THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

published by
The Lepidoptera Research Foundation, Inc.
at
1160 W. Orange Grove Ave., Arcadia, Calif. U.S.A. 91006

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STUDIES ON NORTH AMERICAN PHILOTES
(LYCAENIDAE)

V. TAXONOMIC AND BIOLOGICAL NOTES, CONTINUED

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INTRODUCTION

This paper continues in the format established in Part IV (Shields, 1975) for the remainder of the named subspecies of Nearctic Shijimiaeoides (= Philotes) (except that S. rita rita and S. rita coloradensis will appear in a separate paper with Michael Fisher). Parts II-V are intended to be read as a set and not to be interpreted separately. One more paper in this series is in preparation, describing several new subspecies and reporting a unique collection of John Lane’s from southern California. This project required six years to complete, as Shijimiaeoides ranks with Colias, Euphydryas, Speyeria, and Agathymus in taxonomic complexity. Apologies are extended to contributors for lengthy delays in returning some of their material, due to having all specimens before me for viewing, rather than relying on comparisons drawn from memory. Eriogonum distributions follow Reveal (1969b) for the most part.

NON-HOST ERIOGONUM

Certain Eriogonum species are not used by Shijimiaeoides. I have never seen Shijimiaeoides flying around E. inflatum Torr. & Frem. and E. deflexum Torr. & Ives, two species commonly encountered on field trips, nor around E. elatum Doug. ex Benth. or E. cernuum Nutt. None were seen on blooms of E. fendleri-anum (Benth. in DC.) Small near Vermejo River, Hwy. 64; and 7 mi. S. Raton; both in Colfax Co., New Mexico (VIII-16-70). A visit to the type locality of E. apachense Reveal near Bylas, Arizona (see Reveal, 1969a) on 30 Aug. 1970 produced negative results. None were seen around the blooms of E. pelinophilum Reveal at 8.6 mi. W. of Hotchkiss, Delta Co., Colorado (see Reveal, 1973). No Shijimiaeoides were found on the blooms of E. hieracifolium Benth. in DC. along Hwy. 73 from near Indian
Pine to Carrizo, Navajo & Gila Cos., Arizona, VII-27-70 (Shields #124). Eriogonum abertianum Torr. in Emory var. abertianum grows commonly near Ramsey Canyon, Cochise Co., Arizona, VII-28-70 (Shields #126) and 13-14 mi. NE of Lordsburg, Hidalgo Co., New Mexico, VIII-25-70 (Shields #156) but is not a host of S. rita rita at these locations.

**BEHAVIOUR NOTES**

At 6 rd. mi. S. Sherwin Summit, along Hwy. 395, Mono Co., V-18-70, S. enoptes langstoni flew commonly around the white-flowered Eriogonum kennedyi var. purpusii (one oviposition observed), while S. battoides nr. glaucon avoided this species and alighted on the scarcer yellow-flowered E. umbellatum var. chlorothamnus, in a mixed stand of the two.

At the canyon 3/4 mi. SSE Horse Thief Spgs., Kingston Range, San Bernardino Co., IX-15-70, a fresh male S. enoptes dammersi investigated a male of the white skipper Heliopetes ericetorum that was perched with outstretched wings on the mud. It tried to alight on the skipper ("hovering" over it as if it were a flower) then flew off after this brief encounter. Perhaps significantly, dammersi was associated with the white-flowered Eriogonum wrightii var. wrightii in this canyon.

Shijimiaeoides rita pallescens (Tilden & Downey, 1955)


This was originally described as a separate species, but Mattoni (1965, p. 94) noted that in the shape of the valve it is similar to elvirae and thus considered pallescens to be a subspecies of rita. There is little doubt that Mattoni's decision is correct, as S. rita pallescens intergrades with rita elvirae in extreme western Nevada and eastern California and displays affinities to rita emmeli in western Utah. The holotype male comes from Little Granite Mountain, Dugway Proving Grounds, Tooele Co., Utah, VIII-20-53 (H. E. Cott). The paratype series was taken at this locality, at Dog Area in Dugway Proving Ground, and in the Stansbury Mountains. Tilden & Downey adequately describe pallescens and picture the adults and male valve (in comparison with rita rita). Previously known from only the type locality, pallescens ranges across northern Nevada in scattered locations.

