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CERCYONIS PEGALA (FABRICIUS) (NYMPHALIDAE: SATYRINAE) IN THE GREAT BASIN: NEW SUBSPECIES AND BIOGEOGRAPHY

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The Great Basin is a vast area of mountains and valleys in the western United States, centered on the state of Nevada. At present, the biota of each of these mountain ranges and of the wet areas in the intervening valleys are isolated from biota in like habitats by expanses of shrub desert, dominated by sagebrush. The island-like nature of the montane regions of the Great Basin has been of interest to biogeographers for more than two decades (Austin 1981; Austin and Murphy 1987; Behle 1963, 1978; Billings 1978; Brown 1971, 1978; Grayson 1982, 1983; Harper *et al.* 1978; Johnson 1975, 1978; Pratt 1985; Wells 1983; Wilcox *et al.* 1986). The lowland wet areas have received less attention (Austin 1985a, Johnson 1978) except for studies on fish (Hubbs and Miller 1948; Hubbs *et al.* 1974; Miller 1946, 1958; Smith 1978) and a few other aquatic taxa (Hovingh 1986 and citations therein).

The isolation of Great Basin habitats has led to a diversity of speciation events (Austin and Murphy 1987, Johnson 1978) and centers of differentiation are obvious across several major taxonomic groups (Austin and Murphy 1987; Behle 1963, 1978; Hubbs and Miller 1948; Hubbs *et al.* 1974; Johnson 1970, 1978; Miller 1941; Smith 1978). Generally, the montane regions have been more thoroughly investigated for differentiated, endemic taxa of terrestrial biota. Such surveys have met with limited success; most montane regions

are inhabited by few endemic taxa except in exceptional instances: e.g., the Spring Mountains in southern Nevada (Austin 1981, Clokey 1951, Hall 1946) and the White Mountains on the California-Nevada border (Austin and Murphy 1987, Lloyd and Mitchell 1973).

Intensive studies of riparian habitats in the Great Basin valleys during the last several years have indicated that these areas harbor a greater percentage of differentiated butterfly taxa than the mountains (Austin 1985a, 1987; Austin and Murphy 1987). In retrospect, this is not all that surprising when post-Pleistocene events, including geographical and elevational changes in plant distributions during that period (e.g., Wells 1983), are considered. Biogeographic studies on fish led to the recognition of these areas as speciation centers long ago (Hubbs and Miller 1948; Hubbs *et al.* 1974; Miller 1946, 1958).

Cercyonis pegala (Fabricius) (Nymphalidae: Satyrinae) lives in the wet areas of many of the Great Basin valleys, occurring as several phenotypes (Austin 1985b). The assignment of existing names to these populations has been inconsistent and usually incorrect. Various workers have commented on the taxa involved and/or proposed synonymies (Austin 1985b; Brown 1964, 1965; dos Passos 1964; Emmel 1969, *in* Howe 1975; Ferris and Brown 1981; Miller and Brown 1981), but there has been no uniform consensus in matching names to phenotypes. The most helpful work on this species was by Brown (1964, 1965) who designated lectotypes, illustrated them and fixed type localities for many of the names. Those two papers form a solid starting point for expanded studies of western *C. pegala*. Nevertheless, subsequent workers have largely ignored Brown's work and the original descriptions themselves. This has led to the redescription of one phenotype and the misapplication of a number of names.

The variation of *C. pegala* observed in the Great Basin is obviously complex, thus presenting a taxonomic nightmare. The easiest and most conservative solution is to consider all heavily striated populations as *Cercyonis pegala gabbii* (W. H. Edwards) and all others *Cercyonis pegala nephele* (W. Kirby) as did Scott (1986). Several other combinations have been used in the several papers cited previously. Such simplification ignores the tremendous range of phenotypic variation within the species and undoubtedly masks interesting facets of distribution. Above all, it contradicts the biogeographic and evolutionary history of the species in the Great Basin and elsewhere. It may be merciful (i.e., Emmel *in* Howe 1975) to the taxonomist but it is criminal to the evolutionary biologist to hide these fascinating phenotypes under inappropriate, catchall names.

To aid in sorting out this confusion, I wish to add my observations of the species in the Great Basin. This paper is presented to clear up certain nomenclatural problems concerning Great Basin populations and to make available new names for forthcoming regional books. In addition, the distributions of the various taxa are examined and discussed in the context of the biogeographical history of the Great Basin. This is one of a series of papers (Austin 1986, 1987; Austin and Murphy, *in press*; Austin and Smith, *in press*; Mattoon and Austin, *in press*) to examine patterns of phenotypic variation of Great Basin associated butterflies. Eventually, these studies should lead to a better understanding of patterns observed today in terms of Pleistocene and Holocene events in the region.

Methods

Size is mean forewing length (and range) in mm of 10 specimens (from type series of new taxa; location cited for previously named taxa); "♂" = male and "♀" = female. Capitalized color names are after Smithe (1975, 1981).

THE TAXA

Of the many names applied to populations of *Cercyonis pegala*, the following have been attributed at one time or another to Great Basin populations:

1. *Hipparchia nephele* Kirby (*in* Richardson 1837) - TL: Canada, restricted to western Ontario apparently near the north shore of Lake Huron, vicinity of St. Josephs

- Islands, Ontario, Canada, by Brown (1965, 1966b), type probably lost (Brown 1965).
2. *Satyris ariane* Boisduval (1852) - TL: *dans les forêts* [California], restricted to Tuolumne County, California by Brown (1964), rerestricted to Plumas County, California by Emmel *et al.* (in press a), lectotype male in National Museum of Natural History (Brown 1965).
 3. *Satyris boopis* Behr (1864) - TL: Contra Costa [County, California], type destroyed (Brown 1965), neotype designated by Emmel *et al.* (in press b).
 4. *Satyris gabbi* Edwards (1870) - TL: Oregon, suggested as Lake County by Brown (1964), restricted to the Goose Lake region, Lake County, Oregon, herein, lectotype female in Carnegie Museum (Brown 1964).
 5. *Satyris wheeleri* Edwards (1873) - TL: between the Cascade and Rocky mountains, restricted to Owen's [sic] Lake, Inyo County, California by Brown (1964), lectotype female in Carnegie Museum (Brown 1964).
 6. *Satyris hoffmani* Strecker (1873) - TL: Owen's [sic] Lake, Nevada [=California], lectotype male (designated herein) at Field Museum of Natural History.
 7. *Satyris stephensi* Wright (1905) - TL: northeastern California, suggested as probably Modoc County by Comstock (1924a) and Miller and Brown (1981), restricted to between Lake City and Cedarville, Surprise Valley, Modoc County, California, herein, lectotype female at California Academy of Sciences (Tilden 1975).
 8. *Cercyonis pegala blanca* Emmel and Mattoon (1972) - TL: Dufurrena Ranch, Humboldt County, Nevada, holotype male at University of Florida, Gainesville.

I have examined the types (holotype, lectotype or syntypes) of all the above names except *H. nephele* (lost or unrecognizable, Brown 1965) and *S. boopis* (none exists, Brown 1965). Further, I examined topotypes of all of the above named entities, other series of these taxa, series of unnamed phenotypes in various collections, and amassed extensive material from much of the Great Basin.

THE PHENOTYPES

Most (or all) populations of *Cercyonis pegala* exhibit considerable variation involving color and pattern (e.g., Edwards 1884, Mather 1966) and these have complex patterns of distribution and intergradation (e.g., Shapiro 1966, 1974). Care must thus be exercised in interpreting a single type or short syntype series. This is particularly true when the location of capture was imprecise, as was common for much of the old material on which many of the names were based. I had originally hoped that most or all of the phenotypes present in the Great Basin would fall neatly within the concepts of named taxa. Unfortunately, this was not the case and a number of new taxa will be proposed.

To facilitate the following descriptions, general characteristics of the species are given here (see also Scudder 1889, Emmel 1969). The antennae are black, annulated with white and the club is largely orangish. The palpi are black above and below and whitish laterally with a central black line on their outer faces. The head, body and abdomen are dark gray above and paler beneath (females are more grayish brown). The legs are whitish with some gray scales. The dorsal wing surface of males is a relatively dark brown; females are paler brown. In most populations, the forewing has two large, black submarginal ocelli centered in cells M_1 - M_2 and CuA_1 - CuA_2 , these usually with white pupils and often encircled with yellowish and/or set in a paler (yellow or yellow-brown) field. The pupils (especially on females and on the ventral surface) often appear bluish away from their centers; this is due to translucent whitish scales overlying black ones. Males have a three-parted stigma, slightly darker than ground color, distal to the discal cell in the cells posterior to vein CuA_1 on the forewing. The dorsal hindwing usually has an ocellus in cell CuA_1 - CuA_2 and often smaller ocelli in adjacent cells, some or all encircled with yellowish and often with white pupils. The submarginal area may be yellowish or of ground color. Both wings have thin terminal and marginal lines, a broader submarginal line and sometimes a postmedian line, these darker than ground color and developed to various degrees.

The ventral surface is paler than the dorsum and crossed by dark striations, the width

of which varies. The forewing has the ocelli of the dorsum repeated but with larger pupils. The ocelli are encircled with yellow and then a thin line of brown and often set in a pale, weakly striated field. The hindwing may or may not have submarginal ocelli. When fully developed, these are six in number and arranged in two groups of three; the central ocellus of each group is the largest. These usually have white pupils (at times with blue) and are encircled as on the forewing. The basal portion of the hindwing may be of the same color as the distal portion, may be darker, or may appear darker because of a greater concentration of striations. Both wings have the various lines of the dorsal surface and, often, at least a trace of a postbasal line. Differences between phenotypes involve overall color, amount of yellow, size of forewing ocelli, presence, shape and size of hindwing ocelli and prominence of lines and striations.

General descriptions and diagnoses are given for Great Basin phenotypes emphasizing their overall differences. Several unambiguous characters which vary within and between populations were examined in greater detail as listed below. Information is for the wings on the right side since there is often asymmetry in these characters.

1. the number of dark spots and ocelli on the dorsal hindwing (Table 2).
2. the frequency of specimens with blue associated with the pupil in at least one of the ventral forewing ocelli (Table 2).
3. the size (mm) of the dorsal forewing ocelli and the ocellus in cell CuA_1-CuA_2 on the dorsal hindwing (greatest length parallel to veins, Table 3).
4. the number of ocelli or traces thereof on the ventral hindwing (Table 2).
5. the number of ocelli on the ventral hindwing which were complete with pupil (Table 2).
6. the condition of the posterior two ocelli of the anterior group on the ventral hindwing (Table 2). This was scored as "fused" if the black portions of the two touched and as "not fused" if the yellow margins of one or both intervened (or one ocellus was absent).
7. the shape of the central ocellus of the anterior group on the ventral hindwing (Table 2). This was scored (by eye) as "oval" proximal-distal axis of the black portion longer than anterior-posterior axis) or "not oval" (round or absent).

Cercyonis pegala nephele (W. Kirby)
Figs. 1-4, 9-12

DIAGNOSIS. Size ♂ = 23.9 (22.5-25.1), size ♀ = 27.6 (26.4-29.0). (sample from Juneau County, Wisconsin). Males are dark brown (Prout's Brown to Hair Brown) on the dorsum and females are somewhat paler (Verona Brown to Prout's Brown). The forewing has two black, usually white-pupiled, ocelli as usual; these are relatively small and not or very indistinctly encircled with pale brown on males and moderately-sized and more distinctly (often faintly yellowish) outlined on females. These are in a submarginal patch scarcely paler than ground color on males and in a somewhat more perceptible area on females. The lines on the forewing are all but obsolete except for the submarginal which is a shade darker than ground color. The hindwing of both sexes has a single (or none on some females), often white-pupiled, ocellus in cell CuA_1-CuA_2 . The submarginal line is as on the forewing; the terminal and marginal lines are thinly present.

The ventral forewing of males is medium brown (Brussels Brown to Prout's Brown) with the dorsal ocelli repeated but with larger white pupils and encircled narrowly with dull yellowish (Yellow Ocher to Warm Buff). The basal area is finely striated. The postmedian and submarginal lines are distinct and the outer lines are faint. The hindwing is darker (near Raw Umber, color 223) than the forewing and finely striated. The lines are as on the forewing except the marginal line is more prominent. There are usually six, moderately-sized, round ocelli with white pupils and encircled with dull yellowish. The ventral surface of females is paler than the male (both wings near Army Brown); the basal portion of the hindwing is often darker (Mars Brown). The forewing ocelli are more broadly encircled with yellowish and the pupils usually have bluish distally. The lines are more prominent than on males. The hindwing has a variable number of ocelli (0-6, usually 5 or fewer). Both ventral wings have broader striations than the male.

DISTRIBUTION. There is much disagreement as to the extent of variability that should be recognized within the concept of *C. p. nephele*. Populations from the Great Lakes area from at least central Minnesota to northern New York and adjacent southern Canada are strictly typical (Juneau County, Wisconsin, material described above).

DISCUSSION. In general, the various phenotypes without a yellow forewing patch from the northeastern and northcentral United States northward have been assigned here. Emmel (1969, in Howe 1975) included these brown phenotypes along with all or most of those with a yellow patch in *C. p. pegala*. Scott (1986) included all brown *C. pegala* without strong striations in *C. p. nephele* and all those with a distinct yellow patch in *C. p. pegala*. A complete review of the several concepts and of the variability involved is well beyond the scope of this paper. The taxon is included in this discussion because of the apparent assignment of the name to certain Great Basin populations (Scott 1986). These latter, I believe, are closer to phenotypes in California than to *C. p. nephele* (see below).

***Cercyonis pegala ariane* (Boisduval)**
Figs. 17-20, 23-26

DIAGNOSIS. Size ♂ = 24.2 (23.1-25.2), size ♀ = 26.6 (26.0-27.2 N = 2). (sample from Sierra and Plumas counties, California). This is a relatively dark brown (males Raw Umber, color 223 to Sepia, color 219; females Prout's Brown to Raw Umber, color 223) phenotype with moderate-sized forewing ocelli and very little yellow associated with the forewing ocelli or on the hindwing. The dorsal hindwing usually has one ocellus. The ventral surface is brownish (males Drab to Natal Brown; females Light Drab to Fawn) with some white distally on the hindwing (especially on females) and crossed with striations of medium width. The ventral hindwing has six (or fewer) small ocelli, these usually appearing as set in a brownish smudge. The postmedian and postbasal lines are fairly well developed.

DISTRIBUTION. This taxon occurs in the northern Sierra Nevada of California, mostly on the west slope. Populations with a similar phenotype occur northward into Oregon. Studies of the phenotypes of all the Pacific Coast states are needed before the remainder of the distribution of *C. p. ariane* can be detailed.

DISCUSSION. The name *Cercyonis pegala ariane* has been applied to a wide range of phenotypes and commonly to ones from the western Great Basin (Comstock 1927; Dornfeld 1980; Emmel 1969, in Howe 1975; Garth and Tilden 1986; Tilden and Smith 1986). Nothing, however, could be further from the truth; it does not occur (except as apparent intermediates, see below) east of the Sierra Nevada. This misapplication of the name resulted from not consulting the original description (Boisduval 1852), Oberthur's (1914) figures of Boisduval's specimens, Brown's (1965) designation and figure of the lectotype male and subsequent discussion, or the syntypes (including the lectotype) themselves in the National Museum of Natural History. These all indicate that *Satyrus ariane* refers to a butterfly with small ocelli (some often absent) on the ventral hindwing (especially on females) and a somewhat bicolored ventral surface without the coarse striations seen on many of the Great Basin phenotypes of *C. pegala*. Brown (1965) restricted the type locality to Tuolumne County, California on the west slope of the Sierra Nevada. Based on its known distribution (*C. pegala* does not occur in Tuolumne County) and Lorquin's early travels in California, this is incorrect (*vide* J. F. Emmel). The types were more likely from the Plumas-Sierra counties area further north. Comparison of the syntypes with material from this latter region further suggests this. Emmel *et al.* (in press a) will restrict the type locality to Plumas County, California.

Most figured "*Cercyonis pegala ariane*" are misdetermined: all Comstock's (1927) "*C. ariane*" are *C. p. stephensi* as are Dornfeld's (1980) or *C. p. gabbii*. Those in Holland (1931) are near *C. p. boopis* (plate 26, figs. 5, 6) or near *C. p. gabbii* (plate 63, fig. 20). One of those in Howe (1975; plate 3, fig. 3) is near *C. p. ariane* but the other (plate 3, fig. 15) is of the undescribed Carson Valley, Nevada, phenotype as are both specimens illustrated by Tilden and Smith (1986). The lectotype male was illustrated by Brown (1965); this specimen probably served as the model for Oberthur's (1914) figure.

Cercyonis pegala wheeleri (W. H. Edwards)
Figs. 21, 22, 27, 28

DIAGNOSIS. Size δ = 28.2 (N = 1), size ϕ = 32.0 (N = 1). (Owens Lake, California). This highly distinctive phenotype is characterized by an invariably double apical ocellus on the forewing [all 20 specimens examined by Edwards (1873) and Strecker (1873); 11 examined by me]. No other *C. pegala* regularly has doubled forewing ocelli (occasional specimens from other populations may have a doubled ocellus on one or both forewings; when present, this may involve the anterior or posterior ocellus, Table 1). The pale ventral surface is crossed by coarse striations and the ventral hindwing has six, relatively large, submarginal ocelli, the central one of the anterior group is elongate.

DISTRIBUTION. This taxon, now apparently extinct (Comstock 1927, Emmel 1969), was known only from the Owens Lake region of east-central California (Fig. 214). Recent intensive searches of the area have failed to locate an extant population (*vide* J. F. Emmel).

DISCUSSION. Among Great Basin *C. pegala*, the easiest names to deal with are Edwards' *Satyris wheeleri* and Strecker's straight synonym *Satyris hoffmani*. These names were based on nine females (Brown 1964; called males by Edwards 1873) and one male and ten females (Strecker 1873), respectively, from the same series taken by Ferdinand Bischoff during the Wheeler Expedition of 1871 (Brown 1964, Mead 1875). The type locality was confused from the beginning. Edwards (1873) had no locality data other than "between the Cascade and Rocky Mountains" and other material taken "later by H. W. Henshaw at Apache, Arizona" (Edwards 1884). This latter statement is a mystery as nothing like *C. p. wheeleri* occurs today in northern Arizona and Henshaw apparently did not join the Wheeler Expedition until 1872 nor explore California (Brown 1955, 1966a). Strecker (1873) reported it taken at "Owen's Lake, Nevada" and credited W. J. Hoffman with the collection even though Bischoff is named on his specimen labels. Comstock (1924a, 1927) questioned whether this taxon was actually collected in California. Holland (1931) said that the taxon was "taken by the Wheeler Expedition in Arizona." Brown (1957) suggested the location as southwestern Utah or possibly Cottonwood Springs [Clark County], Nevada. Later, however, Brown (1964) showed that Strecker's (1873) type locality was correct (but in California, not Nevada as stated in the original description). The two names have been variously considered as synonyms (Emmel 1969, *in* Howe 1975) of *C. p. ariane* or as representing a recognizable entity (Comstock 1924b, 1927; dos Passos 1964; Miller and Brown 1981). I concur with the latter opinion as the phenotype is constant and like no other known population of the species.

The 20 specimens of the two type series [plus possibly a few more taken at the same time; *e.g.*, Mead evidently had one (Mead 1875)] are apparently the only ones which existed. Edwards must have had a male before him at some time as he (1874) described and illustrated both sexes; this may have been from the material he received "later". The lectotype female of *S. wheeleri* (designated by Holland 1931, see Brown 1964) and an additional female and a male are at the Carnegie Museum of Natural History. A male and two females (all labeled "orig. type") are in the Strecker collection at the Field Museum of Natural History. Three additional females are at the National Museum of Natural History and two are at the American Museum of Natural History. The male in the Strecker collection is here designated the lectotype of *Satyris hoffmani* and will be labeled with a red printed label: Lectotype/*Satyris hoffmani*/Strecker/designated by/G.T. Austin, 1991.

There are several illustrations of *C. p. wheeleri* published by Brown (1964), Edwards (1884, his plate was the basis for the figures in Mead 1875, the latter copied by Comstock 1927), Holland (1931) and Strecker (1874).

Cercyonis pegala gabbii (W. H. Edwards)
Figs. 29-48

DIAGNOSIS. Size δ = 25.2 (24.3-26.0), size ϕ = 28.1 (27.0-30.8) (sample from Goose Lake, Lake County, Oregon). Males of *C. p. gabbii* are dark brown (Raw Umber, color 223 to Sepia, color 219) above with two white-pupiled, black ocelli on the forewing (the

TABLE 1. Frequency of doubled anterior (ant.) and posterior (post.) forewing ocelli on Great Basin *Cercyonis pegala*.

TAXON	male			female		
	N	% doubled		N	% doubled	
		ant.	post.		ant.	post.
<i>C. p. gabbii</i>	163	0.0	0.0	21	0.0	0.0
<i>C. p. stephensi</i>	386	0.0	1.3	161	0.0	0.0
<i>C. p. paucilineatus</i>	167	3.6	0.6	181	12.2	1.1
<i>C. p. carsonensis</i>	181	0.6	0.6	184	0.0	0.0
<i>C. p. utahensis</i>	150	0.7	0.7	68	5.9	1.5
<i>C. p. pluvialis</i>	150	0.0	0.0	63	0.0	0.0
<i>C. p. wheeleri</i>	3	100.0	0.0	8	100.0	0.0
<i>C. p. walkerensis</i>	208	0.0	0.0	71	0.0	2.8
<i>C. p. paludum</i>	364	0.3	0.0	240	0.8	1.3
blend populations	176	0.0	0.0	108	0.0	0.0
TOTAL (excluding						
<i>C. p. wheeleri</i>)	1945	0.5	0.4	1097	2.6	0.7

anterior one is the smallest). These are usually incompletely and narrowly outlined with dull yellowish and are set in a very slightly paler brown (usually not immediately noticable) submarginal field. The dorsal hindwing has one black, white-pupiled ocellus (frequently encircled narrowly with dull yellow) and often small blind ocelli anteriorly and/or posteriorly. The submarginal area of the hindwing is not paler than the disc. Each wing has an indistinct, nearly blackish, submarginal line.

The ventral ground color is grayish brown (Light Drab to Fawn Color). The wings are coarsely striated with brown streaks; these are heaviest at the base, thus causing the outer third of each wing to appear paler. An irregular brown postmedian line is distinct on both wings. The ocelli of the forewing are larger and more evenly-sized than on the dorsum and are broadly outlined with yellowish. The pupils rarely have a trace of blue. The hindwing usually has a full complement of six, pupiled ocelli. The ocelli are thinly outlined with yellow and then brown. On occasion, the anterior set of three is incomplete and/or with blind ocelli and the central one is often oval.

Females are paler brown (Brussels Brown to Prout's Brown) above than males. The uneven-sized ocelli of the forewing are larger than on males and set in a yellowish to tan field. The hindwing has ocelli (one to three) as on the male, the largest is white-pupiled and all are set in a tan field that is often somewhat yellowish distally.

The venter is pale grayish brown (Cinnamon-Drab to Fawn Color) with heavy dark brown striations, these weaker on the outer third of the wings giving a two-toned effect as on males. The ocelli of the forewing are broadly encircled with yellow in a tan or yellowish field. The pupils frequently have a trace to moderate amount of associated blue. The usually white-pupiled ocelli of the hindwing are as on the male, with a greater tendency towards reduction or absence of the anterior set of three and, occasionally, the anteriormost of the posterior set. A brown postmedian line is present on both wings; this is often faint on the hindwing.

DISTRIBUTION AND PHENOLOGY. This taxon occurs west of the Warner Mountains in the Goose Lake area of Modoc County, California, and Lake County, Oregon, south to Likely, Modoc County, California (at the very southern end of the Goose Lake Basin) and west as a slightly darker phenotype to the Tulelake region of Siskiyou County, California (this latter may eventually prove to be an intermediate phenotype when populations to the west and north are studied in more detail, Fig. 214). Its distribution to the northwest (a different phenotype occurs at Klamath Falls, Klamath County, Oregon) requires further study. The reported occurrence in Utah (Emmel 1969, Emmel and Mattoon 1972, Holland 1931) is incorrect and refers to a phenotype to be described below. The assignment of this name to various Nevada populations (Austin 1985b) is likewise

erroneous. The flight period extends from early July to early August.

