

BULLETIN OF THE ALLYN MUSEUM

Published by
THE ALLYN MUSEUM OF ENTOMOLOGY
Sarasota, Florida

Number 28

3 Sept. 1975

STUDIES ON NORTH AMERICAN PHILOTES (LYCAENIDAE)

IV. Taxonomic and biological notes, and new subspecies

Oakley Shields

Department of Entomology, University of California, Davis, Calif. 95616

"Few butterflies are more completely 'one-plant insects' than members of the genus *Philotes*. Not only do the larvae feed on the flower heads of *Eriogonum*, but the adults visit the flowers for nectar, so all of the food requirements for both larvae and adults may be supplied by one species of plant." (Tilden, 1959: 261)

INTRODUCTION

Philotes as applied in the broad sense is used here only for descriptive convenience to refer to *battoides*, *rita*, and *enoptes* on *Eriogonum*. The group formerly known as the Nearctic "*Philotes*" has been shown (Shields, 1974b) in fact to be a group of sibling species representing *Philotes sonorensis* (Felder & Felder, 1865), *Zizeeria speciosa* (H. Edwards, 1876), *Shijimiaeoides rita* (Barnes & McDunnough, 1916), *S. enoptes* (Boisduval, 1852) and *Caleta battoides* (Behr, 1867). Since then, however, a hybrid specimen of *battoides glaucon* X *enoptes ancilla* has come to my attention, a male from Pattee Canyon, 3500', Missoula Co., Montana, VI-23-62 (J. Scott). Face on, the left valve is like *battoides* and the right valve (though somewhat shorter) is like *enoptes*! Also, two males from 8 mi. N. of Jarbidge, Elko Co., Nevada, VI-28-67 (J. Lane) appear to have somewhat intermediate genitalia between *battoides glaucon* and *enoptes ancilla* (i.e., both have bifurcate valvae but not as deeply as is usual in *battoides*, and one has prominent teeth in a row, as in *enoptes*, along the concave surface. Thus it would appear likely that these three specimens are hybrids between *b. glaucon* and *e. ancilla*, two subspecies that are nearly identical in adult facies and which utilize the same hosts, *Eriogonum umbellatum* and *E. heracleoides*. Consequently, *battoides* should belong in the genus *Shijimiaeoides* along with *enoptes* and *rita*, and should be dropped from the genus *Caleta* where I had tentatively placed it. A close relationship may still exist between *Caleta* and *battoides*, but it now appears doubtful they should reside in the same genus.

P. sonorensis and *Z. speciosa* are readily distinguishable on adult facies alone, but an occasional dwarf form of *enoptes* is mistaken for *speciosa*, and *S. rita*, *enoptes* and *battoides* are often so similar in wing characters that only recourse to their distinctive male (or female) genitalia will place them to proper species

(see Mattoni, 1957). In this study, it was first necessary to examine the male genitalia of all named subspecies, to develop a recognition for the accompanying slight facies differences and to associate each form with its proper *Eriogonum* host(s). Similarly, genitalia of representatives of every new, unplaced population found during the course of study had to be examined to avoid errors. Only after this procedure was strictly adhered to for several years did I allow myself the luxury of determining some populations on facies alone, having then a practiced eye for subtle cues. Even at this stage, however, it was still necessary to examine genitalia of exceptionally close members such as *battoides glaucon-enoptes ancilla-e. columbiae* and *b. comstocki-enoptes* nr. *enoptes* (Tehachapi Mts.). Some 1250 male genitalia were determined and approximately 9,000 specimens were examined in all. Genitalia of representative specimens from many localities were examined (exceptions are some *enoptes mojave* and *rita spaldingi*) by the procedure outlined in Shields (1973).

The male genitalia of *S. battoides* and *S. enoptes* are adequately figured in Langston (1963). (See also, for *battoides*, the figure 23 in Brown, 1970; pl. 17, figs. 3 & 4 of Barnes & McDunnough, 1917; and pl. V, fig. 3 of Williams, 1918. For *enoptes*, see Williams, 1918, pl. 4, 5, fig. 6-10; and Barnes & McDunnough, 1917, pl. 17, figs. 1 & 2.) The male genitalia of *rita* are pictured in Barnes & McDunnough, 1917, pl. 17, figs. 5 & 7; Mattoni, 1965, figs. 2, 3, 4; and drawn in Tilden & Downey, 1955, pl. 11. Barnes & McDunnough, 1917, pl. 17, fig. 6, picture *spaldingi*'s male genitalia but at such an angle that the rudimentary cristae are not visible. *Shijimiaeoides r. spaldingi* appears to be the link between the *rita* type of genitalia (with cristae always present) and the *enoptes* type (its valve being close to *enoptes ancilla* and *e. dammersi*-i.e., terminal end of valve with blunt teeth instead of spines, and general shape of the valve as in *enoptes*). No *enoptes* subspecies possess cristae. Clench's view (1967) that the *pallascens-elvirae* group and the *rita-coloradensis* group may form distinct species is untenable in the light of recent discoveries reported here. Mattoni (1954: 164) using genitalia differentiates female *enoptes* from female *battoides*, and female *enoptes* from female *rita* (1965: 86).

The number of teeth on the terminal end (cucullus) of the valve in the *rita-enoptes* group, for 59 populations and 17 subspecies sampled ($N = 318$), varied from a low of 9 to a high of 35, the lowest being *enoptes ancilla* (averaging 11) and the highest *rita rita* and *rita coloradensis* (averaging 26). The number of teeth was diagnostic for each subspecies.

The terminology used in describing *Philotes* follows that of Nabokov (1944, plate 5) and Mattoni (1954, 1965).

SHIJIMIAEOIDES RELATIVES

Some authors suggest combining the Nearctic species of *Shijimiaeoides* with the Mediterranean-European genus *Pseudophilotes* (*vicrama* extends to Central Himalaya and Tibet) by virtue of their similar facies. The two genera are no doubt closely related, as the genitalia of *vicrama* is like *enoptes* with the "neck" twisted on the valve (with *bavius* probably a *vicrama* derivative), and the *baton* genitalia is quite similar to *battoides* except the bifurcation is upturned (with *abencerragus* probably a *baton* derivative). This reverses my previous opinion (Shields, 1974b) that was based on Hemming's drawings (Beuret's sketches are more instructive). However, the length X width ratios of the aedeagus of the two genera differ considerably (*Pseudophilotes abencerragus* 0.24 (Fig. 37) *P. vicrama* 0.68 (Fig. 34) *P. baton* 0.50 (Fig. 36) *P. bavius* 0.25-0.33 (Fig. 35); *Shijimiaeoides divina barine* 1.73 (Fig. 40), *S. enoptes* 1.43) (Beuret, 1958). In this respect, *Shijimiaeoides* is closer to *Glaucopsyche* (*G. lygdamus* 1.31, *G. alexis cyllarus* 1.77). Likewise, the length X width ratios of the androconia differ in *P. abencerragus* (2.60) and *P. bavius* (1.81-2.41), but are similar in *P. baton* (1.34-1.24), *P. vicrama* (1.19), *S. divina barine* (1.16) and *S. enoptes* (1.10). The male androconial scales of *S. divina barine* and *S. enoptes enoptes* are very similar in form, rib number, and knot

number but differ in size (*barine* = 32mm, *enoptes* = 19mm in width) and are similar to *vicrama* and *baton* but not to *abencerragus* and *bavius* (Beuret, 1958). In view of these morphological differences in genitalia between *Pseudophilotes* and *Shijimiaeoides* (and foodplant differences), I concur with Beuret in designating them as distinct genera. On the basis of male genitalia, other genera that seem closely related to *Shijimiaeoides* are *Palaeophilotes*, *Praepophilotes*, *Scolitantides* (*orion*), *Sinia*, *Shijimia*, *Glaucopsyche* (via *atroguttata* Obth. and *coeligena* Obth.), *Actizera* (via *panagaea* H.-Sch.), *Lycaena*, *Turanana* (*cytis*), and *Zizeeria* (via *speciosa* (Figs. 43-44). Brown (1971) places *pius* in *Glaucopsyche*, a decision I am in agreement with. (I think "*Shijimiaeoides*" lanky Obth. should belong in *Glaucopsyche* because of the shape of the male valve.) Robinson (1971) reports that the modal haploid chromosome number for Lycaenidae is $n = 24$, with *Glaucopsyche*, 4 sp., $n = 23$; *Lycaena*, 7 sp., $n = 24$ (except *heteronea* and *rubidus*); *Pseudophilotes* (*baton*, *bavius*, *vicrama*), $n = 24$; *Scolitantides* *orion*, $n = 23$; *Turanana* *panagaea*, $n = 24$; and *Zizeeria* *maha argia*, $n = 24$.

Beuret (1958: 83) states that the uncus, tegumen, and lateral uncus hooks of *Sinia* are near *Shijimiaeoides* (also the valve tip recalls *enoptes*, though much reduced). However, it shows enough differences from *Shijimiaeoides* in length X width ratios for the androconia and aedeagus to be properly kept as a separate genus. In adult facies, *Sinia* clearly approaches *Shijimiaeoides* (see Beuret, 1958: 78; fig. 26-27). *Sinia leechi* Forst. (Fig. 36) is known from China (Setzschwanz: Kwanhsien) and is very local. Much confusion has centered about the names *S. leechi* and *Shijimia moorei* Leech (Fig. 37). Beuret was unaware that all his discussion, figures, and statistics for *Shijimia moorei* in his 1958 paper referred instead to *Sinia leechi* (= *moorei* auct., nec Leech), but after consulting Forster (1940), he published a correction in 1959.

Jamides pura (Moore) has a very similar bifurcate valve to *S. battoides* (see Eliot, 1973, fig. 95). Another candidate as a close *battoides* relative is the rare *Shijimia moorei*. The male genitalia, as illustrated in Forster (1940: 878), has strongly bifurcate valvae, with the rest of the genitalia somewhat similar also, although apparently modified somewhat from the *battoides*' ground-plan. The brief description in Seitz of the adult seems also to indicate that *moorei* belongs in a separate genus from *battoides*. *Shijimia moorei* flies in central China (Kiukiang and Chang-yang in June and July), southeast Chia (Fuchien: Kuatun), and Formosa.

With *Pseudophilotes* on *Thymus* and *Salvia*, perhaps a nectar source became a larval foodplant (from the unrelated *Eriogonum*). (This idea is attractive because the *Eriogonum* serves as both larval foodplant and nectar source in *Shijimiaeoides*.) There are several records of lycaenids imbibing nectar from Labiatae (*Monarda*, *Monardella*) (Shields, 1972), although I have not seen any doing so on *Salvia* in southern California.

Larvae of *Pseudophilotes vicrama cashmirensis* (Moore) are found particularly on the flowers of *Thymus* (Seitz, 1909: 306). Colin Wyatt (*in litt.*) has found larvae of *Pseudophilotes bavius fatma* (Oberthur) in the Middle Atlas of Morocco feeding on the buds and flowers of a large *Salvia* species with hairy leaves spread out in a rosette around the base of the plant; adults were "very local and only around the foodplant." He reared a series of adults from the larvae.

Shijimiaeoides divina flies in Japan and Korea and feeds as larvae on *Sophora* (Leguminosae) (Shields, 1974b). The species is likely *Sophora flavescens* Ait., a perennial herb with many pale greenish-yellow flowers that blooms in June and July (Ohwi, 1965). The other two *Sophora* species in Japan seem unlikely hosts: *S. franchetiana* is very rare on Kyushu and China, and *S. japonica* is a Chinese tree planted in Japan. *S. flavescens* is common on Honshu, Shikoku, and Kyushu, and ranges to Korea, China, and Siberia (Ohwi, 1965). Today, five species of *Sophora* inhabit the United States and Mexico, and 22 species are scattered through the warm parts of the world (Sargent, 1890: 59-60). Fossil *Sophora* date back to at least Paleocene times in North America (Lamotte, 1952).

ERIOGONUM AND THE COLORADO PLATEAU

The plant genus *Eriogonum* (Polygonaceae) is a large and complex group consisting of some 240 species. It occurs mainly in western North America from northern Mexico to Alaska, with species on the islands in the Gulf of California, in Baja California, and the islands off the coast of Baja and California to the west (Reveal, 1969a,b). At least one species, *E. tomentosum*, occurs along the eastern Coast Plain of the U.S., *E. longifolium* is found from Texas to Florida, and *E. allenii* in Virginia and West Virginia. References to *Eriogonum* species in South America are unfounded.

Most species occupy an arid or semiarid climate (Reveal, 1969b: 232). "*Eriogonum* typically occurs in micro-environments where water is more abundant than elsewhere over long periods of the season," such as road shoulders, washes, and open exposed slopes (Reveal, 1968). Since polyploidy is a sign of ancestry, *Eriogonum* probably originated early as Reveal notes (1969b) that "the vast majority of the modern species are tetraploids." *Eriogonum* species lack an active dispersal mechanism; the small seeds usually fall within a few meters of the parent plants (Reveal, 1969b: 233).

The most primitive *Eriogonum* subgenus, *Eucycla*, has about 14 sections and some 105 species (Reveal, pers. comm.). From a brief analysis of the first 10 sections (90 sp.), by far the greatest area of concentration is Utah with 21 species, mostly endemics. (According to Stebbins & Major, 1965, p. 27, floras in arid regions "are likely to be relatively stable, and most of the endemic species are ancient or at least not recent.") Two-thirds of these 21 species plus four that also range into western Colorado are located east of the major NE-SW Cordillera on or near the Colorado Plateau in Utah, thus a likely place of origin. Going away from Utah, the first 10 sections have species confined to other states but only 3-4 species each (in Arizona, Colorado, Nevada, Baja California, Oregon, except that California has ca. 8 species). The first 10 sections generally range over the western United States west of the continental divide, including island forms, and Baja California, Mexico. *S. rita* and *S. enoptes* subspecies are largely confined to *Eucycla*, as are about half of the *S. battoides* subspecies.

The Colorado Plateau is a great, high-standing crustal block, uplifted 5000 feet since the Eocene, nearly square and 500 miles on a side, whose center is close to the Four Corners area. By what process a block of the earth's crust the size of the Colorado Plateau is uplifted a mile is quite uncertain. The crustal thickness of the Plateau averages 45 km, greater than the average for the western United States, so it has probably thickened, giving rise to the uplift (Gilluly, 1963: 156-157). In eastern Utah, today a desert region, the Uinta Basin on the northern border of the Plateau has Eocene overlying Paleocene sediments, and Paleocene sediments along the Plateau's western border. However, the Plateau from the eastern and southern borders of Utah to the edge of these Early Tertiary sediments consists largely of thick Lower and Upper Triassic redbeds plus Upper Jurassic dune deposits formed in a vast desert, with Upper Cretaceous clastic wedges in some areas, overspread when the Plateau was near sea-level. Rocks of the stable crustal block have been flexed or folded, but gently and on a grand scale, apparently due to the Laramide Revolution, a time of mountain-building in the Rocky Mountain area from Late Cretaceous to Oligocene times. The Colorado Plateau is a region of plateaus, escarpments, and canyons laid out on a grand scale. The Colorado River apparently did not cut through it until the Late Tertiary and has denuded the Mesozoic-Tertiary sequence in the Grand Canyon. (Most of the above discussion was extracted from King, 1959). Perhaps the subgenus *Eucycla* in eastern Utah dates back to the Triassic-Jurassic desert.

Some authors (e.g., Hunt, 1946: 22-23; Gregory, 1938: 94; 1951: 94) reason that Cenozoic formations have been largely stripped away from the interior of the Colorado Plateau by erosional processes. Hunt (1956: 71) estimates that about 80 per cent of the Colorado Plateau has been eroded to formations below the middle of the Upper

Cretaceous, about 60 per cent is lower than the base of the Cretaceous, about 35 per cent is lower than the base of the Jurassic, and about 25 per cent is lower than the base of the Triassic. The total Cenozoic degradation on the Plateau averages about 10,000 feet (Hunt, 1956, p. 71), making the stripping of the Plateau lands a major event in the geologic history of North America (Gregory, 1951: 94). "That sediments and lavas of Tertiary age once covered all or part of this region [southeastern Utah] is suggested by their presence in adjoining regions--the Animas and Mancos Valleys of Colorado, the Chuska Mountains of New Mexico and Arizona, the Uinta Mountains and the High Plateaus of Utah" (Gregory, 1938: 63). Also, Cretaceous strata appear near the Henry and La Sal Mountains (Fisher, Erdmann, & Reeside, 1960). Gregory (1938) notes that today most rains of the San Juan country are short-lived, widely spaced, torrential downpours that run-off from bare rock and are thus affected by evaporation (dry air, and spring and summer high temperatures). The falling rain gathers at once into gullies and flows swiftly to larger drainage channels. Frost is an active agent. Average annual precipitation totals in the southeast Utah region are Hanksville (4200') = 5.41", Bluff (4200') = 6.26", and Kayenta = 8.86". Precipitation falls in the winter and July-September. Characteristic climatic features are the great range of diurnal temperature and the prevalence of clear skies. There are years of heavy rain and years of drought. A post-Eocene to Miocene (?) precanyon erosion cycle, as evidence by the "rock stairway" topography from the Grand Canyon to the High Plateaus of south Utah, is thought responsible for stripping away most of the Tertiary, much of the Mesozoic, and some of the Paleozoic on the Colorado Plateau (Gregory, 1951: 83). Hunt (1956: 71) states that the erosion rate of bedrock on the Colorado Plateau, as determined by sedimentation studies at Lake Mead from 1935-48, would take 21.5 million years to strip 10,000 feet of rock from the Plateau; degradation was dominant during about half of the Cenozoic.

