

TAXONOMY, DISTRIBUTION AND BIOLOGY OF THE GENUS
CERCYONIS (SATYRIDAE). I. CHARACTERISTICS
OF THE GENUS

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Evolution of butterflies in the satyrid genus *Cercyonis* has produced a complex of species groups and variable populations in North America that has not been reviewed thoroughly since the last century. The purpose of this paper and others to follow in the series is to provide a critical, modern synthesis of taxonomic, distributional and biological information on all species and subspecies within the genus, based on extensive studies by the author from 1960 to the present.

In future papers, each species group will be treated intensively, with plates of both sexes of adults of all subspecies, larvae, pupae, figures of eggs, genitalia, androconia, antennae and other important morphological characters, and chromosomes. Genetic data and hybridization crosses will also be summarized in the present series from material to be published in full elsewhere.

TAXONOMY

The Nearctic genus *Cercyonis* has had over thirty specific, subspecific, or varietal names applied to it, and no taxonomic revision has been attempted since the 1880s (Edwards, 1880). On the basis of extensive field work, examination of over 5,000 adult *Cercyonis* specimens, rearing of many of the named forms, and studies of external and internal morphology of all these forms, the following new taxonomic treatment is proposed.¹

- I. *Cercyonis sthenele* (Boisduval, 1852)
 - a. *sthenele sthenele* (Boisduval, 1852)
 - b. *sthenele silvestris* (Edwards, 1861)
 - c. *sthenele paulus* (Edwards, 1879)
 - behrii* (Grinnell, 1905)
 - d. *sthenele masoni* (Cross, 1937)
- II. *Cercyonis oetus* (Boisduval, 1869)
 - a. *oetus oetus* (Boisduval, 1869)
 - b. *oetus charon* (Edwards, 1872)
 - c. *oetus phocus* (Edwards, 1874)
- III. *Cercyonis meadi* (Edwards, 1872)
 - a. *meadi meadi* (Edwards, 1872)

¹ Subspecies names are used as a convenient reference to well-differentiated sets of populations. The term *form* in the taxonomic section refers to a phenotypic form of a subspecies which appears sympatrically with one or more other phenotypic forms in at least one part of the geographic range of the subspecies. In the *Cercyonis pegala* complex especially, there is a tendency for several of the named phenotypes to appear in polymorphic populations.

- melania* (Wind, 1946)
- b. *meadi mexicana* (R. L. Chermock, 1948)
- c. *meadi alamosa* Emmel and Emmel, 1969
- IV. *Cercyonis pegala* (Fabricius, 1775)
 - a. *pegala pegala* (Fabricius, 1775)
 - b. *pegala alope* (Fabricius, 1793)
 - form *nephele* (Kirby, 1837)
 - form *maritima* (Edwards, 1880)
 - form *ochracea* (Chermock and Chermock, 1942)
 - form *carolina* (Chermock and Chermock, 1942)
 - c. *pegala texana* (Edwards, 1880)
 - d. *pegala ino* (Hall, 1924)
 - e. *pegala boopis* (Behr, 1864)
 - olympus* (Edwards, 1880)
 - borealis* (F. H. Chermock, 1929)
 - form *baroni* (Edwards, 1880)
 - form *incana* (Edwards, 1880)
 - f. *pegala ariane* (Boisduval, 1852)
 - form *wheeleri* (Edwards, 1873)
 - hoffmani* (Strecker, 1873)
 - form *gabbii* (Edwards, 1870)
 - form *stephensi* [♀] (Wright, 1905)
 - g. *pegala damei* (Barnes and Benjamin, 1926)

The morphological and general biological differences between the species groups are summarized in Table 1. More specific discussion of biological and regional differentiation within the genus will appear in four future papers in this series.