DISCUSSION. The oldest name correctly applied to populations of *C. pegala* from the Great Basin region is *Satyrus gabbii*, described from a pair taken by "Prof. [William More] Gabb" in Oregon (Edwards 1870). Based on the travels of Gabb, Brown (1964) suggested Lake County, Oregon as the type locality. Assignment of a single specimen of *C. pegala* to a particular population is difficult due to the intrapopulation variability of the species. Long series from several locations in southern Oregon and adjacent northeastern California and northwestern Nevada were examined and compared with the lectotype female (designated by Brown 1964) of *Satyrus gabbii* at the Carnegie Museum of Natural History. A series from the northeast side of Goose Lake, Lake County, Oregon contains several specimens closely matching the lectotype. The phenotypes of populations southward into Modoc County, California are also nearly identical. Populations from adjacent areas to the north and east (Summer and Crump lakes, Lake County, Oregon) have considerably more yellow associated with the forewing ocelli, larger hindwing ocelli, a tendency towards more submarginal yellow on the dorsal hindwing, and a paler and more contrasting ventral surface. These are all *C. p. stephensi* (see below). Material from the west slope of the Warner Mountains (Pine Creek), Modoc County, California is similar but males are somewhat darker and with less dorsal yellow than typical of *C. p. gabbii* and the dorsal hindwing ocelli are often absent on females. These are included within the concept of *C. p. gabbii*. Thus, the Goose Lake region is a reasonable restriction of the type locality of *Satyrus gabbii*.

The literature has nearly uniformly included *C. p. gabbii* as a synonym of *C. p. ariane* (Comstock 1924b; Emmel 1969, in Howe 1975; Miller and Brown 1981) but dos Passos (1964) considered it a recognizable subspecies. Austin (1985b) was unsure if this name applied to western Great Basin populations in Nevada. Scott (1986) used *C. p. gabbii* to represent all western populations with large ventral hindwing ocelli, coarse ventral striations and a flush of yellow on the ventral forewing.

The lectotype female of *C. p. gabbii* was illustrated by Brown (1964). A specimen illustrated by Holland (1931, plate 63, fig. 20) as *C. p. ariane* may also be of this taxon but his figured *C. "gabbii"* is of an undescribed phenotype from Utah (see below). The *C. p. gabbii* illustrated by Scott (1986) are *C. p. stephensi*.

Cercyonis pegala stephensi (W. G. Wright)

Figs. 49-68

DIAGNOSIS. Size ♂ = 27.0 (25.6-28.4), size ♀ = 29.5 (28.6-31.0). (sample from Dufurrena Ranch, Humboldt County, Nevada). Males of *C. p. stephensi* are brown (Hair Brown to Raw Umber, color 223) above. The forewing has relatively large, black, white-pupiled ocelli, usually outlined moderately and completely with yellowish. The hindwing has the usual large, white-pupiled ocellus distinctly outlined with yellow and up to five additional ocelli; the one immediately preceding the largest is also often white-pupiled, and most are outlined with yellow. The submarginal field of the forewing and (usually) hindwing are noticeably paler brown than the basal areas of the wings and often are somewhat yellowish.

The ventral surface is similar to that of *C. p. gabbii* but paler (Light Drab to Drab); some specimens have a very pale gray to almost white ground color. The ventral ocelli on both wings are larger and more broadly outlined with a paler yellowish than dorsal ocelli. The pupils of the forewing ocelli infrequently have a trace of associated blue. There is almost no tendency for a reduction or blindness of the ocelli on the hindwing. These are large and those of the anterior group are often fused. The forewing ocelli are set in a distinctly yellowish to yellowish-brown field. The postmedian lines on both wings are broad and there is often a distinct "V"-shaped mark in the discal cell of the hindwing.

The dorsum of females is tan to medium brown (Fawn Color to Hair Brown). The ocelli of the forewing are usually large and set in an invariably pale yellowish field; this yellow extends distally along the veins, occasionally to the outer margin and as a marginal dusting. The ocelli of the hindwing are as on males and set in a yellowish or yellowish

(distally) and tan field extending distally along the veins and in the marginal area as on the forewing.

The ventral surface has a very pale (Drab-Gray to Light Drab), often pale yellowish (near Cream Color) ground color with heavy brown striations, these weaker distally as on *C. p. gabbii*. The ocelli of the forewing are similar to *C. p. gabbii* but are set in a yellow field; the encircling yellow does not contrast and is often fused. The pupils infrequently have associated blue. The ocelli of the hindwing are usually completely represented and large. The postmedian line, especially on the hindwing, is prominent and there is usually a postbasal line, at least as a shallow "V" in the discal cell.

C. p. stephensi differs from *C. p. gabbii* in several respects. Males of *C. p. stephensi* are paler dorsally and often have a larger complement of ocelli on the hindwing. The venter is paler (whitish), without a reduction of the ocelli on the hindwing and with coarser striations. Similarly, female *C. p. stephensi* are paler; the ocelli of the forewing are set in a yellow field, this yellow extending distally along the veins, and there is much yellow on the hindwing. *C. p. gabbii* females are darker; the ocelli of the forewing are usually in a brown (occasionally yellow-brown) field and have little or no yellow on the hindwing. The ventral surface of the two differ as on the males. In addition, the ocelli of the forewing of *C. p. stephensi* lie in a yellow field; those of *C. p. gabbii* are usually in a tan field.

C. p. stephensi is the known extreme in overall paleness for the species. The name should be restricted to those populations where the dorsal ground color is pale, often yellowish brown on females, the submarginal areas of both wings on females are nearly always yellow, and the venter is whitish and very heavily striated. To the north, *C. p. stephensi* becomes darker with less yellow (see also Newcomer 1965) and has fewer ocelli on the dorsal hindwing. This apparently reflects influence from darker colored populations of other taxa in central Oregon. To the west occur *C. p. gabbii* and phenotypes allied to *C. p. ariane*. To the east in north-central Nevada is an allied but less heavily marked phenotype to be described later. To the south, in the valleys of the upper Truckee and Carson rivers on the lower east slope of the Carson Range is another phenotype which will also be described below.

DISTRIBUTION AND PHENOLOGY. This taxon is known from northeastern Nevada (Dufurrena Ranch, Humboldt County), southern Oregon (Summer and Crump lakes areas, Lake County; the Crump Lake population is intermediate towards the darker phenotype from further north in Oregon) and northeastern California (Surprise Valley, Modoc and Lassen counties, Fig. 214). The flight period extends from late June to late August.

DISCUSSION. The identity of *Satyrus stephensi* has been a comedy of errors from the beginning. Wright (1905) made the first mistakes by figuring a female as a male, figuring males as "*Satyrus gabbii*" and indicating the type locality as simply "northeastern California" in an area that "is a sort of Dead Sea region of wide, sandy wastes, draining into dead salt lakes and marshes that have no outlets." Comstock (1924a) confirmed with the collector of the types, Frank Stephens, that they were taken "a few miles from the Nevada line, and some thirty miles south of the Oregon line" (this is between present-day Lake City and Cedarville). Later, Stephens reported (Comstock 1924a) this as "some miles south of the southernmost Alkali Lake, in Modoc Co." in August 1894. This whole general area perfectly matches Wright's (1905) description of the type locality for *C. p. stephensi* and I further restrict this locality to between Lake City and Cedarville, Surprise Valley, Modoc County, California.

Comstock found *C. pegala* at Goose Lake and Fort Bidwell, both in Modoc County. He correctly pointed out (1924a) that Wright's (1905) male was a female and his male *Satyrus gabbii* were male *Satyrus stephensi* and suggested that the name "stephensi" be retained to refer to the extremely light female form of *Cercyonis gabbii*. Comstock's (1924a) plate showing the "range of variation" of these included specimens from both Goose Lake and the Fort Bidwell area. [Note that among Comstock's material, there are putative Fort Bidwell specimens which appear indistinguishable from Goose Lake material. Since subsequently collected material from the Fort Bidwell area is all undoubtedly *C. p. stephensi*, some of Comstock's specimens must be mislabeled (perhaps when labels were removed for photographs). This combined with his "range of variation" plate has

undoubtedly perpetuated the confusion surrounding the identities of *C. pegala* from northeastern California]. Later, Comstock (1924b) considered *Satyrus gabbii* as a synonym of *C. p. ariane* with "stephensi" as a pale female form. Tilden (1975) called the females illustrated by Wright (1905) *Cercyonis pegala ariane*, female form *stephensi*, also recognized the "male" was actually a female, and designated the female figured as "number 249b" as the lectotype (deposited at the California Academy of Sciences). He identified the males (Wright's figures 250, 250b) as *Cercyonis pegala ariane* form *gabbii*. Newcomer (1965) collected various populations of *C. p. stephensi* and *C. p. gabbii* but thought it doubtful that Stephens entered Surprise Valley. These concepts (extended to include western Great Basin phenotypes, see under *C. p. ariane* above) have more or less persisted to the present (Comstock 1927; Dornfeld 1980; Emmel 1969, in Howe 1975; Garth and Tilden 1986; Scott 1986; Tilden and Smith 1986). What has not been understood was that there are actually two rather pale phenotypes of *C. pegala* in Modoc County, California: *C. p. stephensi* from the Surprise Valley, east of the Warner Mountains and *C. p. gabbii* from the Goose Lake region and southward, west of the Warner Mountains.

C. p. stephensi was renamed *Cercyonis pegala blanca* by Emmel and Mattoon (1972); this is herein (also Austin 1985b, Ferris 1989) considered a subjective junior synonym of *Satyrus stephensi* (e.g., compare figures of the types in Wright 1905 and in Emmel and Mattoon 1972). Miller and Brown (1981) recognized *C. p. stephensi* as distinct but apparently for the wrong reasons as they also recognized *C. p. blanca*. They were aware that western Great Basin *C. pegala* were not *C. p. ariane* and their raising of the name "stephensi" from synonymy appears to have been an attempt to rectify such. This did nothing but further complicate the situation.

This butterfly was illustrated by Comstock (1927, as *C. ariane* and *C. ariane f. stephensi*), Dornfeld (1980, as *C. p. ariane* form "stephensi"), Emmel and Mattoon (1972, as *C. p. blanca*), Ferris and Brown (1981, as *C. p. blanca*), Scott (1986, as *C. p. gabbii*) and Wright (1905, plate 23, fig. 249, b, c are correctly indicated but all are females; fig. 250, b are indicated as *S. gabbii*).

Cercyonis pegala carsonensis ssp. nov.

Figs. 69, 70, 81, 82, 93-112

MALE. Size = 26.5 (25.0-28.4). Dorsum brown (Prout's Brown to Burnt Umber); forewing with two black submarginal ocelli with minute white pupils, posterior ocellus same size to larger than anterior, both outlined narrowly with yellowish (Trogon Yellow), sometimes obscure especially proximally; terminal, marginal and submarginal lines indistinctly darker than ground color. Hindwing with thin marginal and broader submarginal blackish brown lines; white-pupiled (rarely blind) black ocellus in cell CuA₁-CuA₂, this smaller than forewing ocelli, usually outlined with Trogon Yellow at least distally; often small to minute, blind ocelli (sometimes outlined as main ocellus) in one or both adjacent cells and less often extending anteriorly to cell M₂-M₃; fringes brownish on both wings, similar to ground color.

Ventral surface paler than dorsum (Drab to Brussels Brown, often with grayish cast especially on hindwing); forewing ocelli similar to those on dorsum, pupils white but larger than on dorsum and frequently with trace of blue, yellow outlines broader and occasionally fusing narrowly between ocelli, this yellow margined indistinctly with brown, field containing ocelli lightly striated; basal portion of wing moderately striated; postmedian line distinct; thin, dark brown terminal, marginal and submarginal lines. Hindwing moderately striated; terminal, marginal, submarginal and postmedian lines as on forewing; nearly always six ocelli with small white pupils, outlined with Trogon Yellow and then indistinctly with brown, posterior group of ocelli usually roundish and separate, anterior group variable with center ocellus usually drawn out proximally-distally, often fused with ocellus posterior to it.

FEMALE. Size = 29.0 (27.0-31.0). Dorsum pale brown (Prout's Brown to Mikado Brown); forewing with submarginal ocelli as male but larger, outlined more broadly with Trogon Yellow, this usually fused into relatively distinct (but not sharply defined) yellowish

field; terminal, marginal and submarginal lines as on male. Hindwing with ocelli as on male; submarginal area usually Trogon Yellow, this grading gradually into ground color proximally; terminal, marginal and submarginal lines as on male.

Ventral surface paler than dorsum (Cinnamon-Drab to Fawn Color); markings much as on male but field around forewing ocelli paler than ground color, usually yellowish; yellow around ocelli more often fused. Hindwing marked as male; occasional ocelli absent and less fusion among anterior group; area distal to postmedian line whiter than basal area.

TYPES. Holotype ♂ - NV: Douglas Co.; Carson Valley, Scossa Ranch, 26 July 1981, leg. G. T. Austin. Allotype ♀ - same data as holotype. Paratypes (475 ♂, 428 ♀; all same location as holotype; leg. G. T. Austin unless noted otherwise) - 12 July 1989 (8 ♂), 13 July 1980 (2 ♂), 18 July 1981 (108 ♂, 22 ♀), 18 July 1985, leg. G. & A. Austin (46 ♂, 3 ♀), 20 July 1980 (1 ♂), 23 July 1972, leg. P. Herlan (6 ♂, 4 ♀), 24 July 1982 (16 ♂, 3 ♀), 24 July 1984 (44 ♂, 15 ♀), 26 July 1981 (30 ♂, 80 ♀), 27 July 1980 (50 ♂, 3 ♀), 27 July 1983, leg. G. Harjes (7 ♂, 4 ♀), 1 Aug. 1988 (27 ♂, 17 ♀), 3 Aug. 1980 (21 ♂, 8 ♀), 5 Aug. 1980, leg. G. Harjes (25 ♂, 16 ♀), 5 Aug. 1988, leg. P. Savage (25 ♂, 20 ♀), 6 Aug. 1981 (6 ♂, 33 ♀), 8 Aug. 1978, leg. G. Harjes (3 ♀), 10 Aug. 1980 (9 ♂, 32 ♀), 11 Aug. 1964, leg. P. Herlan (36 ♀), 11 Aug. 1978 (8 ♂, 31 ♀), 12 Aug. 1978 (2 ♂, 11 ♀), 13 Aug. 1978 (1 ♂, 4 ♀), 13 Aug. 1979 (14 ♂, 38 ♀), 14 Aug. 1973, leg. A. Pinzl (1 ♂), 14 Aug. 1973, leg. G. Harjes (1 ♀), 15 Aug. 1969, leg. P. Herlan (2 ♀), 17 Aug. 1980 (7 ♂, 25 ♀), 20 Aug. 1985, leg. G. Harjes (5 ♀), 23 Aug. 1981 (3 ♀), 26 Aug. 1976, leg. P. Herlan (1 ♀), 26 Aug. 1976, leg. G. Harjes (4 ♀), 26 Aug. 1983 (8 ♂, 1 ♀), 27 Aug. 1980 (2 ♀), 28 Aug. 1975, leg. P. Herlan (2 ♀), 3 Sept. 1980, leg. G. Harjes (1 ♂, 1 ♀), 8 Sept. 1984 (1 ♂).

DEPOSITION OF TYPES. The holotype, allotype and eight paratypes are deposited at the Allyn Museum of Entomology, Sarasota, Florida. Numerous paratypes are at the Nevada State Museum, Carson City. The remaining paratypes will be distributed to other collections.

TYPE LOCALITY. NEVADA: Douglas County; Carson River Valley, Scossa Ranch, Nevada State Route 206, 3.6 miles south of Nevada State Route 207, 1463 m, T12N R19E S26 on USGS Freel Peak, Calif.-Nev. 15' quadrangle. The area is a lush, marsh area at the base of the Carson Range. Adults take nectar commonly from a variety of white and yellow flowers (Apiaceae, Asteraceae).

DISTRIBUTION AND PHENOLOGY. *C. p. carsonensis* occurs in marshes of the western Great Basin at or near the base of the Carson Range, especially in the Carson Valley from near Stewart, Carson City, Nevada southward into extreme east-central Alpine County, California and the Gardnerville area, Douglas County, Nevada (Fig. 214). There are a few specimens labeled as from the Reno area, Washoe County, Nevada (no recent collections). A population north of Reno in the Red Rock area, Washoe County, Nevada approaches this taxon in phenotype (see below). The single brood flies from early July to early September. Males may appear more than a week before the first females are seen and outnumber them for the first half of the flight season, after which females are more frequently encountered than males (see type data for 1980 above).

ETYMOLOGY. This taxon is named after the Carson River Valley, the upper part of which forms most of the subspecies' range.

DIAGNOSIS AND DISCUSSION. The dorsum of males is similar to that of *C. p. gabbii* but with less contrasting ocelli. It is most similar to *C. p. stephensi* but has, on the average, less yellow associated with the dorsal ocelli of both sexes and less well developed lines on both surfaces. The venter is darker than both the above phenotypes, lacking the grayish aspect of *C. p. gabbii* and the whitish or pale yellowish of *C. p. stephensi*. The ocelli of the forewing and their yellow outlines are more strongly contrasting with the darker ground color than on the other two. There are fewer ocelli on the dorsal hindwing than on *C. p. stephensi*. The ocelli of the ventral hindwing are completely represented as on *C. p. stephensi*, but are often less well developed (all usually present but outer ones of each group are smaller). The center one of the anterior group is nearly always large and is often elongate (sometimes grotesquely so) as on *C. p. stephensi*. All hindwing ocelli are more narrowly outlined with a deeper, nearly orangish, yellow. On *C. p. gabbii*, there is a tendency towards a reduction in number of ocelli and less tendency for these to be elongate. The

postmedian line averages less distinct than on either *C. p. gabbii* or, especially, *C. p. stephensi*.

Females are darker brown with much less yellow on the dorsum than *C. p. stephensi* and resemble the paler females of *C. p. gabbii*. The ground color beneath is more tan than the whitish to pale yellowish color of *C. p. stephensi* and paler and less bicolored on the hindwing than *C. p. gabbii*. As on the male, the ocelli are nearly always completely represented and resemble (large, tendency towards elongation) those of *C. p. stephensi* but are more narrowly encircled with a duller yellow.

C. p. carsonensis was illustrated by Howe (1975, plate 3, fig. 15) as *C. p. ariane* form "stephensi" and by Tilden and Smith (1986) as *C. p. ariane* and *C. p. ariane* form "stephensi".

Cercyonis pegala paucilineatus ssp. nov.

Figs. 71, 72, 83, 84, 113-132

MALE. Size = 26.1 (25.2-27.6). Dorsum brown (Prout's Brown to Sepia, color 219); forewing ocelli relatively large with small white pupils, ocelli encircled (sometimes faintly) with Warm Buff, anterior ocellus with some tendency to be doubled (5% of type series); inconspicuous terminal and marginal lines slightly darker than ground color; submarginal and postmedian lines usually faint or absent. Hindwing with moderately-sized ocellus in CuA_1-CuA_2 encircled with Warm Buff, often flanked anteriorly with smaller ocellus (less commonly anteriorly and posteriorly); thin terminal and marginal lines, broader submarginal line; fringes grayish brown, slightly paler than ground color, whitish posteriorly on forewing and anteriorly on hindwing.

Ventral surface very pale brown (Light Drab to Drab Gray) sometimes with slight yellowish tinge (Tawny-Olive) and moderately striated; forewing ocelli encircled with yellowish, pupils infrequently with trace of blue; outer lines as on dorsum, submarginal line somewhat more prominent, postmedian line weakly developed. Hindwing with two groups of three, white pupiled ocelli, these of moderate size, those of anterior group often elongate but rarely fused; lines weakly developed.

FEMALE. Size = 28.6 (26.7-30.9). Dorsum pale brown (near Fawn Color to Dark Drab); forewing ocelli in pale yellow (Chamois) field, this quite variable in extent, anterior ocellus sometimes doubled (13% of type series); terminal and marginal lines as on male but more conspicuous on paler ground color, submarginal line present or absent, postmedian line present but not prominent. Hindwing with single ocellus in cell CuA_1-CuA_2 (rarely absent, rarely smaller ocelli anteriorly or posteriorly in adjacent cells); submarginal area usually pale yellow grading into ground color proximally; thin terminal and marginal lines and broader submarginal line prominent, postmedian line faint to absent; fringes of ground color, paler or whitish posteriorly on forewing and anteriorly on hindwing.

Ventral surface pale grayish brown (Pale Horn Color to Drab Gray) distally, slightly darker (Light Drab) proximally sometimes with slight yellowish cast and moderately striated; forewing with ocelli encircled with pale yellow, this often fusing and set in large enclosing field, pupils usually with moderate amount of associated blue; all lines weakly developed. Hindwing with variable number of ocelli (0-6), these never large, center one of anterior group often elongate when present, almost never fused with ocellus posterior to it; all lines weakly developed.

TYPES. Holotype ♂ - NV: Humboldt Co.; Quinn River V., US 95, 3.8 mi. S Orovada, 22 July 1984, leg. G. T. Austin. Allotype ♀ - same data as holotype. Paratypes (79 ♂, 83 ♀) - same data as holotype (40 ♂, 50 ♀), same location as holotype, 9 July 1989, leg. G. T. Austin (31 ♂, 4 ♀), 24 July 1987, leg. G. & A. Austin (8 ♂, 29 ♀).

DEPOSITION OF TYPES. The holotype, allotype and four paratypes are deposited at the Allyn Museum of Entomology, Sarasota, Florida. Thirty paratypes are at the Nevada State Museum, Carson City. The remaining paratypes will be distributed to other collections.

TYPE LOCALITY. NEVADA: Humboldt County; Quinn River Valley, U.S. route 95, 3.8 miles south of Orovada, 1304 m, T42N R37E S15 on USGS Orovada, Nev. 15'

quadrangle. This is a low, somewhat wet, grassy area east of the Quinn River channel and adjacent to cultivated fields.

DISTRIBUTION AND PHENOLOGY. This taxon is known only from north-central Humboldt County, Nevada in the Kings River Valley (at and north of the town of Kings River), Quinn River Valley (from Nevada State Route 140 to McDermitt) and eastward in the vicinity of Paradise Valley (Fig. 214). Populations in the Alvord Basin at Trout Creek and near Tum Tum Lake are intermediate towards *C. p. stephensi*. Records for the single brood extend from early July through late August.

ETYMOLOGY. The name reflects the relatively poor development of the terminal, marginal, submarginal and postmedian lines, one of the characteristics of this subspecies.

DIAGNOSIS AND DISCUSSION. This subspecies is most similar to *C. p. stephensi* which occurs in the drainages to the west of *C. p. paucilineatus*. It usually has less yellow on the dorsal surface than *C. p. stephensi* (especially males), has fewer ocelli on the dorsal hindwing, the various lines (especially on the ventral surface) are weaker (the postmedian is sometimes absent), the ventral ground color averages yellower (less whitish), the ventral striations are less coarse and the ventral hindwing ocelli are smaller (several may be absent on females).

This phenotype has been seen by very few collectors and references to it are lacking in the literature. It has not been previously illustrated.

Cercyonis pegala utahensis ssp. nov.

Figs. 73, 74, 85, 86, 133-152

MALE. Size = 26.6 (24.8-28.0). Dorsum medium brown (Prout's Brown to Raw Umber, color 23); forewing ocelli minutely white-pupiled, anterior ocellus smaller than posterior, both usually narrowly encircled (at least distally) with ill-defined Yellow Ocher; terminal and marginal lines faint, submarginal line indistinct or absent, stigma with portion below vein 1A+2A absent or with very few scales. Hindwing with minutely white-pupiled, large ocellus in cell CuA₁-CuA₂, flanked anteriorly and usually posteriorly with smaller (often blind) ocelli, all distinctly to faintly encircled with thin line of Yellow Ocher; terminal and marginal lines faint, submarginal line moderately developed, all slightly darker than ground color; fringes of both wings grayish brown, slightly paler than ground color.