However, a case could also be made for Cenozoic strata never being present over much of the Plateau, with Mesozoic strata eroded *in situ* during the Cenozoic. The rate of chemical and mechanical weathering is extremely slow in the desert because of the lack of moisture and takes place by sand-blasting (abrasion and deflation), cloudbursts, frosts, and wide temperature fluctuations, so soils do not form except for sand (Leet and Judson, 1965: 205-206). It thus appears incongruous that two miles of sediments in 21.5 million years could be eroded away in a region that in Mesozoic and Recent times was desert (and may also have been in the Cenozoic). Axelrod (1972) notes that tropics and deserts are existing side by side today in some regions and no doubt did so in the past. Why were the Paleocene-Eocene strata that are exposed on the northern and northwestern edges of the Colorado Plateau not eroded away as well? They are in closer proximity to the moist Wasatch and Uinta Mountains where streams and rivers flow and where rainfall is high. It would appear ironic that only Early Tertiary sediments *close* to the mountains are preserved when erosion was stripping most of the Colorado Plateau. Why are not the High Plateaus also denuded of their capping Tertiary sediments, especially since they receive higher rainfall amounts? Perhaps the Lower Jurassic and Lower Cretaceous sequences missing in eastern Utah were periods of degradation as is the Cenozoic degradation perhaps occurring on a desert, so that aggradation is not noted in these periods. I thus favor a view of desert conditions persisting in southeastern Utah from the Mesozoic to the present.

Axelrod (1970) reasons on the basis of some desert floral links between North and South America and from the fossil record that an archaic element was present in American deserts prior to Tertiary and Late Cretaceous times, as tropical forests and savannas had prevented any exchange between the Americas during the Cenozoic. Raven (1963) notes two *Chorizanthe* species and one *Oxytheca* (both close relatives of *Eriogonum*) with such a desert distribution today. Axelrod (1970) argues for angiosperm links between dry areas of the Southwest U.S. and Mediterranean being "the remnants of a dry flora that inhabited Gondwanaland prior to its breakup by ocean-floor spreading near the close of medial Cretaceous

time" (p. 309).

The North Atlantic probably began to form in the Upper Jurassic; this age is reported from the northwest coast of Africa and the coast of Spain (Ramsay, 1971, fig. 1). (For the fit of the continents around the Atlantic, see Bullard, Everett, & Smith, 1965). Likewise, the North Pacific's oldest seafloor age appears to be Upper Jurassic, at ca. 140 m.y. (Fischer, *et al.*, 1970; Dietz & Holden, 1971). A major expansion of the earth since Mesozoic times by seafloor spreading appears likely (Meservey, 1969). For the reasoning behind the expanding-earth hypothesis, see, *e.g.*, Egyed (1957), Carey (1958) and Holmes (1965, Ch. 27). The presence of genera related to *Shijimiaeoides* in eastern and western Asia suggests that this genus complex had evolved prior to continental separation in the Upper Jurassic.

It is customary to view the Lepidoptera as quite young (Cenozoic), based on their meager fossil record. However, Forbes (1932) cogently argues that the Lepidoptera arose in the late Carboniferous or early Permian with the first flowers, with butterflies (except Lycaenidae and Riodinidae) arising in the Jurassic with Papilionidae, and Hesperidae before that. Foodplants of some groups of primitive Lycaenidae include lichens, algae, cycads, conifers, etc. and suggest to me that their origin was early, in the late Paleozoic.

SUBSPECIES

During the past two decades, much debate has hotly centered around the worth of the subspecies concept. Even the validity of the species concept has been called into contention by some of the more outspoken numerical taxonomists in recent years. Perhaps the most sobering review of the subspecies "problem" is that of Tilden (1961), who sagely remarks that "defenders of the subspecies are more numerous among entomologists who work with the more plastic groups of insects." I must say that from my training, personal experience, discussions with fellow lepidopterists, and knowledge of the literature, I am strongly in favor of naming subspecies although drawing the line short of extreme splitting such as practiced by some European workers. I certainly do not hold with the negative attitudes of certain numerical taxonomists toward species and subspecies concepts, which if allowed to prevail unchecked would no doubt tear down the hierarchical superstructure of taxonomy. Numerical taxonomy can be used as an adjunct to classical taxonomy (see, *e.g.*, Dobzhansky, 1933; Lidicker, 1960), but hardly as a replacement.

Downey (1956) was faced with much the same problem that one faces with *Philotes* in dealing with the *Plebejus icarioides* complex, *i.e.*, a highly variable species to study and render more intelligible in evolutionary terms. His approach was to analyze the adult characters and run population comparisons both qualitatively and quantitatively, as he thought the variation too great for even subspecific ranking. The result was the characterizing of populations by the summation of qualitative and quantitative differences. He admits that the statistical differences in populations could not be used to approximate subspecific distinctions. Perhaps had he tried correlating the adult variation with *Lupinus* foodplant specificity, much of the complexities might have been resolved.

Bogert, *et al.* (1943) discuss the different criteria for subspecies in various vertebrates. In entomology the criteria for subspecies are usually not nearly as well defined as for the vertebrates, with interpretations often varying depending on the group (see Thorpe, 1930; Linsley, 1944; Remington, *et al.*, 1951). For the purposes of the present study, I have adopted Klots' (1936, p. 167) concept of "food-plant subspecies." In *Philotes*, there appear to me to be numerous distinguishable subspecies that are each specific to a particular species (or in some cases two or more species) of *Eriogonum*, although there are rare exceptions. This rule of thumb clears up almost all of the complex problems of variation in this group that the taxonomist is otherwise faced with.

Problems in naming clinal variation are discussed by Mayr, Linsley, & Usinger (1953), Hubbell (1954), Tilden (1961) and Cohn (1965: 9-10).

SIBLING SPECIES AND MIMICRY

Brown (1959, p. 80) defines sibling, or cryptic, species as reproductively isolated populations that lack obvious distinguishing characters, and reviews the taxonomic problems of closely related species. Sibling species (*i.e.*, those that fit these criteria) in *Philotes* are the *Shijimiaeoides rita*-*S. enoptes*-*S. divina*-*S. battoides* complex. Brown further states that sibling species are like other species except they are more difficult to segregate, especially when sympatric. In *Shijimiaeoides*, proper identification can readily be made by examining the genitalia in cases where the adult facies are nearly identical. Papers dealing with sibling species' examples in Lepidoptera are Corbet (1943), Rawson & Ziegler (1950), Klots & Clench (1952), Smith (1953, 1954), Remington (1953), dos Passos (1969), Cardé, Shapiro, & Clench (1970), Shapiro & Cardé (1970) and Heitzman & dos Passos (1974).

A recent review of the sibling species problem, with numerous examples, is that of Mayr (1966: 33-58, 460-461). He states (p. 57) that recent work in genetics has found much evidence for "a selective premium on the maintenance of the phenotype" in sibling species. This selective factor in *Philotes* presumably is a mimicry condition, with the *Plebejus acmon-lupini* complex the model, and *Shijimiaeoides rita*, *S. enoptes* and *S. battoides* the mimics. Here, *S. rita* does not greatly resemble in facies its immediate ancestor, *Z. speciosa*, which uses other genera as well as *Eriogonum*, but it does closely resemble *Plebejus acmon-lupini* (genitally and phylogenetically quite unrelated) and *rita*'s derived species, *S. enoptes* and *S. battoides*, both only on *Eriogonum*. Often two of the three species (*battoides*, *rita*, *enoptes*) are sympatric and synchronic. *S. rita spaldingi* is distinct from all the other *Philotes* and bears a strong resemblance to *Plebejus melissa* on the underside (Langston, 1969), and the two are often sympatric though using different foodplants. Striking resemblances also occur on the underside between *S. battoides intermedia* and *Plebejus lupini*, and *S. enoptes tildenii* and *Plebejus acmon*, which fly together on the same foodplant, respectively. Also, amazingly close in undersurface facies are *S. enoptes dammersi* and *S. rita rita* (both on *E. wrightii*) and *S. battoides glaucon* and *S. enoptes ancilla* (both on *E. umbellatum*), but in both cases the species are allopatric. This close resemblance I feel is due to a common origin, the former derived from the later in both cases. The selective effect of a nearly identical environment may be responsible for some similarities, rather than mimicry or common ancestry (see Hovanitz, 1941; Ali, 1969).

The original similarity to produce Müllerian mimicry arose by convergence, then continued similarity is maintained by parallel evolution (Brower & Brower, 1972: 64), as perhaps has occurred in the *Philotes* mimic tending toward a *Plebejus* model. Genera with somewhat similar facies to *Shijimiaeoides* but with wholly different genitalia are *Talicada nyseus* Guer. (India, Ceylon, Burma), *Chilades laius* Cr. (Indo-Oriental) and *Luthrodes* Druce (Indo-Australian). These genera also perhaps served as models in the distant past for *Philotes* to mimic and have since become extinct from the North American continent.

COEVOLUTION

According to Janzen (1968), "A species of plant is an island in evolutionary time to the insect species that feed on it." In *Eriogonum* with limited dispersal ability and *Philotes* with the whole life cycle (reproduction, adult nectar source, larval food requirements) of each subspecies usually confined to a particular *Eriogonum* species, the direction of evolution in *Philotes* should parallel the evolutionary development of the *Eriogonum* through time for those species it uses today (*i.e.*, after "jumps" have been recognized, from a perennial onto an annual most frequently). "Allochronic isolation on unrelated plants with different fruiting [or flowering] times" (Bush, 1969: 250) appears to have taken place from *S. enoptes dammersi* on *E. wrightii* (fall) to *enoptes mojave* on *E. pusillum* (spring). In other Lepidoptera that are not so host-specific, the evolutionary pattern would not be

nearly as discernable. For example, the moth *Panaxia dominula* L. uses many different plant genera in 15 families (Cook, 1961). Downey (1962) discusses the taxonomic usefulness of host-specific species.

HABITAT SELECTION

Thorpe (1945) regards geographical, topographical, and ecological isolation as three different scales of spatial isolation. He states, "Habitat change may lead to topographical isolation just as topographical isolation may lead to habitat change." As one example of how an initial separation or fission of a population might take place, Thorpe gives a host-plant preference in which the progeny become selectively adapted and isolated on the new host-plant. Hovanitz has shown, in a series of controversial experiments, that *Pieris* larvae reared on a variety of crucifers preferred to oviposit on the particular larval host they were reared on (see references in Shields, Emmel, & Breedlove, 1969). In *Philotes*, adaptation to a new host would be manifest as foodplant "jumps" evolutionarily, while in most cases a continuum of subspecies can be traced geographically which use phylogenetically related *Eriogonum* species, suggestive of an initial coevolutionary development, with *Philotes* entering a new geographic, topographic, or habitat niche as the *Eriogonum* did so. The resultant habitat isolation would then restrict gene flow and a new subspecies would develop.

COMPETITIVE EXCLUSION

In no instance in my experience with *Philotes* were two or more species using the same *Eriogonum* species at any given locality. Invariably where two species were sympatric and synchronic, each occupied its own particular *Eriogonum* species within the same habitat. However, in three instances, two *Philotes* occupied the same *Eriogonum* species allopatrically. These were: *S. enoptes ancilla* (east) and *S. battoides glaucon* (west) on *E. umbellatum*, *E. wrightii* with *rita rita* (east) and *enoptes dammersi* (west), and *enoptes smithi* (north) and *battoides allyni* (south) on *E. parvifolium*. In the first case they come at least to within 30 air miles of each other in extreme western Nevada, in the second case at least to within 5-10 miles in the vicinity of Cherry and Hillside, Yavapai Co., Arizona, and in the third instance to within 50 miles.

This sort of host-use pattern sketched above strongly suggests that competitive displacement or exclusion is taking place or has often already occurred. If otherwise, at least some instances of sympatric-synchronic coexistence on the same *Eriogonum* host by two or more species would be expected, as in fact exists between certain *Philotes* populations and *Apodemia mormo* (for foodplants, see Opler & Powell, 1961), *Plebejus acmon* and *P. lupini* (for foodplants, see Goodpasture, 1974). For a thorough review of the competitive displacement or exclusion concept, see Hardin (1960), De Bach & Sundby (1963) and De Bach (1966). According to De Bach (1966: 191), "Most cases of competitive displacement in nature have already gone to completion."

"PHILOTES" BEHAVIOR

According to Langston (1963), the appearance of *Philotes* adults is correlated with the early full-bloom of the *Eriogonum*. However, in my experience with *S. rita pallescens* at two Nevada localities that a good flush of fresh adults occurs when plants of *E. kearneyi* are just coming into bloom, and most of the plants are still in bud. *Philotes* adults seem most common when their *Eriogonum* host is just coming into bloom to full bloom. By the time the *Eriogonum* plants mostly reach the full bloom stage, many of the *Philotes* are worn. Adults are scarce or lacking by the time the plants are in past bloom condition. Larvae feed on the flowers. Pupae have been found in sand at the base of *Eriogonum* in one *battoides*, one

rita, and one *enoptes* colony. Each *Philotes* subspecies' life cycle from emergence to pupation is synchronous with that *Eriogonum*'s blooming period (Tilden, 1959: 261). When precipitation was recently rather great or abundant, it triggers the *Eriogonum* to bloom and perhaps initiates the *Philotes* emergence as well (Reveal, *in litt.*).

"The termination of diapause in response to environmental stimuli synchronizes the appearance of reproductive forms at a favorable season" (Harvey, 1962). In *Philotes*, the synchrony is with the blooming time of the host *Eriogonum*, different for each species. Stimuli producing the onset of diapause include photoperiod, temperature, and water, principally photoperiod (Harvey, 1962). Diapause may be induced in any developmental stage, and all stages except the pupa may be receptive to photoperiod (de Wilde, 1962). There is photoperiodism in plants, and in one case with subterranean aphids living at $\frac{1}{2}$ to 2 m in the soil, photoperiod induction of sexual forms was from a "signalling" action via the foodplant (De Wilde, 1962). A similar case has been reported for larvae of the Cabbage-root fly, *Hylemyia brassicae* (Danilevskii, 1965: 80-81). Perhaps a similar situation exists between the *Eriogonum* plant and *Philotes* pupae beneath it in the soil. Cessation of diapause might be caused by hot temperatures following a rainy period, or may also be triggered by some signalling action of the plant such as chemical changes.

Philotes ovipositing females ranged from every hour between 8:30-3:30 (PST & MST, N = 36), with ca. 75% occurring in the morning. Females oviposited mainly on unopened buds and inside flowers, frequently on the inside of the sepals, after much abdominal probing, walking over the flowers, and turning around on flowerheads. Nearly all day long, adults fly around, feed on, and alight to rest on the *Eriogonum* flowers. They fly from plant to plant in a rapid, erratic manner over the blooms. *S. rita emmeli* starts flying at 7:00-8:00 AM and seeks roosting sites around 6:00 PM MST in southeastern Utah. Adults frequently roost on the *Eriogonum* blooms for the night but also on other shrubs (Shields, 1973). Males and occasionally females will come to moisture but do not seem to form mud-puddle "clubs". Occasionally adults are to be found feeding on other flowers (including other *Eriogonum* species, two yellow-flowered composite species, yarrow, aster, a white-flowered crucifer, and *Calyptridium* sp.) especially when their host *Eriogonum* is scarce that year or in past bloom, but this is rather exceptional. The flower colors of the *Eriogonum* species used for foodplants (as well as for nectar sources) include yellow (many)-cream-white (many)-pink-rose. Adults are often common and could play a sizable role in *Eriogonum* pollination in some areas, along with certain other butterflies, Hymenoptera, and some Diptera. Mating apparently takes place on the *Eriogonum* plant; *in copula* pairs were noted at this site at least from 9:00-4:30 (PST & MST), mostly from ca. 10:30-2:30 (N = 42) (Shields & Emmel, 1973). Not uncommonly the female of an *in copula* pair is worn, indicative perhaps of the occurrence of multiple-matings.

ABERRATIONS AND SEX RATIO

Various aberrants are met with not uncommonly in "*Philotes*" (est. less than 1 per cent). These include macules fused or absent, macules present on one side and lacking on the other, wing-shape asymmetry, an occasional striking melanic or "blond" phase, an extension of the aurora in one cell toward the wing base, dwarfs and giants. Individual variation within a given "*Philotes*" population and variation within the range of a given subspecies are often considerable, especially on the undersurface (*e.g. pallescens, glaucon, bernardino*).

During this study one gynandromorph was discovered, an *S. enoptes ancilla* from Sybille Canyon, 6500', Albany Co., Wyoming, 4 July 1966 (R. Hardesty). The specimen is mostly a female with a strip of male blue in a narrow band on the right hindwing upperside only, from the base to the margin, *not* present on the underside. The wings otherwise are uniform brown except for the aurora.

A total of 51 males and 50 females of *S. rita pallescens* emerged over a month's period under uncontrolled lab conditions (from 6:00-8:00 AM PST), from pupae collected at Sand Mountain, Churchill Co., Nevada, by E. M. Perkins and myself in early July, 1974. Similarly, 6 males and 7 females of *S. battoides allyni* emerged from pupae (from ca. 10:00 AM-1:00 PM PST) collected at El Segundo, California, by Perkins. These data help confirm field records of a probable 1:1 sex ratio in *Shijimiaeoides*.

TAXONOMY AND NEW SUBSPECIES

In this section, seven new subspecies are described. Two of these (*battoides allyni* and *b. comstocki*) had been recognized by other workers (unpublished) as distinct, while the remainder were either classed as known subspecies previously or were discovered as new during the course of this survey. At least two other new subspecies will be described in a future paper. The taxonomy of the parent species *battoides*, *rita*, and *enoptes* is discussed, as well as *spaldingi* and *mojave*. Taxonomic notes and biological and distributional data for the other known subspecies of *Philotes* will appear in a future paper.