Number of teeth on terminal end (cucullus) of valve = 11


County undetermined: Montello Wells, 1♂, VIII (CM). UTAH: Tooele Co.: NW Willow Springs, Stansbury Mts., 17♂ 23♀, VIII (AM).

HOSTS AND DISTRIBUTION: Eriogonum kearneyi Tidestr. var. kearneyi. CALIFORNIA: Mono Co.: ca. 5-6 rd. mi. WSW Calif.-Nevada border along Cal. State Hwy. 167, 6700', T3N, R28E, 10♂ 11♀, VII (AM), adult assoc. (Shields #7).

Map 1.—Distribution of *Shijimiaoides rita pallescens* (above dotted line) and *S. r. elvirae* (below).
Ssp. *pallescens* is in flight from early July to September.

One pair in a series of 17 males, 23 female *pallescens* from Willow Springs, Tooele Co., Utah, are like *emmeli*.

One male from 5-6 mi. WSW Calif.-Nev. border along Hwy. 167, Mono Co., California, is unusual in that the aurora is almost absent. Populations on *E. baileyi* in Washoe Co., Nevada, are small and atypical.


*Eriogonum kearneyi* var. *kearneyi* grows in sandy soils from extreme east-central California eastward across central and southern Nevada to western Utah and northwestern Arizona, flowering from July to September. *E. microthecum* var. *foliosum* is widespread and common from southeastern California in eastern San Bernardino and Inyo Cos. eastward across southern and central Nevada into northern Arizona and southern Utah, northward on the Colorado Plateau to Emery and Grand Cos., and in widely scattered locations as far north as the Wyoming state line, entering western Colorado in Mesa Co. and proceeding southward and across southern Colorado to San Luis Valley and across northern New Mexico to the Sangre de Cristo Mts., hence southward to central New Mexico, 4500-7500', flowering from June to October. *E. baileyi* var. *baileyi* occurs in southern and eastern California and western Nevada northward to southeastern Washington and southwestern Idaho, flowering from May to September. Var. *divaricatum* grows in Placer and Nevada Cos., California and from Washoe to Douglas Cos., Nevada, flowering from June to September.

*Shijimiaeoides rita elvirae* (Mattoni, 1965)


The holotype male comes from 3.5 miles southwest of Pearblossom, Los Angeles Co., California, VIII-20-64. Mattoni's detailed verbal description, with black-and-white photographs of a series of adults and male and female genitalia, and a comparison with the other named *rita* subspecies, makes repetition here unnecessary. He recorded the foodplant as *Eriogonum plumatella* and included distributional records. Comstock & Henne (1967) gave a detailed life-history description of *elvirae,*
with a black-and-white painting of the egg, mature larva, and pupa. They noted that the larvae “did not take normally to our coastal *E. fasciculatum.*"

Number of teeth on terminal end (cucullus) of valve = 13 (2), 14 (2), 16 (2), 17 (1), 18 (1), 19 (2); N = 10, average = 16, from Pearblossom mostly, and two other localities.


*Ssp. elvirae* flies from mid June to late September.

There appears to be some gene flow between *pallescens* and *elvirae* based on undersurface characters. Populations from Walker Pass, Kern Co.; Big Pine Creek, Bishop, and Lone Pine, Inyo Co.; and Sherwin Summit, Mono Co., in California; and at Little Washoe Lake, Carson City, and the Lyon-Mineral Co. line on U.S. 95, in Nevada, display a mixed series, some being similar to *elvirae*, others closer to *pallescens*.