DISCUSSION

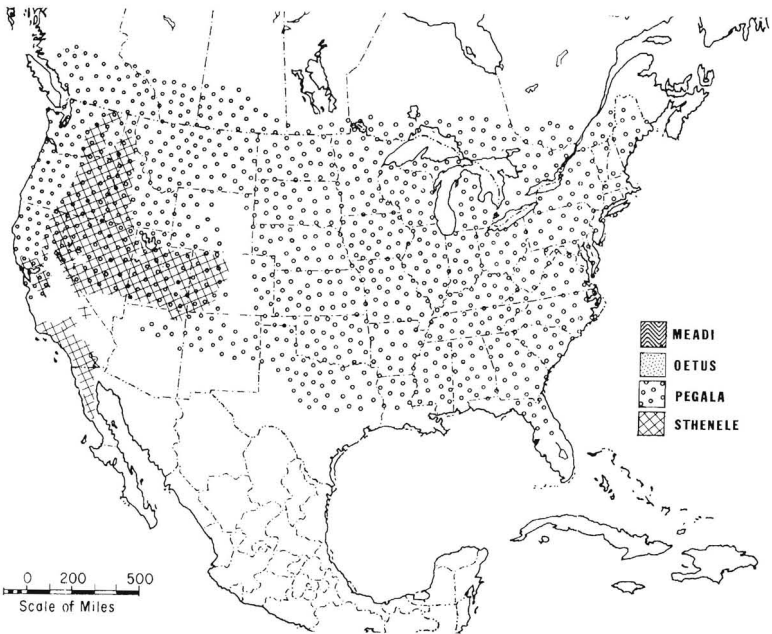
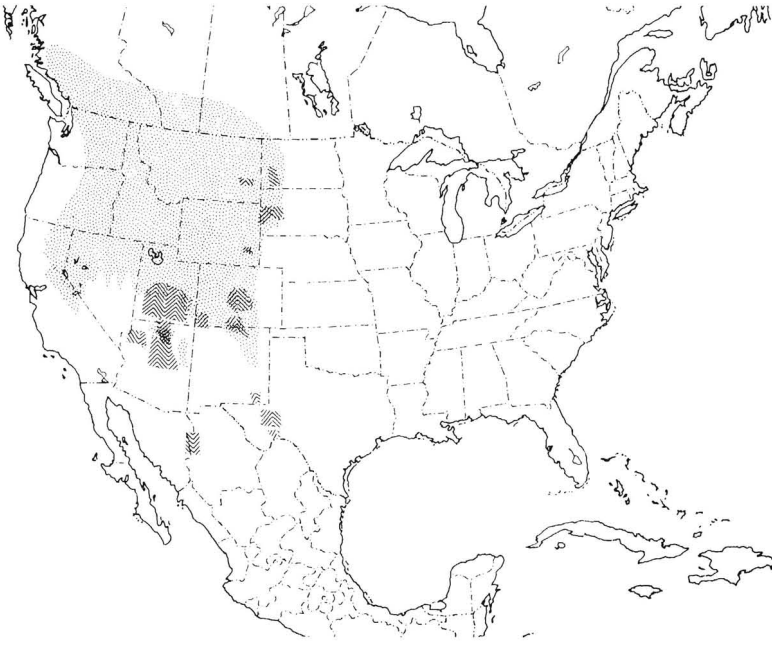
I. *Cercyonis sthenele*:

These small-to-medium-sized *Cercyonis* occur throughout most of the arid Upper Sonoran areas of the western United States. *Cercyonis s. sthenele* is known only from the area now occupied by the city of San Francisco, California, and has been extinct since approximately 1880. *C. s. silvestris* is distributed intermittently from Baja California in Mexico north through California (west of the Sierra Nevada) and Oregon to Washington. Jones (1951) reports it as occurring in the southern interior of British Columbia. *C. s. paulus* is found in eastern California, at scattered localities in eastern Oregon, and throughout Nevada above the desert areas. *C. s. masoni* is known from western Colorado, northeastern Arizona, Utah, and Wyoming; with further collecting, it may be found in northern New Mexico.

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EXPLANATION OF MAPS

The distribution of the four species of *Cercyonis* in North America. Upper map: *C. meadi* and *C. oetus*; lower map: *C. pegala* and *C. sthenele*.



No representatives from the *sthenele* group have been found east of the Continental Divide, north of the Canadian border (with the possible exception of British Columbia), or on the Mexican mainland.

