BULLETIN OF THE ALLYN MUSEUM

Published By
The McGuire Center for Lepidoptera and Biodiversity
Florida Museum of Natural History
University of Florida
P. O. Box 112710
Gainesville, FL 32611-2710

Number 163 5 September 2012

ISSN-0097-3211

A NEW SPECIES OF *CERCYONIS* (LEPIDOPTERA: SATYRIDAE) FROM NORTHERN CALIFORNIA

John F. Emmel[1], Thomas C. Emmel[2], and Sterling O. Mattoon[3]

[1]26500 Rim Road, Hemet, CA 92544

[2]McGuire Center for Lepidoptera & Biodiversity, Florida Museum of Natural History, P. O. Box 112710, Gainesville, FL 32611-2710

[3]2109 Holly Avenue, Chico, CA 95926

ABSTRACT: A previously unrecognized species of the genus *Cercyonis* (Lepidoptera: Satyridae) is described from serpentine grassland-Brewer's Oak woodland habitat in northern California. With phenotypic characteristics close to both *Cercyonis oetus* and *Cercyonis sthenele*, this small *Cercyonis* has been known to collectors and recorded under the name *C. sthenele* subspecies Life history, genitalia, hybridization studies, behavioral and adult morphological traits differentiate the new species from its presumed closest relatives. The new species is more closely related to *Cercyonis oetus* than *C. sthenele*, on the basis of phenotypic and biological characters.

KEY WORDS: endemic, biodiversity, hybridization, life history.

INTRODUCTION

The genus *Cercyonis* is distributed widely in western North America. The single transcontinental large species, *C. pegala* (Fabricius, 1775), has many named subspecies across the Great Basin and Pacific Coast states north into Canada. The other three recognized species occupy somewhat more restricted ranges. *Cercyonis sthenele* (Boisduval, 1852), a medium-sized, variably patterned species, occupies intermediate elevations from southern California north to the Pacific Northwest and east across the Great Basin to western Colorado. *Cercyonis meadii* (W.H. Edwards, 1872), a reddish flushed medium-sized species, is found from Arizona and New Mexico north to Colorado and Wyoming in the pine forests of the Rocky Mountains and high interior brushy valleys such as the San Luis Valley

(8,000' elevation) of Alamosa County in southern Colorado. *Cercyonis oetus* (Boisduval, 1869), a dark and slightly smaller species, is found in the montane pine forest and sagebrush valleys of the Rocky Mountain states from northern Arizona and New Mexico to Montana and Canada, westward to California and eastern Oregon and Washington. The systematics of the group has stabilized (e.g., Emmel, 1969; Sourakov, 1995) around recognition of the one large-sized *Cercyonis pegala* group of taxa and three smaller-sized *Cercyonis* species, with wide subspeciation being recognized in all four species (e.g., Austin, 1992; Emmel and Emmel, 1969, 1971; Emmel and Mattoon, 1972; Emmel, Emmel, and Mattoon, 1998; Emmel and Emmel, 1998a, 1998b; Emmel, Emmel, and Davenport, 2008).

We now report the recent discovery of a previously unrecognized medium-sized *Cercyonis* species that occurs in at least seven northern California counties (Mendocino, Lake, Colusa, Tehama, Trinity, Glenn, and Humboldt) and that, while sharing some characteristics of both *C. oetus* and *C. sthenele*, differs significantly in life history, genetic structure in hybridization experiments, adult ovipositional behavior, and adult morphological traits.

This new *Cercyonis* species is described as follows.

Cercyonis incognita J. Emmel, T. Emmel, & Mattoon, **new species**

Figs. 1, 2 (♂ holotype), 3, 4 (♀ allotype), 14a (♂ genitalia)

