterflies of Southern California*. Natural History Museum of Los Angeles County and Ward Ritchie Press, Los Angeles. 148 pp.
- Emmel, Thomas C., and John F. Emmel. 1973b. Two new subspecies of *Euphydryas chalcedona* from the Mojave Desert of southern California. *J. Res. Lepid.*, 11: 141-146.
- Emmel, Thomas C., and John F. Emmel. 1973c. On *Papilio indra nevadensis* in central Nevada (Lepidoptera: Papilionidae). *Pan-Pacific Entomologist*, 49: 4.
- Emmel, Thomas C., and John F. Emmel. 1974. The biology of *Papilio indra nevadensis* (Papilionidae) in Nevada. *J. Lepid. Soc.*, 28: 107-114.
- Emmel, Thomas C., and John F. Emmel. 1975. A new subspecies of *Euphydryas editha* from the Channel Islands of California. *J. Res. Lepid.*, 13: 131-136.
- Emmel, Thomas C., and John F. Emmel. 1989. Introduction, synonymic list, and bibliography. Reprint edition of Comstock, John A., 1927. *Butterflies of California*. Scientific Publishers, Gainesville, Florida (Nature Guide No. 2). 334 pp., 63 pls.
- Emmel, Thomas C., and John F. Emmel. 1991. Independent evolution of adult and larval characters in butterflies of the *Papilio indra* group. *Evolution*, in press.

- Emmel, Thomas C., and John F. Emmel. 1998a. A Neotype Designation for *Satyrus behrii* Grinnell (Lepidoptera: Satyridae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 117-120.
- Emmel, Thomas C., and John F. Emmel. 1998b. Designation of a Type Locality for *Satyrus silvestris* Edwards (Lepidoptera: Satyridae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 121-122.
- Emmel, Thomas C., and John F. Emmel. 1998c. A New *xerces*-like Subspecies of *Glaucopsyche lygdamus* (Lepidoptera: Lycaenidae) from Santa Rosa Island, California. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 307-312.
- Emmel, Thomas C., and Lowell N. Harris. 1998. A New Subspecies of *Euphydryas anicia* (Lepidoptera: Nymphalidae) from the South Park Area of Central Colorado. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 433-436.
- Emmel, Thomas C., Marc C. Minno, and Boyce A. Drummond. 1992. *Florissant Butterflies: A Guide to Fossil and Modern-day Species*. Stanford University Press, Stanford, California. 118 pp.
- Emmel, Thomas C., Ray E. Stanford, and John F. Emmel. 1973. A check list of the skippers of southern California. University of Florida, Gainesville. 9 pp.
- Emmel, Thomas C., and Sterling O. Mattoon. 1972. *Cercyonis pegala blanca*, a "missing type" in the evolution of the genus *Cercyonis* (Satyridae). *J. Lepid. Soc.*, 26: 140-149.

- Emmel, Thomas C., and Houston R. Trew. 1973. The chromosomes of skipper butterflies from southwestern North America (Lepidoptera, Hesperiiidae). *Cytologia*, 38: 45-53.
- Emmel, Thomas C., Houston R. Trew, and Oakley Shields. 1973. Chromosomal variability in a nearctic lycaenid butterfly, *Philotes sonorensis* (Lepidoptera: Lycaenidae). *Pan-Pacific Entomologist*, 49: 74-80.
- Emmel, Thomas C., and Reinhard A. Wobus. 1965. A southward migration of *Vanessa cardui* in late summer and fall. *J. Lepid. Soc.*, 20: 123-124.
- Endo, K., Y. Maruyama, and K. Sakai. 1985. Environmental factors controlling seasonal morph determination in the small copper butterfly, *Lycaena phlaeus daimo* Seitz. *J. Insect Physiol.*, 31: 525-532.
- Engelhardt, George P. 1930. Dr. William Barnes. *Bulletin of the Brooklyn Entomological Society*, 25: 143-144.
- Essig, E. O. 1926a. *Insects of Western North America*. Macmillan Co., New York. 1,035 pp.
- Essig, E. O. 1926b. A butterfly migration. *Pan-Pacific Entomologist*, 2(4): 211.
- Essig, E. O. 1972. *A History of Entomology* (Facsimile of the Edition of 1931). Hafner Publishing Company, New York. 1,029 pp.
- Evans, William H. 1952. Notes on *Anthocharis sara* and *reakirtii*. *Lepid. News*, 6: 106.
- Evans, William H. 1954. Flight habits of *Anthocharis sara*. *Lepidopterists' News*, 8(1-2): 10.

- Evans, William H. 1955. *A Catalogue of the American Hesperiiidae Indicating the Classification and Nomenclature Adopted in the British Museum. Part IV. Hesperiinae and Megathyminae*. British Museum (Nat. Hist.), London. 449 pp.
- Evans, William H. 1975. Seasonal forms of *Anthocharis sara* (Pieridae). *J. Lepid. Soc.*, 29(1), 52-55.
- Evenden, J. C. 1926. The Pine butterfly, *Neophasia menapia* Felder. *Journal Agricultural Research*, 33(4): 339-344.
- Fadem, C. M., and A. M. Shapiro. 1979. Notes on winter roosting by monarchs (Lepidoptera: Danaidae) at an inland site in California. *Pan-Pacific Entomologist*, 55(4): 309-310.
- Fales, John H. 1959. A field study of the flight behavior of the Tiger Swallowtail butterfly. *Annals Entomol. Soc. America*, 52: 486-487.
- Fales, John H., and D. T. Jennings. 1977. Butterflies as prey for crab spiders (Thomisidae). *J. Lepid. Soc.*, 31(4): 280-282.
- Farquhar, Francis P. 1965. *History of the Sierra Nevada*. Berkeley: University of California Press. 262 pp.
- Farquhar, Francis P., editor. 1966. *Up and Down California in 1860-1864. The Journal of William H. Brewer, Professor of Agriculture in the Sheffield Scientific School from 1864 to 1903*. University of California Press, Berkeley. 583 pp.
- Ferris, Clifford D. 1970. Two new forms of Plebejinae from Wyoming. *J. Res. Lepid.*, 8(3): 91-93. ("1969").

- Ferris, Clifford D. 1973. A revision of the *Colias alexandra* complex (Pieridae) aided by ultraviolet reflectance photography with designation of a new subspecies. *J. Lepid. Soc.*, 27: 57-73.
- Ferris, Clifford D. 1974. Distribution of arctic-alpine *Lycaena phlaeus* L. (Lycaenidae) in North America with designation of a new subspecies. *Bulletin Allyn Museum*, 18: 1-13.
- Ferris, Clifford D. 1976. A proposed revision of non-arctic *Parnassius phoebus* Fabricius in North America (Papilionidae). *J. Res. Lepid.*, 15(1): 1-22.
- Ferris, Clifford D. 1976. A note on the subspecies of *Parnassius clodius* Menetries found in the Rocky Mountains of the United States (Papilionidae). *J. Res. Lepid.*, 15(2): 65-74.
- Ferris, Clifford D. 1977a. A note on the subspecies of *Parnassius clodius* Menetries found in the Rocky Mountains of the United States (Papilionidae). *J. Res. Lepid.*, 15(2): 65-74.
- Ferris, Clifford D. 1977b. Taxonomic revision of the species *dorcas* Kirby and *heloïdes* Boisduval in the genus *Apodemia* Scudder (Lycaenidae: Lycaeninae). *Bulletin of Allyn Museum*, 45: 1-42.
- Ferris, Clifford D. 1988. Revision of several North American Leguminosae-feeding *Colias* species, with description of a new subspecies (Pieridae: Coliadinae). *Bulletin of the Allyn Museum*, 116: 1-28.
- Ferris, Clifford D. 1989. Supplement to: A catalogue/checklist of the butterflies of America north of Mexico. Lepidopterists' Society Memoir No. 3. 103 pp.

- Ferris, Clifford D., and F. Martin Brown. 1981. *Butterflies of the Rocky Mountain States*. University of Oklahoma Press, Norman. 442 pp.
- Ferris, Clifford D., and John F. Emmel. 1982. Discussion of *Papilio coloro* W. G. Wright (= *Papilio rudkini* F. & R. Chermock) and *Papilio polyxenes* Fabricius (Papilionidae). *Bull. Allyn Museum*, 76: 1-13.
- Ferris, Clifford D., and Ray E. Stanford. 1970. *Incisalia fotis shryveri* (Lycaenidae): bionomic notes and life history. *J. Lepid. Soc.*, 24(4): 256-266.
- Field, William D. 1938. Variation in *Habrodais grunus* (Boisduval) (Lepid.: Lycaenidae). *Bulletin Southern California Academy Sciences*, 37(1): 23-29.
- Field, William D. 1971. Butterflies of the genus *Vanessa* and of resurrected genera *Bassaris* and *Cynthia* (Lepidoptera: Nymphalidae). *Smithsonian Contrib. Zool.*, 84, 105 pp.
- Fink, L. S., L. P. Brower, R. B. Wade, and P.R. Spitzer. 1983. Overwintering Monarch butterflies as food for insectivorous birds in Mexico. *Biotropica*, 15(2): 151-153.
- Fisher, Michael S. 1973. Notes on the occurrence of *Hesperia pahaska martini* (Hesperiidae) in Colorado. *J. Lepid. Soc.*, 27(3): 239-240.
- Fletcher, J. 1889. Notes on the preparatory stages of *Carterocephalus mandan*. *Canadian Entomologist*, 21: 115-116.
- Folsom, J. W. 1896. Notes on the oviposition of *Thanaos icelus*. *Psyche*, 7: 403.
- Forbes, Gregory S. 1975. Records of *Calephelis wrighti* (Riodinidae) in southwestern Arizona. *J. Lepid. Soc.*, 29(4): 262-263.
- Forbes, Gregory S. 1981. Description and taxonomic implications of an unusual Arizona population of *Apodemia mormo* (Riodinidae). *J. Res. Lepid.*, 18(3): 201-207. 1979.

- Fox, Charles L. 1924. A new lycaenid (Lep.) from the Pacific Coast. *Entomological News*, 35(4): 140-141.
- Freeman, H. A. 1955. A new species of *Hesperia* from California (Hesperiidae). *Lepidopterists' News*, 9(6): 196-198.
- Freeman, H. A. 1969. Systematic review of the Megathymidae. *J. Lepid. Soc.*, 23, Supplement 1: 1-59.
- Freeman, H. A. 1973. A review of the *Amblyscirtes* with the description of a new species from Mexico (Hesperiidae). *J. Lepid. Soc.*, 27(1): 40-57.
- Friedlander, Tim. 1987. Taxonomy, phylogeny and biogeography of *Asterocampa* Rober 1916 (Lepidoptera, Nymphalidae, Apaturinae). *J. Res. Lepid.*, 25: 215-338.
- Funk, Richard S. 1968. Overwintering of monarch butterflies as a breeding colony in southwestern Arizona. *J. Lepid. Soc.*, 22(1): 63-64.
- Funk, Richard S. 1975. Association of ants with ovipositing *Lycaena rubidus* (Lycaenidae). *J. Lepid. Soc.*, 29(4): 261-262.
- Gall, L. F. 1981. Santa Catalina Island's endemic Lepidoptera. I. The Orange-tips, *Anthocharis cethura catalina* and *Anthocharis sara gunderi* (Pieridae). *Atala*, 7(1): 2-8. ("1979")
- Garland, J. A. 1977. An ecological note on *Polites sabuleti sabuleti* at the northern limit of its range (Hesperiidae). *J. Lepid. Soc.*, 31(1): 70-71.
- Garth, John S. 1934. Butterflies of the Boundary Hill Research Reserve, Yosemite National Park, Calif. *Bull. So. Calif. Acad. Sci.*, 33(3): 131-135.
- Garth, John S. 1935. Butterflies of Yosemite National Park. *Bull. So. Calif. Acad. Sci.*, 34(1): 37-75.

- Garth, John S. and J. W. Tilden. 1963. Yosemite butterflies: an ecological survey of the butterflies of the Yosemite sector of the Sierra Nevada, California. *J. Res. Lepid.*, 2(1): 1-96.
- Garth, John S., and J. W. Tilden. 1986. *California Butterflies*. University of California Press, Berkeley. 246 pp.
- Geiger, Hansjurg. 1980. Enzyme electrophoretic studies on the genetic relationships of Pierid butterflies (Lepidoptera: Pieridae) I. European Taxa. *J. Res. Lepid.*, 19(4): 181-195. 1980.
- Geiger, Hansjurg, and Arthur M. Shapiro. 1986. Electrophoretic evidence for speciation within the nominal species *Anthocharis sara* Lucas (Pieridae). *J. Res. Lepid.*, 25(1): 15-24.
- Gilbert, Lawrence E., and Michael C. Singer. 1975. Butterfly ecology. *Annual Reviews Ecology and Systematics*, 6: 365-397.
- Gillaspy, James E., and Johnny R. Lara. 1984. Rainstorm behavior of Pipevine Swallowtails, *Battus philenor* (L.). *J. Lepid. Soc.*, 38(2): 142-143.
- Goodpasture, Carll. 1973a. A new subspecies of *Plebejus acmon* (Lepidoptera: Lycaenidae). *Pan-Pacific Entomologist*, 49(2): 149-159.
- Goodpasture, Carll. 1973b. Chromosome numbers for *Plebejus (Icaricia) acmon*, *P. lupini*, and *P. neurona* (Lycaenidae). *J. Lepid. Soc.*, 27(2): 109-112.
- Goodpasture, Carll. 1973c. Biology and systematics of the *Plebejus (Icaricia) acmon* group (Lepidoptera: Lycaenidae). I. Review of the group. *Journal Kansas Entomological Society*, 46(4): 468-485.