Ventral surface near Fawn Color; forewing ocelli much as on dorsum (pupils larger, frequently with trace of associated blue) encircled broadly with Warm Buff; wing moderately striated basally, less so distally; postmedian line moderately developed. Hindwing usually with six ocelli, anteriormost of anterior group rarely absent, smaller ocelli occasionally blind; central ocellus of anterior group frequently slightly elongated and/or fused with ocellus immediately posterior to it; entire wing surface moderately striated; lines weakly developed.

FEMALE. Size = 30.6 (27.5-32.1). Dorsum yellowish brown (near Clay Color to Brussels Brown); forewing ocelli considerably larger than on male with larger white pupils (rarely with trace of blue); both ocelli encircled with Yellow Ocher, this color interspersed with brown scales to form more or less distinct enclosing field; terminal, marginal and submarginal lines as on male, but more contrasting; postmedian line moderately developed. Hindwing with ocellus in CuA₁-CuA₂ as on male but larger, flanked similarly with smaller ocelli and all encircled with Yellow Ocher; submarginal area Yellow Ocher grading into ground color proximally; terminal, marginal and submarginal lines as on male but more contrasting; postmedian line weakly developed anteriorly; fringes as on male.

Ventral forewing ground color pale (Drab Gray) occasionally with yellowish cast (near Cream Color), more whitish at apex; ocelli as on dorsum but pupils larger and nearly always with slight to extensive bluish color distally (at least posterior one); wing moderately striated basally, less so distally; outer lines weakly developed; postmedian line moderately developed. Hindwing ground color as forewing or whiter; marked as on male, all ocelli usually present and pupils larger, those of the largest ocelli occasionally with distal bluish, central ocellus of anterior group usually oval and frequently fused with ocellus posterior to it.

TYPES. Holotype ♂ - UT: Utah Co.; Benjamin, 6 July 1989, leg. G. T. Austin. Allotype ♀ - same data as holotype. Paratypes (125 ♂, 56 ♀, all UT: Utah Co.) - same data as holotype (2 ♂, 2 ♀), same location as holotype, 4 June 1979, leg. J. M. Johnson (1 ♂), 25 June 1979, leg. J. M. Johnson (1 ♂), 28 June 1989, leg. J. M. Johnson (5 ♂, 2 ♀), 4 July 1989, leg. J. M. Johnson (4 ♂, 1 ♀), 6 July 1981, leg. J. M. Johnson (1 ♂), 6 July 1981, leg. F. & J. Preston (13 ♂, 3 ♀), 6 July 1989, leg. J. M. Johnson (2 ♂, 2 ♀), 9 July 1984, leg. J. M. Johnson (1 ♂), 10 July 1985, leg. J. M. Johnson (11 ♂, 1 ♀), Spanish Fork River, between Leland and Benjamin, 6 July 1989, leg. G. T. Austin (17 ♂, 4 ♀), 6 July 1989, leg. J. M. Johnson (14 ♂, 4 ♀), Spanish Fork River, Leland, 5 July 1989, leg. P. J. Savage (5 ♂, 4 ♀), 2 mi. S Payson, 6 July 1989, leg. J. M. Johnson (1 ♂), U.S. 6, 2.4 mi. E Goshen, 7 July 1989, leg. G. T. Austin (3 ♂, 1 ♀), Ut. 73, 3.5 mi. W I-15, west of Lehi, 15 July 1988, leg. G. & A. Austin (5 ♂, 4 ♀), Jordan R., St. Hwy. 73, W of Lehi, 9 July 1981, leg. F. & J. Preston (3 ♂), same location, 10 July 1981, leg. F. & J. Preston (5 ♂, 17 ♀), E side Lehi at freeway entrance, 4 July 1982, leg. P. Savage (1 ♂, 1 ♀), 5750W, S of American Fork, just SW of I-15, 5 July 1989, leg. P. J. Savage (14 ♂, 6 ♀), Vineyard, 8 July 1915, leg. T. Spalding (1 ♀), 20 July 1908, leg. T. Spalding (1 ♂), 4 Aug. 1908, leg. T. Spalding (1 ♀), 3 Aug. 1909, leg. T. Spalding (1 ♀), 27 July 1917, leg. ? (1 ♂), 6 July 1908, leg. T. Spalding (4 ♂), 11 July 1923, leg. ? (2 ♂), 19 July 1917, leg. ? (1 ♂), 21 July 1917, leg. ? (1 ♂), 22 July 1917, leg. ? (3 ♂), Provo, 16 July 1917, leg. ? (1 ♂, 1 ♀), 17 July 1917, leg. ? (1 ♂), 29 July 1912, leg. T. Spalding (1 ♂).

DEPOSITION OF TYPES. The holotype, allotype and six paratypes are deposited at the Allyn Museum of Entomology, Sarasota, Florida. The remaining paratypes will be distributed to other collections.

TYPE LOCALITY. UTAH: Utah County; Benjamin, vicinity of 7300S at 2610W, 1390 m, on the farm of Joel M. Johnson of Payson, Utah. Types were taken here in a grassy area along a small stream, in an orchard and in a grassy field. This taxon also flies in tall grass and among willows along river channels. All types are from areas in the vicinity of Utah Lake.

DISTRIBUTION AND PHENOLOGY. This taxon occurs in northcentral Utah from Mona (Juab County) and Goshen (Utah County) north to the Idaho line near Portage (Box Elder County, Fig. 214). Records for the single brood extend from early June through early August.

ETYMOLOGY. *C. p. utahensis* is named after the state of Utah, its type locality and total known distribution.

DIAGNOSIS AND DISCUSSION. *C. p. utahensis* is like *C. p. stephensi* but the male has much less dorsal yellow (the dorsal color of the female is very similar), the ventral surface is less pale, the postmedian line is weakly developed, the ocelli on both surfaces are generally larger, and the striations are less coarse. The dorsal hindwing ocelli flanking the one in cell CuA₁-CuA₂ are present more often and average larger than on the other Great Basin *C. pegala*. The stigma of the male is unique in that the lower element is obsolete or lacking. Other Great Basin *C. pegala* have a distinct, usually bar-shaped, portion of the stigma beneath vein 1A+2A. North of the type locality and east of the Great Salt Lake, both sexes tend to have more spots on the dorsal hindwing and the ocelli average still larger.

The Utah populations of *C. pegala* included here have previously been referred to *C. p. ariane* by Comstock (1927) and Tilden and Smith (1986) or to *C. p. gabbi* (as a form of *C. p. ariane* or as a subspecies) by Emmel (1969, in Howe 1975), Emmel and Mattoon (1972), Holland (1931) and Scott (1986). This phenotype was illustrated by Holland (1931) as *C. gabbi*.

Cercyonis pegala pluvialis ssp. nov.

Figs. 75, 76, 87, 88, 153-172

MALE. Size = 27.7 (26.4-29.0). Dorsum brown (Hair Brown to Raw Umber, color 223); forewing ocelli with small white pupils (occasionally with trace of blue), posterior ocellus same size to larger than anterior; both outlined narrowly with yellowish (Warm Buff),

this sometimes incomplete proximally, especially around posterior ocellus; ocelli set in field slightly paler than ground color; thin terminal and marginal lines, broader submarginal line and broad postmedian bar near end of discal cell darker than ground color; prominent stigma of same darker color; fringe whitish posteriorly, ground color anteriorly. Hindwing with black, white-pupiled ocellus in cell CuA_1-CuA_2 , often flanked on either side with small to minute (often blind) ocelli (sometimes one in cell M_2-M_3), outlined with yellow as on forewing but very narrowly; terminal and marginal lines very dark brown as is prominent submarginal line; faint postmedian line anteriorly on some specimens; fringes ground color, whitish anteriorly.

Ventral surface pale grayish-brown (Drab Gray to Light Drab); forewing ocelli of nearly same size as on dorsum with larger pupils (frequently with trace to moderate amount of associated blue), encircled moderately with Warm Buff, then brown, the yellow areas not fusing; field about ocelli very lightly striated, remainder of wing very heavily striated with dark brown; postmedian line prominent as are terminal, marginal and submarginal lines. Hindwing heavily striated with dark brown; six yellow-encircled, black submarginal ocelli with white pupils; central ocellus of anterior group often somewhat elongate and occasionally fused with posterior ocellus of group; terminal and marginal lines distinct, submarginal and postmedian lines present but not strong.

FEMALE. Size = 30.7 (29.3-32.0). Dorsum pale brown (Brussels Brown to Fawn Color); forewing with considerably larger ocelli than male, posterior invariably larger than anterior, white pupils moderately-sized, that of posterior ocellus usually showing some blue distally; ocelli outlined with Trogon Yellow, this color mixed with brown to form an enclosing field and often extending to outer margin along veins; lines as on male but more prominent. Hindwing ocelli as on male; largest usually with trace of blue associated with pupil; area distal to postmedian line paler than base (mottled yellowish to whitish brown due to ventral striations); lines as on male but more prominent; fringes of both wings pale brownish, whitish posteriorly on forewing and anteriorly on hindwing, indistinctly checkered at vein tips.

Ventral surface very pale, nearly whitish, gray-brown (Drab Gray or paler); area distal to postmedian line tending slightly paler than basal area; both wings heavily striated basally, moderately distally; forewing ocelli larger than on male with large white pupils, these with trace to extensive bluish distally; both ocelli encircled broadly with Trogon Yellow, this yellow often fused; lines as on male. Hindwing ocelli smaller than on male, smaller ones occasionally unpupiled; one or more ocelli (especially of anterior group) may be obsolete or absent, these often oval when present but not fused; lines as on male.

TYPES. Holotype ♂ - NV: White Pine Co.; White River Valley, 1 mi. N Nye Co. line, 15 July 1984, *leg.* G. T. Austin. Allotype ♀ - same data as holotype. Paratypes (74 ♂, 28 ♀) - same data as holotype (43 ♂, 19 ♀), same location as holotype, 12 July 1986, *leg.* G. & A. Austin (24 ♂, 6 ♀), 15 July 1989 *leg.* G. T. Austin (7 ♂, 3 ♀).

DEPOSITION OF TYPES. The holotype, allotype and four paratypes are deposited at the Allyn Museum of Entomology, Sarasota, Florida. Twelve paratypes are deposited at the Nevada State Museum, Carson City. The remaining paratypes will be distributed to other collections.

TYPE LOCALITY: NEVADA: White Pine County; White River Valley, 1 mile north of Nye County line, 1676 m, T10N R61E S11 on USGS Moorman Spring NE, Nev. 7.5' quadrangle. This is a narrow marshy area in the channel of the pluvial White River. Both sexes visit the yellow flowers of composites (Asteraceae) for nectar. Males patrol grassy areas where females perch near the bases of large grass clumps or small shrubs.

DISTRIBUTION AND PHENOLOGY. To date, this subspecies is known from the type locality, in the White River channel southward to extreme northern Nye County, Nevada; at Geysers Ranch in extreme northern Lake Valley, Lincoln County, Nevada; in southern Steptoe Valley (Warm Springs south to the vicinity of Comins Lake), White Pine County, Nevada, along Duck Creek, White Pine County, Nevada and along Deep Creek in the vicinity of Ibapah, Tooele County, Utah (Fig. 214). The first two locations are the only known populations of *C. pegala* from the Colorado River drainage west of central Arizona.

The single brood has been recorded from early July to late August.

ETYMOLOGY. As with many of the Great Basin *C. pegala*, this phenotype is a relict of the last pluvial period, hence the name.

DIAGNOSIS AND DISCUSSION. *C. p. pluvialis* is like *C. p. stephensi* but has less yellow on the dorsum, the postmedian line on the dorsal forewing is better developed, females have more persistent blue associated with pupils of the ventral forewing ocelli, fewer ocelli on the dorsal hindwing and smaller ventral hindwing ocelli (some of these are often absent), the striations on the ventral surface are coarser on both sexes and rather strong indications of ventral striations on the dorsum of the female hindwing (this also occurs on other taxa of the species but is less apparent). Males have less yellow associated with the dorsal ocelli than *C. p. carsonensis* but more than on *C. p. utahensis*. Females tend to have less yellow on the dorsal hindwing than any of the above Great Basin subspecies except *C. p. gabbi*. None of these other subspecies have the dorsal postmedian lines as well marked nor the indications of the ventral striations on the dorsal hindwing of the female.

The populations in Steptoe Valley and at Ibapah are phenotypically closest to this taxon and are so included. They, however, have fewer ocelli on the dorsal hindwing, less bold striations, and females have fewer ocelli on the ventral hindwing. This may be the result of some influence from populations to the north which will be described later.

This phenotype has not, heretofore, been mentioned or illustrated in the literature.

Cercyonis pegala boopis (Behr)

Figs. 5-8, 13-16

DIAGNOSIS. Size ♂ = 26.5 (25.0-27.6, N = 5), size ♀ = 29.1 (27.2-31.0, N = 5) (sample from Contra Costa County, California). This is a relatively dark (male Prout's Brown; female Brussels Brown) butterfly with a strongly bicolored ventral hindwing (male Fawn Color to Cinnamon Brown; female Light Drab to Fawn Color) with fine striations and few or no ocelli on either hindwing surface. Males have only a faint hint of yellow associated with the dorsal forewing ocelli; females have a diffuse yellow-brown field about these, this only slightly paler than the ground color.

DISTRIBUTION. The details of the distribution of *C. p. boopis* await a thorough examination of the *C. pegala* of the Pacific States. The name does not apply to any Great Basin population of the species nor probably to anything very far east of the Pacific Coast.

DISCUSSION. The name *Satyrus boopis*, like *S. ariane*, has been applied to a wide range of phenotypes, from the dark butterfly with a strongly bicolored and often unocellated ventral hindwing occurring in coastal California to a somewhat paler phenotype with a slightly bicolored and weakly ocellated ventral hindwing flying in Oregon to the large and relatively pale phenotypes in northern Arizona. Such a range of sins can be appreciated by consulting almost any book treating western North American butterflies (Brown *et al.* 1957, Comstock 1927, Dornfield 1980, Ferris and Brown 1981, Holland 1931, Howe 1975, Tilden and Smith 1986). I restrict the name *Satyrus boopis* to the first-mentioned phenotype above, the key recorded in Behr's (1864) reference to the bicolored wing ("*Alae subtusdimidiatae pars radicalis brunnea, marginalis griseae, marginem versus brunnescens*") and the type locality of "Contra Costa". The type was lost in the San Francisco earthquake and fire in 1906 (Brown 1965). A neotype will be designated by Emmel *et al.* (in press b).

Many so-called *C. p. boopis* are illustrated in various books. The female illustrated by Tilden and Smith (1986) is typical of Behr's (1864) original concept.

Cercyonis pegala paludum ssp. nov.

Figs. 77, 78, 89, 90, 173-192

MALE. Size = 25.2 (24.2-25.9). Dorsum dark brown (Prout's Brown to Raw Umber, color 223); forewing with relatively small ocelli, posterior larger than anterior, indistinctly

encircled with paler area of mixed brown and yellow scales; terminal and marginal lines thin, faint to obsolete; submarginal line broader but faint; postmedian line absent; fringes grayish brown, paler posteriorly. Hindwing usually with single, relatively small, usually white-pupiled ocellus in cell CuA_1 - CuA_2 , rarely flanked with black dots in adjacent cells; ocellus indistinctly outlined with narrow area of mixed yellow and brown scales; lines as on forewing; fringes grayish brown, paler anteriorly.

Ventral surface pale brownish gray (Drab to Dark Drab); forewing ocelli as on dorsum, distinctly and narrowly outlined with Warm Buff and then medium brown, pupils larger than on dorsum, these infrequently with trace of blue; basal portion of wing rather weakly striated, striations nearly absent distally; terminal, marginal and submarginal lines distinct, dark brown; postmedian line broader and distinct. Hindwing usually with indications of six small ocelli, central one of each group most persistent, sometimes elongate anteriorly but not fused, all narrowly outlined with yellowish; ocelli usually pupiled (not when very small); striations thin over entire wing; lines as on forewing.

FEMALE. Size = 27.2 (26.0-29.2). Dorsum pale brown (Fawn Color to Prout's Brown); forewing with moderately-sized ocelli, these outlined with Warm Buff, this color then interspersed with brown scales to form yellow-brown submarginal field slightly paler than ground color, the yellow occasionally extends along veins distally, pupils rarely with trace of blue; lines as on male. Hindwing with ocellus in CuA_1 - CuA_2 small to obsolete, often blind and vaguely outlined with yellowish, rarely additional adjacent dark spot; submarginal area with some yellow scales distally often creating vague yellowish field; lines as on forewing, submarginal more prominent; faint postmedian line anteriorly; fringes of both wings near ground color, lightly checkered at vein tips.

Ventral surface pale brownish gray (Light Drab to Drab), sometimes grayer (even whitish) distally on hindwing; forewing ocelli as on dorsum, pupils larger with trace to moderate bluish distally; ocelli outlined broadly with Warm Buff, then brownish, these outlines often fused between ocelli; lines and striations as on male. Hindwing without or with some small (rarely oval) ocelli, the one in cell CuA_1 - CuA_2 most persistent and usually pupiled, others often unpupiled; striations and lines as on male.

TYPES. Holotype ♂ - NV: Elko Co.; Pleasant Valley, Nv 227, 3.7 mi. W Lamoille Canyon Rd., 21 July 1984, leg. G. T. Austin. Allotype ♀ - same data as holotype. Paratypes (60 ♂, 37 ♀, all NV: Elko Co.; Pleasant Valley, Nv 227) - same data as holotype (18 ♂, 5 ♀), 4 mi. W Lamoille Canyon turnoff, 15 July 1986, leg. C. Hageman (10 ♂, 7 ♀), 0.9 mi. W Lamoille Canyon Rd., 15 July 1986, leg. G. & A. Austin (9 ♂, 4 ♀), 3.9 mi. W Lamoille Canyon Rd., 15 July 1986, leg. G. & A. Austin (9 ♂, 3 ♀), 4.6 mi. W Lamoille Canyon Rd., 29 July 1988, leg. G. T. Austin (14 ♂, 18 ♀).

DEPOSITION OF TYPES. The holotype, allotype and four paratypes are deposited at the Allyn Museum of Entomology, Sarasota, Florida. Eighteen paratypes are deposited at the Nevada State Museum, Carson City. The remaining paratypes will be distributed to other collections.

TYPE LOCALITY. NEVADA: Elko County; Pleasant Valley, Nevada State Route 227, 3.7-4.0 miles west of Lamoille Canyon Road, 1719 m, T33N R57E S21 on USGS Lee, Nev. 15' quadrangle. The area is a wet grassy meadow along a stream lined with willows.

DISTRIBUTION AND PHENOLOGY. This phenotype occurs in the Humboldt River drainage (along the Humboldt River from north of Lovelock, Pershing County, Nevada, to northeast of Elko, Elko County, Nevada, including many of its upriver tributaries); Salmon Falls Creek, Elko County, Nevada, northward and eastward into at least southern Idaho and northwestern Utah and south into Clover, Butte, Ruby, Newark and northern Steptoe valleys, Elko and White Pine counties, Nevada (Fig. 214). The single brood flies from early June to early September.

ETYMOLOGY. The word "paludum" refers to "swamps or marshes," the habitat of this and other taxa of the species.

DIAGNOSIS AND DISCUSSION. *C. p. paludum* differs from the foregoing Great Basin phenotypes of the species in several respects: the forewing ocelli are smaller, the dorsal hindwing has only one small ocellus (occasionally none), the male nearly lacks distinct yellow on the dorsum, the postmedian line is not evident on the dorsal surface, the yellow

about the dorsal forewing ocelli of the female is faint and does not form an obvious field, the ventral surface is darker and with finer striations, the various lines on the ventral surface (including the postmedian) are weakly developed and there is little yellow flush associated with the ventral forewing ocelli. The ventral hindwing ocelli of males are small; those of females are small or absent. Comparisons with phenotypes outside of the Great Basin will be made under the following taxon.

This taxon has not previously been recognized or illustrated.

Cercyonis pegala walkerensis ssp. nov.

Figs. 79, 80, 91, 92, 193-212

MALE. Size 24.7 (23.8-25.7). Dorsum brown (Prout's Brown to Vandyke Brown, color 121); forewing with relatively small, white-pupiled ocelli, posterior slightly larger than anterior, encircled (often indistinct) with paler area of mixed brown and yellow scales; terminal, marginal and submarginal lines very faint or absent, postmedian line absent; fringe gray-brown, slightly paler than ground color. Hindwing usually with single small ocellus in cell CuA_1 - CuA_2 , vaguely or not encircled with yellowish, pinpoint white pupil; lines as on forewing, fringe as on forewing.

Ventral surface pale brown (Brussels Brown to Hair Brown); forewing ocelli as on dorsum, narrowly but distinctly encircled with Warm Buff and then indistinctly with brown, pupils larger than on dorsum, infrequently with trace of blue; both wings finely striated with brown, heaviest basally (often imparting a slight two-toned aspect), striations nearly absent in area around forewing ocelli; terminal, marginal and submarginal lines dark brown, relatively indistinct; postmedian line present, complete, usually not distinct, especially on hindwing; hindwing generally with at least indications of six ocelli, central one of each group largest, usually with small white pupils; other ocelli smaller, pupiled or not, ocelli not fused, occasionally oval, all outlined with yellowish and then brown.

FEMALE. Size = 26.8 (26.0-28.2). Dorsum pale brown (Cinnamon Brown to Natal Brown); forewing with moderately-sized ocelli, these outlined with Warm Buff, this color often interspersed with brown scales to form faint yellow-brown field surrounding ocelli, occasionally extended along veins distally, pupils occasionally with trace of blue; lines as on male. Hindwing with ocellus in cell CuA_1 - CuA_2 , small, usually indistinct, often absent, with or without white, pinpoint pupil and usually outlined with yellowish; submargin often with light dusting of yellowish scales anteriorly; terminal and marginal lines faint, submarginal line relatively broad and distinct, postmedian line occasionally vaguely represented; fringes of both wings grayish, faintly checked at vein tips with brown.

Ventral surface pale brown (Fawn Color to Cinnamon Brown), usually darker basally; forewing ocelli as on dorsum, pupils larger, nearly all with bluish distally; ocelli outlined broadly with yellow (Cream Color to Warm Buff) and then faintly with brown, the yellow occasionally fused between ocelli; striations as on male. Hindwing usually with two or fewer round ocelli, most persistent in cell CuA_1 - CuA_2 and one posterior to it; striations and lines as on male.

TYPES. Holotype ♂ - CA: Mono Co.; Huntoon Valley, Swanger Creek, U.S. 395, 5.4 mi. NW Bridgeport, Huntoon Camp, 23 July 1989, leg. G. & A. Austin. Allotype ♀ - same data as holotype. Paratypes (70 ♂, 24 ♀; all CA: Mono Co.; Huntoon Valley) - same data as holotype (13 ♂, 7 ♀), same location as holotype, 13 July 1989, leg. G. T. Austin (19 ♂), 24 July 1989, leg. G. & A. Austin (18 ♂, 5 ♀), U.S. 395, Upper Huntoon Valley, 8.1 mi. NW of Bridgeport, 5 August 1979, leg. D. Mullins (9 ♂, 9 ♀), U.S. 395, Huntoon Camp, Swanger Creek, 29 July 1978, leg. C. Hageman (11 ♂, 3 ♀).

DEPOSITION OF TYPES. The holotype, allotype and two paratypes are at the Allyn Museum of Entomology, Sarasota, Florida. Two paratypes are at the Nevada State Museum, Carson City. The remaining paratypes will be distributed to other collections.

TYPE LOCALITY. CALIFORNIA: Mono County; Huntoon Valley, Swanger Creek, U.S. highway 395, Huntoon Camp, 5.4 road miles northwest of Bridgeport, 2048 m on USGS Fales Hot Springs, Calif. - Nev. 15' quadrangle. This is a damp to grassy area along a creek lined with willows. Males patrol along the edges of willows and among the

grasses, especially a tall bunch grass. Females fly little but perch, mainly in the shade, at the bases of willows, sagebrush and tall grass clumps and in rose thickets.

DISTRIBUTION AND PHENOLOGY. This subspecies is known from the north end of the Mono Lake Basin (Mono County, California) and the East Walker River drainage (Mono County, California; southern Lyon and extreme western Mineral counties, Nevada, Fig. 214). Records extend from early July to late August.