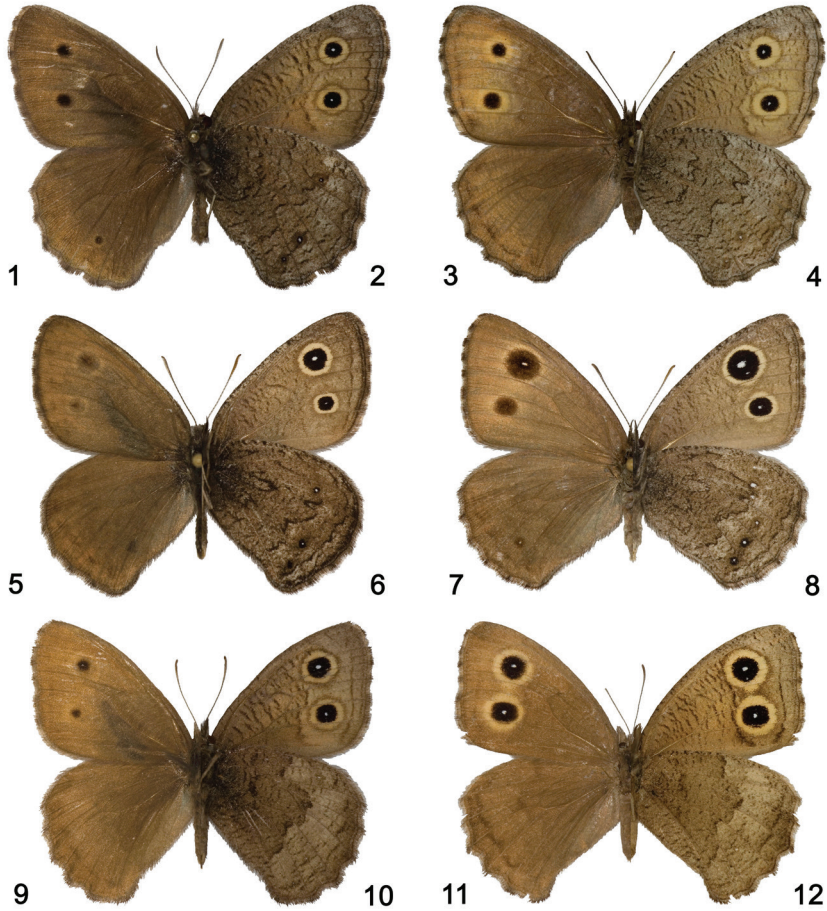
Description. MALE (Fig. 1, 2). Head. Eyes dark red-brown in dried specimens; vertex and palpi covered with long brown scales, these intermixed with short white scales, especially on dorsal surface of palpi antennae dark grayish-brown dorsally, mostly white ventrally, 8-11 mm long.

Thorax. Dorsal surface medium brown, with long brownish gray scales; ventral surface with long dark brown and brownish gray scales, fairly evenly mixed; legs densely covered with short whitish scales and a mixture of long, dense, white and dark brown scales along the posterior edges of the femora.

Abdomen. Dorsum medium brown, covered with short medium round scales; longer scales present especially along anterior half of dorsum; ventral surface with mixture of long white scales and long brown scales; outer edges of valvae covered with short pale brownish gray scales.

Forewing. Holotype forewing length = 23.21 mm. Male forewing mean costal margin length (measured from base to end of R_4, to nearest 0.5 mm) = 21.7 mm (n = 32 males). Dorsal surface. Ground color medium to dark brown; androconial scale patches comprised of dark brown and whitish scales; anterior ocellus present in all specimens, although sometimes obsolescent. Central dot of anterior ocellus ranging in diameter from 0.5 mm to 2 mm; anterior ocellus ringed by pale yellowish brown scales. Posterior ocellus present in about two-thirds of specimens; when present usually smaller than anterior ocellus; also ringed with pale yellowish brown scales, but with less contrast against the background of medium brown to dark brown scales. Costal margin with dense whitish scaling. Outer margin fringe checkered with dark brown scales alternating with white tipped dark brown scales with the all-dark scale groups at the ends of the veins.

Hindwing, dorsal surface. Ground color medium to dark brown. An indistinct submarginal band of dark brown scales is present. Fringe composed of brownish gray



Figures 1-12. *Cercyonis* species from northern California (D-dorsum, V-venter). **1-2)** *C. incognita*, holotype ♂, D,V, from Mendocino County type locality, data in text; **3-4)** *C. incognita*, allotype ♀, D, V, data in text; **5-6)** *C. oetus oetus* topotype ♂ (Mt. Judah, ca. 8200' elev., Placer Co., CA, 25 July 1997), D, V; **7-8)** *C. oetus oetus* topotype ♀ (same data as male), D, V; **9-10)** *C. sthenele behrii* topotype ♂ (Mt. Tamalpais State Park, Pan Toll Campground, Marin Co., CA, 8 July 1968), D, V; **11-12)** *C. sthenele behrii* topotype ♀ (same data as male), D, V.

scales, more uniform than the checkered pattern seen on the outer margin of the forewing. Scaling along inner margin composed of dark brown and pale grayish brown scales. Ocellus in cell CuA_1-CuA_2 present in about 40% of specimens, usually very small and less distinct than in forewing ocelli.