*Ssp. elvirae* from Juniper Hills, Los Angeles Co., often resemble the small form of *battoides ellisii* from the eastern Mojave Desert on the underside. At Walker Pass, Kern Co., *elvirae* is sympatric with *battoides bernardino*, and at Sherwin Summit,

*Eriogonum microthecum* var. *ambiguum* is found in dry rocky places from southern Washoe Co., Nevada and adjacent Nevada Co., California, southward along the eastern flank of the Sierra Nevada and adjacent desert ranges to Mineral and Esmeralda cos., Nevada, and Mono and Inyo cos., California, 6500-10,500', flowering from July to September. *Eriogonum kearneyi* var. *monoense* grows on gravelly soils along the eastern flank of the Sierra Nevada from extreme southern Mono Co. into Inyo Co., California (endemic), flowering from July to October.

*Shijimiaeoides enoptes dammersi* (Comstock & Henne, 1933)

The holotype male was taken at Snow Creek, Riverside Co., California, IX-9-32 (C. Henne). Some 70 paratypes were distributed along USNM, Canadian Museum, LACM, and CAS, collected at Snow Creek (mostly) and Chino Canyon, both located at the base of the San Jacinto Mts. near Palm Springs. The type description leaves no doubt as to the identity of this fall, desert subspecies of *enoptes* from southeastern California, extreme southern Nevada, and northwestern Arizona. The only subspecies that could be confused with *dammersi* is *rita rita*, which is very similar in appearance but is readily separable upon examination of the male genitalia (*rita* has cristae which *enoptes* lacks). Ssp. *rita rita* flies in central and southeastern Arizona, southwestern New Mexico, and extreme western Texas. Foster H. Benjamin examined the male genitalia of *dammersi* for Comstock and Henne and stated that "it is allied to *enoptes*." (I have examined the large series of paratypes in the LACM
collection.) The subspecies is accurately pictured in Emmel & Emmel (1973, pl. 8, figs. 10-12). A description and figures of the egg, larvae, and pupa appear in Comstock & Henne (1965), and the mature larva and pupa are illustrated in Emmel & Emmel (1973, fig. 56).

Number of teeth on terminal end (cucullus) of valve = 10 (1), 11 (2), 12 (7), 13 (9), 14 (11), 15 (3), 16 (3), 17 (3), 18 (2); N = 41, average 13-14, from Banning, Granite Mts., and jct. 79 & 179 mostly, plus two other localities.

DISTRIBUTION (viewed 78 δ gen. from 21 localities):
ARIZONA: Gila Co.: East Verde River, 10 mi. N Payson, 1 δ, ix (UCD); Tonto Bridge, 4900', 72 mi. NE of Phoenix, 1 δ, ix (AM). Maricopa Co.: 1 mi. N Sunflower, 7 δ, ix (KR). Mohave Co.: Hualapai Mts., 6 δ 3 γ, ix (LACM, KH). Yaquapai Co.: Black Hills, 4 δ 1 φ, ix (DB); Hillside, 3 δ 3 γ, ix (DB); 1 mi. S Hillside, 1 δ, ix (JS); nr. Jerome, 3 δ, ix (DB); Mingus Mtn., 5500', 6 δ 1 φ, ix, (DB, CIS); Sycamore Creek, 3500', 1 δ, x (DB); nr. Verde Hot Spr., 4 δ 5 γ, ix (DB). CALIFORNIA: Riverside Co.: Chino Canyon nr. Palm Springs, 3 δ, ix, x (AM, LACM); Palm Springs, 1 δ, x (LACM); Snow Creek, nr. Palm Springs, 13 δ 13 γ, ix, x (LACM, GG, JL, YU, CAS); White-water, 10 δ 7 γ, ix, x (LACM, CAS); Whitewater Canyon, 7 δ 5 γ, ix, x (UCD, LACM, AM). San Bernardino Co.: nr. Barnwell, 1 δ 1 φ, ix (CIS); Cedar Cyn., Mid Hills, New York Mts., 5 δ 6 γ, ix (KH); 5 mi. NW of Cima, 4900', 4 φ, ix (MCZ); Kingston Range, 6400', 1 δ, ix (LACM); Mtn. Pass Sta., Ivanpah Mtns., 1 φ, ix (CIS); New York Mts., 13 δ 10 γ, ix (KH, LACM); Tecopa Pass, 3/4 mi. S of, 4900', 1 δ, ix (AM). San Diego Co.: nr. Camp Ole, Laguna Mts., 4 δ, viii (CIS); Laguna Grade, 5000', Laguna Mts., 1 φ, ix (AM); Hwy. 79 nr. Lake Henshaw, 5 δ 4 γ, viii, ix (KH); Lake Henshaw, Hwy. 79, 4 δ 1 φ, ix (CIS, PO); 2 mi. E Lake Henshaw, 2 γ, ix (LACM); 2 mi. W Manzanita, 4 φ, x (CIS); Mason Valley, Box Canyon, 1 φ, x (LACM); Senetnac Canyon, 1 δ, ix (CM); nr. Warner's Hot Spgs., 1 δ 1 φ, ix (LACM). NEVADA: Lincoln Co.: Meadow Valley Wash, 4200-4400', 8 rd. mi. S turnoff from Caliente, T5S, R46E, 1 δ, ix (AM).