- Goodpasture, Carll. 1974. Foodplant specificity in the *Plebejus (Icaricia) acmon* group (Lycaenidae). *J. Lepid. Soc.*, 28(1): 53-63.
- Gorelick, Glenn A. 1969. Notes on larval host acceptance in a California population of *Plebejus acmon* (Lycaenidae). *J. Lepid. Soc.*, 23(1): 31-32.
- Gorelick, Glenn A. 1971. A biosystematic study of two species of *Callophrys* (*Callophrys*) in California (Lycaenidae). *J. Lepid. Soc.*, 25, Supplement 2: 1-41.
- Gorelick, Glenn A. 1987. Santa Catalina Island's endemic Lepidoptera. III. The Avalon Hairstreak, *Strymon avalona* (Lycaenidae): an ecological study. *Atala*, 14(1): 1-12 ("1986").
- Graham, S. M., W. D. Watt, and L. F. Gall. 1980. Metabolic resource allocation versus mating attractiveness: adaptive pressures on the 'alba' polymorphism of *Colias* butterflies. *Proceedings of the National Academy of Sciences*, 77: 3615-3619.
- Grey, L. P. 1970. On the Gunder collection of Argynnids (Lepidoptera: Nymphalidae). *J. Res. Lepid.*, 8(2): 55-64. ("1969").
- Grey, Lionel Paul. 1988. Memories of Cyril F. dos Passos (1887-1986). *J. Lepid. Soc.*, 42(3): 164-167.
- Grey, L. P., and A. H. Moeck. 1962. Notes on overlapping subspecies. I. An example in *Speyeria zerene* (Nymphalidae). *J. Lepid. Soc.*, 16(2): 81-97.
- Grinnell, Fordyce, Jr.. 1904. An early collector in California. *Entomological News*, 15: 202-204.
- Grinnell, Fordyce, Jr. 1905. Two new butterflies from Mt. Tamalpais, Calif. *Entomological News*, 16: 33-35.

- Grinnell, Joseph and Fordyce Grinnel, Jr. 1907. The butterflies of the San Bernardino Mountains, California. *J. New York Ent. Soc.*, 15: 37-49.
- Grinnell, Fordyce, Jr. 1913a. Notes on the bionomics of *Eugonia* (*Vanessa*) *Californica*. *Bulletin Southern California Academy Sciences*, 12(1): 14-17.
- Grinnell, Fordyce, Jr. 1913b. A Butterfly of the High Sierra Nevada - Behr's Alpine Sulphur. *Sierra Club Bulletin*, 9(2): 99-101.
- Grinnell, Fordyce, Jr. 1916. An unnamed butterfly from San Francisco. *J. Entomol. & Zoology, Pomona College*, 8(2): 83-85.
- Grula, J. W., and O. R. Taylor, Jr. 1979. The inheritance of pheromone production in the sulfur butterflies *Colias eurytheme* and *C. philodice*. *Heredity*, 42: 359-371.
- Grula, J. W., and O. R. Taylor, Jr. 1980a. Some characteristics of hybrids derived from the sulfur butterflies, *Colias eurytheme* and *C. philodice*: Phenotypic effects on the X-chromosome. *Evolution*, 34: 673-687.
- Grula, J. W., and O. R. Taylor, Jr. 1980b. The effect of X-chromosome inheritance on mate-selection behavior in the sulfur butterflies, *Colias eurytheme* and *C. philodice*. *Evolution*, 34: 688-695.
- Gudde, Erwin G. 1969. *California Place Names: The Origin and Etymology of Current Geographical Names*. University of California Press, Berkeley. 416 pp.
- Gudde, Erwin G. 1975. *California Gold Camps*. Berkeley: University of California Press. 467 pp.
- Guillette, Clyde F. 1987. *Nymphalis californica* (Western Tortoiseshell). *Utahensis* (Journal of the Utah Lepidopterists' Society), 7(1): 1-4.

- Gunder, J. D. 1927. New transition forms (Lepid., Rhopalocera). *Canadian Entomologist*, 59: 281-287.
- Gunder, J. D. 1929a. North American institutions featuring Lepidoptera. I. The Natural History Museum, San Diego, California. *Entomological News*, 40(2): 33-34.
- Gunder, J. D. 1929. The genus *Euphydryas* Scud. of boreal America (Lepidoptera Nymphalidae). *Pan-Pacific Ent.*, 6(1): 1-8.
- Gunder, J. D. 1930. The butterflies of Los Angeles County, California. *Bull. So. Calif. Acad. Sci.*, 29: 1-59.
- Gunder, J. D. 1932. A few new butterflies (Lepidoptera, Rhopalocera). *Pan-Pacific Entomologist*, VIII(3): 123-127.
- Guppy, Richard. 1953. *Papilio zelicaon* and hilltops. *Lepidopterists' News*, 7(3): 43-44.
- Guppy, Richard. 1959. Host plants of *Strymon melinus atrofasciata*. *Lepid. News*, 13(3): 170.
- Guppy, Richard, 1962. Collecting *Oeneis nevadensis* (Satyrinae) and other genera on Vancouver Island, with a theory to account for hilltopping. *J. Lepid. Soc.*, 16(1): 64-66.
- Guppy, Richard. 1964. Distribution of *Plebejus saepiolus*, *Lycaena mariposa*, and *Hesperia comma* on Vancouver Island. *J. Lepid. Soc.*, 18(3): 185-188.
- Guppy, Richard. 1989. Evidence for genetic determination of variation in adult size and wing melanism of *Parnassius phoebus* F. *J. Lepid. Soc.*, 43(2): 148-151.
- Hafernik, John E., Jr. 1983. Phenetics and ecology of hybridization in buckeye butterflies (Lepidoptera: Nymphalidae). *Univ. Calif. Publications in Entomology*, 96: 1-109.

- Hammond, Paul C. 1983. The colonization of violets and *Speyeria* butterflies on the ash-pumice fields deposited by Cascadian volcanoes. *J. Res. Lepid.*, 20(3): 179-191. 1981.
- Hammond, Paul C., and David V. McCorkle. 1983. The decline and extinction of *Speyeria* populations resulting from human environmental disturbances (Nymphalidae: Argynninae). *J. Res. Lepid.*, 22: 217-224.
- Hardy, G. A. 1959. On the life history of *Incisalia eryphon* (Lycaenidae) on southern Vancouver Island. *J. Lepid. Soc.*, 13(2): 70.
- Harrison, S., and A. M. Shapiro. 1988. Butterflies of northern California serpentine. *Fremontia*, 15(4): 17-20.
- Haskin, J. R. 1933. *Thecla halesus*, its life cycle and habits (Lepid.: Lycaenidae). *Entomological News*, 44: 72-74.
- Hawks, David A., and John F. Emmel. 1998. New Subspecies of *Cercyonis sthenele* (Lepidoptera: Satyridae) and *Charidryas gabbii* (Nymphalidae) from the Channel Islands of California. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 321-326.
- Hayes, J. L., and C. L. Claussen. 1988. Marking Lepidoptera and the offspring: trace element labeling of *Colias eurytheme* (Pieridae) with rubidium. *J. Lepid. Soc.*, 42(3): 196-203.
- Heitzman, J. R. 1964. The early stages of *Euphyes vestris*. *J. Res. Lepid.*, 3(3): 151-153.
- Heitzman, J. R. 1965. The life history of *Amblyscirtes belli* in Missouri. *J. Res. Lepid.*, 4(1): 75-78.

- Heitzman, J. R., and R. L. Heitzman. 1969. The life history of *Amblyscirtes linda* (Hesperiidae). *J. Res. Lepid.*, 8(3): 99-104.
- Henne, Christopher. 1940. Two new species of Lepidoptera from California. *Bull. So. Calif. Acad. Sci.*, 39(1): 71-74.
- Henne, Christopher. 1957. Charles Henry Ingham (1904-1957). *Lepidopterists' News*, 11(4-5): 169-170.
- Henning, S. F. 1983. Biological groups within the Lycaenidae (Lepidoptera). *J. Entomol. Soc. South Africa*, 46(1): 65-85.
- Heppner, J. B. 1972. The distribution of *Paratrytone melane* and its spread into San Diego County (Hesperiidae). *J. Res. Lepid.*, 10(4): 287-300.
- Herlan, Peter J. 1971. A new subspecies of *Limenitis archippus* (Nymphalidae). *J. Res. Lepid.*, 9(4): 217-222. ("1970").
- Higgins, L. G. 1941. An illustrated catalogue of the palearctic *Melitaea* (Lep. Rhopalocera). *Transactions Royal Entomological Society of London*, 91(7): 175-365.
- Higgins, L. G. 1953. Butterfly colling in USA. *Entomologist*, 86: 207-210.
- Higgins, L. G. 1960. A revision of the Melitaeinae genus *Chlosyne* and allied species (Lepidoptera: Nymphalinae). *Trans. Royal Entomol. Soc. London*, 112: 381-475.
- Higgins, L. G. 1978. A revision of the genus *Euphydryas* Scudder (Lepidoptera: Nymphalidae). *Entomologist's Gazette*, 29: 109-115.
- Higgins, L. G. 1981. A revision of *Phyciodes* Hubner and related genera, with a review of the classification of the Melitaeinae (Lepidoptera: Nymphalidae). *Bulletin of the British Museum Natural History (Ent.)*, 43(3): 77-243.

- Higgins, L. G., and N. D. Riley. 1970. *A Field Guide to the Butterflies of Britain and Europe*. Houghton Mifflin, Boston. 380 pp.
- Hill, H. F., Jr., A. M. Wenner, and P. H. Walls. 1976. Reproductive behavior in an overwintering aggregation of monarch butterflies. *American Midland Naturalist*, 95: 10-19.
- Hoffman, R. J. 1973. Environmental control of seasonal variation in the butterfly *Colias eurytheme*. I. Adaptive aspects of photoperiodic response. *Evolution*, 27: 387-397.
- Hogue, Charles L., Frank P. Sala, Noel McFarland, and Christopher Henne. 1965. Systematics and life history of *Saturnia (Calosaturia) albofasciata* in California (Saturniidae). *J. Res. Lepid.*, 4(3): 173-814.
- Holland, Richard. 1973. Butterflies of middle and southern Baja California. *J. Res. Lepid.*, 11(3): 147-160. (1972).
- Hoover, Mildred Brooke, Hero Eugene Rensch, and Ethel Grace Rensch. 1966. *Historic Spots in California*. Third Edition. Revised by William N. Abeloe. Stanford Univ. Press, Stanford California, 642 pp.
- Hovanitz, William. 1935. Notes on some California butterflies. *Pan-Pacific Entomologist*, 11(4): 190-192.
- Hovanitz, William. 1937a. A new race of *Oeneis chryxus* (Dbld. & Hew.) (Lepidoptera: Satyridae). *Ent. News*, 48(8): 228-230.
- Hovanitz, William. 1937b. Concerning the *Plebejus icarioides* Rassenkreis (Lepidoptera: Lycaenidae), *Pan-Pacific Ent.*, 13(4): 184-189.
- Hovanitz, William. 1937. On *Argynnis coronis* W. H. Edws. (Lepidoptera-Nymphalidae). *Bulletin of the Brooklyn Entomological Society*, 32(4): 166-168.

- Hovanitz, William. 1938. The interpretation of the term subspecies and the status of names applied to lower categories of Lepidoptera. *Ent. News*, 49(2): 39-41.
- Hovanitz, William. 1940. Ecological color variation in a butterfly and the problem of "protective coloration." *Ecology*, 21(3): 371-380.
- Hovanitz, William. 1941. Parallel ecogenotypical color variation in butterflies. *Ecology*, 22(3): 259-284.
- Hovanitz, William. 1942. Genetic and ecologic analysis of wild populations in Lepidoptera, 1: Pupal size and weight variation in some California populations of *Melitaea chalcidona*. *Ecology*, 23(2): 175-188.
- Hovanitz, William. 1943. Geographical variation and racial structure of *Argynnis callippe* in California. *American Naturalist*, 77(772): 400-425.
- Hovanitz, William. 1945. Combined effects of genetic and environmental variations upon the composition of *Colias* populations. *Annals Entomological Society of America*, 38: 482-502.
- Hovanitz, William. 1945. Geographical regularity in the variation and supposed mimicry of a butterfly, *Limenitis bredowii*. *American Naturalist*, 79(784): 472-474.
- Hovanitz, William. 1947. An electronmicroscope study of isolated chromosomes. *Genetics*, 32(5): 500-504.
- Hovanitz, William. 1948. Differences in the field activity of two female color phases of *Colias* butterflies at different times of the day. *Contributions from the Laboratory of Vertebrate Biology*, University of Michigan, Ann Arbor, 41: 1-37.
- Hovanitz, William. 1950a. The biology of *Colias* butterflies. I. A Distribution of North American *Colias*. *Wassman Journal of Biology*, 8(1): 49-75.

- Hovanitz, William. 1950b. The biology of *Colias* butterflies. II. Parallel geographical variation of dimorphic color phases in North American species. *Wassman Journal of Biology*, 8(2): 197-219.
- Hovanitz, William. 1951. The biology of *Colias* butterflies. III. Variation of adult flight in the Arctic and Sub-arctic. *Wassman Journal of Biology*, 9: 1-9.
- Hovanitz, William. 1951. The distribution of the species of the genus *Pieris* in North America. *J. Res. Lepid.*, 1: 73-83.
- Hovanitz, William. 1953. Chromosome structure. I. Analysis of spiral or nodule fragmentations. *Wassman Journal of Biology*, 11(1): 1-22.
- Hovanitz, William. 1953. Isolated chromosomes from calf thymus. *Anatomical Record*, 117(3): 608.
- Hovanitz, William. 1954. Chromosome structure. II. Chromosome of calf thymus. *Wassman Journal of Biology*, 11(3): 257-266. ["1953"]
- Hovanitz, William. 1955. Cytological demonstration of the helical structure of giant chromosomes. *Proceedings of the National Academy of Sciences*, 42(9): 609-613.
- Hovanitz, William. 1958. Distribution of butterflies in the New World. American Association for the Advancement of Science, Publication 51: 321-368.
- Hovanitz, William. 1962. The distribution of the species of the genus *Pieris* in North America. *J. Res. Lepid.*, 1(1): 73-83.
- Hovanitz, William. 1967. Natural habitats [San Gabriel River canyon habitat for *Philotes sonorensis* and *Dudleya lanceolata*]. *J. Res. Lepid.*, 6(3): 199-202.
- Hovanitz, William. 1968. Habitat: General type locality. *J. Res. Lepid.*, 7(2): 126.