Forewing, ventral surface. Ground color pale grayish brown with extensive whitish frosting in apical area. Both anterior and posterior forewing ocelli are present, usually

well developed with blackish pupil and a small whitish dot within the blackish pupil and a surrounding brownish yellow halo. An irregular line of dark brown scaling is present in the postmedial area. Outer margin with a dark brown submarginal line and a checkered fringe similar to the dorsal surface description. Discal cell with numerous small dark irregular lines and dashes.

Hindwing, ventral surface. Ground color pale grayish brown with extensive whitish scale frosting on the outer third of the wing. An irregular band of dark brown-black scaling is present in the postbasal area; a similar irregular blackish brown line is present in the postmedial area. A thin submarginal blackish brown line is also present. Ocellus in cell CuA_1-CuA_2 usually present and small, although distinct. Similar ocellus usually present in cell CuA_2-1A + 2A, but usually slightly smaller than the previously described ocellus. Whitish overscaling present in distal one-third of wing (distal to the postmedial dark line), with a greater concentration of this whitish overscaling in the anterior portion of the postmedial and submarginal area. Fringe composed of dark brown scales and whitish tipped dark brown scales in a less distinct pattern than on the forewing.

FEMALE (Figs. 3, 4). Allotype forewing length = 24.71 mm. Female mean costal margin length = 23.7 mm (n=13 females). Dorsal surface. Ground color of forewing is a paler, dull medium brown than in males. Postmedial two-fifths of wing paler brown with varying amounts of pale brownish yellow scaling especially concentrated around the ocelli. Anterior and posterior ocelli usually present, with the anterior ocellus larger than the posterior one in some specimens, equal in size in other specimens, or with the posterior ocellus larger than the anterior ocellus in some specimens. Anterior ocellus rarely pupiled with a tiny white spot. Posterior ocellus almost never pupiled. Blackish scaling of ocelli usually about 2 mm in diameter, but with some specimens as small as 0.5 mm in diameter and others 2.5 mm. Submarginal and marginal area of wing with two thin, somewhat indistinct lines of dark brown scaling. Fringe of wing checkered as in male. Costal margin with a thin band of dense white scaling.

Hindwing, dorsal surface. Ground color of hindwing similar to forewing. Distal two-fifths of wing with ground color slightly paler than the medial portion of the wing. Submarginal and marginal area of wing with two parallel wavy dark brown lines. Inner margin area covered with light brown long scales. Ocellus in cell CuA1-CuA2 present in about 40% of specimens; if present, shows up as a very small dark dot about 0.5 mm in diameter. Fringe similar to male.

Forewing, ventral surface. Similar to male, except that ground color, particularly in the distal two-fifths of the wing, is paler and ocelli are larger and more frequently pupiled with white.

Hindwing, ventral surface. Similar to male, except that ground color is paler and the distal two-fifths of the wing is whiter due to heavier whitish overscaling. Ocelli in cells CuA_1-CuA_2 and CuA_2-1A + 2A are usually present in specimens that have the corresponding ocellus on the dorsal surface. These ocelli are pupiled with white scaling and are distinct, about 0.5-1 mm in diameter.

Types. Holotype ♂: CALIFORNIA: Mendocino Co.; along USFS Road M1, 0.6-2.0 road miles N. of jct. Road M61, near W. end of Bald Mtn. ridge, 5600-6200 ft. elev.; S5, T20N, R10W, & S32, T21N, R10W. 7 July 2000. *Leg.* S.O. & E.M. Mattoon. Allotype ♀: CALIFORNIA: Mendocino Co.; W. end of Bald Mtn. ridge, along USFS Road M1, 0.8 road mile NW of jct.with USFS Road M61, 6100-6200 ft. elev.; NE 1/4 of S5, T20N, R10W. 27