ETYMOLOGY. The name refers to the Walker River drainage in which most of the taxon's distribution occurs.

DIAGNOSIS AND DISCUSSION. *C. p. walkerensis* is most similar to *C. p. paludum* of the northeastern Great Basin. *C. p. walkerensis* is slightly smaller in size and the forewing appears squarer (less highly arched costa, straighter outer margin). The lines on the dorsum are fainter on *C. p. walkerensis*, the ocelli average smaller and, on the female, are less distinctly outlined with yellowish. The ventral surface is browner and less gray than *C. p. paludum*, the female appears more distinctly two-toned on the hindwing, and the striations are thinner. The ocelli, especially of the males, average smaller.

The dorsum of *C. p. walkerensis* is very similar to *C. p. boopis* but the latter usually lacks ocelli on the dorsal hindwing and has narrower yellow around the forewing ocelli. *C. p. paludum* is grayer than *C. p. boopis* and has much larger forewing ocelli. The venter of *C. p. walkerensis* is paler than that of *C. p. boopis* with a less pronounced two-toned aspect on the hindwing but the fine striations are similar. *C. p. paludum* is paler and grayer with somewhat coarser striations and with an even less distinctly bicolored ventral hindwing. Males and often females of *C. p. walkerensis* and, especially, *C. p. paludum* usually have ventral hindwing ocelli; these are nearly always absent on *C. p. boopis*.

C. p. walkerensis has not been previously recognized or illustrated.

BLEND POPULATIONS

A number of populations occur in the Great Basin that are intermediate phenotypically and geographically with those discussed above. These are briefly characterized and discussed below.

Red Rock Population

In the Red Rock Valley, north of Reno, Washoe County, Nevada, is a population which appears intermediate between *C. p. carsonensis* and *C. p. ariane*. Males are large (size = 25.8 [24.7-27.3]) like *C. p. carsonensis* but are dark brown on the dorsum and have the smaller and unmarginated forewing ocelli of *C. p. ariane*. The ventral surface is intermediate in color between these two taxa, the forewing ocelli are as on *C. p. ariane*, the hindwing ocelli are intermediate in size (but usually all present and may be elongate as on *C. p. carsonensis*), and the striations are coarse as on *C. p. carsonensis*. Females are also the size (28.4 [27.2-29.9]) of *C. p. carsonensis*. Their dorsal surface has intermediate color, ocelli and extent of yellow. The ventral surface is like *C. p. carsonensis* but with hindwing ocelli similar to those of *C. p. ariane* or slightly better developed yet rarely approaching the size of those typical of *C. p. carsonensis*.

Honey Lake Population

Three males from the north shore of Honey Lake, Lassen County, California, have a "gabbii" group aspect (relatively large size, coarse striations, complete set of large ventral hindwing ocelli), but the ventral surface is dark, possibly indicating influence from *C. p. ariane* to the west. I have not seen the material (*leg.* C. Callahan) from just east of Honey Lake near Flanigan, Washoe County, Nevada, nor have I been able to relocate that colony. This is probably of the same phenotype.

Ravendale Population

A population at 19-24 km south of Ravendale, Lassen County, California, appears intermediate between *C. p. gabbii* and *C. p. stephensi*. Both sexes resemble *C. p. gabbii* in size ($\delta = 25.6$ [24.4-26.2], $\phi = 28.8$ [27.8-29.8]), dorsal color and ocelli but the various lines are more prominent as on *C. p. stephensi*. The ocelli of females are enclosed in a somewhat more extensive yellow field than on *C. p. gabbii* but less extensive than is typical of *C. p. stephensi*. The ventral color varies from very pale as on *C. p. stephensi* to the brownish of *C. p. gabbii*. The striations and lines are bold, nearest those of *C. p. stephensi*. The ocelli of the ventral hindwing of males are similar to those on *C. p. gabbii*; the ocelli of females are more persistent than on *C. p. gabbii*, but smaller than on *C. p. stephensi*.

Squaw Creek Population

This population, from west of the Granite Mountains along Squaw Creek, Washoe County, Nevada, is very similar to the Ravendale population, appearing intermediate between *C. p. stephensi* and *C. p. gabbii*.

Crump Lake Population

Newcomer (1965) noted that the Crump Lake (Lake County, Oregon) populations of *C. pegala* contained fewer females of the "*stephensi* form" than other populations he sampled. This population is indeed darker than typical *C. p. stephensi* and appears to be intermediate towards the central Oregon phenotype of *C. pegala* in other characters, also. Both sexes have fewer ocelli (usually one) on the dorsal hindwing, females average fewer ventral hindwing ocelli, there is no fusion of the ventral hindwing ocelli (1 of 51 specimens), and the ocelli are more often round than oval. The ventral color, however, is nearly as pale, the striations are nearly as coarse, and the ocelli are nearly as large as on *C. p. stephensi*.

Alvord and Harney Basin Populations

Populations of the central Alvord drainage, from just west of Denio Junction, Humboldt County, Nevada and in the Tum Tum Lake and Trout Creek region, Harney County, Oregon, are intermediate between *C. p. stephensi* and *C. p. paucilineatus*. The dorsum of the male is darker with less yellow than *C. p. stephensi* and resembles *C. p. paucilineatus*. The dorsum of the female ranges from the phenotype of *C. p. stephensi* to one that is darker with few hindwing ocelli. The ventral surfaces of both sexes are most like *C. p. paucilineatus*, but with more prominent lines and coarser striations, like *C. p. stephensi*. At Frenchglen, Harney County, Oregon, and northward to Burns, both sexes are darker above and browner (less gray-brown) and the ventral surface is darker and browner than either *C. p. paucilineatus* or *C. p. stephensi*. These appear intermediate towards the phenotype from further north in Oregon (see plate 10 in Dornfeld 1980). The population in the southwestern Alvord Basin (Thousand Creek drainage) is typical *C. p. stephensi*.

Utah-Idaho Populations

In the northcentral Utah and southeastern Idaho area, there is a rather abrupt transition from *C. p. utahensis* to a phenotype near *C. p. paludum*. Typical *C. p. utahensis* occurs near Wellsville, Cache County, Utah. At 27 km south of the Idaho state line along highway I-15/U.S. 89, Box Elder County, Utah, occur individuals of fairly typical *C. p. utahensis* and others (females) on which the anterior ocelli on the ventral hindwing are reduced in size or absent. A similar phenotype to the latter flies near Portage, Box Elder County, Utah, and in Richmond and High Creek canyons, Cache County, Utah. Near Malad City, Oneida County, Idaho, and near the Oneida Power Plant, Bear River, Franklin County, Idaho, the females usually have one or two ventral hindwing ocelli and those of males

are also reduced in size and number. There is a parallel transition from coarse to fine striations on the venter and in the amount of dorsal yellow on females (a few of the Idaho females still have the extensive yellow of *C. p. utahensis*). This Idaho material has a darker ventral ground color than either *C. p. paludum* or *C. p. utahensis*, thus apparently showing some intergradation with the darker phenotypes occurring to the north and east (including *Cercyonis pegala ino* Hall).

Beowawe Geysers Population

The *C. pegala* population in the marsh at the outflow of Beowawe Geysers (15 km S of the Humboldt River on the Eureka-Lander County line, Nevada) has a phenotype appearing intermediate between *C. p. paludum* and one of the coarsely striated phenotypes with large ocelli. The dorsal surface is rather typical (little yellow, usually small or absent hindwing ocellus) of *C. p. paludum*. The ventral surface, however, is paler (especially males), and has coarser striations and bolder postmedian lines than *C. p. paludum*. The ventral hindwing ocelli (especially of males) are often larger than is typical of *C. p. paludum* and more often all are present. This surface resembles that of *C. p. pluvialis*. Populations of *C. pegala* just to the north from adjacent to the Humboldt River do not have this aspect and are typical *C. p. paludum*.

DISCUSSION

In the Great Basin, *C. pegala* has, at first glance, a series of seemingly anomalous assortments of phenotypic characters. In color, adults are both pale and dark. Their striations are bold or rather weak. The ocelli of the ventral hindwing are either large or small to absent. The phenotypes, however, do fall into two recognizable groups (Tables 2, 3).

The first (the "gabbii" group) includes *C. p. gabbii*, *C. p. stephensi*, *C. p. carsonensis*, *C. p. wheeleri*, *C. p. paucilineatus*, *C. p. utahensis* and *C. p. pluvialis*. This group is generally characterized by large forewing ocelli, large and persistent ocelli on the dorsal hindwing (very often 2 or more), relatively large and persistent ventral hindwing ocelli (these nearly always pupiled, often fused, often oval), coarse ventral striations (one but often two to three scale rows in width, often uninterrupted across the wing cells), pale ventral ground color, indications on females of a yellow field around the dorsal forewing ocelli, and a yellowish flush in the ocellar area on the ventral forewing.

The second group including *C. p. paludum* and *C. p. walkerensis* (the "paludum" group) is characterized by smaller forewing ocelli, small or absent dorsal hindwing ocelli (usually 1 or none), smaller or absent ventral hindwing ocelli (less often pupiled, not fused and uncommonly oval), fine striations (one or rarely two scale rows in width and often incompletely across wing cells and with scattered pale scales among the dark scales), and little yellow associated with the forewing ocelli.

This pattern of differentiation suggests that at least two separate groups of *C. pegala* populated the Great Basin and subsequently were subjected to range constrictions and isolations. Certain dispersals within the Great Basin can be traced with some degree of confidence. The following scenario is one possibility and is tentative pending studies of other populations from outside the Great Basin.

In any discussion of Great Basin biogeography (as elsewhere), it is necessary to be cognizant of Pleistocene and subsequent events. The distributional patterns of *Cercyonis pegala* phenotypes in the Great Basin can be accounted for within the context of that history for this area and adjacent regions. The major features of the post-Pleistocene in the Great Basin involve a drying climate with a concomitant shrinking of the huge, more-or-less contemporaneous, pluvial lakes which occupied the Great Basin valleys (Fig. 213). This led to the increasing isolation of the wet areas in the various basins as their aquatic connections disappeared. The potential for gene flow obviously decreased between populations of biota in these basins. This effectively allowed differentiation in isolation, potentially enhanced by genetic drift and founder effects.

TABLE 2. Characteristics of Great Basin *Cercyonis pegala*/1.

Taxon	mean #(range) DHW ocelli		mean #(range) VHW ocelli		% VHW ocelli with pupils		% with VHW ocelli fused		% with VHW ocelli oval		% with blue in VFW ocelli/2	
	male	female	male	female	male	female	male	female	male	female	male	female
<i>C. p. gabbii</i>	1.59 (1-3)	1.42 (1-3)	5.88 (5-6)	4.95 (2-6)	95.4	87.3	10.0	0.0	44.0	42.1	10	75
<i>C. p. stephensi</i>	3.02 (1-6)	2.93 (1-6)	6.00	6.00	98.2	96.7	47.0	53.3	57.6	73.3	35	40
<i>C. p. paucilineatus</i>	1.71 (1-4)	1.35 (1-3)	5.99 (5-6)	5.00 (0-6)	96.8	84.6	11.7	1.6	64.0	49.6	30	80
<i>C. p. utahensis</i>	2.98 (1-4)	3.09 (2-4)	5.84 (5-6)	5.94 (5-6)	90.4	95.1	56.8	60.0	63.4	83.9	75	95
<i>C. p. carsonensis</i>	2.00 (1-4)	1.99 (1-4)	6.00	5.86 (3-6)	94.0	92.8	56.3	39.3	73.8	80.9	30	40
<i>C. p. pluvialis</i>	2.44 (1-4)	2.23 (1-3)	6.00	5.88 (5-6)	100.0	91.5	10.0	0.0	62.9	80.8	75	100
<i>C. p. wheeleri</i>	2	3	6	6	100	100	0	0	100	100	0	100
<i>C. p. walkerensis</i>	1.08 (1-2)	0.59 (0-1)	5.08 (2-6)	1.52 (0-6)	75.2	69.1	0.0	0.0	18.0	0.0	25	95
<i>C. p. paludum</i>	1.28 (1-3)	0.90 (0-2)	5.26 (1-6)	2.45 (0-6)	82.7	51.4	0.0	0.0	32.3	9.7	30	100

1/ data are from types and topotypes, sample sizes for all except the final character are as follows: *C. p. gabbii* - 49 ♂, 19 ♀; *C. p. stephensi* - 66 ♂, 15 ♀; *C. p. paucilineatus* - 112 ♂, 128 ♀; *C. p. utahensis* - 80 ♂, 31 ♀; *C. p. carsonensis* - 181 ♂, 184 ♀; *C. p. pluvialis* - 70 ♂, 26 ♀; *C. p. wheeleri* - 1 ♂, 1 ♀; *C. p. walkerensis* - 61 ♂, 22 ♀; *C. p. paludum* - 65 ♂, 31 ♀.

2/ N = 20 except for *C. p. stephensi* - 10 ♀; *C. p. wheeleri* - 1 ♂, 1 ♀.

For the following discussion, the various drainages of the Great Basin and surrounding areas are grouped into drainage units as established by Smith (1978), who based them on physiography and distributions of the Great Basin fish fauna. The geological framework was established with investigations begun in the late nineteenth century (e.g., Gilbert 1882, 1890; Russell 1883, 1885, 1889) and later summarized and correlated with probable pluvial connections and fish distributions (e.g., Hubbs and Miller 1948, Hubbs *et al.* 1974, Mifflin and Wheat 1979, Miller 1946).

Throughout the following discussion, the presence or absence of hydrographic connections between drainage basins since the end of the Pleistocene is emphasized. While the absence of hydrographic connections obviously is not the absolute barrier to *Cercyonis* butterflies that they would be with fish, the presence of connections with associated paludal habitats undoubtedly would have facilitated dispersal of *Cercyonis pegala*. Additionally, shortest distances between possible suitable habitats in the past or between extant colonies are indicated in certain instances. Shortest distance and the existence of continuous surface waters are illustrative of probable routes of dispersal, with the recognition that past movements within and between drainage basins may have been more circuitous in reality.

The most clearly distinguishable and unique *C. pegala* taxa are of the "gabbii" group. These occur as rather isolated populations, generally on the fringes of the Great Basin (Fig. 214). As will be noted in Table 4 and the discussions below, the taxa of the "gabbii" group are now (or recently were) found in eight of the nine drainage units (absent from the Snake) outlined by Smith (1978). This pattern strongly suggests a widespread distribution in the Great Basin during the late Pleistocene or early Holocene. These populations may have been part of a lake shore marsh community. As pluvial lakes dried, their various basins became increasingly isolated from each other and adjacent drainage basins. Eventually, wet areas remained only at sumps, along larger tributaries and at springs. Many of the extant *C. pegala* populations occur in wet areas remaining at the margins of these extinct lakes (Figs. 213, 214; note, however, that much of the current Great Basin marsh habitat also occurs in these same places but that the "gabbii" group phenotypes rarely occur along the Great Basin rivers that have persisted since the last pluvial. The lower portions of these rivers were submerged beneath the pluvial lakes.). The peripheral and disjunct occurrence with little apparent intergradation of these taxa in the Great Basin also argues for an old lake shore fauna hypothesis; these were left behind and increasingly isolated into remaining wet areas as the lakes dried. What we see today is the differentiated remnants of this previously widespread fauna. This argument is further strengthened by the physical and biotic characteristics of present-day drainages. Flow of Great Basin rivers and streams decreases downstream and, often, intermediate portions disappear while headwaters and sumps persist and may parallel the temporal pattern of post-pluvial desiccation. This is consistent with the more diverse upstream butterfly faunas observed in the Great Basin compared with downstream faunas, the converse of the pattern seen in the Colorado River drainage of southern Nevada (Austin 1985a).

The following discussion summarizes the distribution of the "gabbii" group of *C. pegala* in the Great Basin in relation to hydrogeography, physiography and present-day ecology. Each "gabbii" group taxon is now narrowly restricted to part of one (or more than one, closely associated) drainage basin (Table 4; Fig. 214).

C. p. wheeleri was an isolate in the Owens drainage basin, the northernmost of the Death Valley drainage unit. This now isolated system undoubtedly (based on its fish fauna) had early connections with the Colorado River drainage (via troughs to the south and/or east) and with the Lake Lahontan drainage (via Mono Basin) (Hubbs and Miller 1948; Miller 1946, 1981; Miller and Smith 1981). The phenotype of *C. p. wheeleri* (most similar to *C. p. carsonensis* and *C. p. stephensi*) indicates that it is of the "gabbii" group and not closely related to any of the phenotypes in California west of the Sierra Nevada.

The Lahontan drainage unit includes the huge pluvial Lake Lahontan drainage and several smaller drainages which had pluvial connections with the Lahontan basin. None of these smaller drainages have present-day populations of the "gabbii" group (but see discussion of the Beowawe Geysers population above). The pluvial Lake Lahontan basin,

TABLE 3. Size (mm) of dorsal forewing ocelli and ocellus in cell Cu₁-Cu₂ on the dorsal hindwing of Great Basin *Cercyonis pegala*. (all measurements are of types or topotypes, N = 10 except for *C. p. wheeleri* where N = 1 for each sex).

Taxon	males			females		
	anterior FW ocellus	posterior FW ocellus	hindwing ocellus	anterior FW ocellus	posterior FW ocellus	hindwing ocellus
<i>C. p. gabbii</i>	2.8 (2.0-3.1)	3.4 (2.9-4.0)	1.9 (1.5-2.2)	3.8 (2.6-4.7)	4.5 (3.7-5.4)	2.0 (1.0-2.6)
<i>C. p. stephensi</i>	3.3 (2.7-3.8)	4.2 (3.6-4.8)	2.4 (1.8-3.2)	3.9 (3.1-4.4)	4.9 (3.8-6.1)	3.0 (1.9-4.2)
<i>C. p. paucilineatus</i>	3.3 (2.6-4.2)	4.2 (3.2-4.8)	2.1 (1.7-2.9)	3.9 (3.3-4.6)	5.1 (4.2-6.2)	2.4 (1.6-3.2)
<i>C. p. utahensis</i>	3.0 (2.3-4.1)	4.3 (3.4-5.2)	2.7 (2.2-3.2)	4.2 (3.9-4.7)	5.8 (4.7-6.6)	3.3 (2.8-3.9)
<i>C. p. carsonensis</i>	3.2 (2.8-3.8)	4.2 (3.5-5.2)	2.6 (1.9-3.3)	4.0 (3.0-4.8)	5.0 (4.1-5.9)	2.7 (2.0-3.2)
<i>C. p. pluvialis</i>	3.1 (2.7-3.8)	4.0 (3.4-4.6)	2.0 (1.4-2.7)	4.2 (3.7-5.0)	5.6 (4.6-6.6)	2.2 (1.7-2.9)
<i>C. p. wheeleri</i>	2.4	3.1	2.0	3.8	4.8	2.1
<i>C. p. walkerensis</i>	2.3 (1.8-2.5)	2.9 (2.2-3.7)	1.1 (0.5-1.5)	3.8 (3.0-4.5)	4.9 (4.0-5.9)	0.5 (0.0-1.3)
<i>C. p. paludum</i>	2.7 (1.6-3.2)	3.5 (2.6-4.1)	1.3 (0.9-1.7)	3.9 (3.3-4.2)	5.2 (4.3-6.0)	0.7 (0.0-1.4)

itself, has two taxa (plus several blend populations) of the "gabbii" group, both peripheral, occurring in association with the upper tributaries of pluvial Lake Lahontan. *C. p. carsonensis* occurs in the upper portions of the Carson and Truckee rivers. These rivers now drain into the Carson Sink and Pyramid Lake, respectively. *C. p. carsonensis* apparently does not now occur in the Lake Washoe basin, though geographically located between populations in the Carson and Truckee river valleys, but it may have occurred there in the past since this basin had pluvial connections with Lake Lahontan.

A phenotype appearing intermediate between *C. p. carsonensis* and *C. p. ariane* from north of Reno was described above. Populations near *C. p. ariane* occur 40 to 50 km west of here in Sierra and Plumas counties, California. This area is in the vicinity of two pluvial lakes (Lake Laughton, Lake Fred) which evidently had no outlet to pluvial Lake Lahontan (Hubbs and Miller 1948) but were close enough to that lake for *C. pegala* to have reached them.

C. p. paucilineatus occurs in the Quinn River Valley (and along its tributary, the Kings River) which now disappears into the Black Rock Desert. The Black Rock Desert/Smoke Creek subbasin of Lake Lahontan became isolated from the southern basin of the lake sometime between 12,500 and 10,000 years BP (Benson and Thompson 1987b). *C. p. paucilineatus* also occurs in the next valley to the east in the drainages (including Big Cottonwood and Martin creeks) of the northern part of Paradise Valley, these eventually having outlet to the Humboldt River (via the Little Humboldt River) to the south. The phenotype of *C. p. paucilineatus* appears closest to that of *C. p. stephensi* but with the ventral striations, lines and hindwing ocelli less well developed. Known populations of *C. p. paucilineatus* occur within about 50 km of *C. p. stephensi* today and were undoubtedly much closer at pluvial maxima. Apparent intermediate populations between these two taxa in the central Alvord Basin were noted above.

The Oregon Lakes drainage unit is a series of now-isolated basins, mostly in southern Oregon but entering extreme northeastern California and northwestern Nevada, which apparently had a diverse history with uncertain pluvial connections (Hubbs and Miller 1948, Snyder *et al.* 1964). The southernmost of these pluvial lakes, in Surprise Valley, may have had an early connection with pluvial Lake Lahontan and another with pluvial Lake Warner. Even with no connections, the southernmost of these basins was adjacent to the northern arms of pluvial Lake Lahontan (lake shores within 25 km). The Oregon Lakes are inhabited by their endemic *C. p. stephensi* in at least the Summer Lake, south of Albert Lake, Warner Lake (blend with a phenotype from further north in Oregon), Surprise Valley and southern Alvord drainages. At Silver Lake, the phenotype is small and darker, intermediate towards the populations northwestward (*e.g.*, along the Little Deschutes River near La Pine, Deschutes County, Oregon). The characteristics of *C. p. stephensi* undoubtedly indicate a close relationship to other "gabbii" group taxa.

C. p. gabbii occurs in the Goose Lake drainage unit and in part of the Klamath drainage unit (this latter set of populations being somewhat intermediate towards a darker phenotype). Based on its fish fauna, Goose Lake possibly had very early connections with the Lahontan system, highly debatable later connections with the Klamath system, and undoubted connections with the Sacramento River system via the Pit River (Hubbs and Miller 1948, Robins and Miller 1957). The phenotype of *C. p. gabbii*, appearing somewhat intermediate between those of *C. p. stephensi* and *C. p. ariane*, reflects this pluvial history. The Lahontan basin may have been the source of the original *C. pegala* here; the *C. p. ariane* influence may have appeared after the Sacramento River connection.

Intermediate populations between *C. p. gabbii* and *C. p. stephensi*, as described above, occur in localities on or near the west shore of pluvial Lake Lahontan at Squaw Creek and south of Ravendale. It is interesting (perhaps significant) that these occur in Lake Lahontan drainages. Are these "intermediate phenotypes" representative of early *C. pegala* in the Great Basin which subsequently differentiated on either side of the Warner Mountains? *C. p. stephensi* and *C. p. gabbii* also appear to intergrade northward (Tulelake, Crump Lake) with the darker phenotype(s) occurring in central Oregon.

C. p. utahensis is restricted to the eastern portions of the Bonneville drainage unit in the Bear River-Weber River and Provo River-Utah Lake-Jordan River drainages. These

TABLE 4. Distribution of *Cercyonis pegala* taxa among the drainage basins of the Great Basin/1.