II. *Cercyonis oetus*:

These small-sized *Cercyonis* occur throughout most of the mountain ranges of the western United States and north into western Canada. *Cercyonis oetus oetus* ranges from the central Sierra Nevada and Owens Valley (Inyo County) in California north through almost all of Oregon to Yakima and Okanogan counties in Washington. It is also found in southern Idaho and in the mountain ranges of Nevada. *C. o. charon* is found in the Rocky Mountains from northern New Mexico through Colorado and Wyoming to Alberta in Canada. It also occurs in the higher mountains of northern and eastern Arizona, Utah, Montana, eastern Idaho and the Black Hills of South Dakota. *C. o. phocus* is known from British Columbia and from scattered populations in Washington, Montana, and Idaho. Occasional specimens from the mountains of New Mexico show the dark *phocus* phenotype.

No *Cercyonis oetus* populations have been found south of central Arizona or central New Mexico, nor east of the eastern edge of the Rocky Mountains and the Black Hills. Thus, while the range of *C. oetus* is slightly more extensive (to the north) than that of *C. sthenele*, both species are completely restricted to the Nearctic portion of the western half of the Northern American continent.

III. *Cercyonis meadi*:

These medium-sized *Cercyonis* with a reddish forewing flush occur in scattered populations in northern Mexico and the central Southwest, from Upper Sonoran into Transition zone areas. *Cercyonis meadi meadi*, a highland subspecies with blackish underside, is found in Colorado in the moderate elevations (7500–9500 feet) of the Rocky Mountains. *C. m. mexicana*, a lowland subspecies with brownish underside, occurs in northwestern Chihuahua, Mexico, in northern to northwestern Arizona, southern to central Utah, northern New Mexico, the Davis Mountains of Texas, eastern Montana, North Dakota (McKenzie and Slope counties), the Black Hills (near Nemo) of South Dakota, as well as the eastern lowland slopes of the Front Range in Colorado. *C. m. alamosa*, with a silvery-gray underside, is a race endemic to the San Luis Valley (8000 feet) of southern Colorado.

No *C. meadi* occur in Nevada, in the Pacific Coast states, or in the northern states, and the present known distribution is curiously disjunct. The population density varies considerably from year to year in a given area.

IV. *Cercyonis pegala*:

These large-sized *Cercyonis* are the only *Cercyonis* group to be distributed east, as well as west, of the Rocky Mountains. They are found from sea level up to elevations of about 7000 feet. *Cercyonis pegala pegala* is distributed from the Mississippi Valley east to the Atlantic Coast and from the Gulf States north to North Carolina and New Jersey. *C. p. alope* ranges from Virginia and New Jersey north to eastern Quebec and Maine, and into New York; northward and westward, the yellow-patched *alope* intergrades with the completely dark *nephele* and the somewhat lighter *ochracea* (in Ohio). To the south, *alope* blends with *carolina* in the Carolinas. At eastern points in Massachusetts, *alope* intergrades with the darker-yellow form *maritima*. Populations containing two forms of *alope* are frequent in the areas indicated; thus it seems best to treat *nephele*, *maritima*, *ochracea*, and *carolina* as simple phenotypic forms of *alope* that have their particular centers of abundance which interdigitate frequently along their respective margins; it is clear even in the 1870s (Edwards, 1880) that the proportion of these forms varied in observed populations from year to year, and present data show that no stability of gene frequencies has been reached as yet.

Cercyonis p. texana ranges from central Texas north to Kansas and Missouri. *C. p. ino* occurs in Alberta and Manitoba, Canada, and in North Dakota and Montana. *C. p. boopis* ranges from central New Mexico and Arizona north through Colorado to South Dakota and west to the Pacific Coast, from central California north to British Columbia on the coastal side of the Cascades and Sierra Nevada. Several local color or dwarfed forms (*incana* and *baroni*) have been named from northern California, and many other odd-colored forms appear in scattered populations to the north. I have even seen specimens with a greenish underside from near Portland, Oregon. But none are worthy of nomenclatural designation.

Cercyonis p. ariane has a strongly-striated pattern on the ventral surface, with a yellow forewing flush; it occurs in the lowland areas of Utah (form *gabbii*), Nevada (form *wheeleri*, now believed extinct), eastern California, eastern Oregon, and eastern Washington (typical *ariane*). The heavily yellow-washed female form, *stephensi*, occurs mainly in northeastern California populations, but this phenotype also appears among females in Nevada and Oregon.

Cercyonis p. damei occurs only within the Grand Canyon of Arizona; it may represent the result of introgression of reddish-forewing-flush characters from *meadi* populations on the surrounding Kaibab Plateau into a *C. pegala boopis* population formerly residing as a "pure" form in the canyon bottom.