July 2000. *Leg*. S.O. & E.M. Mattoon. Paratypes (84 ♂♂, 68 ♀♀)(all localities Mendocino County, California): l ♂, same data as holotype. 1 ♂, same data as holotype except 6 July 2000. 2 ♂♂, same data as holotype, except 8 July 2000. 5 ♀♀, same data as allotype. 8 ♂♂, W. end of Bald Mtn. ridge, along USFS Road M1, 0.8 road mile NW of jct. with USFS Road M61, 6100-6200 ft. elev.; NE 1/4 of S5, T20N, R10W. 22 July 2001. *Leg.* J.F. Emmel & S.O. Mattoon. 10 ♂♂, 9 ♀♀, same data as previous, reared from ova laid by confined female, emergence dates 4 January 2002 to 11 June 2002. 10 ♂♂, 21 ♀♀, same locality data as previous, reared from ova laid by confined female taken 28 July 2003, emergence dates 13 January 2004 to 8 May 2004. 6 ♂♂, Etsel Ridge, along USFS Road M1, 5.6-10.4 road miles N. of jct. with USFS Road M61, 5200-5800 ft. el.; T21N, R10W. 6 July 2000. *Leg.* S.O. & E.M. Mattoon. 10 ♂♂, 1 ♀, same data as previous except 8 July 2000. 1 ♂, same data as previous except 23 July 2000. 1 ♀, same data as previous except 27 July 2000. 3 ♂♂, 5 ♀♀, SW-facing slope of Etsel Ridge, along USFS Road M1, 0.5 road mile SE of turnoff to Grizzly Flat, 5600-5640 ft.el.; NW 1/4 of S9, T21N, R10W. 23 July 2001. *Leg.* J.F. Emmel & S.O. Mattoon. 16 ♂♂, 9 ♀♀, same data as previous, reared from ova laid by confined Female #1, emergence dates 11 December 2001 to 4 February 2001. 16 ♂♂, 17 ♀♀, same data as previous, reared from ova laid by confined Female #2, emergence dates 15 December 2001 to 27 March 2002.

Deposition of types. The holotype, allotype, and 126 paratypes will be deposited in the collection of the McGuire Center for Lepidoptera & Biodiversity, Gainesville, Florida. Paratypes will be deposited in the following collections: Natural History Museum of Los Angeles County, Los Angeles, California; Entomological Research Museum, University of California, Riverside, California; California Academy of Sciences, San Francisco, California; American Museum of Natural History, New York; U.S. Natural History Museum, Smithsonian Institution, Washington, D.C., C. P. Gillette Museum of Arthropod Diversity, Colorado State University, Ft. Collins, Colorado; the collections of the three authors.

Type locality. CALIFORNIA: Mendocino Co.; along USFS Road M1, 0.6-2.0 road miles N. of jct. Road M61, near W. end of Bald Mtn. ridge, 5600-6200 ft. elev.; S5, T20N, R10W, & S32, T21N, R10W.

Etymology. The specific name *incognita* refers to the fact that this taxon was unrecognized for many years due to its superficial similarity to *Cercyonis sthenele behrii* in the North Coast Range of California.

Distribution and phenology. This species has been found in seven counties in the North Coast Range of California including Mendocino, Lake, Colusa, Glenn, Trinity, Tehama, and Humboldt counties. The characteristic habitat of the species (Fig. 13) consists of scattered thickets of Brewer's oak, *Quercus garryana* Hook. var. *breweri* (Engelm.) Jepson, with abundant growth of blue bunchgrass (*Festuca idahoensis* Elmer) both within the oak thickets and on the open serpentine gravelly slopes between the thickets. This grass is likely the native host of this *Cercyonis*, as several females were observed to oviposit in or near clumps of this grass; additionally, laboratory-reared larvae fed readily on this particular grass. The flight period of this univoltine butterfly is from early July to late August, with a peak flight period in late July.

Life history and habitat. Confined females oviposited readily in the presence of dry grass cuttings. Eggs were not attached to any substrate and were simply dropped to the bottom of the oviposition container. Eggs hatched in approximately 20 days, and the first instar larvae went into diapause without eating. Diapausing first-instar larvae were

Figure 13. Type locality and habitat of *Cercyonis incognita*, at west end of Bald Mountain ridge, Mendocino Co., California. Note multiple bunchgrass clumps of *Festuca idahoensis*, and the very low shrubs in foreground which are Brewer's Oak.

refrigerated for two months with a technique similar to that described for *Speyeria* (see Mattoon *et al.*, 1971). After a period of two months of refrigeration, larvae were brought to room temperature and began feeding immediately on seedlings of *Poa pratensis*. Once they reached third or fourth instar, they were transferred to potted clumps of *Festuca rubra* or *Festuca idahoensis*. The time from breaking of larval diapause to pupation was approximately six weeks and involved five instars. Pupae were variable in color pattern, showing the same range of variation that both *C. oetus* and *C. sthenele* display, with both brown and green morphs and varying degrees of stripes on them. The pupae hatched in approximately 12-14 days with males emerging first, followed closely by females. Females that were confined for ova and fed daily with 3:1 water: sucrose solution lived up to seven weeks. A future paper will describe the life history and biology of *C. incognita* in greater detail.