Shijimiaeoides battoides battoides (Behr), 1867

Behr. 1867. Proc. Calif. Acad. Nat. Sci. 1863-1867, 3: 282; no. 15.

Behr states, "This species was collected at an elevation of eleven thousand feet, on the head-waters of the San Joaquin River, by the Geological Survey." At this elevation in the Sierras, only *S. battoides battoides* and occasionally *S. enoptes enoptes* fly, the former much more abundantly. The description in Latin refers to quadrangular black spots on the underside, the characteristic square-spotting of what today is referred to as *S. battoides battoides*. Further, McDunnough (1914) notes that Behr very aptly compared it with the European *battus* (= *Scolitantides orion* Pallas). Without more to go on, the type locality must lie between Yosemite National Park and Kings Canyon Nat'l Park, Madera and Fresno Co., at 11,000', where it flies abundantly at this elevation. Skinner (1911) presumed that the type was destroyed in the 1906 San Francisco earthquake and fire. Williams (1918) notes that a specimen in the Henry Edwards collection labelled "Lone Mountain, Lake Tahoe" is marked "True to type" [of *battoides*] by Edwards, and agrees with *battoides* figured by Barnes & McDunnough "except that it is not quite so strongly marked below." Barnes & McDunnough (1916) falsely give the type locality as "The headwaters of the Tuolumne River", and so corrected it in 1917. Langston (1969) states the type locality to be "Mineral King, Tulare Co.," surely another error, as this lies two major river drainages to the south of the San Joaquin River. Finally, Skinner (1911) erroneously gives "headwaters of San Joaquin Valley, Calif."

Shijimiaeoides battoides allyni, new subspecies

Figures 1-4

Male: Holotype forewing, 10 mm. UPPER SURFACE, Primaries: light blue with slight violet tinge; marginal band wide, 1 mm, scalloped appearance (black partway along outer veins); fringes white to dark; broad fuscous checkered at vein ends.

Secondaries: marginal band variable, often broken into distinct interneural spots; fringes white with little or no checkering at vein tips; aurora often prominently light orange at CU_1 and CU_2 cells, faint in some; wing margin frequently concave at CU_1 and CU_2 .

UNDER SURFACE, Primaries: ground whitish cream; bold terminal line;

macules heavily marked and square; praeterminal mark at R_4 faint or absent.

Secondaries: terminal line as primaries; aurora orange-brown, in continuous band, usually 1 mm broad; macules bold with haloes; ground color cream, becoming suffused-black basally.

Female: Allotype forewing, 10 mm. UPPER SURFACE, Primaries: ground dark brown; fringes as ♂; discoidal macule faint or distinct.

Secondaries: aurora usually broad band from M_1 to $2A$, solid to terminal line; concave wing margin at CU_1 and CU_2 .

UNDER SURFACE, Primaries: as in ♂. Aurora faint along semimacule band or lacking.

Secondaries as in ♂.

HOLOTYPE ♂: CALIFORNIA: Los Angeles Co., El Segundo, VII-9-65 (R. E. Stanford).

ALLOTYPE ♀: same.

PARATYPES: same, 5♂ 6♀. Also, El Segundo, VII-30-72 (J. F. Emmel), 38♂ 31♀.

Disposition of type material: Holotype and allotype (AM), paratypes (KH, LACM).

Two males, Cedros Island, Mexico, III-18-39 (CIS) also fit this description although with black markings slightly more pronounced; Rindge (1948) noted that they were probably a new, undescribed subspecies.

DISTRIBUTION (viewed 8♂ gen. from 4 localities): CALIFORNIA: *Los Angeles Co.*: El Segundo, 4♂, vii (CAS, PO, KH); El Segundo dunes, 10♂ 1♀, vii, ix (LACM, YU); El Segundo sand dunes, L. A. Airport, 20♂ 20♀, viii (AM, LACM, CIS); "N. Manhattan Beach", 2♂, vii (LACM); Palos Verdes Estates, 1♀, ix (AM); Redondo Beach, 1♂, vii (CIS).

HOST: *Eriogonum parvifolium* Sm. in Rees var. *parvifolium* (Shields #56), several adults reared from larvae collected on this plant, IX-8-69, El Segundo, by J. F. Emmel (AM).

Subspecies *allyni* is on wing from early July to late September.

Occasionally a female within a *battoides bernardino* population appears indistinguishable from *b. allyni*, as, e.g., La Mesa, San Diego Co., v (LACM), and Cushenbury Springs., 5600', San Bernardino Mts., San Bernardino Co., iv (YU). Also one female from Olancho, Inyo Co., x (CAS) appears to be *b. allyni*, although *E. parvifolium* does not occur there.

The closest known relative of *battoides allyni* appears to be *b. bernardino*, approaching *allyni* in size, coloration, overall appearance (though spots much reduced by comparison), sympatry, and closely related foodplant. *S. b. allyni* seems unrelated to *S. battoides battoides*, a subspecies also quite heavily marked on the undersurface.

I take pleasure in naming this distinct subspecies for Arthur C. Allyn, whose generous support has made this project possible.

Eriogonum parvifolium var. *parvifolium* occupies beaches and bluffs or dunes along the coast, from Monterey Co. to San Diego Co., flowering from June to October (Reveal, 1969a). John Emmel and I checked this species on 18 Sept. 1968 at Solano Beach, San Diego Co. (J. F. Emmel #145) without success. Reveal (1969a and in litt.) lists *Eriogonum molle* Greene, *E. fasciculatum* Benth. var. *fasciculatum*, *E. pondii* Greene, *E. wrightii* Torr. ex Benth. in DC. var. *taxifolium* (Greene) Parish, and *E. intricatum* Benth. for Cedros Island. Likely, *E. molle* serves as the host there for *battoides* nr. *allyni* since it is in the same section of *Eriogonum* (*Fasciculata*) as *parvifolium*, though *E. pondii* cannot be ruled out because it resides in the adjacent section (*Ectenomorpha*). Both sections are in the subgenus *Eucycla*. *E. parvifolium* is not known from the island. (It could be on *E. fasciculatum* too, since *battoides bernardino* uses it).

Shijimiaeoides battoides comstocki, new subspecies

Figures 5-8

Male: Holotype forewing, 12 mm. UPPER SURFACE, Primaries: light sky blue (about shade of *bernardino*); terminal band 1 mm wide, only slightly invading veins; checkering broad, alternating with fuscous scales.

Secondaries: marginal fringe usually continuously white, some with mild checkering at vein tips; 5 praeterterminal marks distinct or partially fused to terminal line; margin of Cu_1 and Cu_2 just slightly concave.

UNDER SURFACE, Primaries: ground with distinct yellowish-white cast in fresh specimens; whole under surface has appearance of *enoptes enoptes* from Sierras; macules distinct and rather small.

Secondaries: small first $\frac{1}{2}$ scales of marginal fringe are white underside and black upperside (except at vein ends on underside); aurora from M_1 to Cu_2 (sometimes tinge on Rs) and broken into distinct, small crescent-shaped spots; aurora light orange-brown or yellow-orange.

Female: Allotype forewing, $11\frac{1}{2}$ mm. UPPER SURFACE, Primaries: aurora band sometimes prominent or trace, rarely absent; fringe checkering and color as in ♂; medium brown ground color; discoidal spot faint or somewhat distinct.

Secondaries: praeterterminal macules distinct and form base of a continuous auroral band from M_1 to Cu_2 , 2 mm wide. Aurora to terminal band, or that space filled with brown; sometimes blue scaling light basally on wing.

UNDER SURFACE, Primaries: as in ♂ except auroral band often present.

Secondaries as in ♂.

HOLOTYPE ♂: CALIFORNIA: Kern Co., Tehachapi, VII-22-18 (J. A. Comstock).

ALLOTYPE ♀: same.

PARATYPES: same, 18♂ 27♀.

Disposition of type material: Holotype, allotype, and paratypes (LACM, some paratypes at CAS).

Genitalia of three of the paratype males were determined. The upper and underside and wing shape of both sexes superficially resemble *enoptes* nr. *enoptes* from Blackburn Cyn., Tehachapi Mts., Kern Co., Calif., VII-10-64 (N. La Due). Known only from the type locality and one ♂ from Park City, Summit Co., Utah, VII-2-'95 (CM); host *Eriogonum* unknown. Also at Tehachapi in July flies *battoides bernardino* (1♂, CM).

The closest relative of *b. comstocki* is perhaps *battoides intermedia*. It resembles *comstocki* on the underside but lacks the aurora on the undersurface of the primaries, and male *intermedia* have a much broader black band on the upperside.

Shijimiaeoides battoides ellisii, new subspecies

Figures 9-12

Male: Holotype forewing, 12 mm. UPPER SURFACE, Primaries: iridescent blue cyanic overlay; marginal band medium width, $\frac{3}{4}$ mm wide; fringes white; fuscous checkered at vein ends.

Secondaries: marginal band variable, often broken into distinct interneural spots (= praeterterminal marks showing through), sometimes solid band or nearly so; fringes white with fuscous checkering; aurora faint or pronounced orange spots in most, lacking in some.

UNDER SURFACE, Primaries: ground whitish gray; bold terminal line; macules heavily marked; smoky suffusion toward lower half.

Secondaries: terminal line as primaries; aurora orange, variable from continuous band to nearly dissociated spots, usually broad, 1 mm wide.

Female: Allotype forewing, 12 mm. UPPER SURFACE, Primaries: ground

brown, usually dark or blackish; fringes as ♂; discoidal macule generally definable from ground.

Secondaries: aurora usually broad and pronounced, from light to dark orange, in extent from Cu_2 to M_2 , solid appearance, to the praeterterminal marks.

UNDER SURFACE, Primaries: as in ♂; aurora occasionally present.

Secondaries: as in ♂.

HOLOTYPE ♂: COLORADO: Mesa Co., W. Creek, Unaweep Canyon, 5400', 6 mi. E. of Gateway, VIII-25-67 (S. L. Ellis).

ALLOTYPE ♀: same locality, IX-3-65 (S. L. Ellis).

Disposition of type material: (AM).

DISTRIBUTION (viewed 49♂ gen. from 25 localities): ARIZONA: *Coconino Co.*: 7-8 rd. mi. ESE of jct. of Hwy. 389 & 89A, 5000', ESE Fredonia, "40", viii (AM), Moenkopi formation (Lower Triassic); Hwy. 89A, 8 rd. mi. ESE Fredonia, 30♂ 20♀, viii (KR). COLORADO: *Mesa Co.*: Unaweep Cyn., West Creek, 5400-6000', "common", viii, ix (AM, SE, MF). UTAH: *Grand Co.*: Courthouse Wash, 4 rd. mi. NW Moab, 1♂, viii (AM), Navajo sandstone (Jurassic?). *Kane Co.*: 5 rd. mi. W. Paria River crossing U.S. 89, on U.S. 89, Fivemile Valley, 5000', 2♂, ix (AM). *San Juan Co.*: 1 mi. E Indian Creek State Park, 1♂, viii (AM); 11 rd. mi. NNW Mexican Hat, base of Cedar Mesa, along Hwy. 261, "19", ix (AM), Cedar Mesa sandstone (Permian); 14 rd. mi. SW Mexican Hat, 5400', 2♂ 5♀, ix (AM); Monument Valley, 1♂, viii (KT), Cutler formation (Permian); 8 rd. mi. W of jct. of State Hwys. 95 & 47, on road to Natural Bridges Nat'l Mon., 2♂, ix (AM), Morrison formation (Upper Jurassic); Rainbow Bridge Canyon, Ariz.-Utah line, 1♂, ix (DB), Navajo sandstone (Jurassic?). *Uintah Co.*: jct. of North Willow Creek turnoff & Ouray-Rainbow Rd., ca. 30 mi. SE Ouray, 1♂, viii (AM); Willow Creek, 3♂ 7♀, ix (AM). *Washington Co.*: ½ mi. W West Entrance to Zion Nat'l Park, 1♂, ix (AM), Moenkopi formation (Lower Triassic).

HOSTS AND DISTRIBUTION: *Eriogonum corymbosum* Benth. in DC var. *corymbosum*. ARIZONA: *Coconino Co.*: 7 rd. mi. SE Fredonia, 5000', "73", viii (AM), adult assoc. (*Shields* #49). UTAH: *Duchesne Co.*: 10 rd. mi. S of jct. Hwys. 53 & 216, along Hwy. 53, "45", viii (AM), adult assoc. (*Shields* #22). *Kane Co.*: 1 mi. E. Glendale on rd. to Fourmile Hollow, 6200', "38", viii, ix (AM), adult assoc. (*Shields* #46) Upper Jurassic; 1½ rd. mi. NNW Kanab, 5000', 2♂, viii (AM), adult assoc. (*Shields* #48) Chinle formation (Upper Triassic). *Uintah Co.*: ½ mi. S Bonanza, along Hwy. 45, 6♀, viii (AM), adult assoc. (*Shields* #17); 1 mi. S North Willow Creek turnoff from Ouray-Rainbow Rd., ca. 31 mi. SE Ouray, "5", viii (AM), adult assoc. (*Shields* #20); along Ouray-Rainbow Rd., 18 rd. mi. SW of jct. of 207 & 45, 1♀, viii (AM), adult assoc. (*Shields* #19); along Utah State Hwy. 207, 10 rd. mi. SSE Bonanza, 2♂, viii (AM), adult assoc. (*Shields* #18). *Eriogonum corymbosum* Benth. in DC. var. *glutinosum* (M. E. Jones) M. E. Jones. ARIZONA: *Coconino Co.*: 9.5 rd. mi. NE Winona, on Hwy. to Leupp, "37", ix (AM), oviposition (*Shields* #161); 3.7 rd. mi. S of turnoff to Wupatki Nat'l Mon., along Hwy. 89, "14", ix (AM), adult assoc. (*Shields* #163). *Navajo Co.*: 2.5-3.0 rd. mi. SE Joseph City, along Hwy. 40, 1♂ 1♀, viii (AM), adult assoc. (*Shields* #159). *Eriogonum corymbosum* Benth. in DC. var. *orbiculatum* (S. Stokes) Reveal & Brotherson. UTAH: *Grand Co.*: 1.5 rd. mi. SE of jct. of Hwy. 128 & rd. to Castleton, along rd. to Castleton, "5", ix (AM), adult assoc. (*Shields* #171); 12.5 rd. mi. NE of jct. of Hwy. 128 & rd. to Castleton, along Hwy. 128, "2", ix (AM), adult assoc. (*Shields* #172); 12 rd. mi. W and S of jct. of rd. to Dead Horse Point State Park & U.S. Hwy. 160, 2♂, viii (AM), adult assoc. (*Shields* #25); 14.8 rd. mi. NE of jct. 163 & 128, along Hwy. 128, 1♀, ix (AM), adult assoc. (*Shields* #170). *San Juan Co.*: 10 rd. mi. S of Blanding, "4", viii (AM), adult assoc. (*Shields* #32), Dakota (?) sandstone (Upper Cretaceous); 13 rd. mi. SW of jct. of road to Canyonlands Nat'l Park (via Indian Creek State Park) & U.S. Hwy. 160, "4", viii (AM), adult assoc. (*Shields* #30); Grandview Point, Canyonlands Nat'l Park, "3", viii (AM), adult assoc. (*Shields* #27); 12 rd. mi. N Mexican Hat, along Hwy. 261 at base of canyon, N end Cedar Mesa, 5200', 2♂ 2♀, ix (AM), oviposition (*Shields* #36; *J. F. Emmel* #139), Cedar Mesa sandstone (Permian); 10 rd. mi.

NW of jct. Hwy. 95 & Natural Bridges Nat'l Mon. turnoff, "4", viii (AM), adult assoc. (*Shields* #37), Cedar Mesa sandstone; 19 rd. mi. NW of jct. of Hwy. 95 & Natural Bridges Nat'l Mon. turnoff, 2♂, viii (AM), adult assoc. (*Shields* #38), Cedar Mesa sandstone; 14 rd. mi. WNW of rd. to Needles Overlook & U.S. Hwy. 160, "2", viii (AM), adult assoc. (*Shields* #29). *Eriogonum corymbosum* Benth. in DC. var. *velutinum* Reveal. ARIZONA: Navajo Co.: 7.7 to 8.1 rd. mi. ENE of Kayenta (from jct. Hwy. 464 & 164), just SE of Church Rock, "32", ix (AM), adult assoc. (*Shields* #164), Chinle formation (Late Triassic). *Eriogonum batemanii* M. E. Jones. UTAH: Uintah Co.: Ouray-Rainbow Rd., 22 rd. mi. SE Ouray, "12", viii (AM), oviposition (*Shields* #21). See Maps 1 and 2.

Subspecies *ellisii* flies from mid August to early September (Fig. 29)

S. battoides ellisu is a distinctive subspecies, although populations in the vicinity of Flagstaff and Joseph City, Arizona, approach *b. centralis* from northern New Mexico on the undersurface somewhat. The width of the aurora is highly variable in *ellisii*, sometimes as narrow as in *battoides intermedia*, sometimes as broad as in *battoides martini* (the latter appear very much like *martini* though are larger). Specimens of a rare fall-flying, small *battoides* ssp. from the Clark and Providence Mts. of eastern California appear somewhat similar to *ellisii* (see Emmel & Emmel, 1973, pl. 8, fig. 7), and occur on varieties of *E. heermannii*, while another population in central Nevada on a different variety of *E. heermannii* in June (to be discussed in a later paper) appear closer to *bernardino* than to the Mojave fall form. Near Church Rock, Navajo Co., Arizona, *b. ellisii* and *rita emmeli* occur together. Here, the adults are associated with their proper *Eriogonum* species even when roosting; i.e., in pure stands of each *Eriogonum*, only the proper *Philotes* sp. flew, and where there was a mixed stand, both flew over their respective *Eriogonum*.