- Hovanitz, William. 1969. Present and Ice Age life zones and distributions. *J. Res. Lepid.*, 7(1): 31-34. ["1968"]
- Hovanitz, William 1979. Ecological color variation in a butterfly and the problem of "protective coloration." *J. Res. Lepid.*, 17(Suppl): 10-25. (1978).
- Hovanitz, William. 1979. Parallel ecogenotypical color variation in butterflies. *J. Res. Lepid.*, 17(Suppl.): 26-55. (1978).
- Hovanitz, William, and Vincent C. S. Chang. 1962. The effect of various food plants on survival and growth rate of *Pieris*. *J. Res. Lepid.*, 1(1): 21-42.
- Hovanitz, William, and Vincent C. S. Chang. 1963. The effect of hybridization of host-plant strains on growth rate and mortality of *Pieris rapae*. *J. Res. Lepid.*, 1(2): 157-162.
- Hovanitz, William, and Vincent C. S. Chang. 1963. Change of food plant preference by larvae of *Pieris rapae* controlled by strain selection, and the inheritance of this trait. *J. Res. Lepid.*, 1(2): 163-168.
- Howard, A. Q., and R. A. Arnold. 1980. The Antioch Dunes -- Safe at last? *Fremontia*, 8(3): 3-12.
- Huguenin, J. C. 1918. Early accounts of *Lycaena antiacis* and *Lycaena xerces* in 1917. *Ent. News*, 24(10): 392.
- Hulbirt, E. L. 1935. Two unusual butterflies taken in southern California. *Bull. So. Calif. Acad. Sci.*, 34(3): 210.
- Irwin, Roderick R. 1966. Notes on W. H. Edwards specimens in two midwestern collections. *J. Lepid. Soc.*, 20(3): 156-162.

- Irwin, Roderick R. 1972. Further notes on W. H. Edwards specimens in Illinois museum collections. *J. Lepid. Soc.*, 26(3): 198-199.
- Jaeger, Edmund C. 1956. On desert trails with a naturalist - XXV: the beetle worth its weight in gold. *Desert Magazine*, May 1956: 19-20.
- Jennings, D. T., and M. E. Toliver. 1976. Crab spider preys on *Neophasia menapia* (Pieridae). *J. Lepid. Soc.*, 30(3): 236-237.
- Johnson, John W. 1938. A new subspecies of *Melitaea palla* Boisduval 1852 (Lepidoptera, Nymphalidae). *Bull. So. Calif. Acad. Sci.*, 37(1): 18-20.
- Johnson, John W. 1982a. Another foodplant of *Erynnis tristis tristis* Bdv. (Lepidoptera: Hesperidae). *Atala*, 8(2): 44.
- Johnson, John W. 1982b. A new foodplant for *Satyrium tetra* (Edwards) (Lepidoptera: Lycaenidae). *Atala*, 8(2): 45. ("1980")
- Johnson, John W. 1982c. An extinct population of a third species of southern California satyrid (Lepidoptera: Satyridae). *Atala*, 8(2): 50-51. ("1980")
- Johnson, Kurt. 1976. Three new Nearctic species of *Callophrys* (*Mitoura*), with a diagnosis of all Nearctic consubgenera (Lepidoptera: Lycaenidae). *Bull. Allyn Museum*, 38: 1-30.
- Johnson, Kurt. 1983. The suitability of *Juniperus* (Cupressaceae) for larvae of *Callophrys hesseli* (Rawson and Ziegler) (Lycaenidae). *J. Lepid. Soc.*, 37(1): 78-79.
- Johnson, Kurt, and George Balogh. 1977. Studies in the Lycaeninae (Lycaenidae). 2. Taxonomy and evolution of the nearctic *Lycaena rubidus* complex, with description of a new species. *Bull. Allyn Museum*, 43: 1-62.

- Johnson, Kurt, and Peter M. Borgo. 1976. Patterned perching behavior in two *Callophrys* (*Mitoura*) (Lycaenidae). *J. Lepid. Soc.*, 30(3): 169-183.
- Keller, E. C., Jr., R. H. T. Mattoni, and M. S. B. Seiger. 1966. Preferential return of artificially displaced butterflies. *Animal Behavior*, 14: 197-200.
- Kellner, Clinton V., and Arthur M. Shapiro. 1983. Ecological interactions of *Pieris brassicae* L. (Lepidoptera: Pieridae) and native Pierini in Chile. *Studies on Neotropical Fauna and Environment*, 18: 53-64.
- Kellogg, T. A. 1985. Egg dispersion patterns and egg avoidance behavior in the butterfly *Pieris sisymbrii* Bdv. (Pieridae). *J. Lepid. Soc.*, 39(4): 268-275.
- Kelson, R. B., and M. C. Minno. 1983. Observations of hilltopping *Mitoura spinetorum* and *M. johnsoni* (Lycaenidae) in California. *J. Lepid. Soc.*, 37(4): 310-311.
- Kendall, Roy O. 1966a. Larval food plants for five Texas Hesperiidae. *J. Lepid. Soc.*, 20(1): 35-42.
- Kendall, Roy O. 1966b. Larval food plants and distribution notes for three Texas Hesperiidae. *J. Lepid. Soc.*, 20(4): 229-232.
- Klots, Alexander B. 1951. *A Field Guide to the Butterflies*. Houghton Mifflin Co., Boston. 349 pp.
- Klots, Alexander B., and Cyril F. dos Passos. 1982. Studies of North American *Erora* (Scudder) (Lepidoptera, Lycaenidae). *J. N. V. Entomol. Soc.*, 39(4): 295-331.
- Knowlton, G. F. 1953. Predators of *Vanessa cardui*. *Lepid. News*, 7(2): 55.
- La Due, Lillian. 1964. Oxygen consumption and metabolic rate of *Papilio zelicaon* pupae in a state of delayed eclosion. *J. Res. Lepid.*, 3(4): 197-206.

- Labine, Patricia A. 1964. Population biology of the butterfly, *Euphydryas editha*. I. Barriers to multiple insemination. *Evolution*, 18: 335-336.
- Labine, Patricia A. 1968. The population biology of the butterfly, *Euphydryas editha*. VIII. Oviposition and its relation to patterns of oviposition in other butterflies. *Evolution*, 22: 799-805.
- Langston, Robert L. 1963. *Philotes* of central coastal California (Lycaenidae). *J. Lepid. Soc.*, 17: 201-223.
- Langston, Robert L. 1965. Distribution and hosts of five *Philotes* in California (Lycaenidae). *J. Lepid. Soc.*, 19: 95-102.
- Langston, Robert L. 1969a. *Philotes* of North America: synonymic list and distribution (Lycaenidae). *J. Lepid. Soc.*, 23(1): 49-62.
- Langston, Robert L. 1969b. A review of *Glaucopsyche*, the silvery blues in California (Lycaenidae). *J. Lepid. Soc.*, 23(3): 149-154.
- Langston, Robert L. 1970. *Philotes enoptes bayensis* and *tildeni* Langston - four new localities. *Pan-Pacific Entomologist*, 46(1): 74.
- Langston, Robert L. 1974. Extended flight periods of coastal and dune butterflies in California. *J. Res. Lepid.*, 13: 83-98.
- Langston, Robert L. 1975. Extended flight periods of coastal and dune butterflies in California. *J. Res. Lepid.*, 13: 83-98. ("1974")
- Langston, Robert L. 1980. The Rhopalocera of Santa Cruz Island, California. *J. Res. Lepid.*, 18(1): 24-35. (1979).
- Langston, Robert L., and John Adams Comstock. 1966. Life history of *Philotes enoptes bayensis* (Lepidoptera, Lycaenidae). *Pan-Pacific Ent.*, 42(2): 102-108.

- Lawrence, Donald A., and John C. Downey. 1966. Morphology of the immature stages of *Everes comyntas* Godart (Lycaenidae). *J. Res. Lepid.*, 5(2): 61-96.
- LeGar, Mary Jude, and William Hovanitz. 1952. Genetic and ecological analysis of wild populations in Lepidoptera. II. Color pattern variations in *Melitaea chalcidona*. *Wassman Journal of Biology*, 9(3): 257-310.
- Lekisch, Barbara. 1988. *Tahoe Place Names. The Origin and History of Names in the Lake Tahoe Basin*. Lafayette, California: Great West Books. 173 pp.
- Ley, C., and W. B. Watt. 1989. Testing the 'mimicry' explanation for the *Colias* 'alba' polymorphism: palatability of *Colias* and other butterflies to wild bird predators. *Functional Ecology*, 3: 183-192.
- Lincoln, D. E., T. S. Newton, P. R. Ehrlich, and K. S. Williams. 1982. Coevolution of the checkerspot butterfly *Euphydryas chalcidona* and its larval food plant, *Diplacus aurantiacus*: Larval response to protein and leaf resin. *Oecologia* (Berlin), 52: 216-223.
- Lorquin, Estelle H., editor. 1938. Pierre Joseph Michael Lorquin -- Naturalist-voyageur. An obituary notice read at the meeting of the Entomological Society of France, April 23, 1873, by Dr. Jean Alphonse Boisduval, Honorary Member of the Society. Mimeographed and Published by Lorquin Service, San Francisco [14 pp.]
- MacNeill, C. Don. 1963. *Callophrys fotis* (Strecker), in the San Francisco Bay area. *Pan-Pacific Entomologist*, 39(1): 60.
- MacNeill, C. Don. 1964. The skippers of the genus *Hesperia* in western North America. *Univ. Calif. Publ. Entomol.*, 35: 1-230.

- MacNeill, C. Don. 1967. A unidirectional mass movement by *Satyrium saepium* (Lycaenidae). *J. Lepid. Soc.*, 21(3): 204.
- MacNeill, C. Don. 1970. A new *Pholisora* with notes on *P. alpheus* (Edw.) (Lepidoptera: Hesperiiidae). *Entomol. News*, 81: 177-184.
- Macy, Ralph W. 1931. A new Oregon butterfly (Lepid. Lycaenidae). *Entomol. News*, 42(1): 1-2.
- Macy, Ralph W. 1958. On the occurrence of *Adelpha bredowii* (Nymphalidae) in Oregon. *Lepidopterists' News*, 12(5-6): 199-200.
- Maeki, Kodo, and Charles L. Remington. 1960a. Studies of the chromosomes of North American Rhopalocera. I. Papilionidae. *J. Lepid. Soc.*, 13: 193-203.
- Maeki, Kodo, and Charles L. Remington. 1960b. Studies of the chromosomes of North American Rhopalocera. 2. Hesperiiidae, Megathymidae, and Pieridae. *J. Lepid. Soc.*, 14: 37-57.
- Maeki, Kodo, and Charles L. Remington. 1961a. Studies of the chromosomes of North American Rhopalocera. 3. Lycaenidae, Danainae, Stayrinae, Morphinae. *J. Lepid. Soc.*, 14: 127-147.
- Maeki, Kodo, and Charles L. Remington. 1961b. Studies of the chromosomes of North American Rhopalocera. 4. Nymphalinae, Charaxidinae, Libytheinae. *J. Lepid. Soc.*, 14: 179-201.
- Malicky, Hans. 1970. New aspects on the association between lycaenid larvae (Lycaenidae) and ants (Formicidae, Hymenoptera). *J. Lepid. Soc.*, 24(): 190- .
- Mann, B. P. 1885. Herbert Knowles Morrison. *Psyche*, 4: 287.

- Martin, Lloyd M. 1936. A new southern race of *Euchloe ausonides* (diurnal Lepidoptera). *Bull. So. Calif. Acad. Sci.*, 35(2): 94-95.
- Martin, Lloyd M. 1943. *Polites sonora giris* Edw. raised from the synonymy (Lepid.) *Bull. So. Calif. Acad. Sci.*, 42(1): 46-48.
- Martin, Lloyd M. 1948. Jeane Daniel Gunder (1888-1948). *Lepidopterists' News*, 2(9): 105.
- Martin, Lloyd M. 1971. John Adams Comstock, Jan. 30, 1883-Dec. 26, 1970. *J. Lepid. Soc.*, 25(3): 215.
- Martin, Lloyd M. 1972. John Adams Comstock, 1883-1970. *Bull. So. Calif. Acad. Sci.*, 71(2): 57-68.
- Mason, Larry G., Paul R. Ehrlich, and Thomas C. Emmel. 1967. The population biology of the butterfly, *Euphydryas editha*. V. Character clusters and asymmetry. *Evolution*, 21:85-91.
- Masters, John H. 1972. A new subspecies of *Lycaenides argyrognomon* (Lycaenidae) from the Eastern Canadian Forest Zone. *J. Lepid. Soc.*, 26(3): 150-154.
- Masters, John H. 1979a. The type locality of *Argynnis zerene* Boisduval (Nymphalidae): a correction. *J. Lepid. Soc.*, 33(2): 137-138.
- Masters, John H. 1979b. New foodplant records for *Euphydryas editha* and *Euphydryas chalcedona* (Nymphalidae). *J. Lepid. Soc.*, 33(3): 199-200.
- Masters, John H. 1980. James Mason Hutchings (1824-1902): an early butterfly collector in California. *J. Lepid. Soc.*, 34(1): 68.
- Masters, John H. 1980. Notes on the type and type collector of *Parnassius behrii* (Papilionidae). *J. Lepid. Soc.*, 34(1): 47.