The behavior of *C. incognita* was observed at several sites along Etsel Ridge in Mendocino County. Adults of both sexes tended to stay close to the edges of Brewer's Oak thickets and flew low to the ground, usually staying within a half meter of the soil surface. Females would spend considerable time simply roosting or resting in the *Festuca* clumps or on the ground, whereas males were more active and spent less time resting. The preferred larval host plant throughout the range of this species is undoubtedly *Festuca idahoensis*, as this is the dominant grass in areas where the butterfly flies. Several females were observed to oviposit in clumps of this grass in the field, and larvae reared in the laboratory accepted this *Festuca* readily. *Cercyonis incognita* is invariably associated with Brewer's Oak thickets and *Festuca idahoensis* in our field experience. We have not yet found a locality for the butterfly where either of these plants is absent. Additionally, there are no localities where it is sympatric with *Cercyonis sthenele behrii*, the North Coast Range subspecies of *C. sthenele. Cercyonis sthenele behrii* is found in all of the counties in which *C. incognita* is found, but *C. sthenele behrii* occurs at a generally lower elevation (i.e., below 4,000 feet elevation) and in association with oak forests of species other than Brewer's Oak.

Actually, our first clue that this species was more closely related to *C. oetus* (Figs. 5-8) than to *C. sthenele* (Figs. 9-12) was the observation that females dropped their eggs into grass clumps rather than attaching them to grass blades or grass stems as does *C. sthenele* (Fig. 13) All populations of *C. oetus* in Colorado, California, and Arizona that we have studied exhibit "egg-dropping" oviposition behavior. In contrast, in all *C. sthenele* populations that we have studied, ova are attached during oviposition to the chosen substrate surface.

Diagnosis and discussion. *Cercyonis incognita* is comparable in size to *C. sthenele behrii* (Grinnell) (1905; type locality Mt. Tamalpais, Marin County, California) of the California Coast ranges, whereas *C. oetus oetus* (Boisduval) (1869; type locality west slope of Mt. Judah, south-southeast of Donner Pass, Placer County, California) of the Sierra Nevada averages smaller. The overall aspect of the dorsal surface of *incognita* is more similar to *oetus*, with the forewing ocelli averaging smaller than in *behrii*. Females of *incognita* have a paler aspect both dorsally and ventrally in comparison to *oetus* and *behrii*; this is especially pronounced in the distal half of the forewing. The ventral hindwing pattern in both sexes is more similar to that of *oetus*, but sometimes is very much like that of *C. sthenele silvestris* (W. H. Edwards, 1861) (type locality two air miles southwest of Pulga, north fork Feather River Canyon, California) of the foothills of the Sierra Nevada (compare Figs. 1-4, with Figs. 5-12).