HOSTS AND DISTRIBUTION: Eriogonum wrightii Torr. ex Benth. in DC. var. wrightii. ARIZONA: Mohave Co.: 1.0 to 1.2 road mi. NW of Hualapai Mountain Park, Hualapai Mts., 3 φ, ix (AM), adult assoc. (Shields #180). Yavapai Co.: 4 rd. mi. E of Cherry, 2 δ 1 φ, ix (AM), adult assoc. (Shields #53); 3 rd. mi. NE of jct. Hwy. 79 & 179, along Hwy. 79, 11 δ 7 γ, ix
(AM), adult assoc. (Shields #52). CALIFORNIA: San Bernardino Co.: large canyon just SE of Clark Mtn. (Peak), ca. 5600-6000', 5 rd. mi. NW of Mountain Pass, 1♀, ix (AM), adult assoc. (Shields #177); vicinity of Cove Spring, 4100', T8N, R13E, sec. 8 (SE 1/4) & 17 (NE 1/4), Granite Mts., just SW of Providence Mts., 29δ 8♀, ix (AM), adult assoc. (Shields #59); canyon 3/4 air mi. SSE of Horse Thief Springs, Kingston Range, 6δ 2♀, ix (AM), oviposition (Shields #176); Mid Hills, 5100', NW exposure of ridge, T13N, R15E, NE 1/4 of sec. 31, along road, 8δ 20♀, ix (AM), adult assoc. (Shields #60). Eriogonum wrightii Torr. ex Benth. in DC. var. membranaceum Stokes ex Jeps. CALIFORNIA: San Diego Co.: Power Station, S of Warner's Hot Spgs. at turnoff to Borrego. 1♂, ix (AM), adult assoc. (Shields #183). Eriogonum elongatum Benth. var. elongatum. CALIFORNIA: Riverside Co.: 1½ mi. S Banning, 2300', along Hwy. R1, T3S, R1E, sec. 15 (S center of), 42δ 25♀, ix (AM), adult assoc. (Shields #57). See Map 2.

Ssp. dammersi is on the wing from late August to late October.

At Snow Creek, Riverside Co., one female enoptes dammersi in a series of 13 has blue flecks in a band above the aurora on the upperside of the secondaries. One female in six from Mid Hills, San Bernardino Co., has some basal blue, and four females from Cima, San Bernardino Co., have some basal blue, apparently lacking in other dammersi populations.