- Mattoni, Rudolph H. T. 1954a. Taxonomy and distribution in the genus *Philotes*.
Lepidopterists' News, 8(1-2): 8.
- Mattoni, Rudolph H. T. 1954b. Notes on the genus *Philotes* (Lycaenidae: Lepidoptea).
I: Descriptions of three new subspecies and a synoptic list. *Bull. So. Calif. Acad. Sci.*, 53(3): 157-165.
- Mattoni, Rudolph H. T. 1966. Distribution and pattern of variation in *Philotes rita*. *J. Res. Lepid.*, 4: 81-102. ("1965")
- Mattoni, Rudolph H. T. 1977. The Scolitantidini. I. Two new genera and a generic rearrangement (Lycaenidae). *J. Res. Lepid.*, 16: 223-242.
- Mattoni, Rudolf H. T. 1979. Dr. William Hovanitz, 1915-1977. *J. Res. Lepid.*, 17(Supplement): 1-6. ("1978")
- Mattoni, Rudolf H. T. 1990. Butterflies of Greater Los Angeles. The Center for the Conservation of Biodiversity/Lepidoptera Research Foundation, Inc., Beverly Hills, California. 20 pp.
- Mattoni, Rudolph H. T. 1991. An unrecognized, now extinct, Los Angeles area butterfly (Lycaenidae). *J. Res. Lep.*, 28(4): 297-309. ("1989")
- Mattoni, Rudolph H. T. 1993. Additional taxa of concern in southern California. P. 145.
In New, T. R. (editor), *Conservation Biology of Lycaenidae (Butterflies)*.
International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland. 173 pp.
- Mattoni, Rudolph H. T. 1994. Rediscovery of the endangered Palos Verdes blue butterfly *Glaucopsyche lygdamus palosverdesensis* Perkins and Emmel (Lycaenidae). *J. Res. Lepid.*, 31(3-4): 180-194. ("1992")

- Mattoni, Rudolph H. T., and Marvin S. B. Seiger. 1963. Techniques in the study of population structure in *Philotes sonorensis*. *J. Res. Lepid.*, 1(4): 237-244.
- Mattoon, Sterling O., and George T. Austin. 1998. A Review of *Satyrium fuliginosum* (W. H. Edwards) with the Descriptions of Three New Subspecies (Lepidoptera: Lycaenidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 681-690.
- Mattoon, Sterling O., R. D. Davis, and O. D. Spencer. 1971. Rearing techniques for species of *Speyeria* (Nymphalidae). *J. Lepid. Soc.*, 25(4): 247-256.
- Mattoon, Sterling O., John F. Emmel, and Thomas C. Emmel. 1998. The Distribution of *Polites mardon* (Lepidoptera: Hesperiiidae) in North America, and Description of a New Subspecies from Southern Oregon. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 767-774.
- Mattoon, Sterling O., and James Wilson Tilden. 1998. Re-evaluation of North American *Carterocephalus palaemon* (Pallas) (Lepidoptera: Hesperiiidae) and Description of a New Subspecies. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 641-660.
- McAlpine, W. S. 1971. A revision of the butterfly genus *Calephelis* (Riodinidae). *J. Res. Lepid.*, 10: 1-125.
- McCorkle, David V. 1962. Notes on the life history of *Callophrys (Mitoura) johnsoni* Skinner (Lepidoptera, Lycaenidae). *Proceedings Washington State Entomological Society*, 14: 103-105.

- McCorkle, David V. 1980. Ecological investigation report: Oregon Silverspot butterfly (*Speyeria zerene hippolyta*). U.S.D.A. Forest Service, Siuslaw National Forest, Corvallis, Oregon. 117 pp.
- McCorkle, David V., and Paul C. Hammond. 1985. Observations on the biology of *Parnassius clodius* (Papilionidae) in the Pacific Northwest. *J. Lepid. Soc.*, 39: 156-162.
- McCorkle, David V., and Paul C. Hammond. 1988. Biology of *Speyeria zerene hippolyta* (Nymphalidae) in a marine-modified environment. *J. Lepid. Soc.*, 42(3): 184-195.
- McDunnough, J. 1914. Notes on the synonymy of Boisduval's N. American species of Lycaenidae. *The Entomologist's Record*, 26: 194-203.
- McDunnough, J. 1936. On the identity and type locality of *Euphydryas editha* (Lep. Rhop.) *Bull. So. Calif. Acad. Sci.*, 35(1): 1-2.
- McFarland, Noel. 1964. Notes on collecting, rearing, and preserving larvae of Macrolepidoptera. *J. Lepid. Soc.*, 18: 201-210.
- McFarland, Noel. 1971. Botanical names in entomological papers and habitat studies. *J. Res. Lepid.*, 9(2): 89-96. ("1970").
- McFarland, Noel. 1971. A specialized case of communal roosting in *Pieris rapae*. *J. Lepid. Soc.*, 25(2): 144-145.
- McFarland, Noel. 1972. Notes on describing, measuring, preserving and photographing the eggs of Lepidoptera. *J. Res. Lepid.*, 10(3): 203-214.
- McGuire, William W. 1982. New oviposition and larval hostplant records for North American *Hesperia* (Rhopalocera: Hesperidae). *Bulletin Allyn Museum*, 72: 1-6.

- McGuire, William W. 1998. Description of Three New Subspecies of *Hesperia* (Lepidoptera: HesperIIDae) from the Western United States. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 461-474.
- McHenry, Paddy. 1968. The generic, specific and lower category names of the nearctic butterflies. *J. Res. Lepid.*, 7(2): 127-130.
- Mead, Theodore L. 1875. *Reports of the Wheeler Survey, Vol. 5, Zoology*: 739-794, pls. xxxv-xxxix.
- Mead, Theodore L. 1935. Theodore L. Mead--naturalist, entomologist, and plantsman. An autobiography. *Yearbook, American Amaryllis Society*, 2: 11-22.
- Meadows, Don. 1936. An annotated list of the Lepidoptera of Santa Catalina Island, California. Part I-Rhopalocera. *Bull. So. Calif. Acad. Sci.*, 35(3): 175-180.
- Menetries. 1855. Classis Insectorum. Ordo Lepidopterorum. Pars I. Lepidoptera Diurna. *Enumeratio Corporum Animalium Musei Petropolitanae*, 1: 7.
- Miller, Lee D. 1970. Nomenclature of wing veins and cells. *J. Res. Lepid.*, 8(2): 37-48. ("1969").
- Miller, Lee D. 1983. Chermock, Hovanitz and Weber collections donated to Allyn Museum. *J. Lepid. Soc.*, 37(4): 317-318.
- Miller, Lee D., and F. Martin Brown. 1981. *A Catalogue/Checklist of the Butterflies of America North of Mexico*. The Lepidopterists' Society, Memoir No. 2. 280 pp.
- Miller, Lee D., and F. Martin Brown. 1983. Butterfly taxonomy: a reply. *J. Res. Lepid.*, 20(4): 193-198. (1981).
- Miller, Scott E. 1976. Supplementary notes on the distribution of *Epargyreus clarus* in southern California (HesperIIDae). *J. Res. Lepid.*, 15(4): 206-207.

- Miller, Scott E. 1979. Publications of William Hovanitz. *J. Res. Lepid.*, 17(Suppl): 66-76. ("1978")
- Miller, Scott E. 1984. Type locality of *Papilio indra pergamus* (Lepidoptera: Papilionidae). *J. Res. Lepid.*, 23: 175.
- Miller, Scott E. 1985. Butterflies of the California Channel Islands. *J. Res. Lepid.*, 23(4): 282-296. ("1984")
- Moeck, Arthur H. 1957. *Geographic Variability in Speyeria. Comments, Records and Description of a New Subspecies*. Privately printed, sponsored by Milwaukee Entomological Society. 48 pp.
- Mooney, H. A., P. R. Ehrlich, D. E. Lincoln, and K. S. Williams. 1980. Environmental controls on the seasonality of a drought deciduous shrub, *Diplacus aurantiacus*, and its predator, the Checkerspot butterfly, *Euphydryas chalcedona*. *Oecologia* (Berlin), 45: 143-146.
- Moran, Reid. 1949. *Dudleya stolonifera*, a new species from Orange County, California. *Bull. So. Calif. Acad. Sci.*, 48(3): 105-114.
- Munz, Philip A., and David D. Keck. 1963. *A California Flora*. University of California Press, Berkeley. 1681 pp.
- Murphy, Dennis D. 1983. Nectar sources as constraints on the distribution of egg masses by the checkerspot butterfly *Euphydryas chalcedona* (Lepidoptera: Nymphalidae). *Environmental Entomology*, 12: 463-466.
- Murphy, Dennis D. 1984. Butterflies and their nectar plants: The role of the Checkerspot butterfly, *Euphydryas editha* as a pollen vector. *Oikos*, 43(1): 113-117.

- Murphy, Dennis D., and Paul R. Ehrlich. 1980. Two California checkerspot butterfly subspecies: one new, one on the verge of extinction. *J. Lepid. Soc.*, 34(3): 316-320.
- Murphy, Dennis D., and Paul R. Ehrlich. 1983. On the status of *Euphydryas editha baroni* with a range of extension of *E. editha luestherae*. *J. Res. Lepid.*, 21: 194-198.
- Nabokov, V. 1943. The nearctic forms of *Lycaeides* Hub. (Lycaenidae, Lepidoptera). *Psyche*, 50: 87-99.
- Nabokov, V. 1944. Notes on the morphology of the genus *Lycaeides* (Lycaenidae, Lepidoptera). *Psyche*, 51: 104-138.
- Nabokov, V. 1949. The nearctic members of the genus *Lycaeides* Hubner (Lycaenidae, Lepidoptera). *Bull. Mus. Compar. Zool.*, Harvard, 101: 479-541.
- Nagano, Christopher D., and John Wayne. 1985. A survey of the location of the monarch butterfly (*Danaus plexippus* [L.]) overwintering roosts in the state of California, U. S. A.: First year 1984/1985. Report to the World Wildlife Fund - U.S. The Monarch Project.
- Nakamura, Ichiro, and Shigeru A. Ae. 1977. Prolonged pupal diapause of *Papilio alexanor*: arid zone adaptation directed by larval host plant. *Annals Entomol. Soc. America*, 70(4): 481-484.
- Neck, Raymond W. 1973. Foodplant ecology of the butterfly *Chlosyne lacinia* (Geyer) (Nymphalidae) I. Larval foodplants. *J. Lepid. Soc.*, 27(1): 22-33.
- Neck, Raymond W. 1975. History of scientific study on a larval color polymorphism in the genus *Chlosyne* (Nymphalidae). *J. Res. Lepid.*, 14(1): 41-48.

- Neck, Raymond W. 1976. Lepidopteran foodplant records from Texas. *J. Res. Lepid.*, 15(2): 75-82.
- Neck, Raymond W. 1976. Larval morph variation in *Chlosyne lacinia* (Nymphalidae). *J. Lepid. Soc.*, 30(2): 91-94.
- Neck, Raymond W. 1977. Foodplant ecology of the butterfly *Chlosyne lacinia* (Geyer) (Nymphalidae) II. Additional larval foodplant data. *J. Res. Lepid.*, 16(2): 69-74.
- Neck, Raymond W. 1981. Role of an ornamental plant species in extending the breeding range of a tropical skipper to subtropical southern Texas (Hesperiidae). *J. Res. Lepid.*, 20(3): 129-132. (1983).
- Neck, Raymond W., Guy L. Bush, and Boyce A. Drummond III. 1971. Epistasis, associated lethals and brood effect in larval colour polymorphism of the patch butterfly, *Chlosyne lacinia*. *Heredity*, 26: 73-84.
- Nekrutenko, Yuri P. 1975. Comparative notes on certain West-Palearctic species of *Agriades*, with description of a new subspecies of *A. pyrenaicus* from Turkey (Lycaenidae). *J. Lepid. Soc.*, 28: 278-287.
- Newcomer, E. J. 1911. The life histories of two lycaenid butterflies. *Canad. Ent.*, 43: 83-88.
- Newcomer, E. J. 1963. Biographical reminiscences of McDunnough, Barnes, and Davidson. *J. Lepid. Soc.*, 17(2): 117.
- Newcomer, E. J. 1964. The synonymy, variability and biology of *Lycaena nivalis*. *J. Res. Lepid.*, 2(4): 271-280. ("1963")
- Newcomer, E. J. 1964. Life histories of *Papilio indra* and *P. oregonius*. *J. Res. Lepid.*, 3(1): 49-62.

- Newcomer, E. J. 1966. Butterflies of Yakima County, Washington, additions and corrections. *J. Lepid. Soc.*, 20(4): 253-254.
- Newcomer, E. J. 1966. Life histories of three western species of *Polites*. *J. Res. Lepid.*, 5(4): 243-247.
- Newcomer, E. J. 1973. Notes on life histories and habits of some western Theclinae. *J. Lepid. Soc.*, 27(1): 13-15.
- Nixon, Kevin C., and Kelly P. Steele. 1981. A new species of *Quercus* (Fagaceae) from southern California. *Madrono*, 28(4): 210-219.
- Opler, Paul A. 1962. Some notes on *Callophrys (Mitoura) johnsoni* (Lycaenidae) in California. *J. Lepid. Soc.*, 16(3): 193-194.
- Opler, Paul A. 1966a. Studies on the Nearctic *Euchloe*. Part 1. Introduction. *J. Res. Lepid.*, 5(1): 39-50.
- Opler, Paul A. 1966b. Studies on the Nearctic *Euchloe*. Part 2. Chronological review of the literature and bibliography. *J. Res. Lepid.*, 5(2): 41-50.
- Opler, Paul A. 1966c. Studies on the Nearctic *Euchloe*. Part 3. Complete synonymical treatment. *J. Res. Lepid.*, 5(3): 185-195.
- Opler, Paul A. 1966d. Studies on the Nearctic *Euchloe*. Part 4. Type data and type locality restrictions. *J. Res. Lepid.*, 5: 190-195.
- Opler, Paul A. 1966e. A possible record for the occurrence of *Callophrys (Xamia) xami* (Lycaenidae) in California. *J. Lepid. Soc.*, 20(4): 212.
- Opler, Paul A. 1966f. A gynandromorph of *Lycaena gorgon*. *J. Res. Lepid.*, 5(4): 230.
- Opler, Paul A. 1967. New host plant records for *Anthocharis* (Pieridae). *J. Lepid. Soc.*, 21: 212.