Drainage basins/2 with known <i>C. pegala</i> populations	<i>C. pegala</i> taxon
BONNEVILLE GROUP	
Provo River-Utah Lake-Jordan River	<i>C. p. utahensis</i>
Bear River-Weber River	<i>C. p. utahensis</i> , intermediate towards <i>C. p. paludum</i> northward
Deep Creek	<i>C. p. pluvialis</i>
Thousand Springs	<i>C. p. paludum</i>
SNAKE RIVER GROUP	
Upper Snake River	<i>C. p. paludum</i>
Middle Snake River	<i>C. p. paludum</i>
OREGON LAKES GROUP	
Harney Basin	<i>C. p. paucilineatus</i> (?), intermediate with others northward
Alvord	<i>C. p. stephensi</i> in south, intermediate with <i>C. p. paucilineatus</i> northward
Albert Lake	<i>C. p. stephensi</i>
Summer Lake	<i>C. p. stephensi</i>
Surprise Valley	<i>C. p. stephensi</i>
Warner Lake	<i>C. p. stephensi</i> intermediate
Silver Lake	<i>C. p. stephensi</i> intermediate
GOOSE LAKE	
Goose Lake	<i>C. p. gabbii</i>
KLAMATH SYSTEM	
Upper Klamath	<i>C. p. gabbii</i> intermediate and others
LAHONTAN GROUP	
Lahontan	
Humboldt River	<i>C. p. paludum</i>
Newark Valley	<i>C. p. paludum</i>
Clover - Independence Valley	<i>C. p. paludum</i>
Little Humboldt River	<i>C. p. paucilineatus</i>
Quinn River - Kings River	<i>C. p. paucilineatus</i>
Squaw Valley	intermediate <i>C. p. stephensi</i> / <i>C. p. gabbii</i>
Ravendale	intermediate <i>C. p. stephensi</i> / <i>C. p. gabbii</i>
Honey Lake	intermediate <i>C. p. gabbii</i> / <i>C. p. ariane</i> (?)
Carson River	<i>C. p. carsonensis</i>
Truckee River	<i>C. p. carsonensis</i>
Red Rock Valley	intermediate <i>C. p. carsonensis</i> / <i>C. p. ariane</i>
East Walker River	<i>C. p. walkerensis</i>
RUBY GROUP	
Ruby-Franklin	<i>C. p. paludum</i>
Butte Valley	<i>C. p. paludum</i>
Goshute Valley	<i>C. p. paludum</i>
Steptoe Valley	<i>C. p. pluvialis</i>
COLORADO GROUP	
Meadow Valley Wash	<i>C. p. pluvialis</i> (extreme north only)
White River	<i>C. p. pluvialis</i> (central only)
DEATH VALLEY	
Owens	<i>C. p. wheeleri</i>
Mono Lake	<i>C. p. walkerensis</i>

occur in the vicinity of the east shore of the largest pluvial lake of the Great Basin, Lake Bonneville. The phenotype of *C. p. utahensis* is most similar to that of *C. p. stephensi* and there is little doubt as to its affinities. Lake Bonneville may have had early connections through headwater transfers with the Lahontan and Colorado drainages (Hubbs and Miller 1948).

C. p. pluvialis occurs in the Deep Creek drainage of the Bonneville group of drainages, in the southernmost Ruby drainage unit (southern Steptoe Valley drainage) and in the northern extensions of the Colorado drainage unit into the Great Basin (upper Meadow Valley and White River drainages). The Deep Creek drainage was on the west-central shore of Lake Bonneville. This is within 90 km of a population of *C. p. pluvialis* in Steptoe Valley. Steptoe Valley was thought to have been occupied by two pluvial lakes, Lake Steptoe and Lake Waring separated just south of Currie by a narrows; the pluvial connection of Lake Steptoe was northward into Lake Waring (Hubbs and Miller 1948). More recent evidence, however, suggested that Lake Steptoe did not exist but that Steptoe Valley had extensive paludal habitat draining into Lake Waring (Mifflin and Wheat 1979). The White River Valley is immediately west of the southern end of Steptoe Valley. The pluvial White River undoubtedly had connections with the Colorado River in southern Nevada (Hubbs and Miller 1948). Upper Lake Valley was the site of pluvial Lake Carpenter which probably drained southward via the pluvial Carpenter River, a tributary of the Colorado River (Hubbs and Miller 1948). The Lake Valley Basin is the second valley east of the White River Valley (separated by the now dry Cave Valley). The northern end of Lake Valley is separated by a low pass from Spring Valley, the northern portion of which lies just east of the southern part of Steptoe Valley. No *C. pegala* have been found to date in Spring Valley, yet suitable habitat seems to exist (e.g., the Shoshone, White Pine County, Nevada area). The distribution of *C. p. pluvialis* (undoubtedly a "gabbii" group taxon) is more or less central between that of *C. p. utahensis* on the eastern edge of the Great Basin and those of *C. p. wheeleri* and *C. p. carsonensis* in the extreme western Great Basin. This further supports the theory of a widespread occurrence of this general phenotype in the pluvial Great Basin.

To some degree, the members of the "gabbii" group resemble (yellow associated with the ocelli on both surfaces of the forewing, large ocelli on both surfaces of the hindwing, coarse ventral striations) phenotypes occurring in south-central United States, all currently assigned to *Cercyonis pegala texana* (W. H. Edwards). It is not difficult to envision expansion and subsequent isolation of ancestral "gabbii" group *C. pegala* in western North America during interglacial and glacial events of the Pleistocene similar to those outlined by Mengel (1964). Dispersal westward via a relatively southerly route by an inhabitant of wet areas was certainly possible. Headwaters of various easterly-flowing river systems (e.g., Rio Grande, Arkansas) closely approach those of the Colorado River drainage along the continental divide. The latter, undoubtedly, could have provided a corridor from which dispersal into the Great Basin was possible. I suggest that this "gabbii" group ancestor occupied the marshy areas of the Wisconsin Great Basin or shortly thereafter. It is

1/ *C. pegala* is unknown (u) or apparently absent (a) from the following basins: Bonneville Group - Snake Valley(a), Sevier(a, a Rocky Mountain phenotype occurs in the upper Sevier drainage along Otter Creek), Shoal Creek(u); Snake River Group - Wood River(u), Lost River-Cama Creek(u); Oregon Lakes Group - Alkali Lake(a), Fort Rock-Christmas Lake(u), Catlow Valley(u), Long Valley(a); Lahontan Group - Diamond Valley(a), Eagle Lake(a), Madeline Plains(a), Dixie Valley(a), Big Smokey Valley(a), Fish Lake(a), Colorado Group - Railroad Valley(a), Virgin River(a), Las Vegas(a); Death Valley Group - Mohave(a), Amargosa-Tecopa(a), Pahrump Valley(a). Note that there are additional valleys, especially in south-central Nevada mostly without permanent water (Hubbs and Miller 1948) and thus were not treated by Smith (1978). As far as is known, these all lack *C. pegala* colonies. There are also many valleys within the major drainages included above where *C. pegala* is absent (e.g., Washoe Valley, Reese River Valley, Pyramid Lake, Walker Lake, etc.)

2/ drainage unit terminology after Smith (1978).

noteworthy that a *C. p. texanus*-like phenotype occupies the river valleys in New Mexico while a phenotype similar to that occurring further north in Colorado occurs at middle elevations of the mountains in the same area (S. Cary, M. Toliver, pers. comm.).

The other Great Basin phenotypes of *C. pegala* belong to the "paludum" group. These taxa occur as two relatively undifferentiated phenotypes in a number of drainage basins from at least southern Idaho, northwestern Utah and northeastern Nevada to east-central California including parts of five (Bonneville, Snake, Ruby, Lahontan, Death Valley) of the drainage units outlined by Smith (1978). It is found largely along the main drainages (Humboldt and East Walker rivers) of the Great Basin, the Snake River and the present tributaries of these rivers. The Humboldt and Walker rivers were, respectively, eastern and western tributaries to pluvial Lake Lahontan. The upper Snake River had late pluvial connections with Lake Bonneville (Gilbert 1890, Malde 1968) and this is reflected by the fish fauna (Hubbs and Miller 1948). There is no evidence for a drainage connection between the Bonneville and Lahontan systems, even where they closely approach in northeastern Nevada; the similarities that exist in the fish fauna were attributed to stream capture or stream migration (Hubbs and Miller 1948). The short distances between wet areas of the Bonneville, Snake and Lahontan drainages in northeastern Nevada did not preclude dispersal of *C. pegala* between them. Known populations of this species in the Bonneville drainage (Thousand Springs Creek) are within 55 km of a Humboldt drainage population (East Humboldt Range); the Thousand Springs Creek population is within 40 km of a population in the Snake River drainage (south of Contact). Similarly, a population in the Humboldt drainage (Adobe Summit) is within 55 km of a Snake River drainage population (south of Jack Creek).

C. p. paludum also occurs in a group of four valleys east of the Ruby Mountains-East Humboldt Range axis. These valleys, Clover, Ruby, Butte and northern Steptoe (Goshute), contained pluvial lakes Clover, Franklin, Gale and Waring, respectively. Lake Clover probably had an early (but not later) pluvial discharge into the Humboldt River drainage (Hubbs and Miller 1948, Hubbs *et al.* 1974). Lake Franklin had no later pluvial connections except by intermittent stream connections with Lake Waring and an inflow from Lake Gale (Hubbs *et al.* 1974). The only apparent pluvial connections of Lake Waring were those mentioned above with Lake Franklin. Lake Gale drained northward into Lake Franklin via pluvial Butte River (Hubbs *et al.* 1974).

The occurrence of *C. p. paludum* in this group of valleys is easily explained by dispersal from the Humboldt River drainage via populations occurring in wet areas of the mountains to the west. One such present population occurs in a small marshy area at Angel Creek Campground above Wells in the East Humboldt Range. The Lake Franklin drainage also approaches that of Lake Newark to the southwest (Hubbs *et al.* 1974), another valley with populations of *C. p. paludum*. Newark Valley was occupied by pluvial Lake Newark which probably discharged via Huntington Creek into the Humboldt River (Hubbs *et al.* 1974).

In the western Great Basin, Mono Lake Basin is the northernmost of the Death Valley-associated drainages. Pluvial connections did not exist or were with the Owens River; earlier connections (possibly before *C. pegala* was in the area) seem to have been with Lake Lahontan by the East Walker River through Aurora Valley and then with the Death Valley system (Hubbs and Miller 1948, Miller 1948). Even without a surface water connection, dispersal between the East Walker River and Mono Basin is undoubtedly possible. Known present day colonies occur within 20 km on either side of Conway Summit, Mono County, California.

The distribution of the "paludum" group approaches that of the "gabbii" group in several areas. *C. p. walkerensis* in the Walker River and Mono Lake drainages is distributionally between *C. p. wheeleri* and *C. p. carsonensis* (within 75 km of *C. p. carsonensis*). I can see no phenotypic evidence of gene flow between *C. p. walkerensis* in this area and *C. pegala* of the "gabbii" group. Known populations of *C. p. paucilineatus* and *C. p. paludum* are within 55 km in Humboldt County, Nevada. The reduction in the coarseness of the ventral striations and the size and number of ventral hindwing ocelli of *C. p. paucilineatus* may or may not have resulted through past gene flow from *C. p.*

paludum. The closest known populations of *C. p. paludum* in northern Steptoe Valley (just south of Currie) and *C. p. pluvialis* in southern Steptoe Valley (Warm Springs) are about 70 km apart. As discussed above, there appears to be some phenotypic indication of gene flow between *C. p. paludum* into the northern populations of *C. p. pluvialis* in southern Steptoe Valley and at Ibapah. Steptoe Valley drained into Lake Waring to the north through a narrow channel south of Currie (Hubbs and Miller 1948, Mifflin and Wheat 1979), thus somewhat isolating *C. p. pluvialis* before *C. p. paludum* appeared in northern Steptoe Valley. The blend between *C. p. utahensis* and *C. p. paludum* in northern Utah and southern Idaho was discussed above. The population at Beowawe Geysers was also mentioned above. Beowawe Geysers are just west of Crescent Valley, the drainage for Pluvial Lake Gilbert of the Lahontan drainage.

The occurrence of the "paludum" group along the major river valleys, its absence from the peripheral isolated valleys of the Great Basin, and its relatively constant, very different, phenotype all suggest a later appearance in this region than *C. pegala* of the "gabbii" group. The "paludum" group phenotype must have arrived (or evolved *in situ*) after the initial post-pluvial desiccation but before the disappearance of the corridors of dispersal. Some of the areas occupied today were below water levels from 20,000 to 10,000 years BP (e.g., Benson and Thompson 1987a, 1987b; Curry and Oviatt 1985). Thus the ancestor was able to pass, one way or the other, from the East Walker River drainage to that of the Humboldt River. The Walker River flowed into the lower Carson River and both the Carson and Humboldt rivers flowed into a common sink at least as late as 6900 years ago and possibly later (Davis 1982). Today, the Walker River is separated from the Humboldt by about 150 km. Nearly 250 km separate the nearest known *C. pegala* populations of these two drainages.

The source of ancestral "paludum" group could have been from the north via the Snake River drainage with dispersal southwestward into and through the Humboldt River Valley and into the Walker River Valley; Otherwise it could have been the reverse, from the west or southwest. I prefer this latter option. As noted above, of the Great Basin *C. pegala* phenotypes, those of the "paludum" group most closely resemble *C. p. boopis* and, to a certain degree, *Cercyonis pegala baroni* (W. H. Edwards). The major difference is the presence of ventral hindwing ocelli on *C. p. paludum* males and sometimes females (these may have been acquired during the early initial contact with a member of the "gabbii" group; but note that *C. p. baroni* has ocelli). These form a stepwise progression (in color from brown to gray, number of hindwing ocelli, etc.) from the phenotype of *C. p. boopis* to *C. p. walkerensis* to *C. p. paludum*. The phenotypes to the north and east of the range of *C. p. paludum*, however, are sharply different in color and pattern.

C. p. boopis, the southernmost of the *C. pegala* west of the Sierra Nevada, may be of an old ancestry, possibly derived from a northwestward expansion of an eastern North American stock during one of the earlier Pleistocene interglacials, becoming isolated in California during a subsequent glacial period. If *C. p. boopis* is of such an old Californian stock, it most likely occurred south of its present range during glacial events, giving it access to the Great Basin south of the Sierra Nevada via the Lahontan Trough (a broad, continuous and relatively low elevation area in eastern California and western Nevada, Reveal 1979). Remnants of potential paludal stepping stones exist as springs through the Lahontan Trough today (Mifflin and Wheat 1979). The Lahontan Trough appears to have been a major route of dispersal for both plants and animals into the Great Basin (Reveal 1979, Tanner 1978). This is a more likely source than a direct dispersal across the high crest of the southern Sierra Nevada. The species could also have tracked marshy habitats along the east slope of the Sierra Nevada. These more western populations may well have come into contact with pre-"gabbii" group populations. Once access to the Great Basin was attained, this phenotype would have been able to occupy the vacuum left as the Pleistocene lakes retreated without their "gabbii" group of *C. pegala*, or could have genetically swamped these through intergradation.

An alternative explanation to the above is that all Great Basin phenotypes ("paludum" and "gabbii" groups) are of a single origin. This circumvents the need to explain the absence of the "gabbii" group from the Walker and Humboldt river drainages but creates several

unlikely situations: (1) it requires several differentiations into "gabbii" group phenotypes, (2) it does not explain the presence of the "paludum" group along the major river drainages, (3) it does not explain the absence of the "paludum" group phenotype in any peripheral, now isolated area, (4) it requires convergence of either the "paludum" group towards *C. p. boopis* or of the "gabbii" group phenotypes towards *C. p. texana*, and (5) it does not explain the near absence of intergradation between "paludum" and "gabbii" group populations.

The distribution and differentiation patterns exhibited by *C. pegala* in the Great Basin are strikingly parallel to those of *Polites sabuleti* (Boisduval) (Austin 1987). This hesperiid is another lowland marsh species with a single phenotype (similar to a California phenotype) in the Walker and Humboldt river basins which probably entered the Great Basin from the south and west, similar to the route hypothesized for the "paludum" group. Other phenotypes of *P. sabuleti*, with more restricted distributions, occur in localities in central, eastern and northwestern Nevada in many of the same places where *C. pegala* isolates occur. There is even an anomalous phenotype of *P. sabuleti* at Beowawe Geysers! Both species have a present-day patchwork of distribution with one phenotype dissecting the ranges of two more similar phenotypes. Thus populations of the dark, more finely striated "paludum" group occur north of populations of *C. p. wheeleri*, *C. p. pluvialis*, and *C. p. utahensis*, and south of populations of *C. p. gabbii*, *C. p. carsonensis*, *C. p. paucilineatus*, and *C. p. stephensi* (Fig. 214), all members of the "gabbii" group.

It must be noted in closing that the putative relationships between populations are inferred only from similarities and differences of adult phenotypic characteristics in the framework of known distributions. Additional data (early stages, genetic) may or may not present alternatives to the above. Further study of Great Basin *Cercyonis pegala* would be a fruitful endeavor and may shed additional light on their complex pattern of distribution and variation.

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LITERATURE CITED

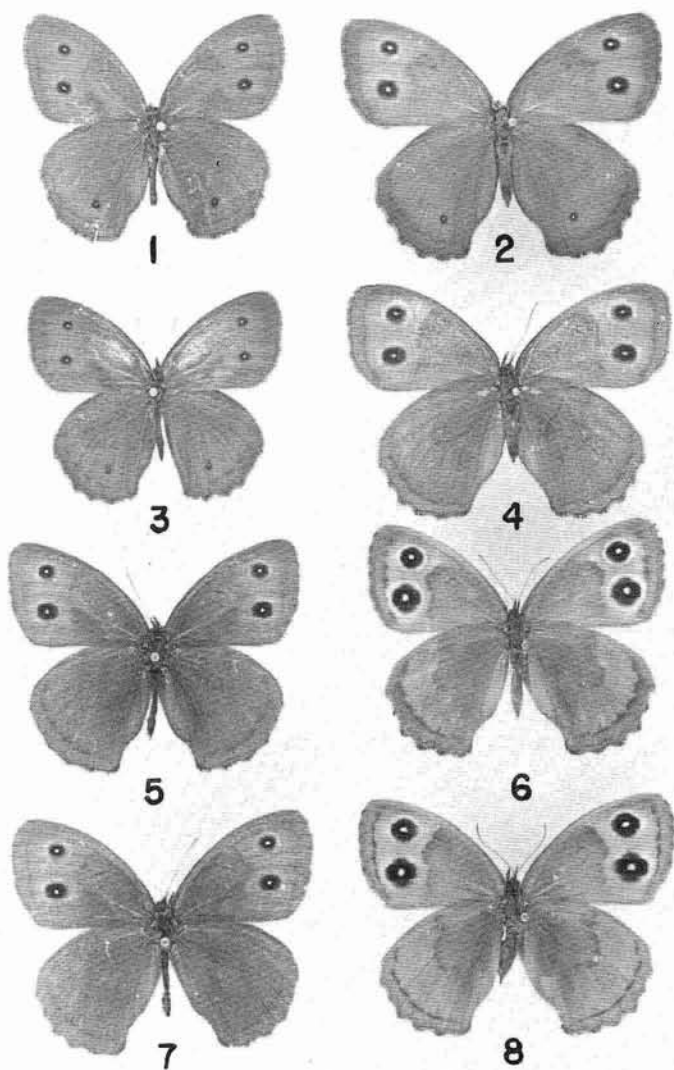
- Austin, G. T. 1981. The montane butterfly fauna of the Spring Range, Nevada. *J. Lepid. Soc.* 35:66-74.
- Austin, G. T. 1985a. Lowland riparian butterflies of the Great Basin and associated areas. *J. Res. Lepid.* 24:117-131.
- Austin, G. T. 1985b. Nevada butterflies: preliminary checklist and distribution. *J. Lepid. Soc.* 39:95-118.
- Austin, G. T. 1986. A review of the satyrine genus *Neominois*, with descriptions of three new subspecies. *Bull. Allyn Mus.*, no. 107.
- Austin, G. T. 1987. Nevada populations of *Polites sabuleti* and the description of five new subspecies. *Bull. Allyn Mus.*, no. 109.
- Austin, G. T. and D. D. Murphy. 1987. Zoogeography of Great Basin butterflies: patterns of distribution and differentiation. *Great Basin Natur.* 47:186-201.
- Austin, G. T. and D. D. Murphy. (in press.) *Euphydryas editha* (Boisduval) (Nymphalidae) of the Great Basin with descriptions of two new subspecies. *Systematics of Western North American Butterflies*. (T. C. Emmel, ed.)
- Austin, G. T. and M. J. Smith. (in press.) Revision of the *Thessalia leanira* complex (Nymphalidae: Melitaeinae): *Thessalia leanira* (C. & R. Felder), with descriptions of four new subspecies. *Systematics of Western North America Butterflies* (T. C. Emmel, ed.)
- Behle, W. H. 1963. Avifaunistic analysis of the Great Basin region of North America. *Proc. 13th Int. Ornithol. Congr.*:1168-1181.
- Behle, W. H. 1978. Avian biogeography of the Great Basin and intermountain region. *Great Basin Nat. Mem.* 2:55-80.
- Behr, H. 1864. Notes on California Satyrids. *Proc. Calif. Acad. Nat. Sci.* 3:163-166.
- Benson, L. and R. S. Thompson. 1987a. The physical record of lakes in the Great Basin. In W. F. Ruddiman and H. E. Wright, Jr., *North America and adjacent oceans during the last deglaciation*. Boulder, CO, Geological Society of North America, vol. K-3.
- Benson, L. and R. S. Thompson. 1987b. Lake-level variation in the Lahontan Basin for the past 50,000 years. *Quaternary Research* 28:69-85.
- Billings, W. D. 1978. Alpine phytogeography across the Great Basin. *Great Basin Nat. Mem.* 2:105-117.
- Boisduval, J. B. A. D. 1852. *Lepidopteres de la California*. *Ann. Soc. Ent. France* (ser. 2) 10:275-324.
- Brown, F. M. 1955. The Wheeler Expeditions to the southwestern United States, 1869-1876. *Lepid. News* 9:124-126.
- Brown, F. M. 1957. Itineraries of the Wheeler Survey Naturalists 1871 - Ferdinand Bischoff. *J. New York Ent. Soc.* 65:219-234.
- Brown, F. M. 1964. The types of satyrid butterflies described by William Henry Edwards. *Trans. Amer. Ent. Soc.* 90:323-413.
- Brown, F. M. 1965. Comments on the genus *Cercyonis* Scudder, with figures of types (Satyridae). *J. Res. Lepid.* 4:131-148.
- Brown, F. M. 1966a. Itineraries of the Wheeler Survey Naturalists: Henry Wetherbee Henshaw. *J. Lepid. Soc.* 20:71-82.
- Brown, F. M. 1966b. Type locality for *Cercyonis nephele* Kirby and "Upper Canada" insects collected in the 1820's. *J. New York Ent. Soc.* 73:240-242.
- Brown, F. M., D. Eff and B. Rotger. 1957. Colorado butterflies. *Denver Museum Nat. Hist.*, Denver, CO.
- Brown, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. *Amer. Nat.* 105:467-478.
- Brown, J. H. 1978. The theory of insular biogeography and the distribution of boreal birds and mammals. *Great Basin Nat. Mem.* 2:209-227.
- Clokey, I. W. 1951. *Flora of the Charleston Mountains, Clark County, Nevada*. Univ. Calif. Press, Berkeley.
- Comstock, J. A. 1924a. Studies in Pacific Coast Lepidoptera. The rediscovery of a "lost species." *Bull. So. Calif. Acad. Sci.* 23:13-16.