This subspecies is named for my good friend Scott L. Ellis, who initially discovered it.

Reveal (1967) gives extensive locality records for *Eriogonum corymbosum* varieties *corymbosum*, *glutinosum*, *orbiculatum*, and *velutinum*. According to Reveal at present, *E. corymbosum* contains six varieties, distributed from southwestern Wyoming southward through eastern and southern Utah and adjacent western Colorado into northern Arizona and northwestern and central New Mexico, flowering from July to October (Reveal, 1969a). John Emmel and I found no *S. battoides ellisii* in late August 1969 on *E. corymbosum* var. *erectum* Reveal & Brotherson, *E. c. var. davidsei* Reveal, *E. duchesense* Reveal (*Shields* #15), *E. lancifolium* Reveal & Brotherson, and *E. saurinum* Reveal, all in the *E. corymbosum* complex, in eastern Utah, and none on *E. c. var. glutinosum* near Cedar City and Shivwits, Utah, although this was used in northern Arizona. Also, Ellis, Toliver, and I found none at the type locality of *E. c. var. velutinum* near San Antonio, New Mexico, on 21 August 1970.

Eriogonum batemanii occurs in northeastern Utah and adjacent northwestern Colorado, flowering from June to September (Reveal, 1969a).

Shijimiaeoides battoides, new unnamed subspecies

On July 29, 1969, John Emmel and I found 8 mature larvae of *Philotes* feeding on the flowers of *Eriogonum shockleyi* S. Wats. var. *shockleyi* (J. F. Emmel #199) on sand dunes 1 air mile south of Blind Spring, 5800', southeast end of Baking Powder Flat, west of Snake Range, T11N, R67E, White Pine Co., Nevada. All the larvae were unusually small when they pupated. All the pupae subsequently died, but one that had matured inside the pupa was dissected out and genitally determined as *battoides*. I feel that collecting in the last two weeks of June at this locality should disclose the presence of a new subspecies.

Eriogonum shockleyi var. *shockleyi* occurs from eastern California to western Utah and northward to southeastern Idaho, flowering from May to July (Reveal, 1969a).

Shijimiaeoides battoides baueri, new subspecies

Figures 13-16

Male: Holotype forewing, 11 mm. UPPER SURFACE, Primaries: light sky blue cyanic overlay; marginal band medium width, $\frac{1}{2}$ mm wide; fringes white; fuscous checkering at vein ends at M_3 , Cu_1 , Cu_2 , and 2A only (sometimes others); black scales from marginal band diffusing out into blue ground slightly, forming patchy spots between veins (= praeterterminal mark on upper side).

Secondaries: marginal band as in upper surface; small black dots at praeterterminal marks distinctly detached from marginal band and somewhat diffuse; fringes white with fuscous checkering; no aurora showing through.

UNDER SURFACE, Primaries: ground pale whitish (snowy white), bold terminal line, $\frac{1}{2}$ mm wide; smoky suffusion from Cu_2 to 2A; macules moderately marked.

Secondaries: terminal line as primaries; aurora light orange, band thin (lacking any orange spot in cell 2A), aurora $2/3$ mm wide.

Female: Allotype forewing, 11 mm. UPPER SURFACE, Primaries: ground color light sky blue with terminal band very broad, sometimes extending nearly to discoidal macule; discoidal macule distinct to absent; black suffusion over blue heavily along veins, lighter between veins.

Secondaries: aurora in medium width band to small spots or absent; praeterterminal marks prominent; aurora not extending to terminal line; blue ground color extensive or blackened in toward Sc and Rs; distinct whitish blue narrow band between praeterterminal marks and terminal line.

UNDER SURFACE, Primaries as in ♂.

Secondaries as in ♂.

HOLOTYPE ♂: CALIFORNIA: Inyo Co., W side Gilbert Pass, 6200', V-23-67 (D. L. Bauer).

ALLOTYPE ♀: same.

PARATYPES: same, 6♂ 9♀.

Disposition of type material: Holotype and allotype (AM), paratypes (DB).

DISTRIBUTION (viewed 12♂ gen. from 8 localities): CALIFORNIA: *Inyo Co.*: pass 4-5 mi. ENE Deep Springs, 1♂, v (DB); Waucoba Cyn., 6000', 16 mi. SE Saline Valley Jct., 1♂, v (GG); Westgard Pass, 2♀, v (UCD). NEVADA: *Churchill Co.*: Buffalo Canyon, Desatoya Mts., 5♂ 2♀, v (NSM); Buffalo Cyn., 5500', 12 mi. S. of Eastgate on road to Ione, W. of O'Donnell Summit, 24♂, v (CAS). *Clark Co.*: Arrow Canyon Range, 1♂ 1♀, v (NSM). *Douglas Co.*: Pine Nut Mts., E. side, 3♂ 1♀, v (AM). *Esmeralda Co.*: 5 mi. S Tonopah, 5500', 1♂, v (DB). *Humboldt Co.*: Winnemucca, 5♂ 3♀, v (CAS, CIS); 10 mi. N. Winnemucca, 2♂, v (CIS). *Lander Co.*: 4.0 road mi. E Carroll Summit, 6700', 1♂, vi (AM). *Lincoln Co.*: Oak Springs, Delamar Range, 4♂ 3♀, v (NSM). *Ormsby Co.*: Clear Creek Cyn., 5 mi. SW Carson City, 1♂, v (PO).

HOSTS AND DISTRIBUTION: *Eriogonum ovalifolium* Nutt. var. *ovalifolium*. CALIFORNIA: *Inyo Co.*: ca. 2 rd. mi. NE Westgard Pass, 7000', 2♂, v (AM), adult assoc. (*Shields* #76), growing mixed in with the abundant *E. caespitosum* Nutt. (*Shields* #77) that was not used. *Eriogonum ovalifolium* Nutt. var. *multiscapum* Gand. NEVADA: *Humboldt Co.*: 10 rd. mi. N Winnemucca, on Hwy. 95, sand dunes area between hwy. & Little Humboldt River, 4350-4450', "few", v (AM), adult assoc. (*J. F. Emmel* #286). Subspecies *baueri* is in flight in May (Fig. 30).

At Westgard Pass near the type locality of *b. baueri*, a distinctive subspecies of *battoides* (near *glaucon*, to be described later, on *E. umbellatum*) flies a month later and appears quite different. However, at the Buffalo Canyon and vicinity of Winnemucca localities, *b. baueri* closely approaches the subspecies *glaucon*, and at Steamboat Hot Spgs., 5 rd. mi. N jct. of Hwy. 3B & 395, on Hwy. 395 SE of Reno, Washoe Co., Nev., VI-19-71, 1♂ *battoides glaucon* was on *Eriogonum ovalifolium* Nutt. var. *nivale* (Canby) M. E. Jones (*Shields* #196) at an alkali spring.

This subspecies is named for David L. Bauer, its original discoverer.

Eriogonum ovalifolium var. *ovalifolium* occupies dry slopes and flats, mostly 5000-7000', east slope Sierra Nevada of California, n. and e. to Alberta, Rocky Mts.; blooms from May to July. Richard Funk and Kilian Roever took a short series of *S. battoides* ssp. (gen. det.) on *E. ovalifolium* Nutt. var. *ovalifolium* (det. by W. B. McDougall and Reveal, *Funk #160*, deposited at the Museum of Northern Arizona, Flagstaff), on V-18-68, Hwy. 89A, 8 road mi. ESE Fredonia, Coconino Co., Arizona. The phenotype is not very similar to *b. baueri* and probably deserves a name. This most intriguing population appears to be not closely related at all to *b. ellisii* and *E. corymbosum* var. *corymbosum* that flies at the same locality some three months later.

***Shijimiaeoides rita rita* (Barnes & McDunnough), 1916**

Barnes & McDunnough. 1916. *Canad. Ent.*, 48: 223-224.

From their type description and the paratype illustration in Barnes & McDunnough, 1916, pl. XI, figs. 3 & 6, there is no question that this is what is currently called *rita rita* from southern Arizona. *S. enoptes dammersi*, with which it might easily have been confused, is not known to enter southern Arizona, and their illustration (1917, pl. 17, figs. 5 & 7) of *rita*'s genitalia clearly establishes it as such (see also Mattoni, 1965: 86). The type locality in the original description reads, "Types-Three ♂'s, S. Arizona (Poling); one ♂, Santa Rita Mts., Ariz.; one ♂, Rio Verde Mts., Ariz.; three ♀'s, S. Arizona (Poling) in Coll. Barnes." Thus the determination of an exact type locality becomes problematical, unless it is assumed that the first mention ("S. Arizona (Poling)") was their intention. If so, Comstock (1953) sheds light on a precise location: "Mr. [Lloyd] Martin has concluded, from a study of various records and dates on material collected by Poling, that the 'S. Arizona' series were taken in the Huachuca Mountains near Ramsay [*sic*] Canyon." Comstock, Martin, Ford, and Thorne subsequently found *rita rita* at the foot of Ramsay [*sic*] Canyon in abundance (700 taken!) on IX-1-53, acting on this hunch. I have determined the genitalia of 17 ♂♂ from this series as *rita rita*. Unless evidence to the contrary eventually emerges, the type locality is hereby designated as near Ramsey Canyon, Huachuca Mts., Cochise Co., Arizona. As noted by Clench (1967), the Rio Verde Mts. are located northeast of Phoenix, based on two Barnes' specimens, and are not synonymous with the Huachuca Mts. as Mattoni (1965: 86) surmised.

***Shijimiaeoides rita emmeli*, new subspecies**

Figures 17-20

Male: Holotype forewing, 11 mm. UPPER SURFACE, Primaries: light blue-lavender (*i.e.* light purplish blue cyanic overlay); terminal fuscous band ½ mm wide; fringes broad, white, with row of black scales at base, black checkering at Cu₂ and 2A vein ends (not pronounced); some black scales along extremities of veins and scattered in cells lightly.

Secondaries: terminal band broad in outer ½ of Sc, outer 1/3 (or less) of Rs, ½ mm wide in M₁ and M₂, becoming distinct spots (praeterterminal marks) in M₃, Cu₁, Cu₂, with light band between these spots and terminal band (sometimes faint or absent); pink aurora usually prominent, from M₃ to Cu₂ or only Cu₁ and Cu₂; outer quarter of veins darkly scaled; wing margin of Cu₂ slightly concave.

UNDER SURFACE, Primaries: ground dull pearly white to gray-white; thin terminal line; semimacules and praeterterminal marks somewhat diffuse, other macules distinct; macules with haloes.

Secondaries: aurora light gold-orange or yellow-orange, prominent band 1 mm wide; extending from M₁ to 1A, occasionally auroral spot in 2A; macules not quite as bold as in *coloradensis*; prominent haloes.

(Male differs from *coloradensis* in smaller size, lighter blue color, less width of terminal band, less pronounced underside macules, and lacking slight melanic suffusion of underside primaries.)

Female: Allotype forewing, 10½ mm. UPPER SURFACE, Primaries: ground color medium brown (usually lighter than *coloradensis*), slightly lighter in basal 1/3 with faint blue-gray scaling; fringe as in ♂; brown color is yellowish (= "orange-green") at ca. 45° to light (same in *coloradensis*); discoidal macule distinct.

Secondaries: pronounced orange aurora from M₂ to 1A (sometimes all or part of M₁); orange occasionally to terminal line but more often stopping at praeterterminal marks (filling between); aurora 1 1/3 mm wide.

UNDER SURFACE, Primaries same as in ♂, though ground color usually more gray-white.

Secondaries same as in ♂, though ground color usually more gray-white.

HOLOTYPE ♂: UTAH: Emery Co., summit of road to 1½ mi. E., of Little Flat Top, 5500', T26S, R13E, ca. 10-11 mi. SE of Utah Hwy. 24, VIII-26-69 (J. F. Emmel & O. Shields).

ALLOTYPE ♀: same.

PARATYPES: Same, 44 adults.

Disposition of type material: holotype, allotype, and paratypes (AM).

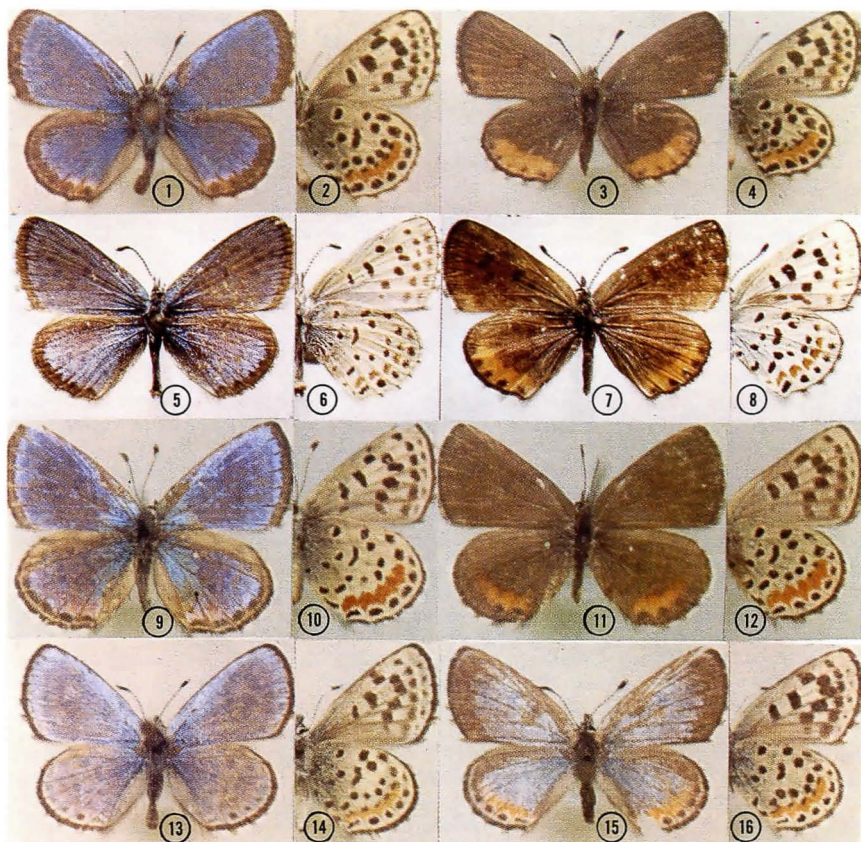
Number of teeth on terminal end (cucullus) of valve = 20 (6), 21 (6), 22 (3), 23 (2), 26 (1); N = 18, average = 20-22, 4 localities = Tuba City, Calf Creek, Dead Horse, Klondyke Bluffs.

The behavioral adaptation of *rita emmeli* to a sandstorm is described in Shields (1974a).

DISTRIBUTION (viewed 38♂ gen. from 18 localities): UTAH: *Emery Co.*: along rd. ½ mi. S. of Goblin Valley turnout from highway 24, 1 mi. SE along this rd. from hiway, 5100', T25S, R12E, 3♀, viii (AM), Upper Jurassic; 10 rd. mi. SE of Hwy. 24, Little Flat Top, Green River Desert, "12", ix (AM), Upper Jurassic; 15.3 rd. mi. SE of Hwy. 24, on road to Orange Cliffs via Little Flat Top, 1♀, ix (AM), Upper Jurassic; San Rafael Desert, 6♂ 5♀, viii (AM). *San Juan Co.*: 20 road mi. S Blanding, 1♂, viii (AM). *Wayne Co.*: 4.0 road mi. S Hanksville, on road to Henry Mts., 1♀, ix (AM).