Ssp. dammersi is sympatric (but allochronic) with battoides martini at Clark Mtn. and Horse Thief Springs, San Bernardino Co., with enoptes mojave in the Providence Mts., and sympatric and synchronic with a dwarf battoides ellisi form at Clark Mtn. At 4 mi. E. Cherry, Yavapai Co., Arizona, dammersi flies, while at Cherry itself, only rita rita is reported. Likewise, these two subspecies are sympatric and synchronic or nearly so at 1 mi. S. Hillside, Yavapai Co. Both species use Eriogonum wrightii var. wrightii at these localities.

Comstock & Henne (1965) observed oviposition and reared adults of dammersi from Eriogonum elongatum at Snow Creek and Chino Canyon near Palm Springs, Riverside Co., California. As they point out, E. elongatum "is more widely distributed in southern California and Baja California than is the associated butterfly." It is also associated with E. elongatum at Banning, Riverside Co., and at Manzanita, San Diego Co. I have checked a number of localities for E. elongatum in southern California during September without locating dammersi.
Map 2.—Distribution of *S. enoptes dammersi*.
E. elongatum var. elongatum occurs in coastal central and southern California and northern Baja California, Mexico, flowering from August to November. E. wrightii var. wrightii is found in southeastern California eastward to western Texas and southward to northern Mexico, flowering from July to September. Var. membranaceum is distributed in southern California and northern Baja California, flowering from August to October.

*Shijimiaeoides enoptes ancilla* (Barnes & McDunnough, 1918)


In 1918 Barnes & McDunnough published a correction to their assertion in 1916 and 1917 that *glaucon* was the Great Basin race of *enoptes*, after viewing the type specimen of *glaucon* and finding it had a *battoides* genitalia (see discussion of *glaucon* under *spaldingi* in Part IV). Thus they erected the name *ancilla* for this *enoptes* subspecies which otherwise so closely resembles *battoides glaucon*. Phenotypically ssp. *ancilla* differs only slightly from *glaucon* in having, especially in females, “a rather rougher squammatation on the underside and a thickening of the black basal fringe line; the males show only traces of fulvous on upper side of secondaries.” Ssp. *glaucon* and *ancilla* are separated with assurance only after examining the male genitalia. “Our type specimens are a series of 6♀, 4♂ from Eureka, [Juab Co.], Utah (July 1-7).” Two of these were figured in black-and-white as *glaucon* in 1916; these leave no doubt about the proper identity of *ancilla*. I have examined a series of 10♀ 4♂ *ancilla* from Eureka, 6500-7500’, Juab Co., Utah, taken in June and July (CM, gen. det.). So far, *glaucon* has not been found in Utah. Langston’s (1969) statement that *ancilla* is geographically sympatric with *rita pallescens* in northwestern Utah is true in the broad sense, but I am unaware of any specific localities where the two fly together.