TABLE 1. MAJOR DIFFERENTIATING CHARACTERS FOR THE FOUR SPECIES OF *CERCYONIS*

CHARACTER	<i>pegala</i>	<i>sthenele</i>	<i>oetus</i>	<i>meadi</i>
Antennal coloration	Brown with proximal half of each segment white.	Brown with proximal fifth or less of each segment white.	Like <i>sthenele</i> on dorsum, all white on venter.	As in <i>sthenele</i> .
Size of ventral forewing ocelli	Equal, or posterior one larger (some ♀♀).	Posterior equal or smaller than anterior in ♂; equal in ♀	Posterior smaller than anterior in ♂; equal in ♀	Posterior usually smaller than anterior in ♂; equal in ♀.
Position of ventral forewing ocelli	Equally distant from wing margin.	Equally distant from wing margin.	Posterior ocellus closer to wing margin than anterior one.	About equally distant from wing margin.
Normal length of forewing	♂, 25–27 mm, ♀, 28–31 mm. Larger in many eastern populations.	♂, 21–23 mm, ♀, 22–26 mm	19–22 mm	♂, 20–24 mm, ♀, 23–25 mm
Coloration of central forewing (dorsal and ventral)	Dark brown in western populations; yellow in most eastern populations; russet or reddish in Grand Canyon populations.	Dark brown; occasionally slightly yellow or tan around ocelli (♀) but not over whole FW.	As in <i>sthenele</i> .	Chocolate brown, with reddish or rusty area in limbal zone, varying towards base of wing, always present on underside if not also dorsally.
Sex patch on FW of males	Three medium- to large-sized, below Cu ₁ , Cu ₂ , and 2V.	Four medium- to large-sized, below M ₃ , Cu ₁ , Cu ₂ , and 2V. Patch Cu ₂ with smoothly convex basal edge.	Four large, below M ₃ , Cu ₁ , Cu ₂ , and 2V. Patch Cu ₂ with sharp notch in basal edge.	Variable in northern Arizona and Utah: 2 to 4 (Cu ₁ and Cu ₂ always present). Elsewhere, only Cu ₁ and Cu ₂ patches present, the Cu ₂ patch divided horizontally.

TABLE 1—Continued

CHARACTER	<i>pegala</i>	<i>sthenele</i>	<i>oetus</i>	<i>meadi</i>
Ventral hindwing ocellus pupil	Oblong or a linear dash; thin layer of white scales makes the pupil a dull white. Often a mixture of black and white scales near pupil margins produces blue.	In <i>masoni</i> usually large and rounded; with heavy layer of white scales, bright white. Similar in <i>paulus</i> . In <i>silvestris</i> , a tiny white dot. In <i>s. sthenele</i> , a small white dot. Never BLUE.	Usually round and bright white (heavy scaling).	Round and bright white (heavy scaling).
Ventral hindwing ocellus outer ring	A prominent light tan ring surrounds the black spot; a dark brown ring outside the tan ring.	Tan ring barely indicated around black spot; most ocelli surrounded by large brown rings which touch each other between the ocelli.	No tan ring; usually not even a trace of an outer dark brown ring.	As in <i>oetus</i> .
General ventral hindwing color	Light mottled tan in southeast U.S. to Texas (<i>p. pegala</i> and <i>p. texana</i>), Utah (<i>p. gabbi</i>), and northeast California, southeast Oregon, and Nevada (<i>stephensi</i> form). Dark mottled brown elsewhere (various shading combinations, random geographically).	Dark mottled brown with whitish scaling over most of the species' range; pale brown in southern and central California.	Dark brown; also zigzag pattern in the far west, mottling in Rocky Mountains, and uniform slate black-brown in British Columbia and adjacent areas.	Dark, finely-mottled brown in higher Rocky Mountains; light and dark mottled brown elsewhere, except in <i>alamosa</i> , heavy, white mottling.
Larval instars	Six	Five	Five	Five

BIOLOGY

All four species of *Cercyonis* are univoltine. *Cercyonis sthenele* flies in June and July, *C. oetus* in July and August, *C. meadi* from late July to early September, and *C. pegala* from June to August, depending on the area (earlier in eastern and western coastal populations, later in inland populations as in Colorado).