HOSTS AND DISTRIBUTION: *Eriogonum leptocladon* Torr. & Gray var. *leptocladon*. UTAH: *Emery Co.*: 10 road mi. NE of Goblin Valley turnout from Hwy. 24, on Hwy. 24, Green River Desert, "19", ix (AM), adult assoc. (Shields #169), Upper Jurassic. *Garfield Co.*: Poison Spring Cyn., 1 mi. S Wayne Co. line, along Hwy. 95, 18 road mi. SE Hanksville, 3♂ 1♀, viii (AM), adult assoc. (Shields #39). *Grand Co.*: ½ mi. N of Courthouse Wash, along U.S. Hwy. 160, ca. 17 road mi. NW Moab, 1♂ 6♀, viii (AM), oviposition (Shields #23) Morrison formation (Upper Jurassic); sand hillocks 5 rd. mi. W of jct. of rd. to Dead Horse Point State Park & U.S. Hwy. 160, NW of Moab, "53", viii (AM), oviposition (Shields #24); 3 rd. mi. S & W on road to Klondyke Bluffs from jct. of this rd. with rd. to Devils Garden, Salt Valley, "7", viii (AM), adult assoc. (Shields #28). *San Juan Co.*: 8 rd. mi. S of jct. of rd. to Dead Horse Point State Park & Canyonlands Nat'l Park, 1♂, viii (AM), adult assoc. (Shields #26); 8 rd. mi. NW past turnout at Dugout Ranch, along rd. to Canyonlands Nat'l Park, via Indian Creek State Park, "13", viii (AM), adult assoc. (Shields #31). *Wayne Co.*: 6 rd. mi. SE Hanksville, "9", viii (AM), adult assoc. (Shields #40); 20.7 rd. mi. SE of Hwy. 24, on road to Orange Cliffs via Little Flat Top, "6", ix (AM), adult assoc. (Shields #167) Upper Jurassic. 30.6 road mi. SE of Hwy. 24, on rd. to Orange Cliffs via Little Flat Top, "19", ix (AM), oviposition (Shields #168) Upper Jurassic. *Eriogonum leptocladon* Torr. & Gray var. *ramosissimum* (Eastw.) Reveal. ARIZONA: *Coconino Co.*: 5.0 rd. mi. NE Sunrise Trading Post, N of Leupp, 1♀, ix (AM), adult assoc. (Shields #162); 14 rd. mi. NE Tuba City, "15", viii (AM), adult assoc. (Shields #50); 9 rd. mi. SW of jct. with Hwy. 89, & rd. thru Wupatki Nat'l Mon., 1♂ 1♀, viii (AM), adult assoc. (Shields #51). *Navajo Co.*: 2½ rd. mi, N

Joseph City, 5200', "11", viii (AM), adult assoc. (Shields #160); 7.7 to 8.1 rd. mi. ENE Kayenta (from jct. Hwy. 464 & 164), just SE Church Rock, "14", ix (AM), adult assoc. (Shields #165), Chinle formation (Late Triassic). UTAH: Kane Co.: 8 rd. mi. SSE Mt. Carmel Junction, 5800', along Hwy. 89, 2♂, viii (AM), adult assoc. (Shields #47). San Juan Co.: at SW base of a bluff, 3 rd. mi. N & 1 rd. mi. E of Bluff, 5000', T40S, R22E, "17", viii (AM), adult assoc. (Shields #33), Morrison formation (Upper Jurassic); 5 rd. mi. WSW Bluff, "20", viii (AM), adult assoc. (Shields #34), San Rafael group (Upper Jurassic); 6.8 rd. mi. SW Mexican Hat, along Hwy. 163, "29", ix (AM), adult assoc. (Shields #166); 2 rd. mi. NW of jct. Hwy. 261 & 47, along Hwy. 261 (5 mi. N. Mexican Hat), "5", viii (AM), adult assoc. (Shields #35),



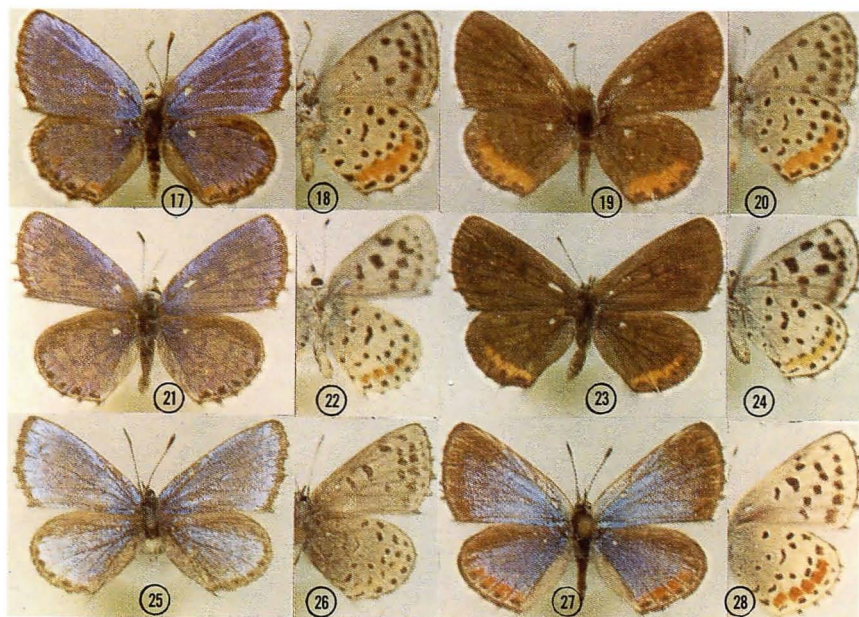
Figures 1-16: new *Shijimiaeoides battoides* subspecies. 1-4: *S. b. allyni*, new subspecies; Holotype ♂ upper (1) and under (2) surfaces; Allotype ♀ upper (3) and under (4) surfaces; CALIF.: Los Angeles Co.: El Segundo, vii.9.1965 (R. E. Stanford). 5-8: *S. b. comstocki*, new subspecies; Holotype ♂ upper (5) and under (6) surfaces; Allotype ♀ upper (7) and under (8) surfaces; CALIF.: Tehachapi, vii. 22.1918 (J. A. Comstock). 9-12: *S. b. ellisii*, new subspecies; Holotype ♂ upper (9) and under (10) surfaces; Allotype ♀ upper (11) and under (12) surfaces; COLORADO: Mesa Co.: Unaweep Canyon, viii.16.1969 (S. L. Ellis). 13-16: *S. b. baueri*, new subspecies; Holotype ♂ upper (13) and under (14) surfaces; Allotype ♀ upper (15) and under (16) surfaces; CALIF.: Inyo Co.: W side Gilbert Pass, 6200', v.23.1967 (D. L. Bauer).

Pennsylvanian. Wayne Co.: 5 rd. mi. NE Hanksville, 4600', "4", viii (AM), adult assoc. (Shields #44), Upper Jurassic. *Eriogonum leptocladon* Torr. & Gray var. *papiliunculi* Reveal. UTAH: Garfield Co.: 5 rd. mi. SSW Calf Creek Recreation Area, 12 rd. mi. E Escalante on Hwy. 54, 5800', T35S, R4E, 6S 5Q, viii (AM), oviposition and 1♀ reared from larva (Shields #45). See Map 3.

Subspecies *emmeli* is on wing in late August and early September.

In the vicinity of the type locality on VIII-26 & 27-69, at 1½ mi. E. Little Flat Top, Upper Jurassic, 24 adults were on *E. leptocladon* var. *ramosissimum* (Shields #41). Some adults were on *E. leptocladon* var. *leptocladon* (Shields #42) and *E. smithii* Reveal (oviposition, Shields #43) at the summit (Fig. 31-32). About 1 miles east is a mixed stand where all three *Eriogonum*'s occur together.

S. rita emmeli in parts of northern Arizona occasionally bears a strong resemblance to *rita rita*, and in northwestern New Mexico populations of *rita* that are clinal between *rita rita* and *rita coloradensis*, on *E. effusum*, also approach *emmeli*. Reveal (1971: 2) states that recently in Kane Co., Utah, intergrades were discovered between *E. leptocladon* var. *ramosissimum* and *E. kearneyi*, the later being the principle foodplant of *rita pallescens* (Shields, unpubl.), while on the eastern flank var. *ramosissimum* is approached by the New Mexican phase of *E. effusum* var. *effusum*. Thus, *rita emmeli* appears to be related to the *rita rita-r. coloradensis* series on the one hand, and (perhaps *rita pallescens* on the other. In valve teeth number it lies intermediate between the two (averages, *rita rita*



Figures 17-28: new *Shijimiaeoides*. 17-20: *S. rita emmeli*, new subspecies; Holotype ♂ upper (17) and under (18) surfaces; Allotype ♀ upper (19) and under (20) surfaces; UTAH: Emery Co.: 1.5 mi. E Little Flat Top, ca. 5500', viii.26.1969 (J. F. Emmel & O. Shields). 21-24: *S. rita mattonii*, new subspecies; Holotype ♂ upper (21) and under (22) surfaces; Allotype ♀ upper (23) and under (24) surfaces; NEVADA: Elko Co.: 4 mi. W Charleston Reservoir, 6600', vii.24.1969 (J. F. Emmel & O. Shields). 25-28: *S. enoptes langstoni*, new subspecies; Holotype ♂ upper (25) and under (26) surfaces; Allotype ♀ upper (27) and under (28) surfaces; CALIF.: Mono Co.: 1.6 mi. N Inyo-Mono Co. line on Hwy. 395, 5700', v.18.1970 (O. & R. Shields).

and *r. coloradensis* = 24-26, *rita emmeli* = 20-22, *rita pallescens* = 19-21).

This subspecies is named for Dr. John F. Emmel, my companion on many summer trips, in appreciation for his efforts with this subspecies.

For *Eriogonum leptocladon* var. *leptocladon* and var. *ramosissimum*, specific localities are listed in Reveal (1965). They range from SE Utah, NE Arizona, extreme SW Colorado, and adjacent New Mexico, flowering from June to October. White-flowered var. *ramosissimum* is confined mostly to white "blowsand", while yellow-flowered var. *leptocladon* is confined to red "blowsand" (Reveal, 1969a). The var. *papiliunculi*, with its white flowers and glabrous stems, ranges from Garfield Co., Utah, southward to northern Coconino and Apache Cos., Arizona (Reveal, 1974). *E. smithii* is known only from the vicinity of Little Flat Top, Emery Co., Utah, flowering from late July to September (Reveal, 1967). John Emmel and I separately have checked a closely related species from Imperial Co., Calif., *E. deserticola* S. Wats., that blooms from November to February, without success.

***Shijimiaeoides rita mattonii*, new subspecies**

Figures 21-24

Male: Holotype forewing, 10 mm. UPPER SURFACE, Primaries: lavender blue cyanic overlay; marginal line $\frac{1}{2}$ mm wide, black scales extending *ca.* outer $\frac{1}{3}$ of veins and scattered black scales over rest of veins (veins almost outlined thinly in black in several), blue scales lightly dusted with black scales over ground; fringe white with black checkering at vein tips (but usually lacking for M_1 and M_2); small $\frac{1}{3}$ length fringe scales black, uneven.

Secondaries: fringe white except Cu_1 , Cu_2 , small row black and uneven; terminal band partially or nearly filling cells Sc and Rs; praeterterminal macules fused on lower $\frac{1}{2}$ to terminal line, giving scalloped appearance to band from M_1 to Cu_2 , or separate; some black scales dusting over blue ground overlay; aurora faintly present in Cu_1 , Cu_2 of one, absent in the others; black scaling on outer $\frac{1}{3}$ of veins M_2 to Cu_2 , boxing in the praeterterminal macules, veins M_1 and Rs completely covered with black scales.

UNDER SURFACE, Primaries: ground is snowy white with slight grayish cast in several; terminal line thin; macules heavily marked (except for faint praeterterminal marks), slight or extensive smoky suffusion in cell Cu_2 .

Secondaries: aurora golden orange or yellowish orange, $\frac{1}{3}$ mm wide, continuous band from M_1 to Cu_2 (except one discontinuous), scalloped appearance; praeterterminal marks separate from aurora; macules smaller than those of forewing.

Female: Allotype forewing, 11 mm. UPPER SURFACE, Primaries: ground dark brown, solid; discoidal spot distinct.

Secondaries: aurora $\frac{3}{4}$ mm wide, from M_1 to Cu_2 ; fringe white without checkering; solid dark brown ground.

UNDER SURFACE, Primaries as in ♂ except smoky suffusion below Cu_2 .

Secondaries: as in ♂ except aurora 1 mm wide.

HOLOTYPE ♂: NEVADA: Elko Co., ridge 4 air mi. W. of Charleston Reservoir, 6600', SW corner of T43N, R57E, SW of Jarbidge Mts., VII-24-69 (J. F. Emmel & O. Shields).

ALLOTYPE ♀: same.

Disposition of type material: (AM).

Number of teeth on terminal end (cucullus) of valve = 15, 18, 19, N = 3, from Charleston Reservoir and Beaver Creek.

DISTRIBUTION: NEVADA: *Elko Co.*: West Fk., Beaver Creek, 2♂, vii (DB).

HOST: *Eriogonum microthecum* Nutt. var. *laxiflorum* Hook. At the type locality, oviposition (Shields #10).

Subspecies *mattonii* flies in July.

Named in honor of Dr. R. H. T. Mattoni's major contributions to this complex genus.

S. rita mattonii appears to have no known close relatives, though perhaps it is anciently related to *rita coloradensis* on *E. effusum* by virtue of *microthecum* and *effusum* both residing in the *E. microthecum* complex. Certainly the two *rita* subspecies, though, are today quite disparate. Certain *rita* forms, as yet unplaced, from central Nevada and eastern California, also use *E. microthecum* varieties but bear no obvious resemblance to *rita mattonii*.

Eriogonum microthecum var. *laxiflorum* is widespread and common in western U.S., from 5,000-10,500', flowering from June to October (Reveal, 1971; see fig. 6). Hence, *rita mattonii* may prove to be much more widespread than is presently known.

***Shijimiaeoides rita spaldingi* (Barnes & McDunnough), 1917**

Barnes & McDunnough, 1917. Contrib. Nat. Hist. Lepid. N. Amer., 3: 215-216; 262, 264; pl. 16, figs. 9-11; pl. 17, fig. 6.

There is no doubt from the original description that *spaldingi* refers to a form similar to *enoptes* in male genitalia, with the primaries of both sexes possessing a broad submarginal orange band on the underside, and with the female upperside having the subterminal orange band of the secondaries continued on the primaries for half the length. The type series is mixed: "our types are 2♂, 1♀ from Provo, Utah (Aug. 1-7), 1♂ from Silver Lake, Utah (July 24-30) and 1♂ (very large) from Stockton, Utah, the latter in the collection of Mr. Spalding." Plate 16, fig. 9 & 11, are of the ♂ and ♀ "Type" from Provo, Utah, hereby designated the type locality. In the past, much confusion has centered about the names *glaucon* and *spaldingi*, apparently stemming from the fact that the genitalia of *glaucon* was unknown (see McDunnough, 1914; Williams, 1918). In the original description of *glaucon*, the male being pruinose blue (like *Everes comyntas*), underside gray-brown, etc. would also fit *spaldingi*. Barnes & McDunnough (1918: 79), however, note that the type description of *glaucon* does not apply to *spaldingi* in certain particulars.

Both Barnes & McDunnough (1918: 77-79) and Brown (1970: 406-409) come to the same conclusion, apparently independently, that Henry Edwards' *glaucon* type was number "251" and has a *battoides* male genitalia. They note that this number referred to Storey Co., Nevada, from "mountain pastures". Barnes & McDunnough further restrict this locality to "the hills around Virginia City", though on what basis is unclear. Brown (1970: 407), also found an entry in Hy. Edwards' catalogue mentioning Virginia City. Likewise, Williams (1918: 101) says the type specimens probably came from near Virginia City. Unless evidence to the contrary is brought to light, near Virginia City, Storey Co., Nevada, is hereby designated the type locality, for *glaucon*. *S. b. glaucon* has been taken at 7 mi. Canyon, Virginia City, V-18-69, leg. D. L. Bauer (gen. det.). I feel that part of the confusion surrounding *glaucon* is due to the type description being a composite of specimens of what today are known as *glaucon*, *enoptes ancilla*, and *spaldingi*; a similar opinion was expressed by Barnes & McDunnough (1916: 117; 1917: 215; 1918: 79). Williams (1918: 101) indeed thought that *glaucon* and *spaldingi* were synonymous. A male *spaldingi* specimen I have seen in the MCZ Collection, bears the labels "Colorado. *glaucon* Edw. Col. Gift of H. C. Fall." I have proposed (1973: 2) that *spaldingi* be considered a subspecies of *rita*. This decision is based on the presence of cristae on the male genitalia of *spaldingi*, a trait universally present in *rita* and lacking in *enoptes* forms.

The number of teeth on terminal end (cucullus) of valve = 11 (3), 12 (3), 13 (8), 14 (10), 15 (8), 16 (1), 17 (1), 18 (1), N = 35, average = 13-15, localities = North Rim, Indian Hollow, Robbers Roost, Bee Spring, Schilling's Spring (most), Alamosa Reservoir (many), Swain Creek.

DISTRIBUTION (viewed 37♂ gen. from 17 localities): ARIZONA: *Coconino*

Co.: Bee Springs, Kaibab Plateau, 5♂, vi, vii (DB, LACM); Bee Spring, 7800', Kaibab Plateau, 3♂, vii (KR) Kaibab formation (Upper Permian); Indian Hollow, 6800', Kaibab Plateau, 3♂, vii (KR) Kaibab formation; North Rim, Grand Canyon, 2♂, vii (LACM); Robbers Roost Spr., 8200', N. Rim, Grand Canyon Nat'l Park, 2♂, vii (KR) Kaibab formation. *Navajo Co.*: Gomez Crk., Upper Log Rd., 6 mi. E. Hwy. 73, Fort Apache Indian Res., 1♂, viii (AM). **COLORADO**: *Archuleta Co.*: 2 mi. S Pagosa Springs, vi (RM); Trujillo, vii (NL). *Conejos Co.*: ½ mi. N of E end Alamosa Reservoir, 3♂, vii (JS); W end Alamosa Res., large series, vii (JS); Aspen Glade Recreation Area, Rio Grande Nat. For., "1", vii (CC); Schilling's Spring, large series, vii (JS); ½ mi. SE Schilling's Spring, large series, vii (JS). *Dolores Co.*: 3 mi. E Dove Creek (MF). *Gunnison Co.*: Almont, 8000', 2♂, vii (SE); 1.5 mi. N Almont, Hwy. 135, 1♂, vii (RL); Jack's Cabin, 3♂, vii, viii (CIS, YU). *La Plata Co.*: Rockwood, 7360', vii (in Brown, 1955). *Montezuma Co.*: Mesa Verde Park, 1♀, viii (LACM); Morefield Canyon, Mesa Verde Nat'l Park, 5♂, vii (CIS, AM) Mesa verde sandstone (Upper Cretaceous); Prater Canyon, Mesa Verde Nat'l Park, 4♂ 3♀, vii (RL) Mesa verde sandstone (Upper Cretaceous). *Montrose Co.*: Black Canyon, 1♂, vii (RL); Cimarron, 7000', 2♂, vii (SE). *San Miguel Co.*: Wilson Draw, 8000', 6 mi. SE Egnar, San Juan Nat'l For., 12♂, vii (SE). **NEW MEXICO**: *Catron Co.*: nr. Mangas, Apache Nat. For., "1", vii (CC). *McKinley Co.*: 4 mi. S Fort Wingate, 1♂, vii (CAS). *Rio Arriba Co.*: 4 mi. S Tierra Amarilla (RL). *San Juan Co.*: Shiprock, 1♂ 5♀, viii (LACM). *Torrance Co.*: Capillo Peak Summit, 9200', Manzano Mts., 1♀, vii (CM); 1 mi. S. Capillo Peak, 9000', Manzano Mts., 1♂, vii (RH). **UTAH**: *Garfield Co.*: Bryce Nat'l Park, 1♂, vii (CAS); near Panguitch, vii (KR). *Juab Co.*: Eureka, 7500', 2♂, (CM). *Kane Co.*: nr. Strawberry Creek, 1♂, vii (KT); nr. Swain Creek, Hwy. 14 mile 36, 1♂ 1♀, vii (KH, JL). *Tooele Co.*: S. Willow Cr., Stansbury Mts., 1♂, vii (SE). *Utah Co.*: Springville, left fork Hobbie Creek, 1♂, vii (DB). *Wasatch Co.*: Provo Canyon, 1♂, vii (LACM). *Washington Co.*: Pine Valley C. G., Pine Valley Mts., 1♂, vii (KR). See Map 4.