- Opler, Paul A. 1968a. New host plant records for *Anthocaris* (Pieridae). *J. Lepid. Soc.*, 21(3): 212.
- Opler, Paul A. 1968b. Myrmecophily reported for *Icaricia acmon* and *Philotes enoptes bayensis* (Lepidoptera: Lycaenidae). *Pan-Pacific Entomologist*, 44(1): 79-80.
- Opler, Paul A. 1970. Studies on the Nearctic *Euchloe*. Part 5. Distribution. *J. Res. Lepid.*, 7: 65-86. ("1968")
- Opler, Paul A. 1971. Studies on the Nearctic *Euchloe*: Part 6. Systematics of adults. *J. Res. Lepid.*, 8: 153-168. ("1969")
- Opler, Paul A. 1974. Studies on the Nearctic *Euchloe*. Part 7. Comparative life histories, hosts and the morphology of immature stages. *J. Res. Lepid.*, 13: 1-20.
- Opler, Paul A. 1986. A new *Euchloe* (Pieridae) from northwestern Mexico. *J. Lepid. Soc.*, 40(3): 188-190.
- Opler, Paul A., and Harry K. Clench. 1983. Studies on the Nearctic *Euchloe*. 8. *Euchloe olympia*. *Ann. Carnegie Mus.*, 52: 41-54.
- Opler, Paul A., and Robert L. Langston. 1968. A distributional analysis of the butterflies of Contra Costa County, California. *J. Lepid. Soc.*, 22(2): 89-107.
- Opler, Paul A., and J. A. Powell. 1961. Taxonomic and distributional studies on the western components of the *Apodemia mormo* complex (Riodinidae). *J. Lepid. Soc.*, 15: 145-171.
- Oppewall, Jeannice. 1979. From the Gold Rush to the Hollywood rushes: Some notes on the history of butterfly farming in California. *Terra* (Magazine of the Natural History Museum Alliance of Los Angeles County), 17(4): 30-35.
- Orsak, Larry J. 1974. Project Atossa--Preliminary report. *Atala*, 2(2): 5-8.

- Orsak, Larry J. 1974. Charles Rudkin collection at the University of California, Irvine.
J. Lepid. Soc., 28(4): 363.
- Orsak, Larry J. 1976. Recent captures of *Anthocharis cethura catalina* Meadows. *J. Res. Lepid.*, 14(2): 85-89. ("1975")
- Orsak, Larry J. 1977. Management recommendations for populations of the Bright Blue Copper Butterfly (*Lycaena heteronea clara*) of southern California. *Atala*, 4(1-2): 10-18. ("1976")
- Orsak, Larry J. 1977. The butterflies of Orange County, California. Center for Pathobiology: Misc. Publ. No. 3, Museum of Systematic Biology Research Series No. 4. University of California, Irvine. 339 pp.
- Orsak, Larry J., and Scott E. Miller. 1980. Habitat: *Lycaena heteronea clara* (Lepidoptera: Lycaenidae). *J. Res. Lepid.*, 17(3): 204-206. (1978).
- Orsak, Larry J., and Douglas W. Whitman. 1987. Chromatic polymorphism in *Callophrys mossii bayensis* larvae (Lycaenidae): spectral characterization, short-term color shifts, and natural morph frequencies. *J. Res. Lepid.*, 25(3): 188-201.
- Perkins, Edwin M., and John F. Emmel. 1978. A new subspecies of *Glaucopysche lygdamus* from California (Lepidoptera: Lycaenidae). *Proc. Entomol. Soc. Wash.*, 79: 468-471.
- Perkins, E. M. and W. C. Meyer. 1973. Revision of the *Boloria epithore* complex, with description of two new subspecies (Nymphalidae). *Bull. Allyn Museum*, 11: 1-23.
- Perkins, E. M., and S. F. Perkins. 1966. A new race and discussion of the *Boloria epithore* complex (Nymphalidae). *J. Lepid. Soc.*, 20: 103-117.

- Perkins, E. M., Jr., and S. F. Perkins. 1966. A review of the *Limenitis lorquini* complex (Nymphalidae). *J. Lepid. Soc.*, 20(3): 172-176.
- Perkins, Stephen F., and Edwin M. Perkins, Jr. 1967. Revision of the *Limenitis weidemeyerii* complex, with description of a new subspecies (Nymphalidae). *J. Lepid. Soc.*, 21(4): 213-234.
- Petersen, Bjorn. 1963. A method for breeding *Pieris napi* and *Pieris bryoniae*. *J. Res. Lepid.*, 1(4): 275-279.
- Piazza, Enrico. 1975. Old Timers. *J. Res. Lepid.*, 14(2):P 90-92.
- Platt, Austin P. 1983. Evolution of North American Admiral butterflies. *Bull. of Ent. Soc. of America*, Fall 1983: 11-22.
- Porter, Adam H., and Hansjürg Geiger. 1988. Genetic and phenotypic population structure of the *Coenonympha tullia* complex (Lepidoptera: Nymphalidae: Satyrinae) in California: No evidence for species boundaries. *Canadian Journal of Zoology*, 66: 2751-2765.
- Porter, Adam H., and Sterling O. Mattoon. 1989. A new subspecies of *Coenonympha tullia* (Müller) (Nymphalidae: Satyrinae) confined to the coastal dunes of northern California. *Journal of the Lepidopterists' Society*, 43(3): 229-238.
- Poulton, Edward B. 1908. Mimetic North American species of the genus *Limenitis* (s.l.) and their models. *Transactions Entomol. Society London*, 1908 (Part III): 447-488.
- Powell, Jerry A. 1957. A previously unrecorded host plant for *Pieris beckerii* Edwards (Lepidoptera: Pieridae). *Pan-Pacific Entomologist*, 33: 156.
- Powell, Jerry A. 1958. Additions to the knowledge of the butterfly fauna of Baja California Norte. *Lepid. News*, 12: 26-32.

- Powell, Jerry A. 1964. *Univ. California Publications in Entomology*, 32: 5.
- Powell, Jerry A. 1968a. A study of area occupation and mating behavior in *Incisalia irioides* (Lepidoptera: Lycaenidae). *J. New York Ent. Soc.*, 76: 47-57.
- Powell, Jerry A. 1968b. Foodplants of *Callophrys (Incisalia) iroides*. *J. Lepid. Soc.*, 22(4): 225-226.
- Powell, Jerry A. 1969. North American annual summary for 1969: California, life histories. *News of the Lepidopterists' Society*, 1969(3): 7.
- Powell, Jerry A. 1972. Mass movements of *Nymphalis californica* (Boisduval) in the San Francisco Bay area during 1971 (Lepidoptera: Nymphalidae). *Pan-Pacific Entomologist*, 48(2): 144.
- Pratt, Gordon F. 1988. The evolution and biology of *Euphilotes* biotypes. Ph.D. dissertation, University of California, Riverside. 653 pp.
- Pratt, Gordon F., and Gregory R. Ballmer. 1986. Clarification of the larval host plant of *Epidemia mariposa* (Lycaenidae) in northern California. *J. Lepid. Soc.*, 40(2): 127.
- Pratt, Gordon F., and Gregory R. Ballmer. 1991. Three biotypes of *Apodemia mormo* (Riodinidae) in the Mojave Desert. *Journal of the Lepidopterists' Society*, 45(1): 46-57.
- Pratt, Gordon F., and John F. Emmel. 1998a. Revision of the *Euphilotes enoptes* and *E. battoides* Complexes (Lepidoptera: Lycaenidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 207-270.
- Pratt, Gordon F., and John F. Emmel. 1998b. A New Subspecies of *Euphilotes pallescens* (Lycaenidae) from the Death Valley Region of California. *Systematics of*

Western North American Butterflies. Mariposa Press, Gainesville, Florida. Pp. 271-276.

Priestaf, Richard C. 1970. Courtship and mating between *Chlosyne neumoegeni* and *Chlosyne californica* (Nymphalidae). *J. Lepid. Soc.*, 24: 226.

Priestaf, Richard C. 1972. Observed mating between *Pieris rapae* and *Pieris protodice* (Pieridae). *J. Lepid. Soc.*, 26(2): 104.

Priestaf, Richard C. 1974. *Phyciodes texana* (Nymphalidae) in California. *J. Lepid. Soc.*, 28(3): 242.

Priestaf, Richard C. 1974. Hybrid between *Colias eurytheme* and *Colias harfordi* (Pieridae) captured in California. *J. Lepid. Soc.*, 28(4): 358.

Priestaf, Richard C., and John F. Emmel. 1998a. An Extraordinary New Subspecies of *Philotiella speciosa* from Santa Barbara County in California (Lepidoptera: Lycaenidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 283-286.

Priestaf, Richard C., and John F. Emmel. 1998b. A New Subspecies of *Thessalia leanira* (Lepidoptera: Nymphalidae) from Coastal Central California. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 327-332.

Pronin, George F. 1955. Notes on the life-history and methods of rearing the Giant Tiger Swallowtail, *Papilio multicaudatus*. *Lepid. News*, 9(4-5): 137-140.

Pyle, Robert Michael. 1974. *Watching Washington Butterflies*. Seattle Audubon Society, Seattle, Washington. 109 pp.

- Pyle, Robert Michael.. 1980. *The Audubon Society Field Guide to North American Butterflies*. Alfred A. Knopf, New York. 916 pp.
- Raguso, Robert A. 1988. A response to "ovular head start in *Anthocharis* and *Pontia*." *News Lepid. Soc.*, 1988(No. 5): 80.
- Raven, Peter H. 1963. A flora of San Clemente Island. *Aliso*, 5: 289-347.
- Raven, Peter H. 1977. The California flora. Pp. 109-137. In Barbour, Michael G., and Jack Major, eds. 1977. *Terrestrial Vegetation of California*. John Wiley & Sons, New York. 1002 pp.
- Raven, Peter H., and Daniel I. Axelrod. 1978. Origin and relationships of the California flora. *Univ. Calif. Publications in Botany*, Volume 72. 134 pp.
- Rawson, G. W. 1961. The early stages of *Brephidium pseudosea* (Morrison) (Lepidoptera, Lycaenidae). *New York Ent. Soc.*, LXIX: 88-91.
- Reinhard, H. V. 1981. Notes on early stages of *Nymphalis californica* (Nymphalidae). *J. Lepid. Soc.*, 35(3): 243-244.
- Remington, Charles L. 1954. Obituary notes: John L. Sperry. *Lepidopterists' News*, 8(1-2): 30.
- Remington, Charles L. 1958. New records of larval host plants of *Mitoura spinetorum*, (Lycaenidae). *Lepid. News*, 12(1-2): 14.
- Remington, Charles L. 1958. Portion of Ingham collection acquired by Yale University. *Lepidopterists' News*, 12(3-4): 94.
- Remington, Charles L. 1968. A new sibling *Papilio* from the Rocky Mountains, with genetic and biological notes (Insecta, Lepidoptera). *Postilla*, 119: 1-40.

- Remington, Charles L., and Roger W. Pease. 1955. Studies in foodplant specificity. 1. The suitability of Swamp White Cedar for *Mitoura gryneus* (Lycaenidae). *Lepid. News*, 9(1): 4-6.
- Rickard, Mike A., and John B. Vernon. 1975. *Lycaeides melissa* (Lycaenidae) in Texas: confirmation of an old record. *J. Lepid. Soc.*, 29: 150.
- Riddell, Janet. 1941. Some remarkable forms and aberrations in the subgenus *Zerene* Hubner (Lepidoptera, Pieridae). *Transactions Royal Entomological Society London*, 91(9): 447-457.
- Ritland, David B. 1991. [Viceroy/Queen - p. 159, Sixth Draft]
- Ritland, David B., and J. Mark Scriber. 1985. Larval development rates of three putative subspecies of tiger swallowtail butterflies, *Papilio glaucus*, and their hybrids in relation to temperature. *Oecologia (Berlin)*, 65: 185-193.
- Robinson, John W. 1990. *Trails of the Angeles: 100 Hikes in the San Gabriels*. Wilderness Press, Berkeley. 230 pp.
- Roer, H. 1970. Untersuchungen zum Migrationsverhalten des Trauermanels (*Nymphalis antiopa*). *Z. angew. Ent.*, 65: 368-396.
- Roever, Kilian. 1962. Notes on *Erora* (Lycaenidae). *J. Lepid. Soc.*, 16: 1-4.
- Roever, Kilian. 1964. Bionomics of *Agathymus* (Megathymidae). *J. Res. Lepid.*, 3(2): 103-120.
- Roever, Kilian 1998. Descriptions of New *Agathymus* (Lepidoptera: Megathymidae) from the Southwestern United States. *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 491-500.

- Ross, Gary N. 1964. Life-history studies of Mexican butterflies. III. Early stages of *Anatole rossi*, a new myrmecophilous metalmark. *J. Res. Lepid.*, 3: 81-94.
- Ross, Gary N. 1964. Life-history studies of Mexican butterflies. III. Nine Rhopalocera (Papilionidae, Nymphalidae, Lycaenidae) from Ocotil Chico, Veracruz. *J. Res. Lepid.*, 3(4): 207-229.
- Ross, Gary N. 1966. Life-history studies on the Mexican butterflies. IV. The ecology and ethology of *Anatole rossi*, a myrmecophilous metalmark (Lepidoptera: Riodinidae). *Ann. Entomol. Soc. Amer.*, 59: 985-1004.
- Rudkin, Charles N. 1936. Interrelationship of *Anthocharis cethura* F. & F. and *A. pima* Edw. (Lepid. Rhopal.). *Bull. So. Calif. Acad. Sci.*, 35(1): 3-5.
- Rutkowski, Frank. 1971. Notes on some Florida Lepidoptera. *J. Lepid. Soc.*, 25(2): 137-139.
- Rutkowski, Frank. 1983. Courtship behavior of the dainty sulfur butterfly, *Nathalis iole* with a description of a new, facultative male display (Pieridae). *J. Res. Lepid.*, 20(3): 161-169. (1981).
- Rutowski, Ronald L. 1979. Courtship behavior of the Checkered White, *Pieris protodice* (Pieridae). *J. Lepid. Soc.*, 33(1): 42-49.
- Rutowski, Ronald L., and John Schaefer. 1984. Courtship behavior of the Gulf Fritillary, *Agraulis vanillae* (Nymphalidae). *J. Lepid. Soc.*, 38(1): 23-31.
- Sakai, T., and S. Masaki. 1965. Photoperiod as a factor causing seasonal forms in *Lycaena phlaeas daimio* Seitz (Lepidoptera: Lycaenidae). *Kontyu*, 33: 275-283.
- Schaus, William. 1920. New species of Lepidoptera in the United States National Museum. *Proc. U.S. Nat. Mus.*, 57: 107-111.