- Comstock, J. A. 1924b. Studies in Pacific Coast Lepidoptera. Notes on the genus *Cercyonis*. Bull. So. Calif. Acad. Sci. 23:174-176.
- Comstock, J. A. 1927. Butterflies of California. Publ. by the author, Los Angeles, CA.
- Curry, D. R. and C. G. Oviatt. 1985. Durations, average rates, and probable causes of Lake Bonneville expansions, standstills, and contractions during the last deep-lake cycle 32,000 to 10,000 years ago. Geog. J. Korea 10:1085-1099.
- Davis, J. O. 1982. Bits and pieces: the last 35,000 years in the Lahontan area. Pp. 53-75 in D. B. Madsen and J. F. O'Connell (eds.) *Man and environment in the Great Basin*. Soc. Amer. Archaeol. Papers, no. 2.
- Dornfeld, E. J. 1980. The butterflies of Oregon. Timber Press, Forest Grove, OR.
- dos Passos, C. F. 1964. A synonymic list of the Nearctic Rhopalocera. Lepid. Soc. Mem., no. 1.
- Edwards, W. H. 1870. Descriptions of new North American diurnal Lepidoptera. Trans. Amer. Ent. Soc. 3:189-196.
- Edwards, W. H. 1873. Descriptions of diurnal Lepidoptera found within the United States. Trans. Amer. Ent. Soc. 4:343-348.
- Edwards, W. H. 1884. The butterflies of North America. Second Series. Houghton, Mifflin & Co., Boston, MA.
- Emmel, J. F., T. C. Emmel and S. O. Mattoon. (in press a.) The types of California butterflies named by Jeane Alphonse Boisduval: designation of lectotypes and neotype, and fixation of type localities. Systematics of Western North American Butterflies. (T. C. Emmel, ed.)
- Emmel, J. F., T. C. Emmel and S. O. Mattoon. (in press b.) The types of California butterflies named by Herman Behr: designation of neotypes and fixation of type localities. Systematics of Western North American Butterflies. (T. C. Emmel, ed.)
- Emmel, T. C. 1969. Taxonomy, distribution and biology of the genus *Cercyonis* (Satyridae). I. Characteristics of the genus. J. Lepid. Soc. 23:165-175.
- Emmel, T. C. and S. O. Mattoon. 1972. *Cercyonis pegala blanca*, a "missing type" in the evolution of the genus *Cercyonis* (Satyridae). J. Lepid. Soc. 26:140-149.
- Ferris, C. D. (ed.). 1989. Supplement to: A catalogue/checklist of the butterflies of America north of Mexico. Lepid. Soc. Memoir, no. 3.
- Ferris, C. D. and F. M. Brown (eds.). 1981. Butterflies of the Rocky Mountain states. Univ. Oklahoma Press, Norman.
- Garth, J. S. and J. W. Tilden. 1986. California butterflies. Univ. California Press, Berkeley.
- Gilbert G. K. 1882. Contributions to the history of Lake Bonneville. Ann. Rep. U.S. Geol. Surv. 2:167-200.
- Gilbert, G. K. 1890. Lake Bonneville. Monogr. U.S. Geol. Surv. 1:1-438.
- Grayson, D. K. 1982. Toward a history of Great Basin mammals during the past 15,000 years. Pp. 82-101 in D. B. Madsen and J. F. O'Connell (eds.), *Man and environment in the Great Basin*. Soc. Amer. Archaeol. Papers, no. 2.
- Grayson, D. K. 1983. Paleontology of Gatecliff Shelter - small mammals. In D. H. Thomas, J. O. Davis, D. K. Grayson, W. N. Melhorn, T. Thomas and D. Trexler, *The archaeology of Monitor Valley. 2. Gatecliff Shelter*. Anthropol. Papers Amer. Mus. Nat. Hist., vol. 59.
- Hall, E. R. 1946. Mammals of Nevada. Univ. Calif. Press, Los Angeles.
- Harper, K. T., D. C. Freeman, W. K. Ostler and L. G. Klikoff. 1978. The flora of Great Basin mountain ranges: diversity, sources, and dispersal ecology. Great Basin Nat. Mem. 2:81-103.
- Holland, W. J. 1931. The butterfly book. Revised edition. Doubleday, Doran and Co., Garden City, NY.
- Hovingh, P. 1986. Biogeographic aspects of leeches, mollusks, and amphibians in the intermountain region. Great Basin Nat. 46:736-744.
- Howe, W. H. 1975. The butterflies of North America. Doubleday, Garden City, NY.
- Hubbs, C. L. and R. R. Miller. 1948. The zoological correlation between fish distribution and hydrographic history in the desert basins of western United States. Bull. Univ. Utah Biol. Ser. 38:17-166.
- Hubbs, C. L., R. R. Miller and L. C. Hubbs. 1974. Hydrographic history and relict fishes

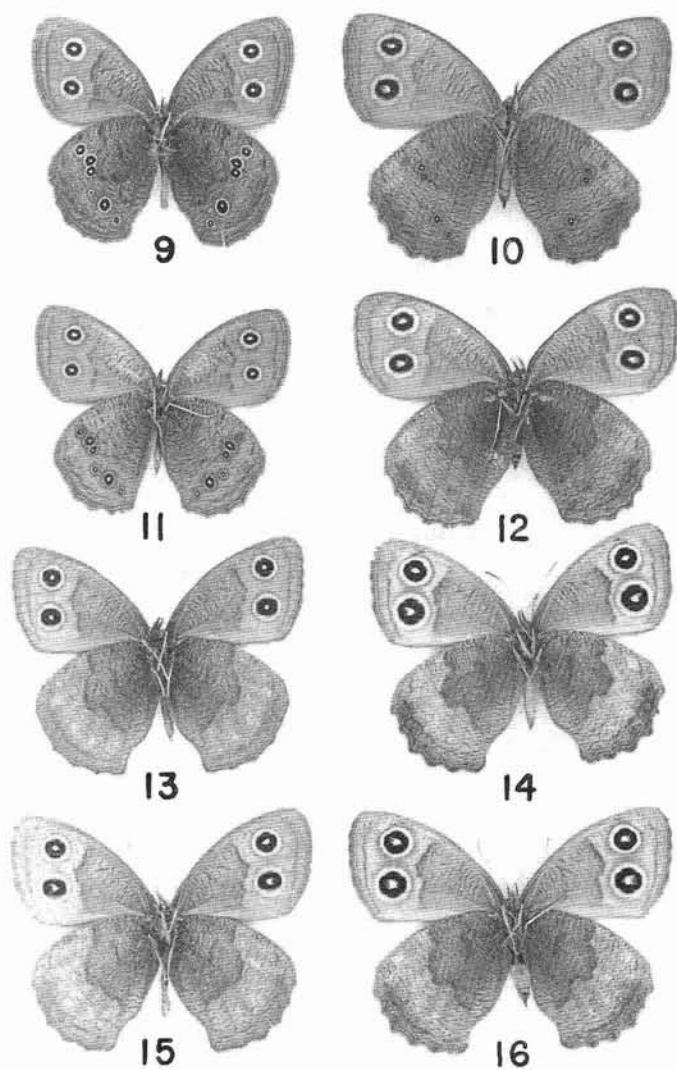
- of the north-central Great Basin. Mem. Calif. Acad. Sci. 7:1-259.
- Johnson, N. K. 1970. The affinities of the boreal avifauna of the Warner Mountains, California. Occ. Pap. Biol. Soc. Nevada, no. 22.
- Johnson, N. K. 1975. Controls of number of bird species on montane islands in the Great Basin. Evol. 29:545-567.
- Johnson, N. K. 1978. Patterns of avian geography and speciation in the intermountain region. Great Basin Nat. Mem. 2:137-159.
- Lloyd, R. M. and R. S. Mitchell. 1973. A flora of the White Mountains, California and Nevada. Univ. Calif. Press, Berkeley.
- Malde, H. H. 1968. The catastrophic late Pleistocene Bonneville flood in the Snake River plain, Idaho. U.S. Geol. Surv. Prof. Pap. 596:1-52.
- Mather, B. 1966. *Cercyonis pegala pegala* (Satyridae): occurrence in Mississippi and variation in forewing maculation. J. Lepid. Soc. 20:186-188.
- Mattoon, S. O. and G. T. Austin. (in press.) A review of *Satyrium fuliginosum* (W. H. Edwards) with the description of three new subspecies. Systematics of Western North American Butterflies. (T. C. Emmel, ed.)
- Mead, T. L. 1875. Report upon the collections of diurnal Lepidoptera made in portions of Colorado, Utah, New Mexico, and Arizona during the years 1871, 1872, 1873, and 1874, with notes upon all species known to inhabit Colorado. Reports of Surveys West of the 100th Meridian 5:739-794, Washington, D.C.
- Mengel, R. M. 1964. The probable history of species formation in some northern wood warblers (Parulidae). Living Bird 3:9-43.
- Mifflin, M. D. and M. M. Wheat. 1979. Pluvial lakes and estimated pluvial climates of Nevada. Nevada Bureau of Mines and Geology, Bull. 94.
- Miller, A. H. 1941. A review of centers of differentiation for birds in the western Great Basin region. Condor 43:257-267.
- Miller, L. D. and F. M. Brown. 1981. A catalogue/checklist of the butterflies of America north of Mexico. Lepid. Soc. Mem., no. 2.
- Miller, R. R. 1946. Correlation between fish distribution and Pleistocene hydrography in eastern California and southwestern Nevada, with a map of the Pleistocene waters. J. Geol. 54:43-53.
- Miller, R. R. 1948. The cyprinodont fishes of the Death Valley system of eastern California and southwestern Nevada. Misc. Publ. Mus. of Zool., Univ. Mich., no. 68.
- Miller, R. R. 1958. Origin and affinities of the freshwater fish fauna of western North America. Pp. 187-222 in C. L. Hubbs (ed.), *Zoogeography*. Amer. Assoc. Adv. Sci., publ. no. 51, Baltimore, MD.
- Miller, R. R. 1981. Coevolution of deserts and pupfishes (genus *Cyprinodon*) in the American southwest. Pp. 39-94 in R. J. Naiman and D. L. Soltz (eds.) *Fishes of North American Deserts*, J. Wiley & Sons, New York, NY.
- Miller, R. R. and G. R. Smith. 1981. Distribution and evolution of *Chasmistes* (Pisces: Catostomidae) in western North America. Univ. Mich. Mus. Zool., Occ. Pap., no. 696.
- Newcomer, E. J. 1965. Type locality of *Cercyonis stephensi* revisited. J. Lepid. Soc. 19:161-164.
- Oberthur, C. 1914. Les lepidopteres de la Californie par le Docteur Boisduval. Etudes de Lepid. Comp. 9(2):73-86 (pl. 253-264).
- Pratt, W. L. 1985. Insular biogeography of central Great Basin land snails: extinction without replacement. J. Arizona/Nevada Acad. Sci. (1985 Proc. Suppl.):20:14 (abstract).
- Reveal, J. L. 1979. Biogeography of the intermountain region, a speculative appraisal. *Mentzelia*, no. 4.
- Richardson, J. 1837. Fauna Boreali-Americana; or the zoology of the northern parts of British America: containing descriptions of the objects of natural history collected on the late Northern Land Expeditions, under command of Captain Sir John Franklin, R. N. Josiah Fletcher, Norwich, England.
- Robins, C. R. and R. R. Miller. 1957. Classification, variation, and distribution of sculpins, genus *Cottus*, inhabiting Pacific slope waters in California and southern Oregon, with a key to the species. Calif. Fish and Game 43:213-233.

- Russell, I. C. 1883. Sketch of the geological history of Lake Lahontan. *Ann. Rep. U.S. Geol. Surv.* 3:189-235.
- Russell, I. C. 1885. Geological history of Lake Lahontan, a Quaternary Lake of northwestern Nevada. *Monogr. U.S. Geol. Surv.* 11:1-288.
- Russell, I. C. 1889. Quaternary history of Mono Valley, California. *Ann. Rep. U.S. Geol. Surv.* 8:261-394.
- Scott, J. A. 1986. The butterflies of North America, a natural history and field guide. Stanford Univ. Press, Stanford, CA.
- Scudder, S. H. 1889. The butterflies of the eastern United States and Canada with special reference to New England. Publ. by author, Cambridge, MA.
- Shapiro, A. M. 1966. Butterflies of the Delaware Valley. *Amer. Ent. Soc.*, special publication.
- Shapiro, A. M. 1974. Butterflies and skippers of New York state. *Search* 4:1-60.
- Smith, G. R. 1978. Biogeography of intermountain fishes. *Great Basin Nat. Mem.* 2:17-42.
- Smithe, F. B. 1975. Naturalist's color guide. *Amer. Mus. Nat. Hist.*, NY.
- Smithe, F. B. 1981. Naturalist's color guide part III. *Amer. Mus. Nat. Hist.*, NY.
- Snyder, C. T., G. Hardman and F. F. Zdenak. 1964. Pleistocene lakes in the Great Basin. *U.S. Geol. Surv., Misc., Geol. Invest. Map* 1-416.
- Strecker, H. 1873. *Lepidoptera, Rhopaloceres and Heteroceres*. Part 4, pp. 25-32. Publ. by author, Reading, PA.
- Strecker, H. 1874. *Lepidoptera, Rhopaloceres and Heteroceres*. Part 8, pp. 61-70. Publ. by author, Reading, PA.
- Tanner, W. W. 1978. Zoogeography of reptiles and amphibians in the intermountain region. *Great Basin Nat. Mem.* 2:43-53.
- Tilden, J. W. 1975. An analysis of the W. G. Wright butterfly and skipper plesiotypes in the collection of the California Academy of Sciences. *Occ. Pap. Calif. Acad. Sci.*, no. 118.
- Tilden, J. W. and A. C. Smith. 1986. A field guide to western butterflies. Houghton Mifflin, Boston, MA.
- Wells, P. V. 1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. *Ecol. Monogr.* 53:341-382.
- Wilcox, B. A., D. D. Murphy, P. R. Ehrlich and G. T. Austin. 1986. Insular biogeography of the montane butterfly faunas in the Great Basin: comparison with birds and mammals. *Oecologia* 69:188-194.
- Wright, W. G. 1905. The butterflies of the west coast of the United States. Publ. by the author, San Francisco, CA.

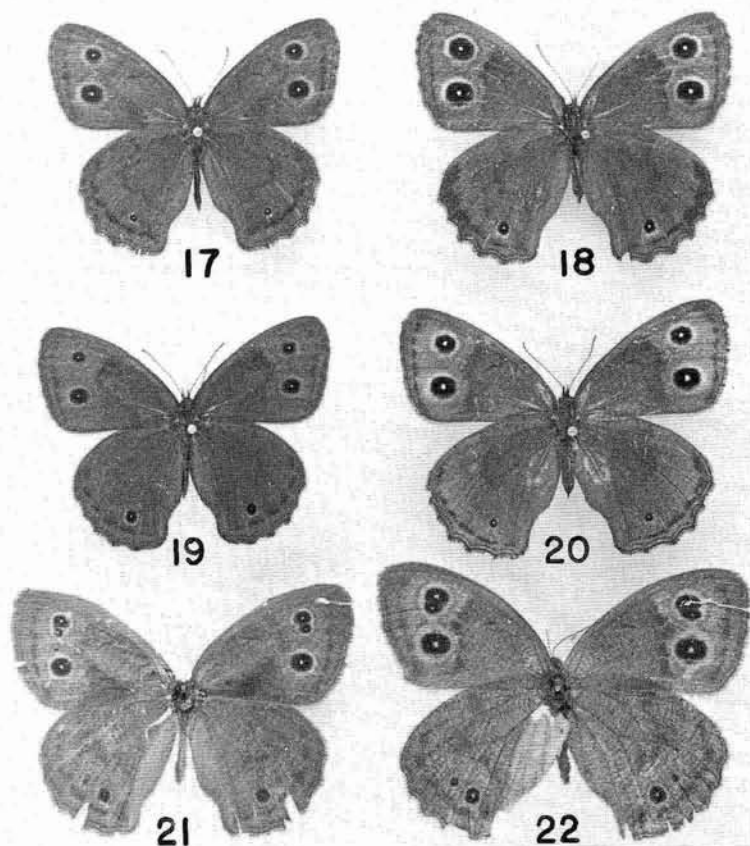
FIGURES 



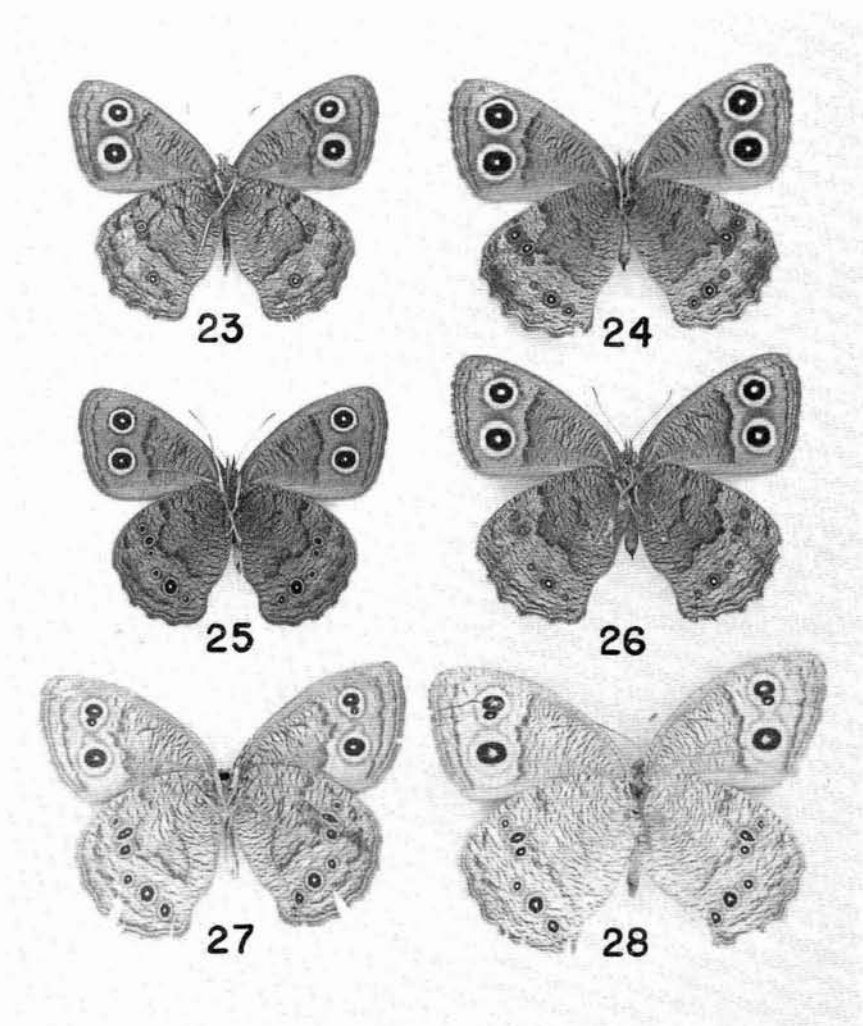
Figures 1-8. *Cercyonis pegala* subspecies (dorsal surface, males on left, females on right). 1-4. *C. p. nephele*, WI: Juneau Co.; Necedah Township, leg. T. Kral (1) 28 June 1977, (2) 25 July 1984, (3) 12 July 1982, (4) 28 July 1984; 5-8. *C. p. boopis*, CA: Contra Costa Co.; Point Richmond, leg. J. Scott (5, 7) 14 June 1972, (6, 8) 18 June 1971.



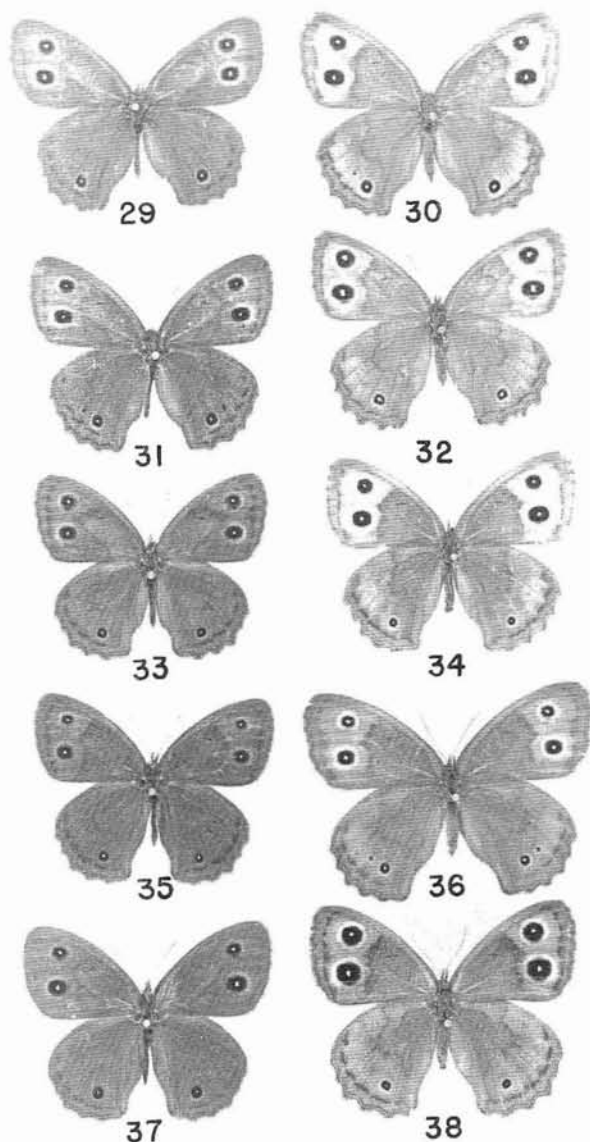
Figures 9-16. *Cercyonis pegala* subspecies (ventral surface). 9-12. *C. p. nephele*, same specimens as in Figures 1-4; 13-16. *C. p. boopis*, same specimens as Figures 5-8.



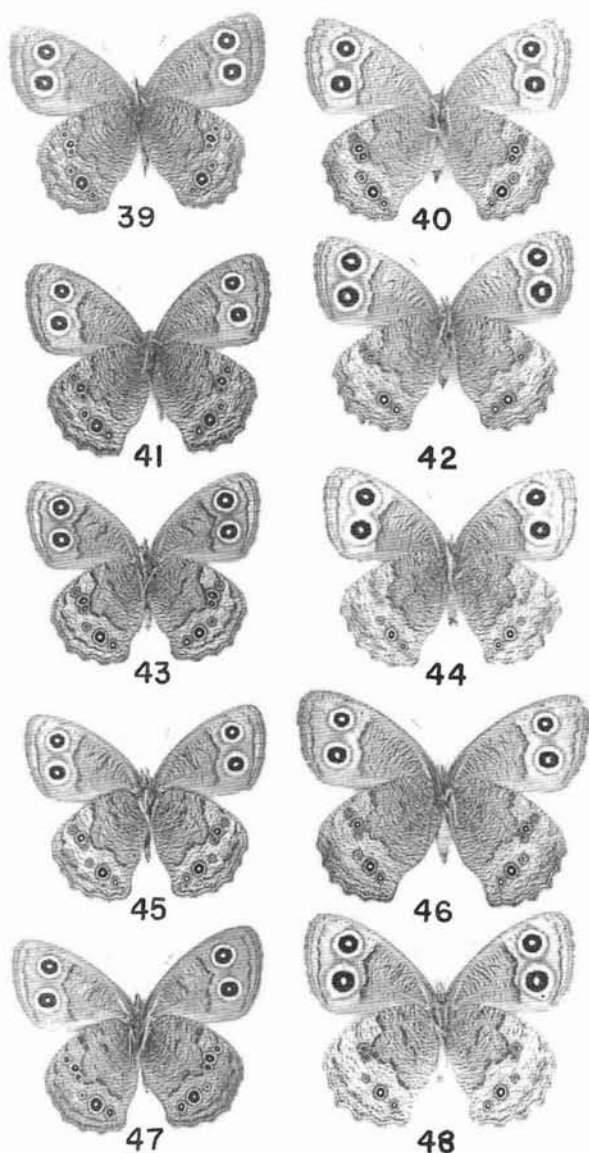
Figures 17-22. *Cercyonis pegala* subspecies (dorsal surface, males on left, females on right). 17-20. *C. p. ariane* (17) CA: Plumas Co.; Ca 70, 4.1 mi. E Ca 89, 30 June 1985, leg. G. T. Austin; (18) CA: Sierra Co.; Hwy. 49, 1.4 mi. N Hwy. 89, 3 Aug. 1987, leg. C. Hageman; (19-20) CA: Plumas Co.; Ca 70, 1.4 mi. E Ca 89, 30 June 1985, leg. G. T. Austin; 21-22. *C. p. wheeleri* (21) "Ariz/a", (22) "Owens Lake, Nev."