HOST: *Eriogonum racemosum* Nutt. **COLORADO**: *Conejos Co.*: W end Alamosa Res., NW of Capulin, viii (no adults; JS took large series here) (*Shields #140*). *Montezuma Co.*: hillside ca. 1 mi. W Park Point Fire Lookout (with water tank at summit), Mesa Verde Nat'l Park, "8", viii (AM), adult assoc. (*Shields #136*). Also sympatric here was *Plebejus melissa*, 9 adults, flying around legumes, feeding on flowers other than *racemosum*, or roosting on sagebrush. Though sympatric, *spaldingi* and *melissa* had different flight patterns and behaviors. Scott, Ellis, & Eff (1968) also record *spaldingi*'s foodplant as *racemosum*. Subspecies *spaldingi* is in flight from latest June to mid August (Map 4).

Brown (1955) gives a good phenotypic description of *spaldingi*. Garth (1950: 36) lists four North Rim, Grand Canyon records.

The relationship of *spaldingi* to the other *rita* subspecies remains unclear. However, the general heavily sclerotized valves, their overall form, and teeth number on terminal end of valve of *spaldingi* closely approach *enoptes ancilla* and *e. dammersi*. *S. e. dammersi* feeds on *Eriogonum elongatum* and *E. wrightii*, both related to *E. racemosum*. *S. rita rita* also feeds on *E. wrightii* but appears to intergrade with *rita coloradensis* on *E. effusum*, of the Sect. *Corymbosa*, a taxon quite different from *Racemosa*, and both *rita rita* and *r. coloradensis* average 26-28 valve teeth, exactly double that for *spaldingi*. The subspecies with teeth number nearest *spaldingi* found so far is the Mojave Desert *r. elvirae* on *E. plumatella*, but *elvirae* facies do not resemble those of *spaldingi* in the slightest. Perhaps a connecting link between *spaldingi* and the known *rita* subspecies will eventually turn up on the species most closely related to *E. racemosum*: *E. panamintense*, *E. rupinum* and *E. zionis*. Another possibility is that *rita rita-r. coloradensis* were the ancestral subspecies to *spaldingi* (*r. rita* has reduced cristae, as does *spaldingi*; both are comparable to *spaldingi* in size; rarely there is a trace of an aurora on the underside primaries of *r. emmeli*, *rita rita* and *r. coloradensis*; males are similar on the upperside of *rita rita*, *r. coloradensis* and *r. spaldingi*), in which an aberration in genitalia isolated *spaldingi* (i.e., heavy sclerotized parts, fusion of teeth

to form $\frac{1}{2}$ the original number). It would have been maintained because of its selective advantage in mimicing *Plebejus melissa*. *S. e. dammersi* and *S. rita rita*, except for genitalic differences, appear nearly identical in facies, and both use *E. wrightii*. Although *E. wrightii* and *E. effusum* (the latter being the host of *rita coloradensis*) are widely separated by Reveal, these two *Eriogonums* have a generally similar appearance and *E. effusum* is largely replaced by *E. wrightii* in New Mexico, but occupy almost an identical ecological niche. *S. r. spaldingi* does overlap the range of *enoptes ancilla* and approaches the range limits of *enoptes dammersi* south of the Grand Canyon, but is temporally isolated from both.

In Utah, *spaldingi* and *ancilla* are sympatric in the Stansbury Mts. and the vicinity of Eureka. In the Wasatch Range, *ancilla* comes down as far as Alta (8600'), Salt Lake Co., and *spaldingi* comes up to the vicinity of Provo and Springville, Utah Co. There are no *ancilla* records for Arizona and New Mexico, where *spaldingi* flies. In Colorado, the two are known to be sympatric in the vicinity of Almont, Gunnison Co., and at Mesa Verde National Park. One female *spaldingi* from nr. Swain Creek, Kane Co., Utah, has a strong tendency toward *ancilla* on both dorsal and ventral surfaces.

Eriogonum racemosum ranges (5000-10,000') from central and eastern Nevada to most of Utah, northern Arizona, northern New Mexico, and southwestern Colorado, flowering from June to September. In view of the distribution of *E. panamintense* and *E. rupinum*, perhaps two old California *spaldingi* specimens I have seen in the MCZ Coll. are authentic, viz: 1♂, "Ariz. or Cal./L. battoides Behr/C. J. Paine Collection," and 1♂, "Cal. '89, ~~Ariz.~~ [struck out in pencil] battoides/C. J. Paine Collection."

***Shijimiaeoides enoptes enoptes* (Boisduval), 1852**

Boisduval, 1852. Ann. Soc. Ent. France, (2) 10: 298-299, no. 36. (From article: Lépidoptères de la Californie.)

According to Williams (1918), Oberthür figured the types (Etud. Lep. Comp. IX. Pl. 237, fig. 1948♂, 1949♀) in 1913 and sent a photograph to Williams of the male genitalia of the type in his collection (Plate IV of Williams' article). It possesses ca. 17 valve teeth and is certainly an *enoptes*-type of genitalia. The original description (as translated by Skinner, 1911) compares favorably with what today is known as *enoptes enoptes*; "it is found in May in the dry [or barren] places" (California). Perhaps an exact type locality may never be known. Barnes & McDunnough (1917: 215) say their specimens from Truckee, Calif., exactly match Oberthür's figures of the types, and that a series from Mineral King, Calif., is nearly identical. The Oberthür figures to me appear fairly typical of Sierran *enoptes enoptes*.

***Shijimiaeoides enoptes langstoni*, new subspecies**

Figures 25-28

Male: Holotype forewing, 11 mm. UPPER SURFACE, Primaries: ground uniform light bright blue cyanic overlay; terminal band narrow, 2/3 mm wide; fringe white with pronounced black checkering at vein tips and row of small dark scales of uneven length.

Secondaries: praeterterminal macules small but distinct, from M_1 to 2A; cell Sc nearly black with light blue scales scattered basally, cell Rs partially so.

UNDER SURFACE, Primaries: ground whitish gray; terminal line very thin; checkering at vein tips, rest of fringe white; macules distinct, semimacules well-developed; smoky suffusion in cells 1A and 2A (partial or complete).

Secondaries: aurora golden orange, from M_1 to Cu_2 , $\frac{1}{2}$ mm wide, crescents fused or separate; praeterterminal marks distinct and separate from aurora; terminal

line thin; ground uniform over wing.

Female: Allotype forewing, 12 mm. UPPER SURFACE, Primaries: ground black with sky blue cyanic overlay, varying from none (1) to partial to nearly complete except outer quarter, blue diffuse toward outer perimeter (one = diffuse throughout); fringe as in ♂; whitish blue band just inside terminal line (in 4 of 6); discoidal macule rather distinct to absent.

Secondaries: blue overlay variable (lacking in one), mostly black in Sc and Rs; thin whitish blue band just inside terminal line (in 4 of 6); fringe white with black scales for basal ½ at vein tips; aurora golden orange and continuous with praeterminal macules (separate in one).

UNDER SURFACE, Primaries: trace of aurora in lower ½ or absent; macules distinct and prominent; fringe as in ♂.

Secondaries: macules distinct to reduced; aurora in continuous band or separate spots, 1 mm wide; fringe mostly white with basal ½ all white or black-white, some slight checkering at vein tips.

HOLOTYPE ♂: CALIFORNIA: Mono Co., 1.6 rd. mi. N of Mono-Inyo Co. line, Hwy. 395, ca. 6 rd. mi. S of Sherwin Summit, ca. 5700', V-18-70 (O. & R. Shields). ALLOTYPE ♀: same.

PARATYPES: same, 2♂ 6♀.

Disposition of type material: (AM).

DISTRIBUTION (viewed 4♂ gen. from 2 localities): CALIFORNIA: Inyo Co.: Carroll Crk., 9 mi. SW Lone Pine, 3♂ 1♀, v (CIS).

HOST: *Eriogonum kennedyi* Porter ex Wats. var. *purpusii* (Brandg.) Reveal in Munz. At type locality, oviposition (Shields #81). Subspecies *langstoni* is on wing in May (Fig. 33).

Number of teeth on terminal end (cucullus) of valve = 14, 15, 16, N = 3, from Carroll Creek. Named for Robert L. Langston, a keen student of the genus.

S. enoptes langstoni's closest relative is doubtless *e. mojave*, from which it differs in its larger size, different foodplant, and females with prominent aurora and extensive blue on the upperside.

Eriogonum kennedyi var. *purpusii* occupies dry granitic flats and slopes, 5000-8000', east slope of Sierra Nevada from Mono Co. s. to Argus and Coso Mts., Inyo Co., flowering May-June.

***Shijimiaeoides enoptes mojave* (Watson & W. P. Comstock), 1920**

Watson & W. P. Comstock, 1920. Bull. Amer. Mus. Nat. Hist.; 42: 455-456; no illust.

This was originally described as a subspecies of *enoptes* but seems to have been referred to as a separate species by various workers (W.J. Holland, Mattoni, dos Passos, Langston, J. A. Comstock) ever since for no apparent reason. After viewing many specimens of *enoptes mojave* from different localities, examining the male genitalia of 23 specimens, and comparing the adults with the other subspecies of *enoptes*, I am convinced it belongs as a subspecies of *enoptes* and not as a separate species. The original authors note that the male genitalia of *e. mojave* is definitely related to *enoptes* and not *rita* (see also Mattoni, 1954: 157), while both sexes bear a strong resemblance in facies to *enoptes enoptes* but are only three-fourths the size. The subspecies is adequately pictured in Emmel & Emmel (1973: pl. 8, figs. 17-19). The type specimen was collected in the "Mojave Desert, California, April 18, 1913." "These three specimens were obtained through a dealer and no further information than that given above was available." Thus a more precise type locality does not appear forthcoming.

Number of teeth on terminal end (cucullus) of valve = 11 (1), 12 (4), 13 (3), 14 (3), 15 (7), 16 (2), 17 (1), 19 (1), 20 (1), N = 23, average = 3-15, localities = Jawbone Canyon, Pinyon Crest, Rock Corral, and most from Juniper Hills, Bob's Gap, and Littlerock. A detailed life history description for this subspecies

appears in Comstock (1966). He records the larval foodplant as *Eriogonum pusillum* Torr. & Gray.

DISTRIBUTION (viewed 23♂ gen. from 8 localities): CALIFORNIA: *Inyo Co.*: Argus Mts., 3♂, iv, v (LACM, CAS); Argus Mts., 6000' [N. of Argus Peak], 1♂, v (LACM). *Kern Co.*: Dove Well, 1♂, v (CIS); Last Chance Canyon, El Paso Mts., 2♂, iii (AM); E. branch Last Chance Canyon, E. off Hwy. 6, 4 mi. N Ricardo, 1♂, iv (CIS); Mojave, 1♂, iv (LACM); nr. Randsburg, Mojave Desert, 2♂, iv (LACM); 16 mi. S Weldon, 1♂, iv (CIS). *Los Angeles Co.*: Bob's Gap, 16♂ 2♀, iii, iv (PO, KH, JL); Bob's Gap (Holcomb Ridge), nr. Llano, 4000', 10♂ 2♀, iii-v (AM); Juniper Hills, 3600-3700', Mojave Desert, nr. Pearblossom, 18♂, iii-v (LACM, KH, AM); Littlerock, 8♂, iii, iv (PO, JL); 1 mi. W Little Rock, 1♂, iv (CIS); Littlerock Dam 8♂ 3♀, iii, iv (KH, GG). *Riverside Co.*: 6 mi. S Cottonwood Spr., Joshua Tree Nat'l Mon., 2♀, iv (CIS); Pinyon Crest, 12 rd. mi. SW Palm Desert, 15♂ 6♀, iv (CIS, LACM); Pinyon Crest Jct. on Hwy. 74, 13 mi. SW Indio, 3400', "24", iv (LACM); E. entrance nr. 29 Palms, Joshua Tree Nat'l Mon., 1♀ iii (GG). *San Bernardino Co.*: Apple Valley, 1♂, v (CIS) W. of Barstow, 1♀, iv (LACM); Bighorn Canyon, 4000', 43 mi. ESE Victorville, 1♂, iv (RL); Bonanza King, Providence Mts., 1♂, iv (LACM); Bonanza King Cyn., 5000', Providence Mts., 1♀, iv (PO); sect. 1, extreme NE corner of T2S, R15E, N end Coxcomb Mts., 2000', 1♂, iii (AM); Kramer Hills, 1♂, iv (LACM); 5 mi. S Lucerne Valley, 4500', 23 mi. ESE Victorville, 1♀, iv (RL); Monarch Flat, 4200', 29 mi. ESE Victorville, 1♀, iv (RL); 4 mi. SSW Rabbit Dry Lake, 4300', 16 mi. SE Victorville, 5♂ 3♀, iv (RL); mts. S Rabbit Dry Lake, 5 air mi. SW Lucerne Valley, 5♂ 2♀, iv (CIS); Rattlesnake Canyon [NW of Yucca Valley], 3♂ 1♀, iv (LACM); Rock Corral, ca. 20 mi. NW Yucca Valley, "abundant", iv (CS, KH); 1 mi. SE Sheephole Summit, Sheephole Mts., 2♀, iv (CIS); Sunflower Wash, 3200', Old Woman Mts., 5♂ 3♀, iv (CIS); 21 mi. ESE Victorville, 4100', 1♂, iv (RL); 22 mi. SE Victorville, 4700', iv (NL).

HOSTS: *Eriogonum pusillum* Torr. & Gray. CALIFORNIA: *Los Angeles Co.*: Bob's Gap, 3800', reared 2♂ 3♀ from larvae coll. v (TE). *Riverside Co.*: Pinyon Crest Jct., "series", iv (FT), adult assoc. *Eriogonum nudum* Dougl. ex Benth. var. *pubiflorum* Benth. in DC. CALIFORNIA: *Kern Co.*: canyon 2.2 rd. mi. SW Jawbone Canyon turnoff on St. Hwy. 14, 2600', 2♂, iii (AM), adult assoc. (*J. F. Emmel #51*); Last Chance Canyon, El Paso Mts., 3♂, iv (AM), adult assoc. (*J. F. Emmel, "A"*). See Map 5.

Subspecies *mojave* flies from mid March to mid May.

S. enoptes mojave probably is a close relative of *S. enoptes dammersi*, as it is sympatric (but allochronic) with it in part of its range, both possess similar male valve teeth number counts (*mojave* av. = 13-15, *dammersi* av. = 14-15), and both have rather similar facies. Its nearest relative, however, is probably *enoptes langstoni*.

Eriogonum pusillum ranges from southern California northward to SE Oregon and SW Idaho, and across southern Nevada to SW Utah and western Arizona, flowering from March to July (Reveal, 1969a). It is noteworthy that so far *enoptes mojave* is only known from southern California (Map 5). One of *Z. speciosa's* larval foodplants, *E. reniforme*, is closely related to *pusillum*. I suspect that *e. mojave* has secondarily come on to *E. pusillum* and certainly is quite unrelated to *speciosa*.

ACKNOWLEDGEMENTS

I thank the following individuals for making available loans and/or records (* = *in litt.*): (AM) Allyn Museum of Entomology, Lee D. Miller; (DB) David L. Bauer; (CAS) Calif. Acad. Sci., Paul Arnaud & Thomas W. Davies; (CIS) Calif. Insect Survey, Robert L. Langston & Jerry A. Powell; (CM) Carnegie Museum, Harry K. Clench; (CC) *C. R. Cushing; (SE) Scott Ellis; (TE) *Thomas C. Emmel; (MF) Michael Fisher; (GG) Glenn A. Gorelick; (RH) *Richard Holland; (KH)

Keith Hughes; (NL) Noel La Due; (JL) John Lane; (RL) *Robert L. Langston records; (LACM) Los Angeles County Museum of Nat. Hist., Julian P. Donahue; (RM) *R. H. T. Mattoni; (MCZ) Museum of Comparative Zoology, John Burns; (NSM) Nevada State Museum, Peter Herlan; (PO) Paul A. Opler; (KR) Kilian Roeber; (JS) James A. Scott; (FT) Fred T. Thorne; (KT) Kenneth B. Tidwell; (YU) Yale Univ. Coll., Douglas C. Ferguson & Charles L. Remington. Special thanks are due Dr. James L. Reveal for identifying the *Eriogonum* species, and for placing voucher specimens on file at the United States National Arboretum (NA) in Washington, D.C. John F. Emmel, Stanley K. Dvorak, David P. Levin, Scott L. Ellis, and Michael Toliver assisted me in the field work. Scott Ellis and Scott L. Ellis kindly provided some pertinent geology literature. This study was supported by grants from the Allyn Museum of Entomology (Arthur C. Allyn and Lee D. Miller), the Los Angeles County Museum (Julian P. Donahue, Charles Hogue, and Lloyd M. Martin), John M. Burns, Theodore J. Cohn, and Charles L. Remington, and an N.S.F. graduate traineeship. This aid enabled me to cover ca. 40,000 miles in four summers, in the states of Calif., Oreg., Nev., Ariz., Utah, Colo., and New Mexico, in quest of *Philotes* and *Eriogonum*. All my personal *Philotes* material will be deposited with the Allyn Museum of Entomology. Paddy McHenry made available some needed type descriptions. J. F. Emmel and my brother Dick took the photographs. Drs. J. F. Emmel, W. H. Lange, J. L. Reveal, and R. W. Thorp reviewed the paper and offered helpful suggestions. This series of papers is submitted in partial fulfillment of the degree, Doctor of Philosophy, University of California, Davis, California.