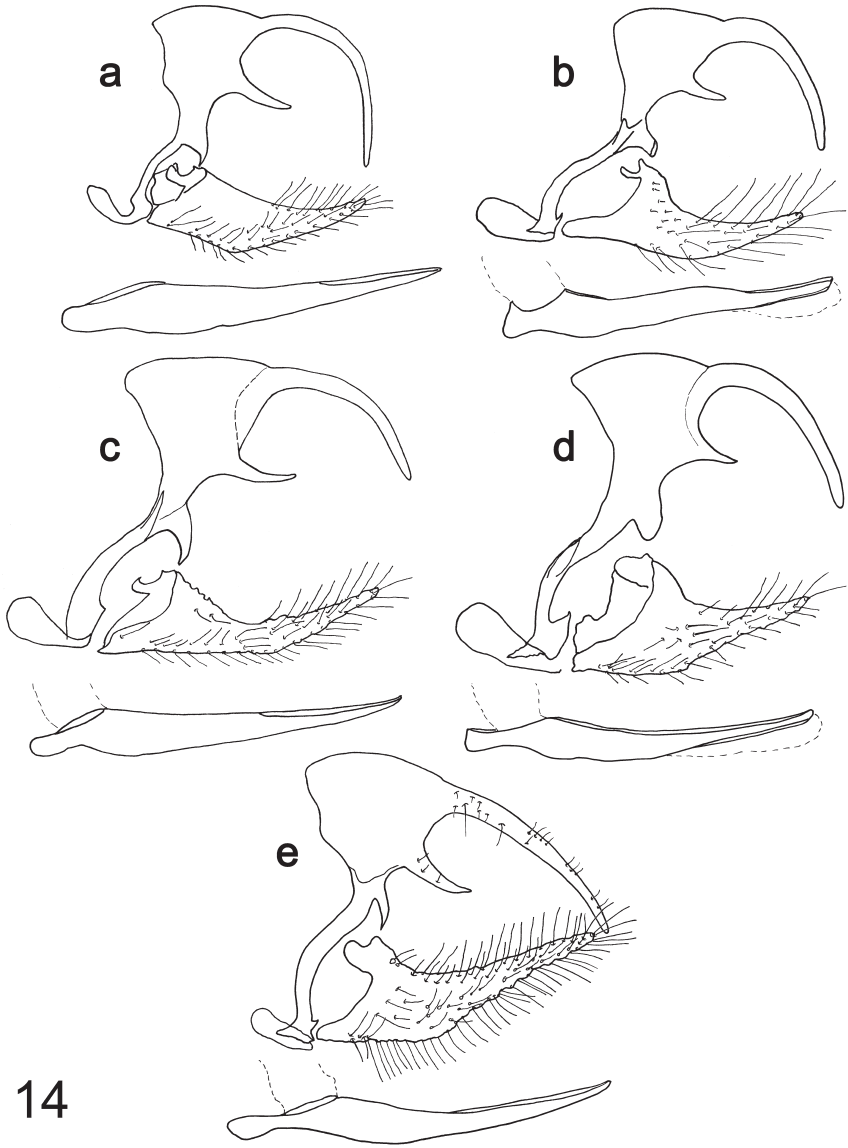


Figure 14. Lateral views of male genital structures, with aedeagus below: **a)** *Cercyonis incognita*, paratype male (Bald Mountain ridge, Mendocino Co., CA, 22 July 2001); **b)** *C. oetus oetus*, male (Sweetwater Mountains, Sawyer Creek, Mono Co., CA, 26 July 1970); **c)** *C. sthenele paulus*, male (8 miles W. of Lone Pine, Inyo Co., CA, 3 July 1963); **d)** *C. sthenele silvestris*, male (Frazier Park, Kern Co., CA, 6 June 1979); **e)** *C. sthenele behrii*, male (Pan Toll Campground, Marin Co., CA, 8 July 1968).

GENITALIC EVIDENCE FOR SPECIES DISTINCTION

In comparing the male genitalic structures (Fig. 14) of the new *Cercyonis incognita* to *C. oetus oetus, C. sthenele behrii, C. sthenele paulus*, and *C. sthenele silvestris* from California, the new species differs from the other small *Cercyonis* taxa in the following characters: (1) the shape of the posterior end of the aedeagus in *incognita* (a) is a wide blunt thumb-shaped projection, whereas it is shorter and heel-like in *oetus* (b), thinner and projected in *paulus* (c), and extended, heel-like and more flattened in *silvestris* (d); (2) the shapes of the juxta and of the valva are quite different in all five taxa, the outlined structure of the juxta and valves being most similar to *oetus* while diverging noticeably in *paulus* and *silvestris*; (3) the uncus and gnathos differ in minor ways (primarily in relative length of the gnathos); (4) the shapes of the protrusions at the lower part of the tegumen that meet the upper posterior end of the valva vary in minor ways between *incognita* and *oetus*, and also *behrii, paulus* and *silvestris*; and (5) the pattern and number of spines of various lengths on the valvae of all five taxa differ in notable ways from each other.

Overall, the male genitalic characters suggest that the degrees of differences existing between *C. incognita* and either *C. oetus* or *C. sthenele* cumulatively combine with other morphological and biological differences to define species in this complex of smaller *Cercyonis* taxa. Female genitalia were not studied.

HYBRIDIZATION STUDIES

Matings between the taxa treated in the present paper were obtained by the method of hand-pairing as described by Clarke & Sheppard (1956). The results of these matings are summarized in Table 1. No backcross matings were obtained due to unavailability of parental stock individuals when the hybrid adults emerged.