Number of teeth on terminal end (cucullus) of valve = 9 (3), 10 (3), 11 (3), 12 (3), 13 (3), 14 (5), 15 (3); N = 23, average = 13-14. The localities are mostly Kingston Canyon and Bonanza Gulch, Nevada; others are singletons from seven localities.
DISTRIBUTION (viewed 225 $\delta$ gen. from 105 localities):
COLORADO: Adams Co.: Denver, 1 $\sigma$, vii (CM). Boulder Co.: Boulder, 1 $\delta$ 1 $\varphi$, vi (AM); Boulder Canyon, 14 $\delta$ 5 $\varphi$, v, vii (YU, AM); Buckingham Pk., 6500', 1 $\delta$, vi (YU); Chatqua Mesa, 6 $\delta$ 5 $\varphi$, v (JS); Eldora, 2 $\delta$, vii (YU); Flagstaff Mt., 7 $\delta$ 6 $\varphi$, vi, vii (AM, YU, LACM, DG); 4-Mile Creek above Sunset, 7 $\delta$, vi (AM, JS, LACM); 4-Mile Canyon nr. Sunset, 8 $\delta$, vi, vii (PO, SE, AM, LACM); Gregory Canyon, Boulder, 36 $\delta$ 2 $\varphi$, v-vii (YU, LACM, JS, AM); Lefthand Canyon, 4 $\delta$, vi (AM, LACM); Magnolia, 1 $\delta$, vii (YU); Nederland, 1 $\varphi$, vii (AM); Pennsylvania Gulch, near Sunset, 1 $\delta$ 1 $\varphi$, vii (JS, AM); Sawmill Hill, nr. Ward, 1 $\delta$, vii (LACM); Six Mile Canyon, 1 $\delta$, v (LACM); R. R. Grade, NW Sugarloaf, 2 $\varphi$, vi (PO). Clear Creek Co.: Clear Creek, 4 $\delta$ (CM); Fall River Rd., 7500', 2 mi. W Idaho Springs, 7 $\delta$ 1 $\varphi$, vi, vii (MF); nr. Morrison, 1 $\delta$ 1 $\varphi$, v (BM); Mt. Evans, 13,000', 1 $\delta$, vii (CM); York Gulch, 8000', Fall River, 1 $\delta$, vi (JS). Delta Co.: Black Ridge, 6500', Smith Fork Canyon, 14 $\delta$ 9 $\varphi$, vi (SE, LACM). Gunnison River, 5 mi. S Austin, 6000', 2 $\varphi$, vi (SE); S end of Landing Field, E side Redlands Mesa, NE ¼ of SW ¼, sec. 16, T14S, R93W, 6300', 21 $\delta$ 2 $\varphi$, v (AM); Rogers Mesa, 5850', nr. Filter Plant, 3 $\delta$, v (SE); Smith Fork Canyon, 5500', 4 $\delta$ 2 $\varphi$, v, vi (SE, LACM); Smith Fork of Gunnison R., W Hotchkiss, 1 $\delta$, v (SE); 2 mi. S Smith Fork Canyon, 6500-7000', 4 $\delta$, vi (SE). Eagle Co.: 2 mi. N Basalt, 7500', 1 $\delta$, vi (SE). Garfield Co.: E. Elk Creek, 6800-7000', 8 $\delta$, vii (SE); No Name Creek, 6400-7400', 1 $\delta$, vii (SE). Gilpin Co.: Golden, 2 $\delta$ 1 $\varphi$, vi (UCD, CM); 1 mi. into N. Fork Clear Creek Canyon, 16 $\delta$ 7 $\varphi$, vii (JS); Rollinsville, 1 $\delta$, vii (AM). Grand Co.: Beaver Creek, 1 $\delta$, vii (JS); Grand Lake, 1 $\delta$, vii (CM). Gunnison Co.: 1.5 mi. N Almont, Hwy. 135, 1 $\varphi$, vii (AM); Black Mesa, 8500', 1 $\delta$, vii (SE); Black Mesa Rd., 8500', 7 $\delta$ 1 $\varphi$, vii (SE); Cement Creek, 1 $\delta$, vii (CIS); Curecanti Creek, 9000', 1 $\varphi$, vi (SE); Gothic, 9500-10,500', 4 $\delta$, vi, vii (YU, AM); Hwy. 50, 5 mi. W Gunnison, 7000', 9 $\delta$ 6 $\varphi$, vi (SE); Vulcan, 7 mi. S Iola, 1 $\delta$, vi (SE). Jefferson Co.: Bear Crk. Canyon, 6000', nr. Morrison, 14 $\delta$ 1 $\varphi$, vii (MF); Castle Rock nr. Golden, 24 $\delta$ 26 $\varphi$, v (JS, LACM); Chimney Gulch, 5 $\delta$ 6 $\varphi$, v, vi (CM); gulch ¼ mi. S Chimney Gulch, 11 $\delta$, vi (JS, GG); Clear Creek Canyon, 2 $\delta$ 1 $\varphi$, vi (SE, LACM); Cub Creek, Evergreen, 1 $\delta$, vi (AM); Dedisse Park, Evergreen, 1 $\delta$ 3 $\varphi$, vii (AM); Deer Creek Canyon & Hwy. 75, 1 $\delta$, vii (CIS); Golden Gate Canyon, 1 $\delta$, vi (JS); Indian Hills, 3 $\delta$ 1 $\varphi$, vii (AM); Lookout Mt., 6500-7200', above Golden, 9 $\delta$ 6 $\varphi$, vi, vii (DG,
BM, LACM, MF); Mother Cabrini Shrine, 3♀ 1♂, vi (JS, AM); Phillipsburg, 4♀ 4♂, vii (JS); Platte Canyon, 2♀ 1♂, v (CM); Red Rocks Park, 25♀ 8♂, vi (CIS, JS, LACM); Rooney Ranch, 1♀, v (AM); Table Mtn., 2♀, v (JS); E end of S. Table Mtn., 7♀ 3♂, v (JS); Whitehall, 1♂, vii (CM). Larimer Co.: 3 mi. W Bellevue, 6700', 3♀ 1♂, vi (MF); Copeland Lake, Long's Plk. Trail, Estes Park, 1♂, (MCZ); Horsetooth Res. Area, 5400', 1♂ 1♀, vi (MF); Lily Lake, Estes Park, 1♀, (MCZ); Long's Plk. Inn, Estes Park, 9500', 20♂ 6♀, (MCZ); Soldier Canyon, 6000', 1♂, vi (MF). Moffat Co.: Juniper Mtn. W of Craig, 1♂ 2♀, vi (SE); Plug Hat Picnic Area, 7000', Dinosaur Nat'l Mon., 1♂, vi (SE). Montezuma Co.: Navajo Canyon, 8000', Mesa Verde Nat'l Park, 1♀, vi (AM). Pitkin Co.: Aspen Area, 7500-9500', 3 mi. W., 1♂, vi (MF). Routt Co.: 4 mi. N Hayden, 10♀ 3♂, vi (LACM, SE). IDAHO: Cassia Co.: Bostetter Cmpgd., Rock Cr.-Oakley Rd., 7000', Sawtooth Nat'l For., 3♀ 1♂, vii (AM); 2 mi. E. Bostetter Cmpgd., 7000', 1♀, vii (AM); Divide N. of Cache Peak, Oakley-Elba Rd., Sawtooth Nat'l For., 7500', 28♂, vii (AM); Rock Creek, S. of the village of Rock Crk., Sawtooth Nat'l For., 6000', 3♂, vii (AM). MONTANA: Madison Co.: Three Forks, 2♂, vi (CM). Sweet Grass Co.: sage hilltop nr. Big Timber Creek, 4400', 1♂, vi (JS); Little Timber Creek, 5743', Crazy Mts., 1♂, vi (YU). County undetermined: Big Timber Canyon, ca. 6500', (Half Moon Park), Crazy Mts., 1♂, vi (AM); Rock Creek & Madison River, Gallatin Nat'l For., 1♂ 3♀, (CM); Teepee Creek & Madison River, Gallatin Nat'l For., 2♂ 2♀, (CM). NEVADA: Elko Co.: Angel Lake, 8100', Ruby Mts., 13 mi. SW Wells, 1♂, viii (AM); Horns Gulch, Mountain City, 1♂, vi (CIS); Jarbidge, 6500', 2♂, vii (KH); approx. 