BIBLIOGRAPHY

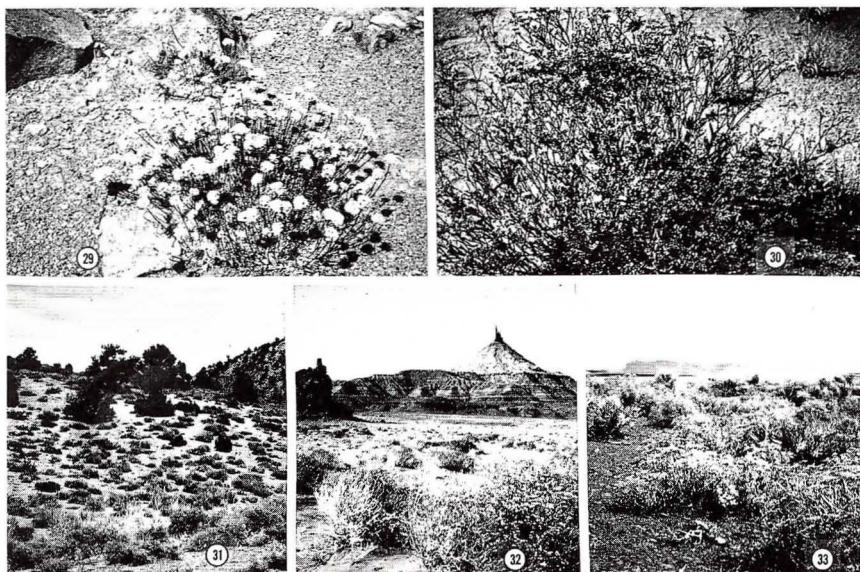
- Ali, S. I., 1969. The role of environment in evolution. *Phyton* 13: 249-265.
- Axelrod, D. I., 1970. Mesozoic paleogeography and early angiosperm history. *Bot. Rev.* 36: 277-319.
- Axelrod, D. I., 1972. Edaphic aridity as a factor in angiosperm evolution. *Amer. Nat.* 106: 311-320.
- Barnes, W., & J. H. McDunnough, 1916. Notes on North American diurnal Lepidoptera. Papilionidae. *Contrib. Nat. Hist. Lepid. North Amer.* 3: 116-117, 152-153.
- , 1917. Further notes on *Philotes battoides* and its allies. *Contrib. Nat. Hist. Lepid. North Amer.* 3 (4): 213-216, 262-265.
- , 1918. Notes and new species; Lycaenidae. *Contrib. Nat. Hist. Lepid. North Amer.* 4: 77-79.
- Beuret, H., 1955. *Zizeeria Karsandra* Moore in Europa und die systematische Stellung der Zizeerinae (Lepidoptera, Lycaenidae). *Mitteilungen der Entomologischen Gesellschaft Basel* 5: 123-130.
- , 1958. Zur systematischen Stellung einiger wenig bekannter Glaucopsychidi (Lep., Lycaenidae). *Mitteilungen der Entomologischen Gesellschaft Basel* 8: 61-79, 81-100.
- , 1959. Zur Taxonomie einiger palaearktischer Bläulinge (Lep., Lycaenidae). *Mitteilungen der Entomologischen Gesellschaft Basel* 9: 80-84.
- Bogert, C. M., W. F. Blair, E. R. Dunn, E. R. Hall, C. L. Hubbs, E. Mayr, & G. G. Simpson, 1943. Criteria for vertebrate subspecies, species and genera. *Ann. N. Y. Acad. Sci.* 44: 105-188.
- Brower, L. P., & J. V.-Z. Brower, 1972. Parallelism, convergence, divergence, and the new concept of advergence in the evolution of mimicry. *Trans. Connecticut Acad. Arts & Sci.* 44: 58-67.
- Brown, F. M., 1955. Colorado Butterflies. *Proc. Denver Mus. Nat. Hist.*, part III. Libytheidae, Riodinidae, Lycaenidae, pp. 113-176 (p. 174).
- , 1970. The types of lycaenid butterflies named by William Henry Edwards. Part III. Plebejinae. *Trans. Amer. Entomol. Soc.* 96: 353-433.
- , 1971. The "Arrowhead Blue", *Glaucopsyche piasus* Boisduval (Lycaenidae):

- Plebejinae). *J. Lepid. Soc.* 25: 240-246.
- Brown, W. J., 1959. Taxonomic problems with closely related species. *Ann. Rev. Entomol.* 4: 77-98.
- Bullard, E. C., J. E. Everett, & A. C. Smith, 1965. The fit of the continents around the Atlantic. *Phil. Trans. Roy. Soc. London, Ser. A*, 258: 41-51.
- Bush, G. L., 1969. Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). *Evolution* 23: 237-251.
- Cardé, R. T., A. M. Shapiro, & H. K. Clench, 1970. Sibling species in the *eurydice* group of *Lethe* (Lepidoptera: Satyridae). *Psyche* 77: 70-103.
- Carey, S. W., 1958. The tectonic approach to continental drift. In: S. W. Carey (Convener). *Continental Drift, a Symposium*. Geol. Dept. Univ. Tasmania, Hobart, pp. 177-355.
- Clench, H. K., 1967. Further distribution records and taxonomic notes on *Philotes rita* (Lycaenidae). *J. Lepid. Soc.* 21: 141-142.
- Cohn, T. J., 1965. The arid-land katyids of the North American genus *Neobarrettia* (Orthoptera: Tettigoniidae): their systematics and a reconstruction of their history. *Mus. Zool., Univ. Michigan, Misc. Publ.* no. 126, 179 pp.
- Comstock, J. A., 1953. Life history notes on four southern Arizona butterflies. *Vull. So. Calif. Acad. Sci.* 52 (pt. 3): 127-136.
- , 1966. Life history of *Philotes mohave* (Lepidoptera: Lycaenidae). *Trans. San Diego Soc. Nat. Hist.* 14: 133-136.
- Cook, L. M., 1961. Food-plant specialization in the moth *Panaxia dominula* L. *Evolution* 15: 478-485.
- Corbet, A. S., 1943. Taxonomy of the moths infesting stored food products. *Nature* 152: 742-743.
- Danilevskii, A. S., 1965. *Photoperiodism and Seasonal Development of Insects*. (Transl. by J. Johnston). Oliver & Boyd, Edinburgh & London, 283 p.
- De Bach, P., 1966. The competitive displacement and coexistence principles. *Ann. Rev. Entomol.* 11: 183-212.
- De Bach, P., & R. A. Sundby, 1963. Competitive displacement between ecological homologues. *Hilgardia* 34: 105-166.
- Dietz, R. S., & J. C. Holden, 1971. Pre-Mesozoic oceanic crust in the eastern Indian Ocean (Wharton Basin) ? *Nature* 229: 309-312.
- Dobzhansky, T., 1933. Geographical variation in lady-beetles. *Amer. Nat.* 67: 97-126.
- Downey, J. C. 1956. Intraspecific variation and evolution in populations of *Glebejus icarioides* (Bdv.) (Lepidoptera, Lycaenidae). Unpubl. Ph. D. diss. U. C. Davis, Entomology. 120 pp.
- , 1962. Host-plant relations as data for butterfly classification. *Syst. Zool.* 11: 150-159.
- Egyed, L., 1957. Investigations on the interior of the earth. *Budapest. Tudomány-egyetem Eötvös. Annales. Sectio geologica* vol. 1: 37-77.
- Eliot, J. N., 1973. The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. *Bull. British Mus. (Nat. Hist.) Entomol.* 28(6): 371-505.
- Emmel, T. C., & J. F. Emmel, 1973. The butterflies of southern California. *Nat. Hist. Mus. Los Angeles Co., Sci. Ser.* 26: 1-148.
- Fischer, A. G., & 9 others, 1970. Geological history of the western North Pacific. *Science* 168: 1210-1214.
- Fisher, D. J., C. E. Erdmann, & J. B. Reeside, Jr., 1960. Cretaceous and Tertiary formations of the Book Cliffs, Carbon, Emery, and Grand Counties, Utah, and Garfield and Mesa Counties, Colorado. *U. S. Geol. Surv. Prof. Paper* 332, 80 p.
- Forbes, W. T. M., 1932. How old are the Lepidoptera? *Amer. Nat.* 66: 452-460.
- Forster, W., 1940. Neue Lycaeniden-Formen aus China. I. *Münchener Entomologische Gesellschaft Mitteilungen* 30: 870-883.
- Garth, J. S., 1950. Butterflies of Grand Canyon National Park. *Grand Canyon*

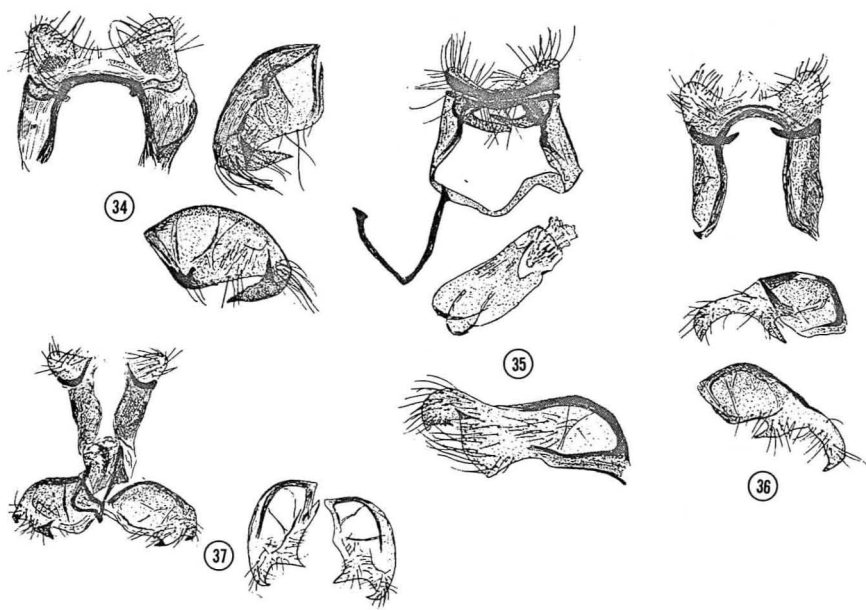
- Nat. Hist. Assoc., Bull.* no. 11, 52 p.
- Gilluly, J., 1963. The tectonic evolution of the western United States. *Quart. J. Geol. Soc. London* 119: 133-174.
- Goodpasture, C., 1974. Foodplant specificity in the *Plebejus (Icaricia) acmon* group (Lycaenidae). *J. Lepid. Soc.* 28: 53-63.
- Gregory, H. E., 1938. The San Juan Country: a geographic and geologic reconnaissance of southeastern Utah. *U.S. Geol. Surv. Prof. Paper* 188, 123 p.
- , 1951. The geology and geography of the Paunsaugunt region, Utah. *U. S. Geol. Surv. Prof. Paper* 226, 116 p.
- Hardin, G., 1960. The competitive exclusion principle. *Science* 131: 1292-1297.
- Harvey, W. R., 1962. Metabolic aspects of insect diapause. *Ann. Rev. Entomol.* 7: 57-80.
- Heitzman, J. R., & C. F. dos Passos, 1974. *Lethe portlandia* (Fabricius) and *L. anthedon* (Clark), sibling species, with descriptions of new subspecies of the former (Lepidoptera: Satyridae). *Trans. Amer. Entomol. Soc.* 100: 52-99.
- Holmes, A., 1965. *Principles of Physical Geology*, 2nd. ed. The Ronald Press Company, New York, 1288 p.
- Hovanitz, W., 1941. Parallel ecogenotypical color variation in butterflies. *Ecology* 22: 259-284.
- Hubbell, T. H., 1954. The naming of geographically variant populations. *Syst. Zool.* 3: 113-121.
- Hunt, C. B., 1946. *Guidebook to the Geology of Utah. No. 1. Guidebook to the Geology and Geography of the Henry Mountain Region.* Utah Geol. Soc., Salt Lake City, 51 pp.
- , 1956. Cenozoic geology of the Colorado Plateau. *U. S. Geol. Surv. Prof. Paper* 279, 99 p.
- Janzen, D. H., 1968. Host plants as islands in evolutionary and contemporary time. *Amer. Nat.* 102: 592-595.
- King, P. B., 1959. *The Evolution of North America.* Princeton Univ. Press; Princeton, New Jersey, 189 pp.
- Klots, A. B., 1936. The interrelationships of the species of the genus *Lycaena* Fabricius (Lepidoptera, Lycaenidae). *Bull. Brooklyn Entomol. Soc.* 31: 154-171.
- Klots, A. B., & H. K. Clench, 1952. A new species of *Strymon* Huebner from Georgia (Lepidoptera, Lycaenidae). *Amer. Mus. Nov.* no. 1600, 19 pp.
- Lamotte, R. S., 1952. Catalogue of the Cenozoic plants of North America through 1950. *Geol. Soc. Amer. Mem.* 51: 1-381.
- Langston, R. L., 1963. *Philotes* of central coastal California (Lycaenidae). *J. Lepid. Soc.* 17: 201-223.
- Langston, R. L., 1969. *Philotes* of North America: synonymic list and distribution (Lycaenidae). *J. Lepid. Soc.* 23: 49-62.
- Leet, L. D., & S. Judson, 1965. *Physical Geology*, 3rd ed. Prentice-Hall; Englewood Cliffs, New Jersey, 406 pp.
- Lidicker, W. Z., Jr., 1960. An analysis of intraspecific variation in the Kangaroo Rat *Dipodomys merriami*. *Univ. Calif. Publ. Zool.* 67: 125-218.
- Linsley, E. G., 1944. The naming of infra-specific categories. *Entomol. News* 55: 225-232.
- McDunnough, J., 1914. Notes on the synonymy of Boisduval's N. American species of Lycaenidae. *Entomol. Rec.* 26: 194-203 (pp. 201-202).
- Mattoni, R. H. T., 1954. Notes on the genus *Philotes* (Lycaenidae: Lepidoptera) I: Descriptions of three new subspecies and a synoptic list. *Bull. So. Calif. Acad. Sci.* 53: 157-165.
- , 1957. The significance of the genitalia to taxonomic studies of the Lepidoptera. *Lepid. News* 11: 5-7.
- , 1965. Distribution and pattern of variation in *Philotes rita*. *J. Res. Lepid.* 4: 81-102.
- Mayr, E., 1966. *Animal Species and Evolution.* The Belknap Press, Cambridge,

- Mass., 797 pp.
- Mayr, E., E. G. Linsley, & R. L. Usinger, 1953. *Methods and Principles of Systematic Zoology*. McGraw-Hill Book Co., New York, 336 pp.
- Meservey, R., 1969. Topological inconsistency of continental drift on the present-sized earth. *Science* 166: 609-611.
- Nabokov, V., 1944. Notes on the morphology of the genus *Lycaeides* (Lycaenidae, Lepidoptera). *Psyche* 51: 104-138.
- Ohwi, J., 1965. *Flora of Japan* (in English). Smithsonian Institution, Washington, D.C., 1067 p.
- Opler, P., & J. A. Powell, 1961. Taxonomic and distributional studies on the western components of the *Apodemia mormo* complex (Riodinidae). *J. Lepid. Soc.* 15: 145-171.
- dos Passos, C. F., 1969. *Lethe eurydice* (Johansson) and *L. fumosus* (Leussler), sibling species (Lepidoptera: Satyridae). *J. N. Y. Entomol. Soc.* 77: 117-122.
- Ramsay, A. T. S., 1971. Occurrence of biogenic siliceous sediments in the Atlantic Ocean. *Nature* 233: 115-117.
- Raven, P., 1963. Amphitropical relations in the flora of North and South America. *Quart. Rev. Biol.* 38: 151-177.
- Rawson, G. W., & J. B. Ziegler, 1950. A new species of *Mitoura* Scudder from the pine barrens of New Jersey (Lepidoptera, Lycaenidae). *J. N. Y. Entomol. Soc.* 58: 69-82.
- Remington, C. L., 1953. The sibling species of budworm moths in Canada. *Lepid. News* 7: 57-58.
- Remington, C. L., M. M. Cary, A. B. Klots, B. P. Beirne, E. Munroe, & L. P. Grey, 1951. Geographic subspeciation in the Lepidoptera. *Lepid. News* 5: 17-35.
- Reveal, J. L., 1965. Notes on three Utah *Eriogonums*. *Utah Acad. Proc.* 42 (pt. II): 287-292.
- , 1967. Notes on *Eriogonum*-V. A revision of the *Eriogonum corymbosum* complex. *The Great Basin Naturalist* 27: 183-229.
- , 1968. Notes on *Eriogonum*-IV. A revision of the *Eriogonum deflexum* complex. *Brittonia* 20: 13-33.
- , 1969a. A revision of the genus *Eriogonum* (Polygonaceae). Ph. D. dissertation. Brigham Young Univ.; Univ. Microfilms, Inc., Ann Arbor, Michigan. 70-4714.
- , 1969b. The subgeneric concept in *Eriogonum* (Polygonaceae), pp. 229-249. In: J. E. Gunckel, editor. *Current Topics in Plant Science*. Academic Press, New York, 461 p.
- , 1971. Notes on *Eriogonum*-VI. A revision of the *Eriogonum microthecum* complex (Polygonaceae). *Brigham Young Univ. Sci. Bull., Biol. Ser.* 13(1): 1-45.
- , 1974. Two shrubby novelties in *Eriogonum* (Polygonaceae) from the deserts of Utah and Arizona. *Brittonia* 26: 90-94.
- Rindge, F. H., 1948. Contributions toward a knowledge of the insect fauna of Lower California. No. 8 Lepidoptera: Rhopalocera. *Proc. Calif. Acad. Sci., 4th Ser.*, 24(8): 289-312 (pp. 304-305).
- Robinson, R., 1971. *Lepidoptera Genetics*. Pergamon Press, Oxford, 687 pp.
- Sargent, C. S., 1890. *The Silva of North America*. vol. 3. Peter Smith, New York, 141 p.
- Scott, J. A., S. L. Ellis, & D. Eff, 1968. New records, range extensions, and field data for Colorado butterflies and skippers. *J. Lepid. Soc.* 22: 159-171.
- Seitz, A., 1909. *The Macrolepidoptera of the World*. vol. 1. *The Palearctic Butterflies*. Alfred Kernen, Stuttgart, 379 p., 89 pls.
- Shapiro, A. M., & R. T. Cardé, 1970. Habitat selection and competition among sibling species of satyrid butterflies. *Evolution* 24: 48-54.
- Shields, O., 1972. Flower visitation records for butterflies (Lepidoptera). *Pan-Pac. Entomol.* 48: 189-203.
- , 1973. Studies on North American *Philotes* (Lycaenidae). I. Roosting behavior, tending ants, parasites, and predators, *Bull. Allyn Mus.* no. 10, 5 p.