Cercyonis pegala subspecies have six larval instars while the other three species have five instars. The larval food is grass, and most do not seem to be narrowly restricted in host choice; the only species that seems on circumstantial evidence to be restricted to very few grass species is *C. meadi*. Mating can occur almost immediately after the female's emergence from the pupa, but the male is several days old before he makes any mating attempts. Eggs are deposited singly on dried or living grass stems; five to thirty per day may be laid for up to thirty days (in the lab) by a female. Normal egg production is 100–150 eggs in *C. oetus*, *C. sthenele*, and *C. meadi*, and 200–300 eggs in *C. pegala*. The adults can live up to 45 days in the laboratory, but the normal life span in natural populations is only 5–10 days (capture-recapture data; Emmel, unpublished).

At 25° C the eggs hatch 10 days after oviposition, and the first-instar larvae go into diapause immediately. The site for diapause in nature is likely in the base of grass clumps. During the fall and winter, the diapausing larvae shrink to one-half their former length. In late spring, probably April in most localities, larvae come out of diapause and begin feeding. In the wild they are probably strictly nocturnal feeders; in the laboratory, daytime feeding occurs also.

At 25° C, the larvae can reach a mature state in three to four weeks, but in nature this requires two months for *C. oetus*, and two and one-half to three months for *C. meadi*, *C. sthenele*, and *C. pegala*. The natural site for pupation is near the base of a grass clump, where the pupa is hung from bent-over grass blades. The pupa hatches in ten to twelve days at 25° C, and probably in about twenty days in most wild populations.

SYMPATRIC DISTRIBUTION

In a number of localities, two or three species of *Cercyonis* are found flying together, often alighting on the same flowers, or are at least in close enough proximity that the adults may have visual contact with each other. In all such sympatric populations, there is a partial separation of flight periods of adults, and there are usually different habitat preferences by the respective species. For instance, near Florissant, Colorado, *Cercyonis oetus* adults reach their peak of activity the last week of July and the first week of August, while *Cercyonis meadi*, flying in the same

meadows, does not reach its peak of abundance until the latter half of August. Where *Cercyonis pegala boopis* and *Cercyonis sthenele masoni* occur together (e.g., at Glenwood Springs, Colorado), *C. p. boopis* flies mainly in oak thickets while *C. s. masoni* flies in grassy sagebrush areas adjoining the oak forest.

The species that are sympatric in the western states may be listed as follows: *Cercyonis pegala boopis* or *C. p. ariane* frequently with *Cercyonis sthenele masoni* or *C. s. paulus* through the intermountain west; in Colorado, *C. p. boopis* occasionally also with *Cercyonis oetus*. *Cercyonis sthenele* occasionally is sympatric with *Cercyonis oetus* in eastern California and the Northwest, and again in Colorado. *Cercyonis meadi* is sympatric with *C. oetus* at scattered points in central Colorado and with *C. pegala boopis* near Colorado Springs.

No natural *Cercyonis* hybrids are known to the author except in one area on Fruitland Mesa, Delta County, Colorado. Here, *Cercyonis pegala boopis* and *C. sthenele masoni* both occur in the same habitat and adults fly at the same time; judging from wing and genitalic characters, hybridization seems to be fairly frequent. Also, judging from present distributions and phenotypic characters, it is possible that the populations of *C. pegala damei* in the Grand Canyon are the result of past hybridization between *Cercyonis meadi mexicana* on the North Rim and *C. pegala boopis* populations along the bottom of the gorge. A future paper in this series will discuss these situations further.

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A CASE OF AUTHORSHIP, *MELITAEA RUBICUNDA*
(NYMPHALIDAE)

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A series of synopses of the butterflies of North America appeared in the first series of the Bulletin of the Brooklyn Entomological Society. They were published between 1878 and 1885. Most of these articles carry no author's name, yet some of them are nomenclatorially important. The authorship for the majority is indicated in a letter from George D. Hulst, of the Brooklyn Society, to Herman H. Strecker. This was written September 28, 1880, and in part reads "By the way, Graef & Tepper run the Synopsis of the Butterflies in the Bulletin and that of *Argynnis* has been made out by Mr. W. H. Edwards entirely" (Hulst, 1880).