- Schaus, William, August Busck, and Carl Heinrich. 1930. William Barnes. *Proc. Ent. Soc. Wash.*, 32(6): 114-115.
- Schiier, R. D., N. J. Cullenward, P. R. Ehrlich, and R. R. White. 1976. The structure and genetics of the montane population of the Checkerspot butterfly, *Chlosyne palla*. *Oecologia* (Berlin), 25: 279-289.
- Scott, James A. 1965. North American season summary for 1964: California, life history observations. *News Lepid. Soc.*, 1965(3): 3.
- Scott, James A. 1968. The life history and habits of *Chlosyne fulvia* (Nymphalidae). *J. Lepid. Soc.*, 22(4): 237-240.
- Scott, James A. 1970. Hilltopping as a mating mechanism to aid the survival of low density species. *J. Res. Lepid.*, 7(4): 191-204. ("1968").
- Scott, James A. 1973a. Down-valley flight of adult Theclini (Lycaenidae) in search of nourishment. *J. Lepid. Soc.*, 27(4): 283-287.
- Scott, James A. 1973b. Convergence of population biology and adult behaviour in two sympatric butterflies, *Neominois ridingsii* (Papilionoidea: Nymphalidae) and *Amblyscirtes simius* (Hesperioidea: Hesperiiidae). *J. Animal Ecology*, 42: 663-672.
- Scott, James A. 1974a. Population biology and adult behavior of *Lycaena arota* (Lycaenidae). *J. Lepid. Soc.*, 28(1): 64-72.
- Scott, James A. 1974b. Early stages and biology of *Phyciodes orseis* (Nymphalidae). *J. Res. Lepid.*, 12(4): 236-242. ("1973")
- Scott, James A. 1975. Movement of *Precis coenia*, a "pseudoterritorial" submigrant (Lepidoptera, Nymphalidae). *J. Animal Ecology*, 44: 843-850.

- Scott, James A. 1975. Variability of courtship of the Buckeye Butterfly, *Precis coenia* (Nymphalidae). 9, 14(3): 142-147.
- Scott, James A. 1975a. Movements of *Euchloe crusonides* (Pieridae). *J. Lepid. Soc.*, 29(1): 24-31.
- Scott, James A. 1975b. Mate-locating behavior of western North American butterflies. *J. Res. Lepid.*, 14: 1-40.
- Scott, James A. 1975c. Early stages of seven Colorado *Hesperia* (Hesperiidae). *J. Lepid. Soc.*, 29(3): 163-167.
- Scott, James A. 1975d. *Pyrgus xanthus* (Hesperiidae): systematics, foodplants and behavior. *J. Lepid. Soc.*, 29(4): 213-220.
- Scott, James A. 1976. Early stages of *Phyciodes pallida*, *P. orseis*, and *P. mylitta* (Nymphalidae). *J. Res. Lepid.*, 14(2): 84. ("1975")
- Scott, James A. 1980. A survey of valvae of *Euphydryas chalcedona*, *E. c. colon*, and *E. c. anicia*. *J. Res. Lepid.*, 17(4): 245-252. ("1978").
- Scott, James A. 1980. Geographic variation in *Lycaena xanthoides*. *J. Res. Lepid.*, 18(1): 50-59. ("1979").
- Scott, James A. 1981. Hibernial diapause of North American Papilionoidea and Hesperioidea. *J. Res. Lepid.*, 18(3): 171-200. ("1979").
- Scott, James A. 1983. An apparent interspecific F₁ Hybrid *Speyeria* (Nymphalidae). *J. Res. Lepid.*, 20(3): 174-175. ("1981").
- Scott, James A. 1986. *The Butterflies of North America*. Stanford University Press, Stanford, California. 583 pp.

- Scott, James A., and John A. Justice. 1982. Intergradation between *Callophrys dumetorum oregonensis* and *Callophrys dumetorum affinis* in northwestern U.S. (Lycaenidae). *J. Res. Lepid.*, 20(2): 81-85. ("1981").
- Scott, James A., Norbert G. Kondla, and Stephen M. Spomer. 1998. *Speyeria hesperis* and *Speyeria atlantis* are distinct species. *Papilio New Series*, No. 8: 1-31.
- Scott, James A., and Sterling O. Mattoon. 1982. Early stages of *Speyeria nokomis* (Nymphalidae). *J. Res. Lepid.*, 20(1): 12-15. ("1981").
- Scott, James A., and Paul A. Opler. 1975. Population biology and adult behavior of *Lycaena xanthoides* (Lycaenidae). *J. Lepid. Soc.*, 29(1): 63-66.
- Scott, James A., Oakley Shields, and Scott L. Ellis. 1977. Distribution and biology of a Pleistocene relict: *Ochlodes yuma* (Hesperiidae). *J. Lepid. Soc.*, 31(1): 17-22.
- Scriber, J. M. 1982. Foodplants and speciation in the *Papilio glaucus* group. Proc. 5th Int. Symp. Insect-Plant Relationships, Wageningen, 1982: 307-314.
- Scudder, Samuel H. 1861. Notice of some North American species of *Pieris*. *Proceedings Boston Society Natural History*, 8: 178-185.
- Scudder, Samuel H. 1889. The Butterflies of the Eastern United States and Canada with Special Reference to New England. Cambridge: Published by the author.
- Sette, Oscar Elton. 1962. Variation in the silvering of *Argynnis (Speyeria) callippe* in the interior mountain area of south central California. *J. Res. Lepid.*, 1(1): 3-20.
- Shapiro, Arthur M. 1967. The origin of Autumnal "false broods" in common Pierid butterflies. *J. Res. Lepid.*, 6(3): 181-193.
- Shapiro, Arthur M. 1968. Biological notes on three Pyrginae in New York (Hesperiidae). *J. Lepid. Soc.*, 22(3): 179-180.

- Shapiro, Arthur M. 1973a. An attempted interfamilial mating (Lycaenidae, Nymphalidae). *J. Lepid. Soc.*, 27(2): 159.
- Shapiro, Arthur M. 1973b. Recurrent aberration in *Cynthia annabella*: A review with four new records (Lepidoptera: Nymphalidae). *Pan-Pacific Entomologist*, 49(4): 289-293.
- Shapiro, Arthur M. 1973c. Host records for *Brephidium exilis* (Lycaenidae). *J. Lepid. Soc.*, 27(3): 157-158.
- Shapiro, Arthur M. 1973d. A yellow aberration of *Lerodea eufala* (Hesperiidae). *J. Lepid. Soc.*, 27(4): 238.
- Shapiro, Arthur M. 1973d. Altitudinal migration of butterflies in the central Sierra Nevada. *J. Res. Lepid.*, 12(4): 231-235.
- Shapiro, Arthur M. 1974a. Host-plant utilization by *Pieris napi* populations in California (Lepidoptera: Pieridae). *Psyche*, 81: 361-366.
- Shapiro, Arthur M. 1974b. Movements of *Nymphalis californica* (Nymphalidae) in 1972. *J. Lepid. Soc.*, 28(1): 75-78.
- Shapiro, Arthur M. 1974c. A note on the phenology of *Plebejus acmon* (Lycaenidae). *J. Lepid. Soc.*, 28(4): 371-372.
- Shapiro, Arthur M. 1974d. Natural and laboratory occurrence of "Elymi" phenotypes in *Cynthia cardui* (Nymphalidae). *J. Res. Lepid.*, 13(1): 57-62.
- Shapiro, Arthur M. 1974e. Altitudinal migration of central California butterflies. *J. Res. Lepid.*, 13(3): 157-161.
- Shapiro, Arthur M. 1974f. Butterflies of the Suisun Marsh, California. *J. Res. Lepid.*, 13(3): 191-206.

- Shapiro, Arthur M. 1974g. A new northern record for *Philotes sonorensis* (Lepidoptera: Lycaenidae). *Pan-Pacific Entomologist*, 50(1): 442-443.
- Shapiro, Arthur M. 1975a. *Papilio "gothica"* and the phenotypic plasticity of *P. zelicaon*. *J. Lepid Soc.*, 29: 79-84.
- Shapiro, Arthur M. 1975b. The butterfly fauna of the Sacramento Valley, California. *J. Res. Lepid.*, 13: 73-82, 115-122, 137-148. ("1974")
- Shapiro, Arthur M. 1975d. The role of watercress, *Nasturtium officinale*, as a host of native and introduced Pierid butterflies in California. *J. Res. Lepid.*, 14(3): 158-168.
- Shapiro, Arthur M. 1975e. Ecological and behavioral aspects of coexistence in six crucifer-feeding Pierid butterflies in the central Sierra Nevada. *Amer. Midland Naturalist*, 93(2): 424-433.
- Shapiro, Arthur M. 1975f. Developmental and phenotypic responses to photoperiod in uni- and bivoltine *Pieris napi* in California. *Trans. Royal Ent. Soc. London*, 127(1): 65-71.
- Shapiro, Arthur M. 1975g. Interspecific competition and the history of *Pieris rapae* in North America. *Entomologists' Rec. J. Variation*, 87: 17-19.
- Shapiro, Arthur M. 1975h. Why do California tortoiseshells migrate? *J. Res. Lepid.*, 14(2): 93-97.
- Shapiro, Arthur M. 1975i. Supplementary records of butterflies in the Sacramento Valley and Suisun Marsh, lowland central California. *J. Res. Lepid.*, 14(2): 100-102.

- Shapiro, Arthur M. 1976a. The biological status of nearctic taxa in the *Pieris protodice-occidentalis* group (Pieridae). *J. Lepid. Soc.*, 30(4): 289-300.
- Shapiro, Arthur M. 1976b. Habitat: *Pieris occidentalis* (Pieridae). *J. Res. Lepid.*, 15(3): 182-183.
- Shapiro, Arthur M. 1977a. The alpine butterflies of Castle Creek, Nevada County, California. *Great Basin Naturalist*, 37: 443-452.
- Shapiro, Arthur M. 1977b. Sacramento Valley butterflies and their known host plants in the valley. Unpublished update of 1975c paper, Davis, California. 7 pp.
- Shapiro, Arthur M. 1977c. *Pieris castoria* Reakirt, 1867 (Insecta, Lepidoptera): proposed suppression under the plenary powers. Z. N. (S.) 2170. *Bulletin of Zoological Nomenclature*, 33(3/4): 221-227.
- Shapiro, Arthur M. 1977d. Autumnal false broods of multivoltine butterflies at Donner Pass, California. *J. Res. Lepid.*, 16(2): 83-86.
- Shapiro, Arthur M. 1977e. Photoperiod and temperature in phenotype determination of Pacific Slope Pierini: biosystematic implications. *J. Res. Lepid.*, 16(4): 193-200.
- Shapiro, Arthur M. 1977f. The alpine butterflies of Castle Peak, Nevada County, California. *Great Basin Naturalist*, 37(4): 443-452.
- Shapiro, Arthur M. 1978. A new weedy host for the Buckeye, *Precis coenia* (Nymphalidae). *J. Lepid. Soc.*, 32(3): 224.
- Shapiro, Arthur M. 1979a. Weather and the lability of breeding populations of the Checkered White butterfly, *Pieris protodice* Boisduval and Le Conte. *J. Res. Lepid.*, 17(1): 1-23. ("1978")

- Shapiro, Arthur M. 1979b. *Nymphalis milberti* (Nymphalidae) near sea level in California. *Journal of the Lepidopterists' Society*, 33: 200-201.
- Shapiro, Arthur M. 1979c. Does *Hesperia juba* (Hesperiidae) hibernate as an adult? *J. Lepid. Soc.*, 33: 258-260.
- Shapiro, Arthur M. 1980a. Genetic incompatibility between *Pieris callidice* and *Pieris occidentalis nelsoni*: differentiation within a periglacial relict complex (Lepidoptera: Pieridae). *Canadian Entomologist*, 112: 463-468.
- Shapiro, Arthur M. 1980b. Mediterranean climate and butterfly migration: an overview of the California fauna. *Atalanta*, 11(3): 181-188.
- Shapiro, Arthur M. 1981a. The Pierid red egg syndrome. *American Naturalist*, 117: 276-294.
- Shapiro, Arthur M. 1981b. The pierid fauna of jewel flower at a mid-elevation Sierran locality. *J. Lepid. Soc.*, 35(4): 322-324.
- Shapiro, Arthur M. 1981c. Egg-mimics of *Steptanthus* (Cruciferae) deter oviposition by *Pieris sisymbrii* (Lepidoptera: Pieridae). *Oecologia (Berlin)*, 48: 142-143.
- Shapiro, Arthur M. 1981. Canalization of the phenotype of *Nymphalis antiopa* (Lepidoptera: Nymphalidae) from subarctic and montane climates. *J. Res. Lepid.*, 19(2): 82-87. ("1980").
- Shapiro, Arthur M. 1982. A new elevational record for *Pieris protodice* in California (Lepidoptera: Pieridae). *Pan-Pacific Entomologist*, 58(2): 162.
- Shapiro, Arthur M. 1982. The biological and systematic significance of red fecal and meconial pigments in butterflies: a review with special reference to the Pieridae. *J. Res. Lepid.*, 20(2): 97-102. ("1981").