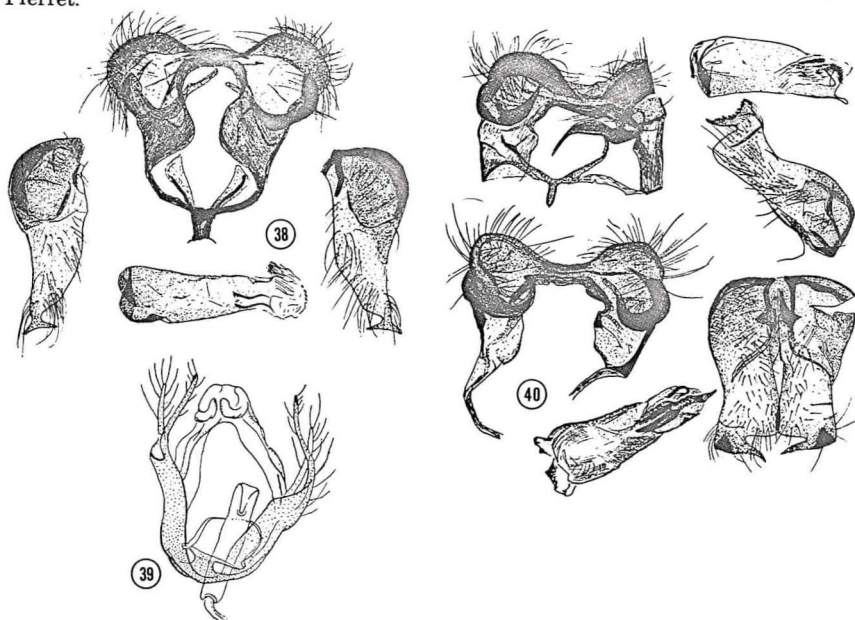
- , 1974a. *Philotes rita* (Lycaenidae) in a sandstorm. *J. Lepid. Soc.* 28: 78.
- , 1974b. Studies on North American *Philotes* (Lycaenidae). III. Generic reassignments and the biology of *speciosa*. *Bull. Allyn Mus.* no. 19, 10 p.
- Shields, O., & J. F. Emmel, 1973. A review of carrying pair behavior and mating times in butterflies. *J. Res. Lepid.* 12: 25-64.
- Shields, O., J. F. Emmel, & D. E. Breedlove, 1969. Butterfly larval foodplant records and a procedure for reporting foodplants. *J. Res. Lepid.* 8: 21-36.
- Skinner, H., 1911. *Lycaena enoptes*, *battoides* and *glaucon* (Lepid.). *Entomol. News* 22: 259-262.
- Smith, S. G., 1953. Reproductive isolation and the integrity of two sympatric species of *Choristoneura* (Lepidoptera: Tortricidae). *Canad. Entomol.* 85: 141-151.
- , 1954. A partial breakdown of temporal and ecological isolation between *Choristoneura* species (Lepidoptera: Tortricidae). *Evolution* 8: 206-224.
- Stebbins, G. L., & J. Major, 1965. Endemism and speciation in the California flora. *Ecol. Monogr.* 35: 1-35.
- Thorpe, W. H., 1930. Biological races in insects and allied groups. *Biol. Rev.* 5: 177-212.
- , 1945. The evolutionary significance of habitat selection. *J. Anim. Ecol.* 14: 67-70.
- Tilden, J. W., 1959. The butterfly associations of Tioga Pass. *Wasmann J. Biol.* 17: 249-271.
- , 1961. Certain comments on the subspecies problem. *Syst. Zool.* 10: 17-23.
- Tilden, J. W., & J. C. Downey, 1955. A new species of *Philotes* from Utah (Lepidoptera, Lycaenidae). *Bull. So. Calif. Acad. Sci.* 54 (pt. I): 25-29.
- Wilde, J. de, 1962. Photoperiodism in insects and mites. *Ann. Rev. Entomol.* 7: 1-26.
- Williams, R. C., 1918. The genus *Lycaena*, *enoptes* group (Lep.). *Entomol. News* 29: 99-102, pls. IV-VI.



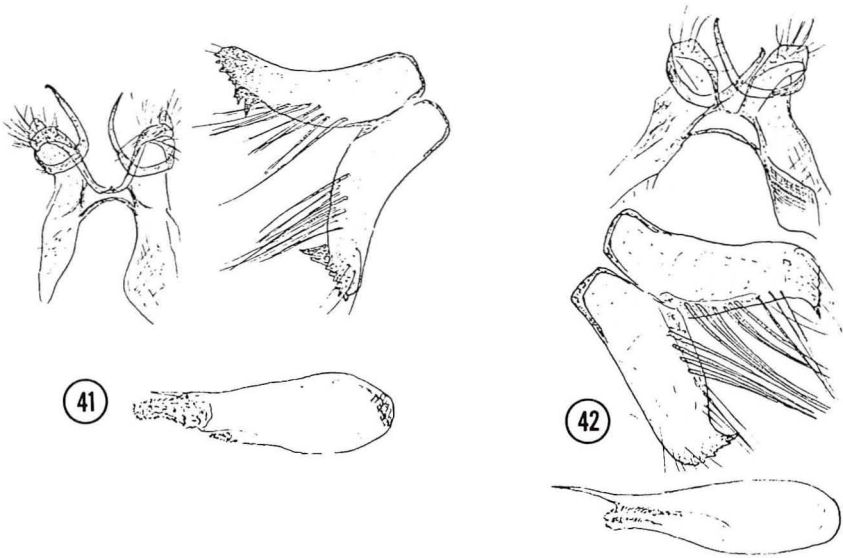
Figures 29-33: habitat and *Eriogonum* photographs. 29: Habitat of *S. battoides ellisii*, new subspecies, with its foodplant *Eriogonum corymbosum* var. *corymbosum* in foreground; ARIZ.: Coconino Co.: 7 mi. SE Fredonia, 5000'. 30: Habitat of *S. battoides baueri*, new subspecies, where its foodplant *E. ovalifolium* var. *ovalifolium* grows; CALIF.: Inyo Co.: 2 mi. NE Westgard Pass, 7000'. 31: Habitat of *S. rita emmeli*, new subspecies, 8 mi. NW past turnoff to Dugout Ranch along road to Canyonlands Natl. Prk, San Juan Co., UTAH; *E. leptocladon* var. *leptocladon* growing on red Entrada blowsand. 32: Another foodplant of *S. rita emmeli*, new subspecies, *E. smithii*, at type locality for insect. 33: foodplant of *S. enoptes langstoni*, new subspecies, *E. kennedyi* var. *purpusii*, at type locality of insect.



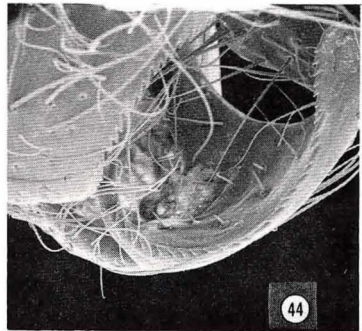
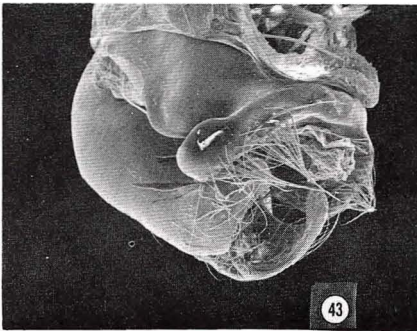
Figures 4-7: ♂ genitalia of *Pseudophilotes* (all after Beuret, 1958). 34: *P. vicrama* Moore. 35: *P. bavius* Eversmann. 36: *P. baton* Bergsträsser. 37: *P. abencerragus* Pierret.



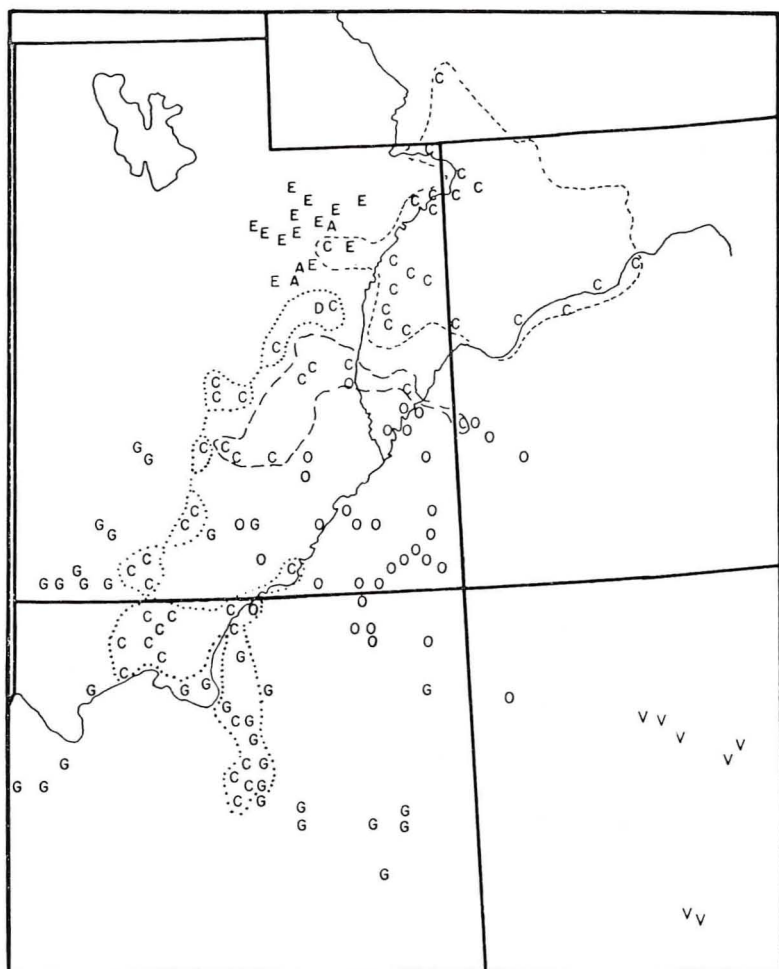
Figures 38-40: ♂ genitalia of *Philotes* relatives. 38: *Sinia leechi* Forster (after Beuret, 1958). 39: *Shijimia moorei* Leech (after Forster, 1940). 40: *Shijimiaeoides divina barine* Leech (after Beuret, 1958).



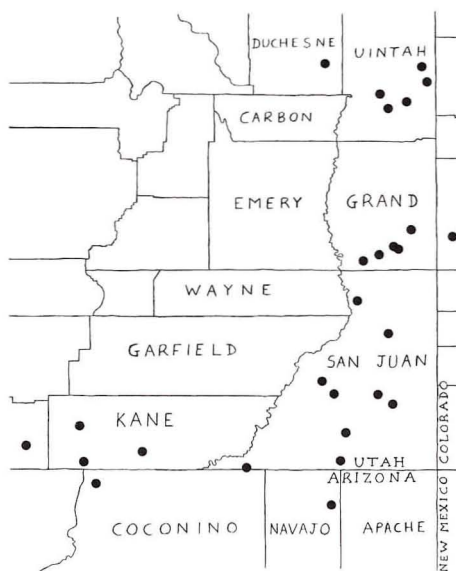
Figures 41-42: ♂ genitalia of *Zizeeria* (after Beuret, 1955). 41: *Z. karsandra* Moore. 42: *Z. knysa* Trimen.



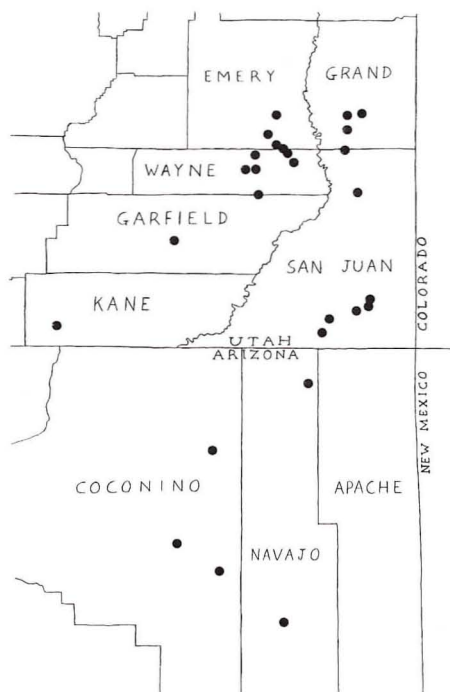
Figures 43-44: ♂ genitalia of *Zizeeria speciosa* Hy. Edwards; NEVADA: Churchill Co.: S end Stillwater Range, 28-29 road mi. SE Fallon. 43: entire view of genital capsule, approx 100x; cristae not visible. 44: same specimen showing detail of valve teeth, 30 in number, approx 280x. SEM photographs courtesy R. O. Schuster.



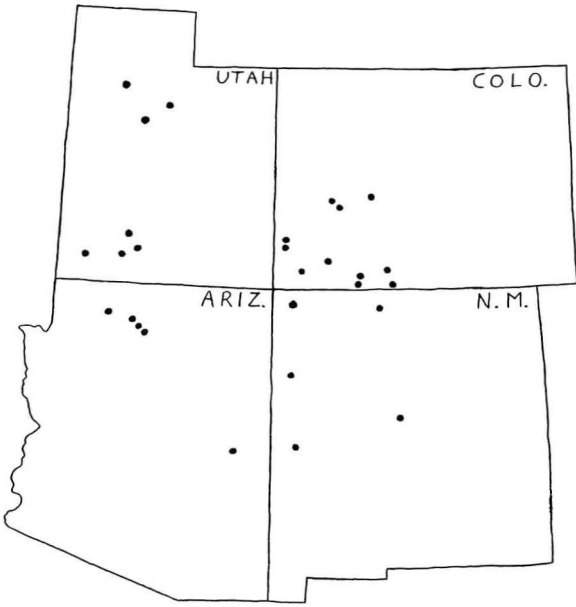
Map 1. Distribution in Utah, Colorado, Arizona, and New Mexico of *Eriogonum corymbosum*, var. *corymbosum* (C) with short dash lines showing the form of the variety represented by the type, the long dash lines showing the desert form, and the dotted line which represents the low mountain and southern form; var. *erectum* (E); var. *davidsei* (D); var. *albogilvum* (A); var. *orbiculatum* (O); var. *velutinum* (V); and var. *glutinosum* (G) (from Reveal, 1967, Map 3).



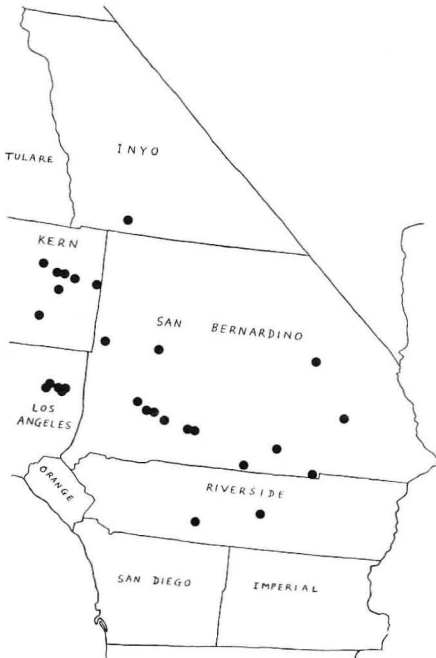
Map 2. Distribution of *Shijimiaeoides battoides ellisii* (three Arizona localities not shown).



Map 3. Distribution of *Shijimiaeoides rita emmeli*.



Map 4. Distribution of *Shijimiaeoides rita spaldingi*.



Map 5. Distribution of *Shijimiaeoides enoptes mojave*.