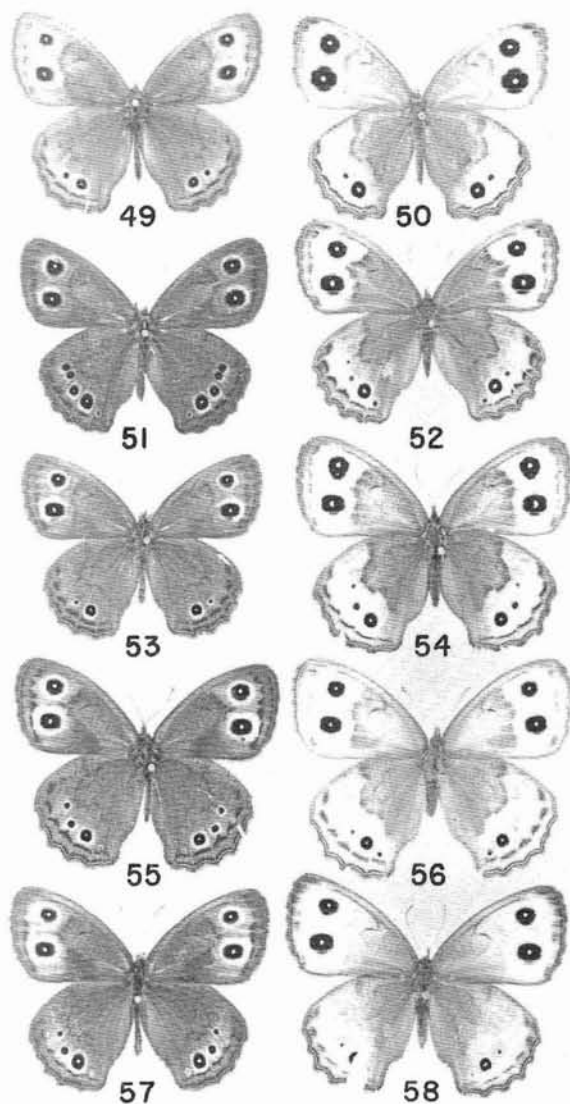
Figures 23-28. *Cercyonis pegala* subspecies (ventral surface). 23-26. *C. p. ariane*, same specimens as in Figures 17-20; 27-28. *C. p. wheeleri*, same specimens as in Figures 21-22.



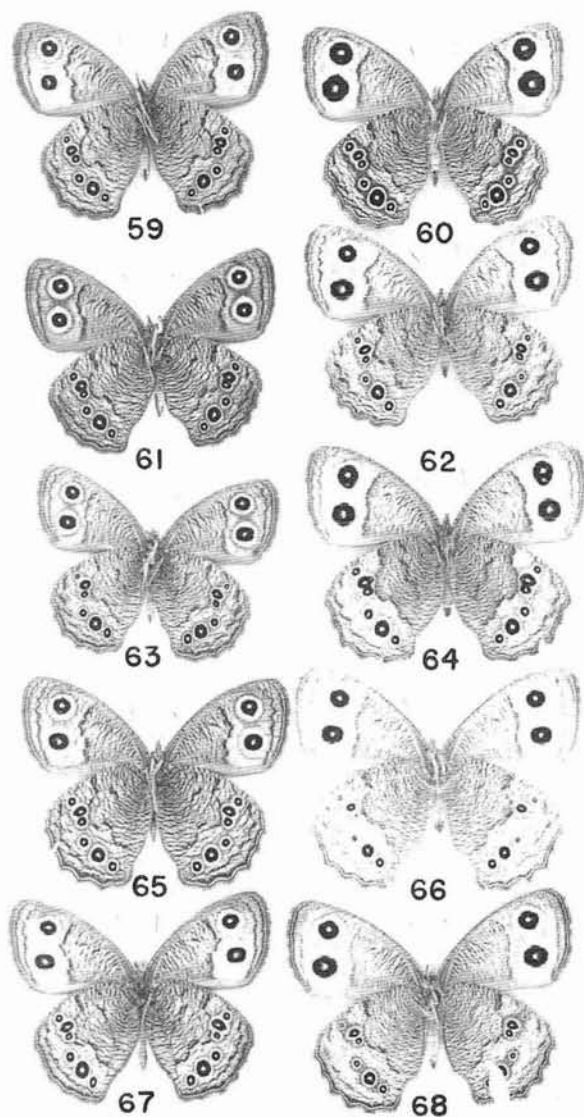
Figures 29-38. *Cercyonis pegala gabbii* (dorsal surface, males on left, females on right). (29-32, 34, 36, 38) OR: Lake Co.; E side Goose Lake, US 395, 7.0 mi. N Calif. line, 18 July 1986, leg. G. & A. Austin; (33, 35) OR: Lake Co.; Goose Lake area, US 395, 6.5 mi. N Pine Creek, 10 July 1989, leg. G. T. Austin; (37) CA: Modoc Co.; US 395, 5.1 mi. S Oregon line, 10 July 1989, leg. G. T. Austin.



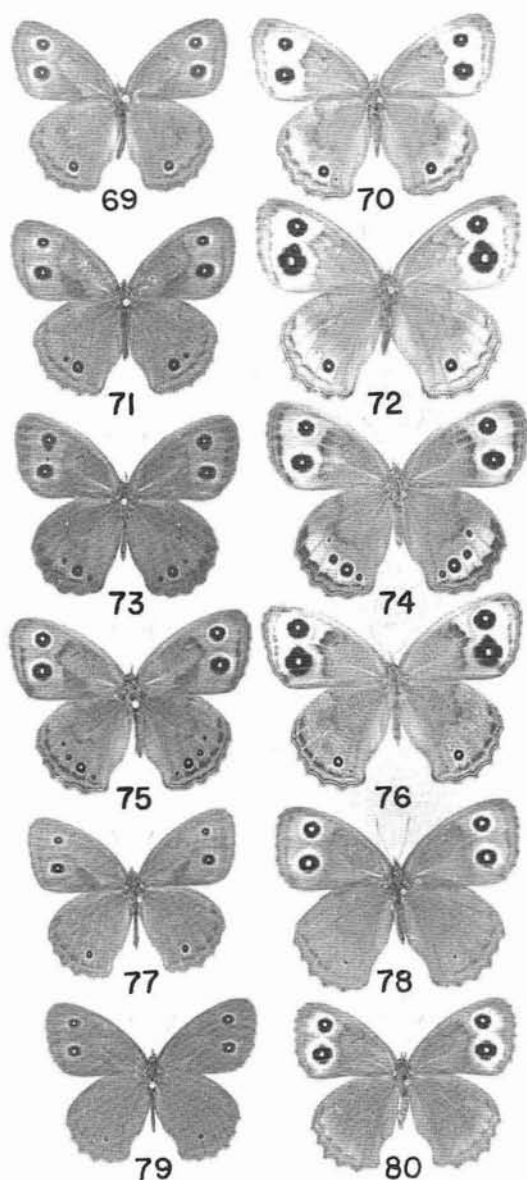
Figures 39-48. *Cercyonis pegala gabbii* (ventral surface). Same specimens as in Figures 29-38.



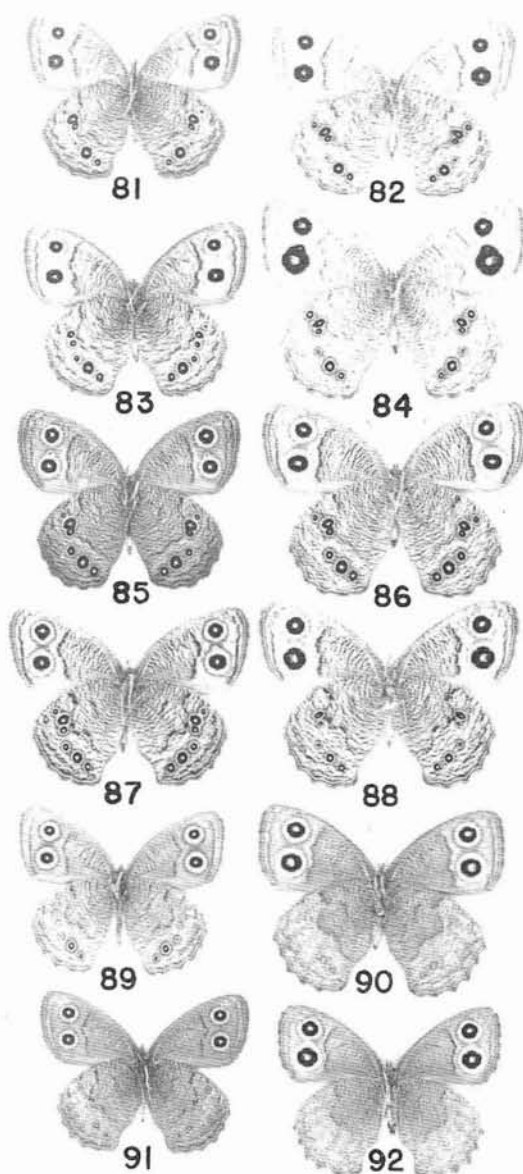
Figures 49-58. *Cercyonis pegala stephensi* (dorsal surface, males on left, females on right). (49 51, 57) CA: Modoc Co.; Surprise Valley, Ft. Bidwell Rd., 8.2 mi. S Eagleville, 20 July 1986, leg. G. & A. Austin; (50) CA: Lassen Co.; Ft. Bidwell Rd., 1.2 mi. S Modoc Co. line, 20 July 1986, leg. G. & A. Austin; (52) CA: Modoc Co.; Ft. Bidwell Rd., 4.5 mi. N Fandango Pass Rd., 19 July 1986, leg. G. & A. Austin; (53) CA: Modoc Co.; Ft. Bidwell Rd., 4.3 mi. S Cedarville, 20 July 1986, leg. G. & A. Austin; (54, 55, 58) CA: Modoc Co.; Ft. Bidwell Rd., 6.5 mi. S Eagleville, 20 July 1986, leg. G. & A. Austin; (56) CA: Modoc Co.; Co. Rt. 1, 2.0 mi. N Lassen Co. line, 8 Aug. 1981, leg. G. T. Austin.



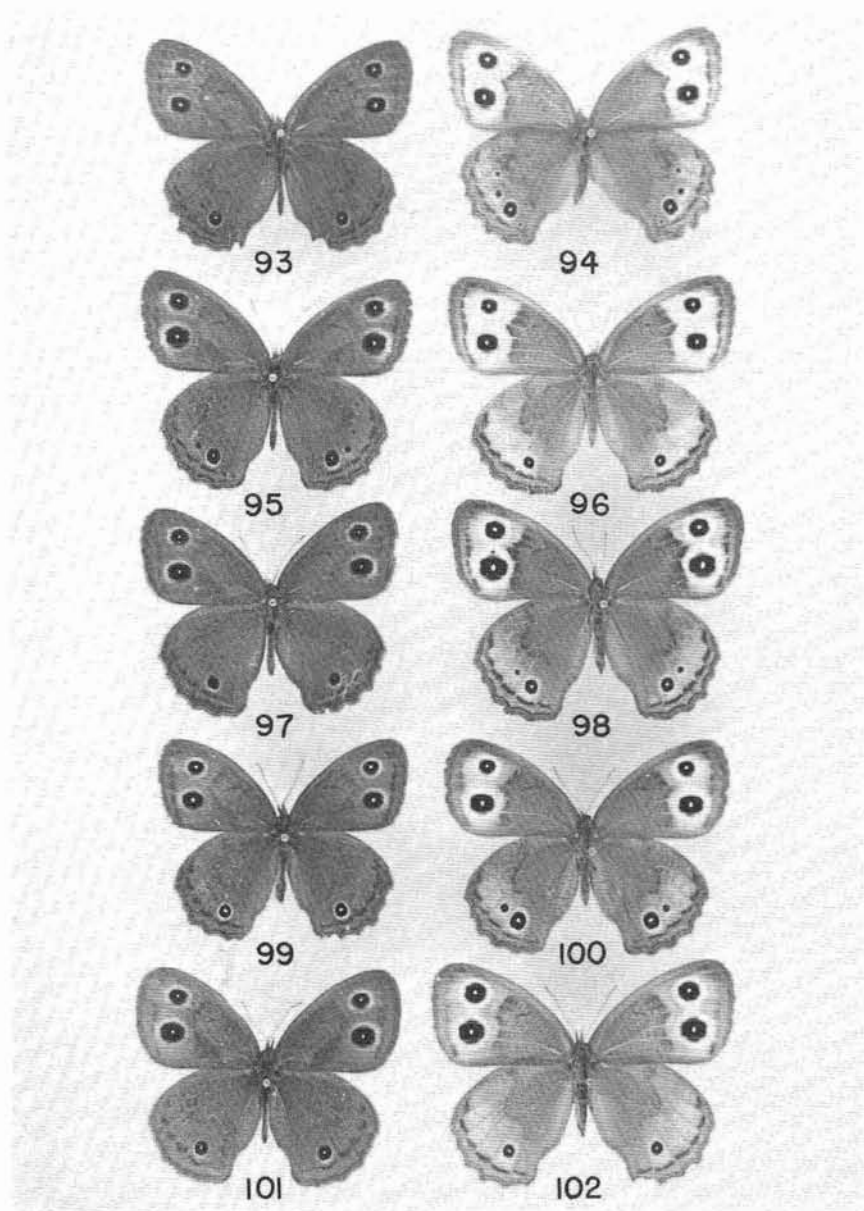
Figures 59-68. *Cercyonis pegala stephensi* (ventral surface). Same specimens as in Figures 49-58.



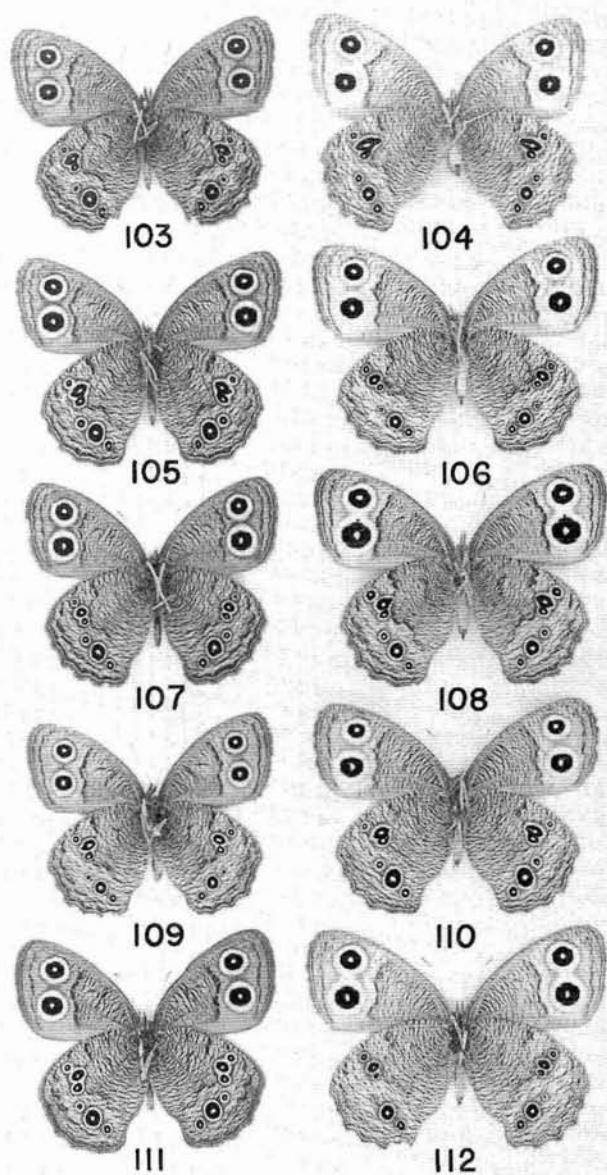
Figures 69-80. *Cercyonis pegala* subspecies (dorsal surface, holotype males on left, allotype females on right, data in text). (69-70) *C. p. carsonensis*, (71-72) *C. p. paucilineatus*, (73-74) *C. p. utahensis*, (75-76) *C. p. pluvialis*, (77-78) *C. p. paludum*, (79-80) *C. p. walkerensis*.



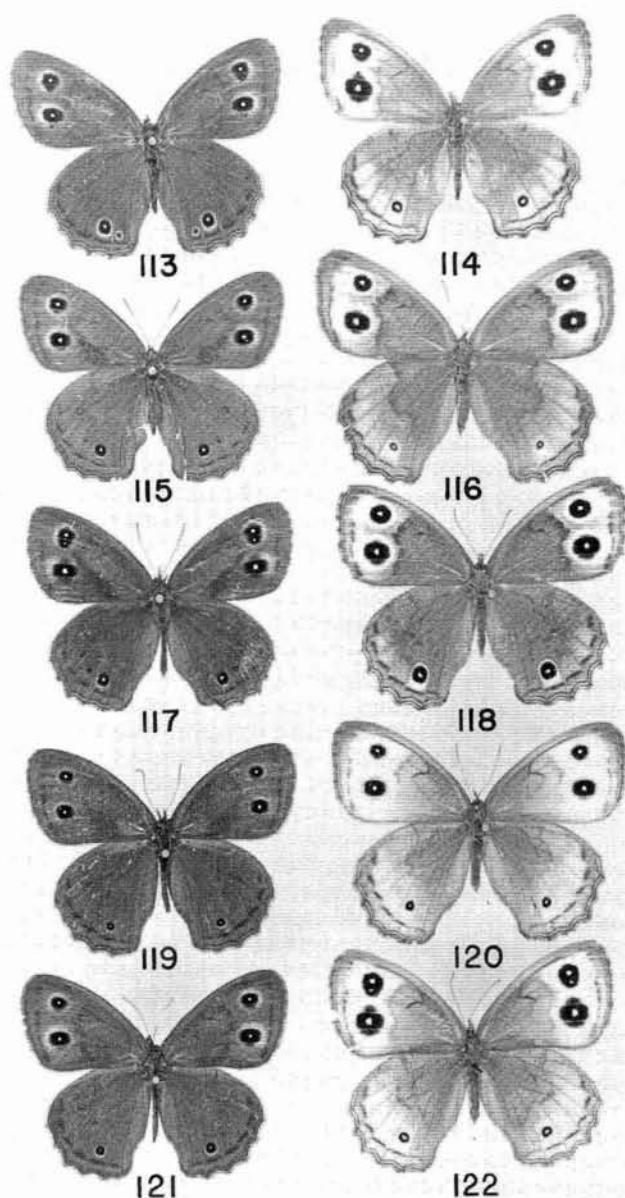
Figures 81-92. *Cercyonis pegala* subspecies (ventral surface). 81-82. *C. p. carsonensis*, same specimens as in Figures 69-70; 83-84. *C. p. paucilineatus*, same specimens as in Figures 71-72; 85-86. *C. p. utahensis*, same specimens as in Figures 73-74; 87-88. *C. p. pluvialis*, same specimens as in Figures 75-76; 89-90. *C. p. paludum*, same specimens as in Figures 77-78; 91-92. *C. p. walkerensis*, same specimens as in Figures 79-80.



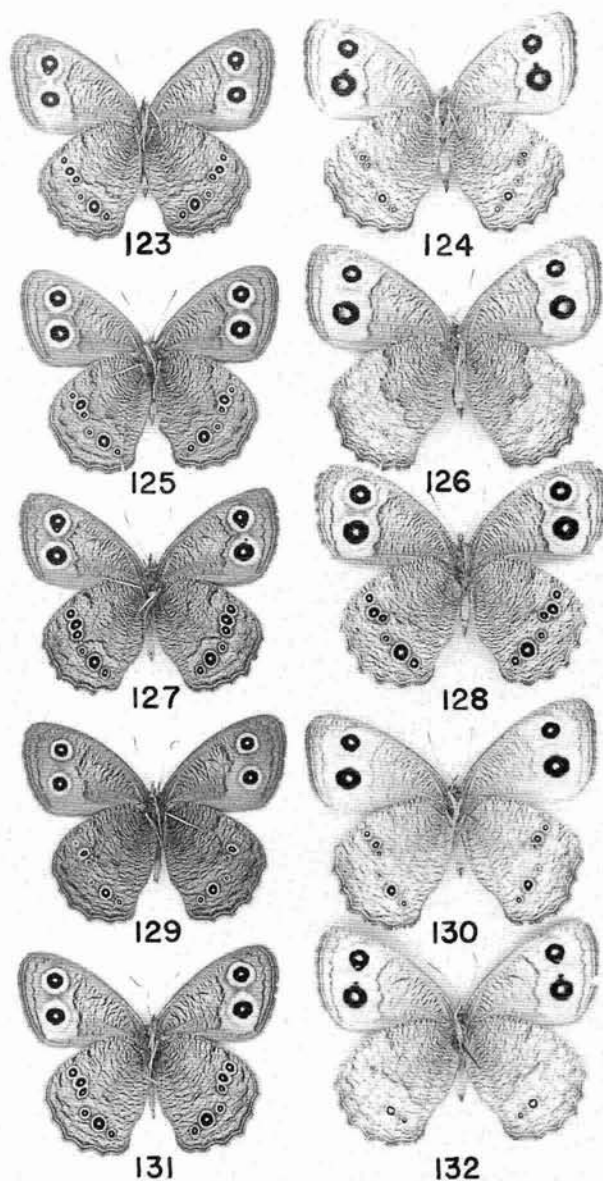
Figures 93-102. *Cercyonis pegala carsonensis* (dorsal surface, males on left, females on right). NV: Douglas Co.; Carson Valley, Scossa Ranch, leg. G. T. Austin. (93, 95, 101) 24 July 1984, (94) 11 Aug. 1979, (96, 98, 100) 26 July 1981, (97) 26 Aug. 1983, (99) 24 July 1982, (102) 6 Aug. 1981.



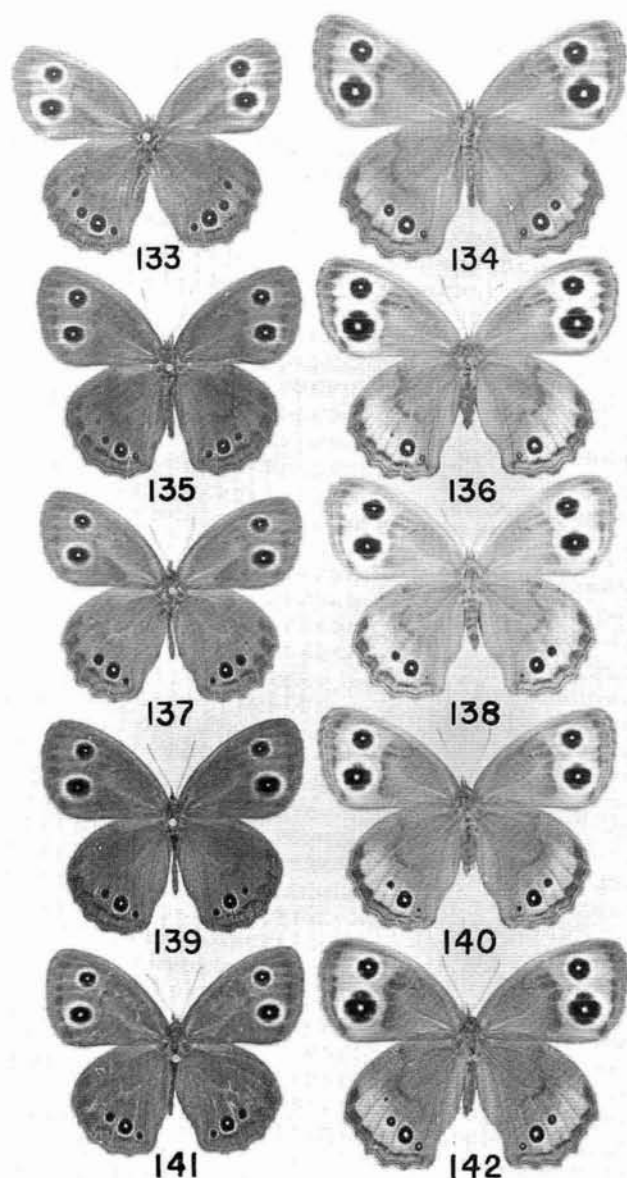
Figures 103-112. *Cercyonis pegala carsonensis* (ventral surface). Same specimens as in Figures 93-102.