- Shapiro, Arthur M. 1983. A new record of *Vanessa virginiensis* "ab. *ahwashtee*" from northern California (Lepidoptera: Nymphalidae). *J. Res. Lepid.*, 20(3): 176-177. ("1981").
- Shapiro, Arthur M. 1984a. Non-diapause overwintering by *Pieris rapae* (Lepidoptera: Pieridae) and *Papilio zelicaon* (Lepidoptera: Papilionidae) in California: Adaptiveness of type III diapause-induction curves. *Psyche*, 91: 161-169.
- Shapiro, Arthur M. 1984b. *Anthocharis lanceolata* (Pieridae) feeding on a rare endemic *Streptanthus* species (Cruciferae). *J. Lepid. Soc.*, 38(3): 251-252.
- Shapiro, Arthur M., Sterling O. Mattoon, George T. Austin, and Oakley Shields. 1990. Northward dispersal of *Euptoieta claudia* (Nymphalidae) in California and Nevada in 1988. *J. Lepid. Soc.*, 44(3): 201-202.
- Shapiro, Arthur M., Cheryl A. Palm, and Karen L. Wcislo. 1981. The ecology and biogeography of the butterflies of the Trinity Alps and Mount Eddy, northern California. *J. Res. Lepid.*, 18(2): 69-152. ("1979")
- Shapiro, Arthur M., and Rutowski. 19 .
- Shapiro, Irene. 1975. Courtship and mating behavior of the Fiery Skipper, *Hylephila phylaeus* (Hesperiidae). *J. Res. Lepid.*, 14(3): 125-141.
- Sharp, Margaret A., and David R. Parks. 1973. Habitat selection and population structure in *Plebejus saepiolus* Boisduval (Lycaenidae). *J. Lepid. Soc.*, 27(1): 17-22.
- Shepard, Jon H. 1964. The genus *Lycaeides* in the Pacific Northwest. *J. Res. Lepid.*, 3(1): 25-36.

- Shepard, Jon H. 1998. The Correct Name for the *Boloria chariclea/titania* Complex in North America (Lepidoptera: Nymphalidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 727-730.
- Shepard, Jon H., and Thomas R. Manley. 1998. A Species Revision of the *Parnassius phoebus* Complex in North America (Lepidoptera: Papilionidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 717-726.
- Shepard, Jon H., Lars Crabo, and J. P. Pelham. 1998. Revision of *Boloria natazhati* (Gibson) (Lepidoptera: Nymphalidae). *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Florida. Pp. 731-736.
- Shields, Oakley. 1965. *Callophrys (Mitoura) spinetorum* and *C. (M.) johnsoni*: their known range, habits, variation, and history. *J. Res. Lepid.*, 4(4): 233-250.
- Shields, Oakley. 1966. The butterfly fauna of a yellow pine forest community in the Sierra Nevada, California. *J. Res. Lepid.*, 5(2): 127-128.
- Shields, Oakley. 1967. Hilltopping. An ecological study of summit congregation behavior of butterflies on a southern California hill. *J. Res. Lepid.*, 6(2): 69-178.
- Shields, Oakley. 1972. Flower visitation records for butterflies (Lepidoptera). *Pan-Pacific Entomologist*, 48: 189-203.
- Shields, Oakley. 1973a. Studies on North American *Philotes* (Lycaenidae). I. Roosting behavior, tending ants, parasites and predators. *Bull. Allyn Museum*, No. 10: 1-5.
- Shields, Oakley. 1973b. Studies on North American *Philotes* (Lycaenidae). II. The biology, distribution, and taxonomy of *Philotes sonorensis* (F. & F.). *Bull. Allyn Museum*, No. 15: 1-16.

- Shields, Oakley. 1974a. Studies on North American *Philotes* (Lycaenidae). III. Generic reassignments and the biology of *speciosa*. *Bull. Allyn Museum*, No. 19: 1-10.
- Shields, Oakley. 1974b. *Philotes rita* (Lycaenidae) in a sandstorm. *J. Lepid. Soc.*, 28(1): 78.
- Shields, Oakley. 1975. Toward a theory of butterfly migration. *J. Res. Lepid.*, 13(4): 217-238. ("1974")
- Shields, Oakley. 1977. Distribution of *Shijimiaeoides rita*, especially *S. r. rita* and *S. r. coloradensis* (Lycaenidae). *J. Res. Lepid.*, 16(3): 162-172.
- Shields, Oakley. 1977. Studies on North American *Philotes* (Lycaenidae). V. Taxonomic and biological notes, continued. *J. Res. Lepid.*, 16(1):1-67.
- Shields, Oakley. 1978. *Erynnis brizo lacustra* and *Hesperia columbia* in the Sierra Nevada. *J. Lepid. Soc.*, 32(1): 61-62.
- Shields, Oakley. 1984. A revised, annotated checklist of world Libytheidae. *J. Res. Lepid.*, 22: 264-266.
- Shields, Oakley. 1985. Zoogeography of the Libytheidae (Snouts or Beaks). *Tokurana (Acta Rhopalocerologica)* (Mishima-shi, Japan), No. 9: 1-58.
- Shields, A. Oakley. 1987a. A review of migration in *Nymphalis californica* [Lepidoptera: Nymphalidae: Nymphalinae]. *Utahensis* (Journal of the Utah Lepidopterists' Society), 7(1): 5-13.
- Shields, Oakley. 1987b. Updates to the biology and distribution of *Philotiella speciosa* (Lepidoptera: Lycaenidae). *Atala*, 15(1-2): 14-15.
- Shields, Oakley. 1987c. Presence of pterin pigments in wings of Libytheidae butterflies. *Journal of Chemical Ecology*, 13(8): 1843-1847.

- Shields, Oakley. 1987d. A review of migration in Libytheidae. *Tokurana (Reports on Rhopalocera)*, No. 12 (pt. 2): 1-14.
- Shields, Oakley, and J. F. Emmel. 1973. A review of carrying pair behavior and mating times in butterflies. *J. Res. Lepid.*, 12: 25-64.
- Shields, Oakley, J. F. Emmel, and D. E. Breedlove. 1970. Butterfly larval foodplant records and a procedure for reporting foodplants. *J. Res. Lepid.*, 8(1): 21-36. ("1969")
- Shields, Oakley, and Johnson C. Montgomery. 1966. The distribution and bionomics of arctic-alpine *Lycaena phlaeus* subspecies in North America. *J. Res. Lepid.*, 5(4): 231-242.
- Shields, Oakley, and James R. Mori. 1979. Another *Anthocaris lanceolata* x *A. sara* hybrid. *J. Res. Lepid.*, 17(1): 53-55. ("1978").
- Sicher, Harry. 1953. Migration of *Vanessa carye*. *Lepidopterists' News*, 7(2): 53.
- Simms, H. M. 1920. Butterflies observed in Dead Horse Canyon, California, during 1917 season. *Southwest Science Bulletin* (Southwest Museum), No. 1: 9-12.
- Sims, Steven R. 1979. Aspects of mating frequency and reproductive maturity in *Papilio zelicaon*. *American Midland Naturalist*, 102(1): 36-50.
- Sims, Steven R. 1980. Diapause dynamics and host plant suitability of *Papilio zelicaon* (Lepidoptera: Papilionidae). *American Midland Naturalist*, 103(2): 375-384.
- Sims, Steven R. 1983a. Prolonged diapause and pupal survival of *Papilio zelicaon* Lucas (Lepidoptera: Papilionidae). *J. Lepid. Soc.*, 37(1): 29-37.
- Sims, Steven R. 1983b. Inheritance of diapause induction and intensity in *Papilio zelicaon*. *Heredity*, 51(2): 495-500.

- Sims, Steven R. 1983c. The genetic and environmental basis of pupal colour dimorphism in *Papilio zelicaon* (Lepidoptera: Papilionidae). *Heredity*, 50(2): 159-168.
- Sims, Steven R. 1984. Reproductive diapause in *Speyeria* (Lepidoptera: Nymphalidae). *J. Res. Lepid.*, 23(3): 211-216.
- Sims, Steven R., John G. Brittnacker, and Francisco J. Ayla. 1979. Genetic confirmation of the specific status of the *Speyeria adiastra* group in California (Lepidoptera: Nymphalidae). *Pan-Pacific Entomologist*, 55(2): 111-116.
- Sims, Steven R., and Arthur M. Shapiro. 1983a. Pupal colour dimorphism in California *Battus philenor* (L.) (Papilionidae): Mortality factors and selective advantage. *J. Lepid. Soc.*, 37(3): 236-243.
- Sims, Steven R., and Arthur M. Shapiro. 1983b. Pupal colour dimorphism in California *Battus philenor* (L.): Pupation sites, environmental control, and diapause linkage. *Ecological Entomology*, 8: 95-104.
- Sims, Steven R., and Arthur M. Shapiro. 1983c. Seasonal phenology of *Battus philenor* (L.) (Papilionidae) in California. *J. Lepid. Soc.*, 37(4): 281-288.
- Singer, Michael C. 1971. Evolution of food-plant preferences in the butterfly, *Euphydryas editha*. *Evolution*, 25: 383-389.
- Singer, Michael C. 1972. Complex components of habitat suitability within a butterfly colony. *Science*, 176: 75-77.
- Singer, Michael C., and Paul R. Ehrlich. 1979. Population dynamics of the Checkerspot butterfly, *Euphydryas editha*. *Fortschr. Zool.*, 25(2/3): 55-60.

- Singer, M. C., C. D. Thomas, H. L. Billington, and C. Parmesan. 1989. Variation among conspecific insect populations in the mechanistic basis of diet breadth. *Animal Behaviour*, 37: 751-759.
- Skinner, Henry. 1882. New species of Rhopalocera. *Entomological News*, 3(1): 15.
- Skinner, Henry. 1893. A new *Eudamus*. *Entomological News*, 4(2): 64-65.
- Skinner, Henry. 1902. A new *Papilio* [and California record of *Apargyreus exadeus*]. *Entomological News*, 13(6): 183.
- Skinner, Henry. 1911. The larger boreal American Hesperidae (sic), including *Eudamus*, *Erycides*, *Pyrrhopyge* and *Megathymus*. *Trans. Amer. Entomol. Soc.*, 37: 169-209, pl. 10.
- Skinner, Henry, and R. C. Williams, Jr. 1922. On the genitalia of the larger Hesperidae of North America. *Trans. Amer. Entomol. Soc.*, 48: 109-127.
- Smith, Michael J., and Jim P. Brock. 1988. A review of the *Thessalia leanira* complex in the southwestern United States (Nymphalidae: Melitaeinae), with a description of two new subspecies of *Thessalia fulvia*. *Bulletin Allyn Museum of Entomology*, No. 118: 1-21.
- Sperling, Felix A. H. 1991. Mitochondrial DNA phylogeny, speciation, and hostplant coevolution of *Papilio* butterflies. Ph.D. dissertation, Cornell University, Ithaca, New York. 132 pp.
- Sprague, M. 1941. Climate of California. *U.S. Yearbook of Agriculture Climate and Man*. U.S. Government Printing Office, Washington, D.C. Pp. 783-797.

- Stallings, Don B., and J. R. Turner. 1956. Description of a new subspecies of the *Megathymus yuccae* (Boisd. & LeC.) Complex. *Bull. So. Calif. Acad. Sci.*, 55(3): 150-152.
- Stallings, Don B., J. R. Turner, and Viola N. Stallings. 1966. Two new species and two new subspecies of Megathymidae from Mexico and the United States. *J. Lepid. Soc.*, 20: 163-172.
- Stanford, Ray E. 1973. *Apodemia mormo* near *dialeuca* (Riodinidae) from montane southern California: new for U.S.A. *J. Lepid. Soc.*, 27(4): 304-305.
- Steiner, John. 1990. Bay area butterflies: the distribution and natural history of San Francisco region Rhopalocera. California State University, Hayward, M. S. Thesis. 307 pp.
- Sternitzky, R. S. 1937. A race of *Euphydryas editha* Boiduval (Lepidoptera). *Canadian Entomologist*, 69: 203-205.
- Stoner, E. A. 1954. Further notes on the migration and breeding of *Nymphalis californica*. *Lepidopterists' News*, 8(3-4): 103.
- Storer, T. I. 1933. *Aglaia californica* in California during 1932. *Pan-Pacific Ent.*, 9(2): 67-68.
- Tebis, L., Jr. 1953. An outbreak of *Nymphalis californica* near Lake Almanor, California. *Pan-Pacific Ent.*, 29(4): 201-202.
- Thorne, Fred. 1959. The distribution of *Lycaena hermes*. Minutes of the Sixth Annual Meeting of the Pacific Slope Section of the Lepidopterists' Society, 29 and 30 August, 1959. *J. Lepid. Soc.*, 13(4): 238-239.

- Thorne, Fred. 1961. Extensions of range and a new host plant for *Philotes speciosa* (Lepidoptera: Lycaenidae). *Bull So. Calif. Acad. Sci.*, 60(1): 37-39.
- Thorne, Fred. 1962. Larval notes on *Chlosyne lacinia* and *C. californica*. *J. Lepid. Soc.*, 16: 61.
- Thorne, Fred. 1963. The distribution of an endemic butterfly, *Lycaena hermes*. *J. Res. Lepid.*, 2(2): 143-150.
- Thorne, Robert F. 1976. The vascular plant communities of California. Pp. 1-31. In Latting, June, editor. *Plant Communities of Southern California*. Special Publication No. 2. California Native Plant Society, Berkeley, California. 164 pp.
- Thorne, Robert F., Barry A. Prigge, and James Henrickson. 1981. A flora of the higher ranges and the Kelso Dunes of the eastern Mojave Desert in California. *Aliso*, 10(1): 71-186.
- Tietz, H. M. 1972. *An Index to the Described Life Histories, Early Stages and Hosts of the Macrolepidoptera of the Continental United States and Canada*. Vols. 1 and 2. A. C. Allyn, Sarasota, Fla. 1041 pp.
- Tilden, J. W. 1942a. *Erynnis lacustra* (Wright) from near the type locality (Lepidoptera, Nymphalidae). *Pan-Pacific Ent.*, 18(1): 8.
- Tilden, J. W. 1942b. An unusual record of *Ochlodes yuma* (Edwards) (Lepidoptera, Hesperidae). *Pan-Pacific Ent.*, 18(1): 29.
- Tilden, J. W. 1944. Breeding of *Phoebis sennae marcellina* Cran. in San Jose, California (Lepidoptera, Pieridae). *Pan-Pacific Ent.*, 20(3): 117.
- Tilden, J. W. 1947. An occurrence of the pupa of *Glaucopsyche lygdamus behrii* (Edwards) in an ant nest. *Pan-Pacific Ent.*, 23(1): 42-43.