These crosses utilized reared virgin adults, which were examined also for typical phenotypic characters. Leg samples were preserved for future molecular analyses. The egg fertility and rearing results were as follows in these crosses.

1) Intraspecific fertility in eggs from *C. incognita* x *C. incognita* was 97.1%. There were 231 ova out of 238 deposited which showed fertility change (egg color changes from white to reddish-brown within 48-72 hours after oviposition). Subsequently, 92% of the 238 eggs laid produced larvae. These larvae then showed high survivorship, with 180 adults being obtained from 238 eggs.

2) In contrast, three *C. oetus* x *C. incognita* crosses resulted in 1 adult being obtained out of 918 eggs laid (with only 183 ova, or 19.9%, showing a fertility change).

3) Likewise, with three *C. sthenele behrii* x *C. incognita* crosses, 13 adults resulted from 423 eggs laid (with only 153 ova, or 36.2%, showing a fertility change).

4) These data indicate virtually complete genetic isolation (coupled with total geographic isolation) between Sierra Nevadan *C. oetus* and Coast Range *C. incognita*, and a major degree of genetic isolation between *C. sthenele behrii* and *C. incognita* in the northern Coast Range areas where these two taxa could potentially come in contact.

5) In previous genetic crosses between all four previously described species of the genus *Cercyonis* (Emmel, 1967; Emmel & Emmel, in prep.), *C. oetus* x *C. pegala* or *C. oetus* x *C. sthenele* crosses showed 0-0.5% fertility and no adults resulted.

6) CONCLUSION: The slightly greater genetic compatibility between *C. incognita*

Table 1. Results of crosses involving reared virgin adults of *Cercyonis incognita, C. oetus*, and *C. sthenele* from California populations.

cross	# ova	# showing fertility change	# hatching	# surviving diapause	# adults obtained
2003-C-6 ***incognita* F** (Summit Spring, Colusa Co., CA) × ***incognita* M** (Summit Spring, Colusa Co., CA)	238	231	221	216	180
2002-C-1 ***oetus* F** (Sonora Pass, Mono Co., CA) × ***incognita* M** (Summit Spring, Colusa Co, CA.)	216	56	14	6	0
2002-C-2 ***incognita* F** (Summit Spring, Colusa Co., CA) × ***oetus* M** (Sonora Pass, Mono Co., CA)	321	26	6	4	0
2003-C-3 ***incognita* F** (Summit Spring, Colusa Co., CA) × ***oetus* M** Sonora Pass, Mono Co., CA)	381	101	16	12	1M
2005-C-1 ***sthenele behrii* F** (Garner Valley, Riverside Co., CA) × ***incognita* M** (Pattymocus Butte, Tehama Co., CA)	138	73	62	28	8M, 1F
2005-C-2 ***sthenele behrii* F** (Garner Valley, Riverside Co., CA) × ***incognita* M** (Pattymocus Butte, Tehama Co., CA)	132	55	51	16	3M, 1F
2005-C-5 ***incognita* F** (Pattymocus Butte, Tehama Co., CA) × ***sthenele behrii* M** (Garner Valley, Riverside Co., CA)	153	25	4	0	0

and *C. s. behrii* versus *C. incognita* and *C. oetus* in crosses is likely due to shared physiological adaptations to similar mid-elevation montane oak-thicket habitat conditions, versus the quite different conditions in the high-elevation montane sagebrush habitat of *C. oetus*. Evolutionarily speaking, from both phenotype and egg-dropping behavior, *C. incognita* and *C. oetus* were likely derived from the same parental stock and yet now are more isolated genetically due to selection for oak-thicket habitat adaptation in the coastal mountains for *C. incognita*. Thus in the hybridization studies to date, *C. incognita* and *C. oetus* and *C. sthenele* all appear to be strongly isolated genetically and behave as good species in crosses involving entire genomes.

ACKNOWLEDGEMENTS

We are indebted to Ken Hansen of McKinleyville, California, who collected live females of the Humboldt County populations of this species and sent them to the senior author for rearing. Ken Hansen also collected a series of adults from the Humboldt County population for us to study. We thank Ian K. Segebarth for his expert digital photography of the specimens illustrated in the accompanying figures. Male genitalia were drawn by Thomas C. Emmel from specimens selected by John F. Emmel and Jacqueline Y. Miller, and dissected by Deborah Matthews Lott. Christine M. Eliazar and Deborah Matthews Lott at the McGuire Center rendered valuable contributions in plate and manuscript preparation. We thank editor Jacqueline Y. Miller and anonymous reviewers for helpful comments on this paper.