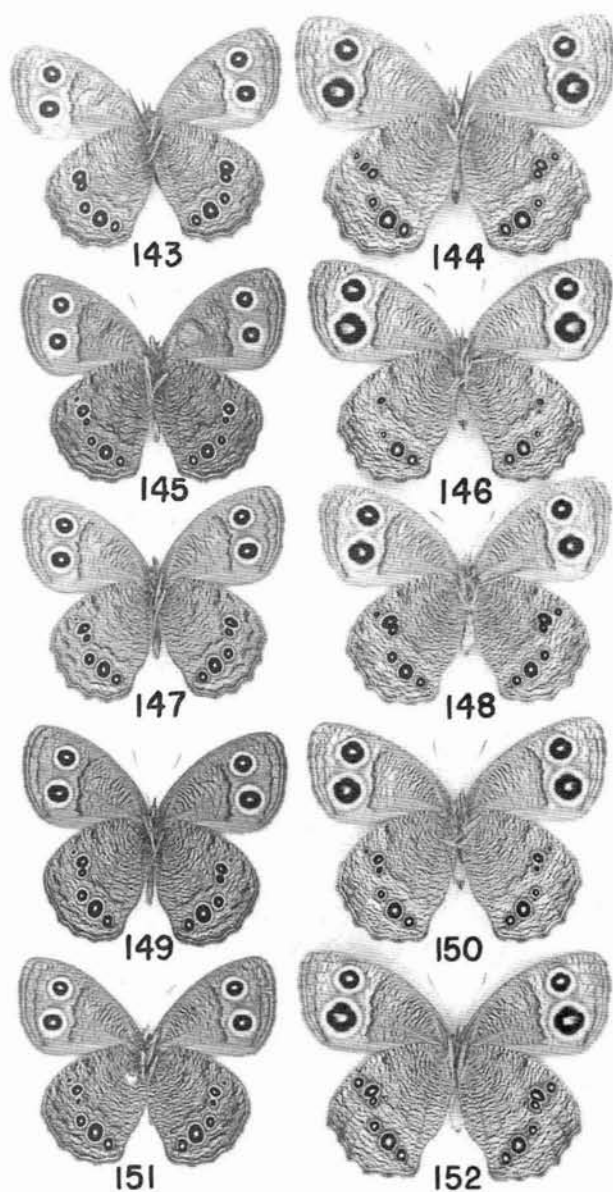
Figures 113-122. *Cercyonis pegala paucilineatus* (dorsal surface, males on left, females on right). NV: Humboldt Co.; Quinn River Valley, US 95, 3.8 mi. S Orovada. (113, 115, 119, 121) 9 July 1989, leg. G. T. Austin; (114, 118) 24 July 1987, leg. G. & A. Austin; (116, 117, 120, 122) 22 July 1984, leg. G. T. Austin.



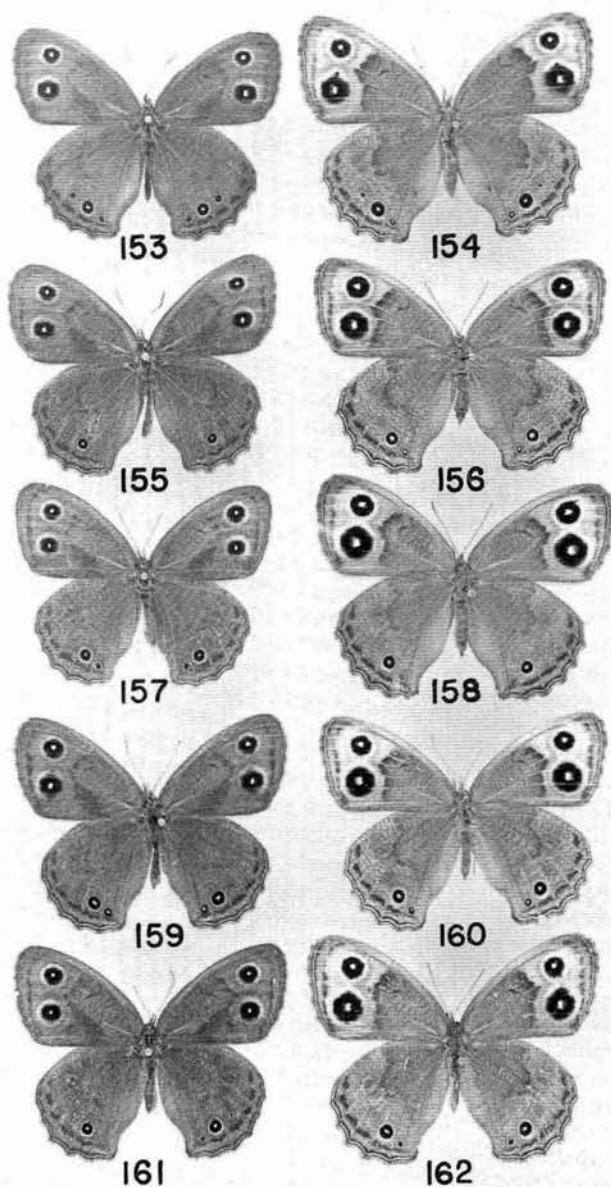
Figures 123-132. *Cercyonis pegala paucilineatus* (ventral surface). Same specimens as in Figures 113-122.



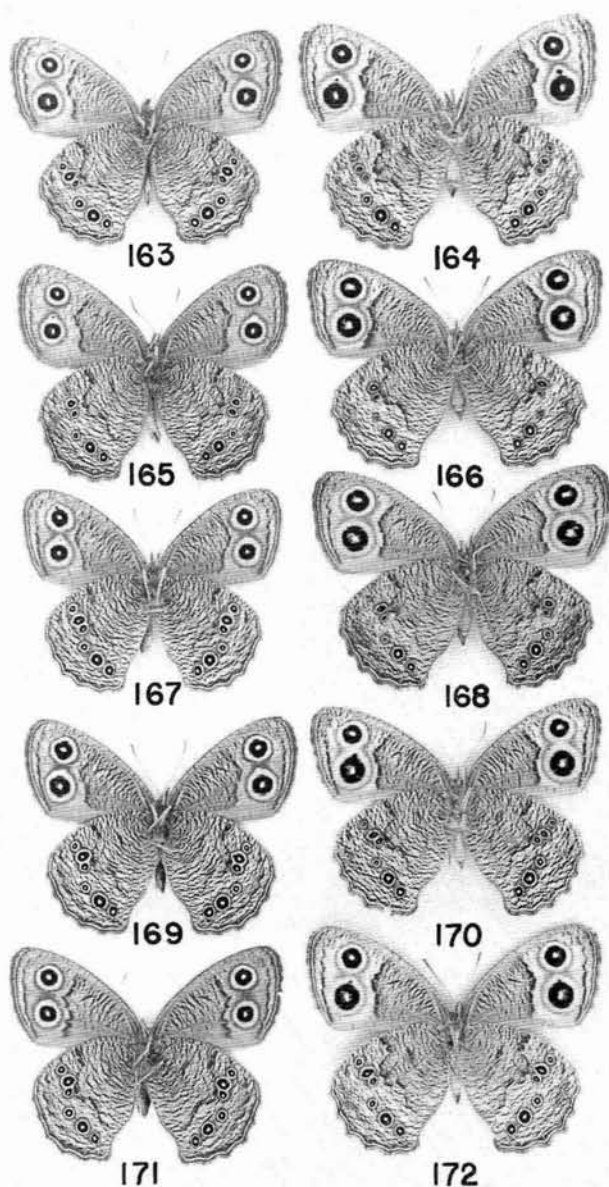
Figures 133-142. *Cercyonis pegala utahensis* (dorsal surface, males on left, females on right). UT: Utah Co. (133) Benjamin, 28 June 1989, leg. J. M. Johnson; (134, 135) Spanish Fork River, between Leland and Benjamin, 6 July 1989, leg. J. M. Johnson; (136, 142) Benjamin, 6 July 1989, leg. J. M. Johnson; (137, 139, 141) Spanish Fork River, between Leland and Benjamin, 6 July 1989, leg. G. T. Austin; (138, 140) Benjamin, 6 July 1989, leg. G. T. Austin.



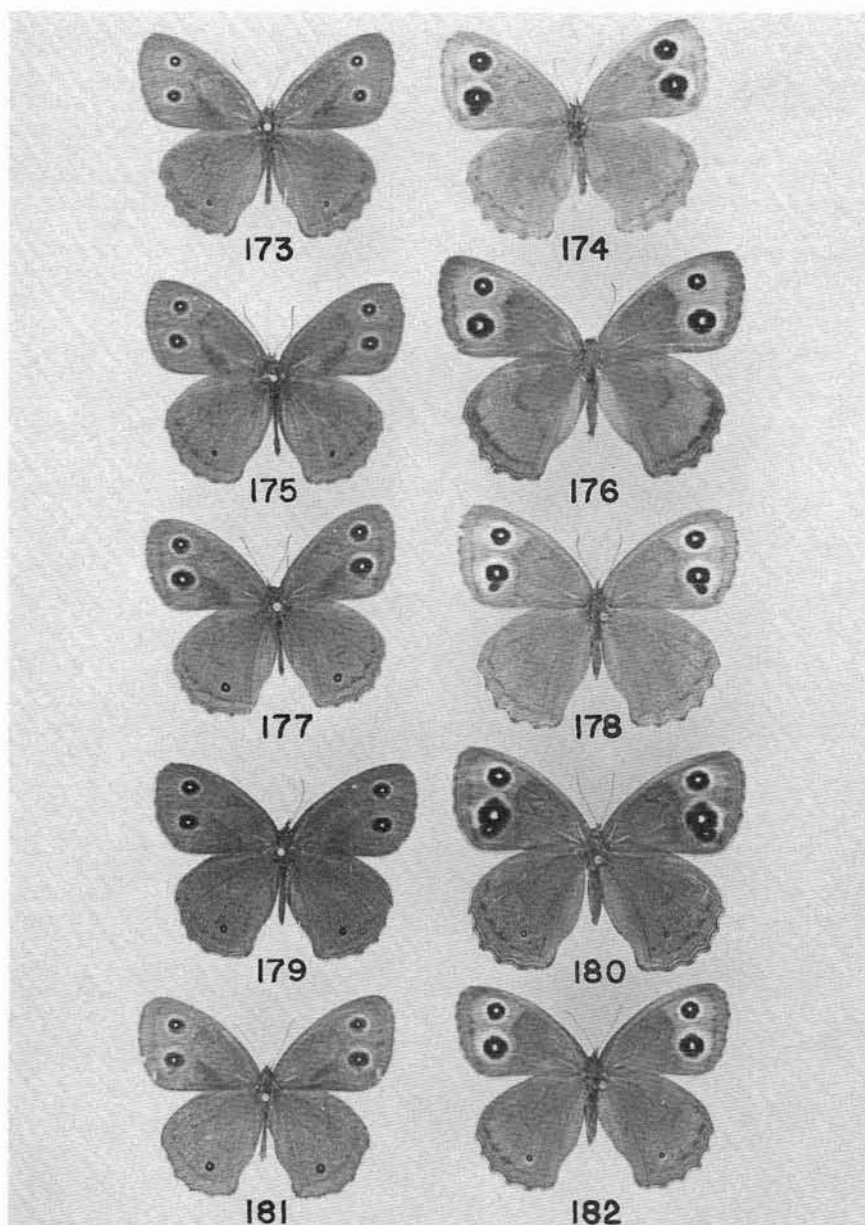
Figures 143-152. *Cercyonis pegala utahensis* (ventral surface). Same specimens as in Figures 133-142.



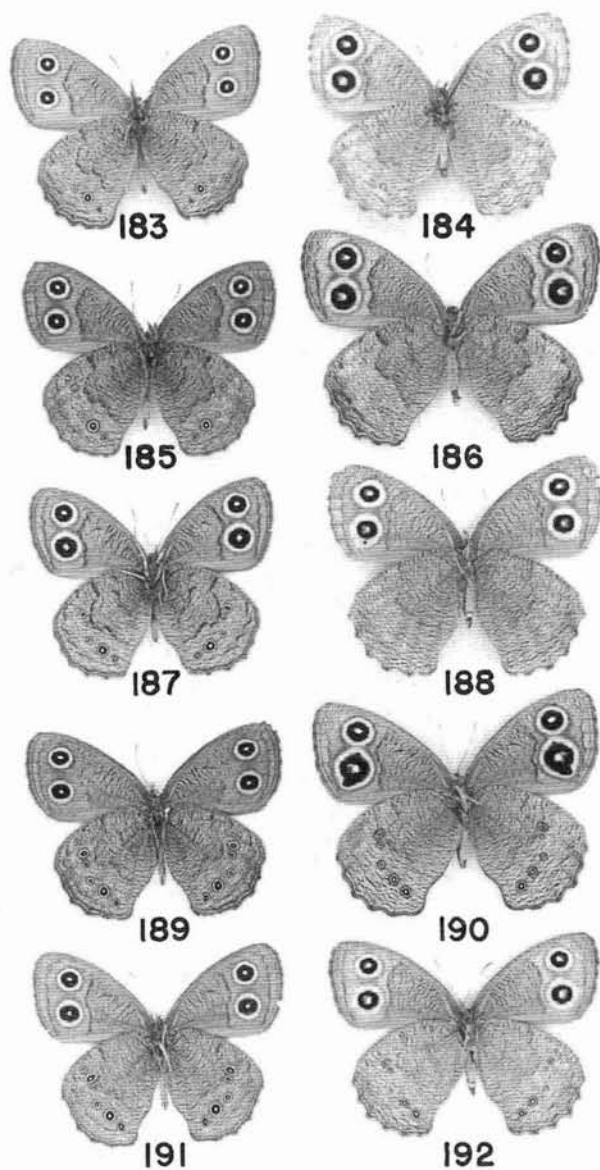
Figures 153-162. *Cercyonis pegala pluvialis* (dorsal surface, males on left, females on right). NV: White Pine Co.; White River Valley, 1.0 mi. N Nye Co. line. (153, 162) 12 July 1986, leg. G. & A. Austin; (154-161) 15 July 1984, leg. G. T. Austin.



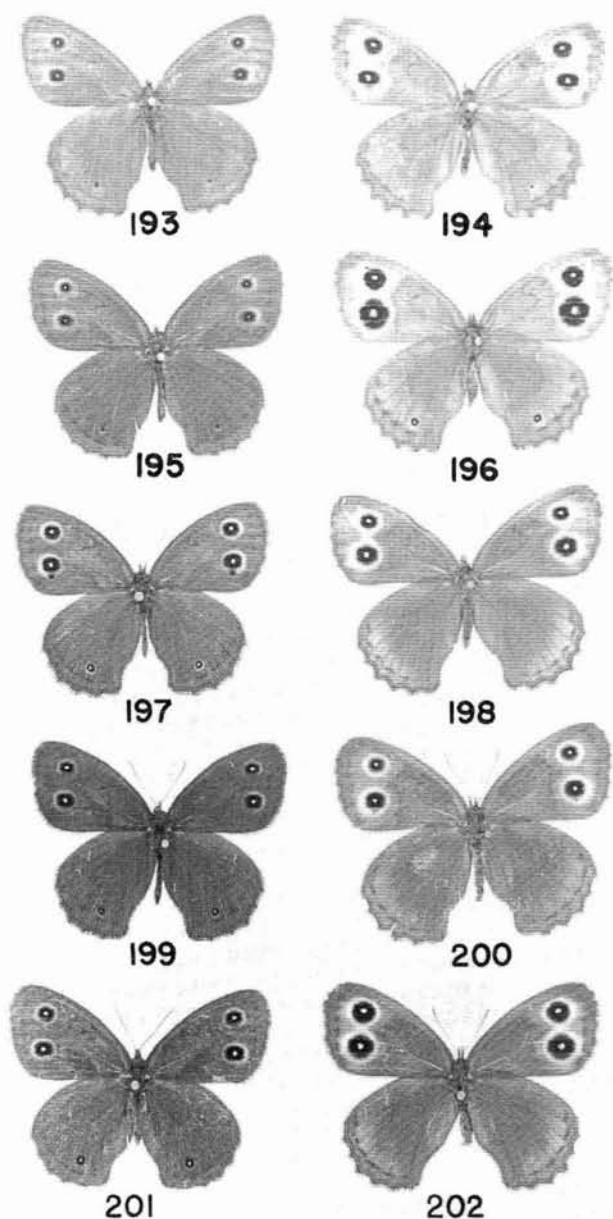
Figures 163-172. *Cercyonis pegala pluvialis* (ventral surface). Same specimens as in Figures 153-162.



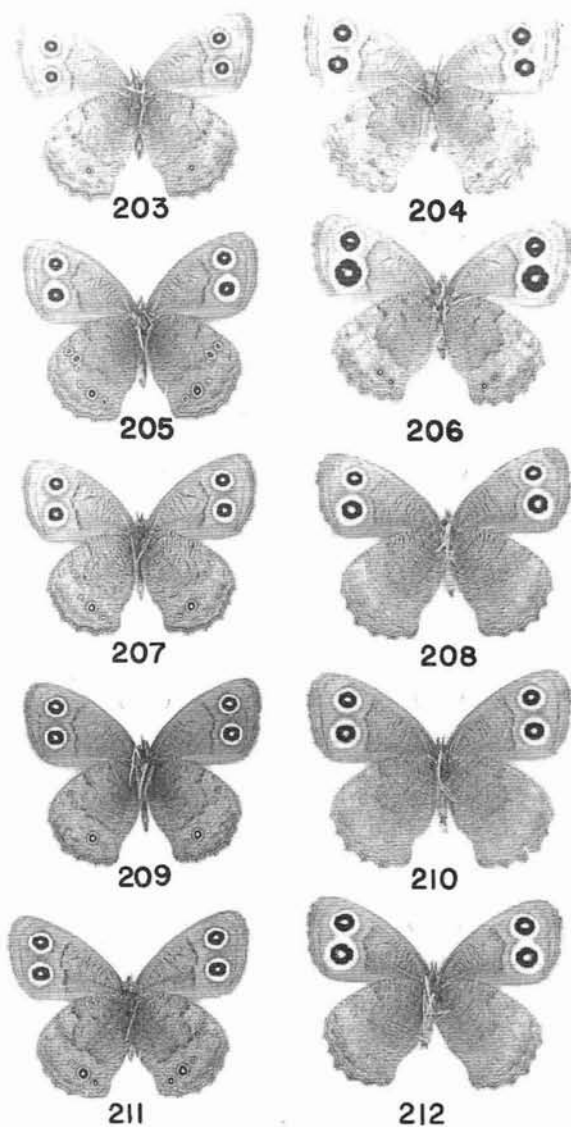
Figures 173-182. *Cercyonis pegala paludum* (dorsal surface, males on left, females on right). NV: Elko Co.; Pleasant Valley, Nv 227. (173-175) 3.7 mi. W Lamoille Canyon Rd., 21 July 1984, leg. G. T. Austin; (176, 178-180) 4.6 mi. W Lamoille Canyon Rd., 29 July 1988, leg. G. T. Austin; (177, 181, 182) 0.9 mi. W Lamoille Canyon Rd., 15 July 1986, leg. G. & A. Austin.



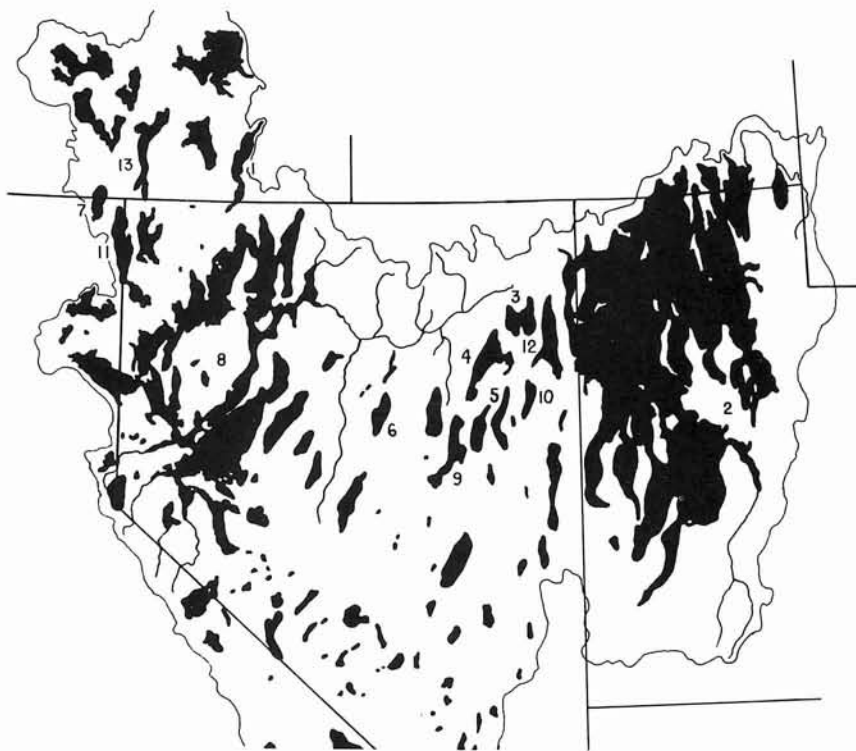
Figures 183-192. *Cercyonis pegala paludum* (ventral surface). Same specimens as in Figures 173-182.



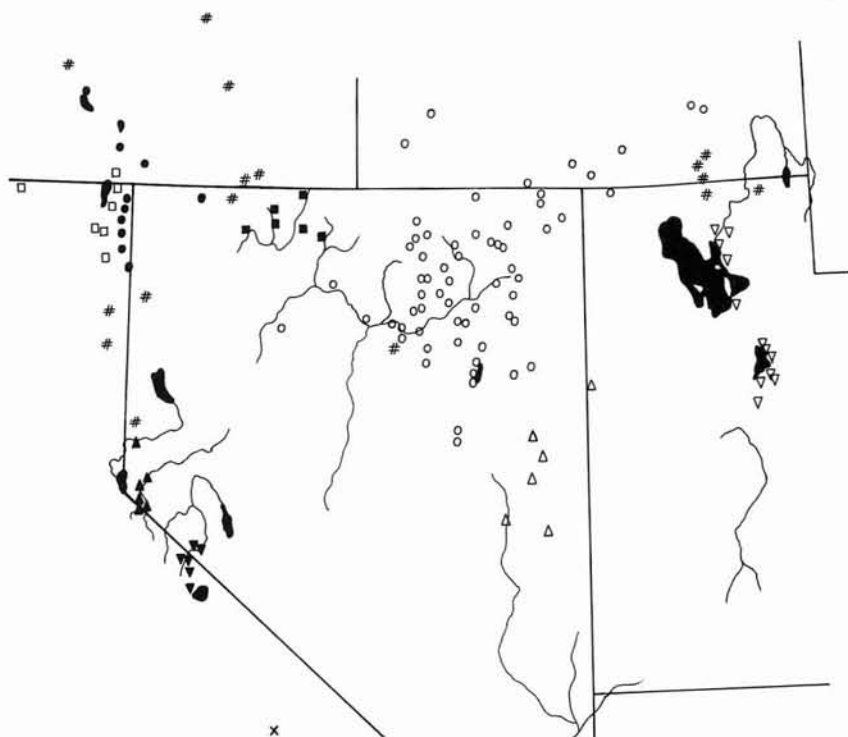
Figures 193-202. *Cercyonis pegala walkerensis* (dorsal surface, males on left, females on right). CA: Mono Co.; Hunttoon Valley, Swanger Creek, Hunttoon Camp, US 395, 5.4 mi. NW Bridgeport. (193, 194, 198, 202) 24 July 1989, leg. G. & A. Austin; (195, 197, 199) 13 July 1989, leg. G. T. Austin; (196, 200, 201) 23 July 1989, leg. G. & A. Austin.



Figures 203-212. *Cercyonis pegala walkerensis* (ventral surface). Same specimens as in Figures 193-202.



Figures 213. Major Pleistocene lakes of the northern Great Basin at their approximate maximum elevation; line indicates hydrological limit of internal drainage. Lakes mentioned in text include: (1) Alvord, (2) Bonneville, (3) Clover, (4) Franklin, (5) Gale, (6) Gilbert, (7) Goose, (8) Lahontan, (9) Newark, (10) Steptoe, (11) Surprise, (12) Waring, (13) Warner.



Figures 214. Northern Great Basin showing major waters that exist at present and the distribution of *Cercyonis pegala*: *C. p. wheeleri* (X), *C. p. carsonensis* (closed upright triangle), *C. p. gabbii* (open square), *C. p. stephensi* (closed circle), *C. p. paucilineatus* (closed square), *C. p. pluvialis* (open upright triangle), *C. p. utahensis* (open reversed triangle), *C. p. paludum* (open circle), *C. p. walkerensis* (closed reversed triangle).

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