- Tilden, J. W. 1951. A new subspecies of *Mitoura siva* Edwards. *Bull. So. Calif. Acad. Sci.*, 50(2): 96-98.
- Tilden, J. W. 1952. Concerning the identity of *Mitoura nelsoni mui*ri. *Lepid. News*, 6(6-8): 95-96.
- Tilden, J. W. 1954. Notes. *Pan-Pacific Entomologist*, 30: 85.
- Tilden, J. W. 1955. A revision of *Tharsalea* Scud. (s. str.) with description of a new subspecies. *Bull So. Calif. Acad. Sci.*, 54(2): 67-77.
- Tilden, J. W. 1956. San Francisco's vanishing butterflies. *Lepidopterists' News*, 10(3-4): 113-115.
- Tilden, J. W. 1957a. A record of *Stanleya* as a foodplant of *Pieris beckeri* (Lepidoptera: Pieridae). *Pan-Pacific Entomol.*, 33: 169.
- Tilden, J. W. 1957b. *Carterocephalus palaemon* in California (Hesperiidae). *Lepidopterists' News*, 11(1-3): 43.
- Tilden, J. W. 1957c. Taxonomic history and distribution of *Ochlodes yuma* (Hesperiidae). *Lepid. News*, 11: 151-152.
- Tilden, J. W. 1958a. Notes on the life history of *Euphydryas editha bayensis*. *Lepid. News*, 12(1-2): 33-35.
- Tilden, J. W. 1958b. Distributional oddities. *Lepid. News*, 12: 203-204.
- Tilden, J. W. 1960. An additional note on the life history of *Mitoura spinetorum* (Hewitson) (Lepidoptera: Lycaenidae). *Pan-Pacific Ent.*, 36(1): 40.
- Tilden, J. W. 1962. General characteristics of the movements of *Vanessa cardui* (L.). *J. Res. Lepid.*, 1(1): 43-49.

- Tilden, J. W. 1963. The *Argynnis* populations of the Sand Creek area, Klamath Co., Oregon. *J. Res. Lepid.*, 1(2): 109-113.
- Tilden, J. W. 1963. An analysis of the North American species of the genus *Callophrys*. *J. Res. Lepid.*, 1(4): 281-300.
- Tilden, J. W. 1965. A note on *Pyrgus communis* and *Pyrgus albescens* (Hesperiidae). *J. Lepid. Soc.*, 19: 91-94.
- Tilden, J. W. 1965. *Butterflies of the San Francisco Bay Region*. University of California Press, Berkeley. 88 pp.
- Tilden, J. W. 1967. A previously unrecognized subspecies of *Philotes speciosa*. *J. Res. Lepid.*, 6(4): 281-284.
- Tilden, J. W. 1968. Records of two species of exotic Lepidoptera captured in California. *J. Lepid. Soc.*, 22: 187.
- Tilden, J. W. 1971. Comments on the nearctic members of the genus *Precis* Huebner. *J. Res. Lepid.*, 9(2): 101-108. ("1970")
- Tilden, J. W. 1973. Specific entities of the subgenus *Icaricia* Nabokov (Lycaenidae). *J. Res. Lepid.*, 12(1): 11-20.
- Tilden, J. W. 1973. A name for *Glaucopsyche lygdamus* Behrii Auct., not Edwards 1862. *J. Res. Lepid.*, 12(4): 213-215.
- Tilden, J. W. 1973. *Junonia* and *Precis*. A correction. *J. Res. Lepid.*, 12(4): 216.
- Tilden, J. W. 1975. An analysis of the W. G. Wright butterfly and skipper plesiotypes in the collection of the California Academy of Sciences. *Occasional Papers Calif. Academy of Sciences*, No. 118: 1-44.
- Tilden, J. W. 1975. Hesperiid notes. *J. Lepid. Soc.*, 29(1): 60-62.

- Tilden, J. W. 1976. *Urbanus simplicius* (Stoll), a new record for California. *J. Res. Lepid.*, 15(1): 40.
- Tilden, J. W. 1976. A proposed terminology for the types of diapause occurring in the Order Lepidoptera. *J. Res. Lepid.*, 15(1): 33-39.
- Tilden, J. W., and J. C. Downey. 1955. A new species of *Philotes* from Utah (Lepidoptera, Lycaenidae). *Bull. So. Calif. Acad. Sci.*, 54(1): 25-29.
- Tilden, J. W., and A. C. Smith. 1986. *A Field Guide to Western Butterflies*. Houghton Mifflin Company, Boston. 370 pp.
- Tong, Mark L., and Arthur M. Shapiro. 1989. Genetic differentiation among California populations of the Anise Swallowtail butterfly, *Papilio zelicaon* Lucas. *Journal of the Lepidopterists' Society*, 43(3): 217-228.
- Truman, P. C. 1890. Butterflies of San Diego. *The West American Scientist*, 7(51): 19-20.
- Tuskes, P. M., and Lincoln P. Brower. 1978. Overwintering ecology of the Monarch butterfly, *Danaus plexippus* L., in California. *Ecological Ent.*, 3: 141-153.
- Urquhart, Fred A. 1960. The Monarch Butterfly. Royal Ontario Museum, Toronto. 361 pp.
- Urquhart, F. A., and N. R. Urquhart. 1977. Overwintering areas and migratory routes of the Monarch butterfly (*Danaus plexippus*, Lepidoptera: Danaidae) in North America, with special reference to the western population. *Canadian Ent.*, 109: 1583-1589.

- Urquhart, F. A., P. Beard, and R. Brownlee. 1965. A population study of a hibernial roosting colony of the Monarch butterfly (*D. plexippus*) in northern California. *J. Res. Lepid.*, 4(4): 221-226.
- Urquhart, F. A., and R. W. Stegner. 1966. Laboratory techniques for maintaining cultures of the Monarch butterfly. *J. Res. Lepid.*, 5(3): 129-136.
- Urquhart, F. A., N. R. Urquhart, and F. Munger. 1970. A study of a continuously breeding population of *Danaus plexippus* in southern California to a migratory population and its significance in the study of insect movement. *J. Res. Lepid.*, 7(4): 169-181. ("1968").
- Van Devender, Thomas R. 1977. Holocene woodlands in the southwestern deserts. *Science*, 198: 189-192.
- Van Doren, Phyllis. 1983. Remembering Doc Comstock. *Environment Southwest*, Winter 1983: 14-19.
- Wade, J. S. 1928. A bibliography of biographies of entomologists, with special reference to North American workers. *Annals Entomological Society America*, 21: 489-520.
- Wallace, Gary D. 1985. Vascular plants of the Channel Islands of Southern California and Guadalupe Island, Baja California, Mexico. *Natural History Museum of Los Angeles County Contributions in Science*, No. 365. 136 pp.
- Watson, Frank E., and Wm. P. Comstock. 1920. Notes on American Lepidoptera with descriptions of new varieties. *Bulletin Amer. Museum of Natural History*, 42: 447-457.

- Watt, Ward B. 1968. Adaptive significance of pigment polymorphisms in *Colias* butterflies. I. Variation of melanin pigment in relation to thermoregulation. *Evolution*, 22: 437-458.
- Watt, Ward B. 1969. Adaptive significance of pigment and polymorphisms in *Colias* butterflies. II. Thermoregulation and photoperiodically controlled melanin variation in *Colias eurytheme*. *Proceedings National Academy Sciences, U.S.A.*, 63: 767-774.
- Watt, Ward B. 1983. Adaptation at specific loci. II. Demographic and biochemical elements in the maintenance of *Colias* PGI polymorphism. *Genetics*, 103: 691-724.
- Watt, Ward B., D. Han, and B. Tabashnik. 1979. Population structure of pierid butterflies. II A "native" population of *Colias philodice eriphyle* in Colorado. *Oecologia*, 44: 44-52.
- Watt, W. B., C. Kreman, and P. Carter. 1989. Testing the 'mimicry' explanation for the *Colias* 'alba' polymorphism: patterns of co-occurrence of *Colias* and Pierine butterflies. *Functional Ecology*, 3: 193-199.
- Webster, R. P., and M. C. Nielsen. 1984. Myrmecophily in the Edwards' Hairstreak butterfly *Satyrrium edwardsii* (Lycaenidae). *J. Lepid. Soc.*, 38(2): 124-133.
- Weissman, K. G. 1972. The population biology of *Coenonympha tullia* on Jasper Ridge: Strategies of bivoltine butterfly. Ph.D. dissertation, Stanford University. 95 pp.
- Welling, Eduardo C. 1973. A massive migration of *Kricogonia* (Pieridae) in Campeche, Mexico. *J. Lepid. Soc.*, 27(2): 154-155.
- Wells, Mary P. 1987. Ilya Voznesensky, an early Russian collector. *Fremontia (Journal of the California Native Plant Society)*, 14(4): 16-19.

- Wells, P. V. 1983. Paleobiogeography of the montane islands of the Great Basin since the last glaciopluvial. *Ecological Monographs*, 53: 341-382.
- Wells, Philip V., and Rainer Berger. 1967. Late Pleistocene history of coniferous woodland in the Mohave Desert. *Science*, 155: 1640-1647.
- Wesley, David J., and Thomas C. Emmel. 1975. The chromosomes of neotropical butterflies from Trinidad and Tobago. *Biotropica*, 7(1): 24-31.
- West, David A. 1983. Hand-pairing of *Battus philenor* (Papilionidae). *J. Lepid. Soc.*, 37(1): 90.
- West, David A., and W. N. Hazel. 1979. Natural pupation sites of swallowtail butterflies (Lepidoptera: Papilioninae): *Papilio polyxenes* Fabr., *P. glaucus* L., and *Battus philenor* (L.). *Ecological Ent.*, 4: 387-392.
- West, David A., and W. N. Hazel. 1982. An experimental test of natural selection for pupation site in swallowtail butterflies. *Evolution*, 36: 152-159.
- White, Raymond R. 1974. Foodplant defoliation and larval starvation of *Euphydryas editha*. *Oecologia* (Berlin), 14: 307-315.
- White, Raymond R. 1986. Pupal mortality in the Bay Checkerspot Butterfly (Lepidoptera: Nymphalidae). *J. Res. Lepid.*, 25(1): 52-62.
- White, Raymond R., and Michael C. Singer. 1974. Geographical distribution of hostplant choice in *Euphydryas editha* (Nymphalidae). *J. Lepid. Soc.*, 28(2): 103-107.
- Whittaker, P. L. 1984. Population biology of the Great Purple Hairstreak, *Atlides halesus*, in Texas (Lycaenidae). *J. Lepid. Soc.*, 38(3): 179-185.

- Wielgus, Ronald S. 1974. Artificial diet: the key to the mass rearing of *Megathymus* larvae. *J. Res. Lepid.*, 13(4): 271-277.
- Wielgus, Ronald S., and Dale Wielgus. 1973. Some techniques for the rearing of *Megathymus* larvae. *J. Res. Lepid.*, 11(4): 245-250. ("1972").
- Wilkinson, Ronald S. 1988. Cyril Franklin dos Passos (1887-1986). *J. Lepid. Soc.*, 42(3): 155-163.
- Wilkinson, Ronald S. 1988. Annotated bibliography of the entomological publications of Cyril F. dos Passos (1887-1986). *J. Lepid. Soc.*, 42(3): 168-183.
- Williams, C. B. 1930. *The Migration of Butterflies*. Oliver and Boyd, Edinburgh. 473 pp.
- Williams, C. B. 1938. Recent progress in the study of some North American migrant butterflies. *Ann. Ent. Soc. Amer.*, 31(2): 211-239.
- Williams, C. B. 1970. The migration of the Painted Lady butterfly, *Vanessa cardui* (Nymphalidae), with special reference to North America. *J. Lepid. Soc.*, 24: 157-175.
- Williams, Francis X. 1908. The life history of *Lycaena antiacis* Bdv., with notes on other species. *Entomological News*, 19: 476-483.
- Williams, Francis X. 1910. The butterflies of San Francisco, California. *Ent. News*, 21: 30-41.
- Williams, Francis X., and Fordyce Grinnell, Jr. 1905. A trip to Mt. Diablo in search of Lepidoptera. *Entomological News*, 16: 235-238.
- Wind, Robert G. 1943. Notes on *Apodemia* (F. & F.) and other southern butterflies occurring in northern California. *Bull. of Brooklyn Ent. Soc.*, 38: 42-43.

- Wind, Robert G. 1947. A new subspecies of *Melitaea* (Lepidoptera). *Pan-Pacific Entomologist*, 23: 171.
- Woodbury, A. M., J. W. Sugden, and C. Gillette. 1942. Notes on migrations of the Painted Lady Butterfly in 1941. *Pan-Pacific Entomologist*, 18(4): 165-176.
- Wourms, M. K., and F. E. Wasserman. 1985. Bird predation on Lepidoptera and the reliability of beak-marks in determining predation pressure. *J. Lepid. Soc.*, 39: 239-261.
- Wright, William Greenwood. 1905. *The Butterflies of the West Coast of the United States*. San Francisco: Whitaker and Ray Co. 257 pp.
- Wright, William Greenwood. 1906. *The Butterflies of the West Coast of the United States*. Second Edition. San Bernardino, California: published by the author. 257 pp.
- Young, Allen M. 1980. Some observations on the natural history and behaviour of the Camberwell Beauty (Mourning Cloak) butterfly *Nymphalis antiopa* (Linnaeus) (Lepidoptera: Nymphalidae) in the United States. *Entomological Gazette*, 31: 7-18.
- Ziegler, J. Benjamin. 1953. Notes on the life history of *Incisalia augustinus* and a new host plant record (Lycaenidae). *Lepid. News*, 7(2): 33-35.
- Ziegler, J. Benjamin. 1960. Preliminary contribution to a redefinition of the genera of North American hairstreaks (Lycaenidae) north of Mexico. *J. Lepid. Soc.*, 14(1): 19-23.
- Zimmerman, Elwood C. 1969. Francis Xavier Williams, 1882-1967. *Pan-Pacific Entomologist*, 45(2): 135-146.