LITERATURE CITED

Boisduval, J. A. 1852. *Annales de la Société Entomologique de France* (2)10(2): 308-309.

Boisduval, J. A. 1869. Lèpidoptéres de la Californie. *Annales de la Societe Entomologique de Belgique* 12: 1-28, 37-94.

Clarke, C. A., and P. M. Sheppard. 1956. Hand-pairing of butterflies. *The Lepidopterists' News* 10 (nos. 1-2): 47-53.

Edwards, W. H. 1861. Descriptions of certain species of diurnal Lepidoptera, found within the limits of the United States and of British America. *Proceedings of the Academy of Natural Sciences of Philadelphia* 13: 160-164.

Edwards, W. H. 1872. *Transactions of the American Entomological Society (Philadelphia)* 4(1/2): 61, 70.

Emmel, T. C. 1967. Genetic and phenetic differentiation in two complexes of western American butterflies. Stanford University, Stanford, California. Ph.D. dissertation. 101 pp.

Emmel, T. C. 1969. Taxonomy, distribution, and biology of the genus *Cercyonis* (Satyridae). I. Characteristics of the genus. *Journal of the Lepidopterists' Society* 23(3): 165-175.

Emmel, T. C., and J. F. Emmel. 1969. A new subspecies in the *Cercyonis meadi* group (Satyridae). *Journal of the Lepidopterists' Society* 23(3): 161-164.

Emmel, T. C., and J. F. Emmel. 1971. An extraordinary new subspecies of *Cercyonis oetus* from central Nevada (Lepidoptera: Satyridae). *The Pan-Pacific Entomologist* 47(2): 155-157.

Emmel, T. C., and S. O. Mattoon. 1972. *Cercyonis pegala blanca*, a "missing type" in the evolution of the genus *Cercyonis* (Satyridae). *Journal of the Lepidopterists' Society* 26(3): 140-149.

Emmel, J. F., T. C. Emmel, and K. Davenport. 2008. A new subspecies of *Cercyonis pegala* (Lepidoptera: Satyridae) from the southern Sierra Nevada of California. *Bulletin of the Allyn Museum* 157: 1-5.

Emmel, J. F., T. C. Emmel, and S. O. Mattoon. 1998. The types of California butterflies named by Jean Alphonse Boisduval: designation of lectotypes and a neotype, and fixation of type localities. Pp. 3-76. *In* Emmel, T. C., editor. *Systematics of Western North American Butterflies*. Gainesville, Florida: Mariposa Press. 878 pp.

Emmel, T. C., and J. F. Emmel, 1998a. A neotype designation for *Satyrus behrii* Grinnell (Lepidoptera: Satyridae). Pp. 117-120. *In* Emmel, T. C., editor. *Systematics of Western North American Butterflies*. Gainesville, Florida: Mariposa Press. 878 pp.

Emmel, T. C., and J. F. Emmel, 1998b. Designation of a type locality for *Satyrus silvestris* W. H. Edwards (Lepidoptera: Satyridae). Pp. 121-122. *In* Emmel, T. C., editor. *Systematics of Western North American Butterflies*. Gainesville, Florida: Mariposa Press. 878 pp..

Fabricius, J. C. 1775. Systema Entomologiae, sistens Insectorum classes, ordines, genera, species, adjectis synonymis, locis, descriptionibus, observationibus. Flensburgh and Leipzig, Library Kortii. 832 pp. (p. 494).

Grinnell, F., Jr. 1905. Two new butterflies from Mt. Tamalpais, California. *Entomological News* 16(2): 33-35.

Mattoon, S.O., R. D. Davis, and O. D. Spencer. 1971. Rearing techniques for species of *Speyeria* (Nymphalidae). *Journal of the Lepidopterists' Society* 25(4): 247-258.

Munz, Philip A. 1959. *A California Flora*. Berkeley, California: University of California Press. 1681 pp.

Sourakov, A. 1995. Systematics, evolutionary biology and population genetics of the *Cercyonis pegala* group (Lepidoptera: Nymphalidae: Satyrinae). *Holarctic Lepidoptera* 2(1): 1-20.

Numbers of the *Bulletin of the Allyn Museum* are published at irregular intervals.
Price $1.92