3 mi. S Jarbidge, 6500', 4♂, vii (JL, KH); Jarbidge Wilderness, Pine Creek Camp Rd., 1♀, vii (AM); Pine Creek, nr. Jarbidge, 2♂, vii (GG). Humboldt Co.: Indian Crk., 6000', Santa Rosa Mts., 4♂, vii (AM); Martin Creek Ranger Station, 7000', Santa Rosa Range, 2♂, vii (AM). Lander Co.: lower end Birch Creek Canyon, 6200-6500', Toiyabe Range, 2♀, vi (AM); 4 rd. mi. E. Carroll Summit, 6700', 9♂ 10♀, vi (AM); Kingston Canyon, Toiyabe Range, 5♂ 1♀, vii, viii (JL, AM); S & W-facing slopes of Victorine Canyon, 8000-10,000', S side of Bunker Hill, Toiyabe Range, 67♂ 41♀, vii (AM). Nye Co.: Summit Canyon, 7000-7200', E side Toiyabe Range, 30♂ 1♀, vi, vii (AM). Pershing Co.: Buena Vista Creek, 5700-6300', E slope Humboldt Range, 2♀, vii (AM). Washoe Co.: "T. H. Ranch Ca. Pyramid Lake", 7♂, vi (LACM). OREGON: Harney Co.: ½ mi. W Burns P.O.,
4100', 3 5 5 9, vi (CIS); Devine Canyon, 12 mi. N Burns, 5036', 1 9, vi (CIS). UTAH: Cache Co.: Green Canyon, nr. Logan, 9 9, vii (AM). Davis Co.: Mill Creek Canyon, 5300', 1 9, vi (CIS); Mueller Park, Wasatch Mts., 1 9, vi. (AM). Duchesne Co.: Wolf Crk. Cyn., 7320', 14 mi. NW Tabiona, 4 9, vi (CIS). Emery Co.: Big Spring Wash, 2 4 9, v (KT). Juab Co.: Eureka, 6500-7500', 10 4 9, vi, vii (CM). Salt Lake Co.: Alta, 4 2 9, vii (MCZ); City Creek Canyon, 5300', 4 9, vi (CIS, MCZ, CM); Lamb's Canyon, Wasatch Mts., 2 9, vii (AM); Mill Crk.,6000', Wasatch Mts., 2 9, vii (AM); Mineral Fork, Big Cottonwood Canyon, 1 9, vii (KT); Parleys Canyon, Eureka, 6000', 1 9, vi (CIS). Summit Co.: Co-op Creek, Uintah Mts., 1 9, vii (KT); East Canyon, 1 9, vi (CIS); 5 mi. E Kambs, 7500', 4 9, vi (CIS); 1/2 mi. S Kimball Jct., Uintah Mts., 4 3 9, vi (LACM, AM); Park City, 11 5 9, vii (CM); N. Fork Provo River, 7500', Uintah Mts., 5 2 9, vii (LACM, AM, KT); Shingle Creek, Uintah Mts., 11 5 9, vi, vii (JS, KT, LACM); Snyderville, 21 9, vi (AM, DG, JS, KT, LACM); nr. Snyderville, 3 9, vii (JS, KT); St. Hwy. 105, 7000', 4 8 9, vii (DB). Tooele Co.: Bennion Crk., Sheeprock Mts., 3 9, vi (AM); South Willow Creek, Stansbury Mts., 4 9, vii, vii (SE, KT, CIS); Stockton, 7 9, 2 9, vi (CM). Uintah Co.: Blue Mtn. Plateau, 8000', Dinosaur Nat'l Mon., 1 9, vi (SE); S slope Blue Mtn., 8000', 1 9, vi (CM). WYOMING: Albany Co.: Johnson Creek, Sybille Canyon, 1 9, vi (DG); Sybille Canyon, 6500', 6 3 9, vii (DG). Lincoln Co.: Swift Creek, nr. Afton, 6 1 9, vi (AM). Park Co.: Roosevelt Camp, Yellowstone Nat'l Park, 1 9, vii (CAS). Sublette Co.: Elkhart Park, 1 9, vii (DG). Teton Co.: Blacktail Butte, Teton Mts., 1 9, vi, vii (MCZ); Grant Teton Nat'l Park, 8 4 9, vi (CAS); 4 mi. E. Jackson, 13 9, vii (AM); 6 mi. N. Jackson, 1 9, vii (DG); Jackson Hole, 1 9, vi (CAS); Jenny Lake, Teton Mts., 32 13 9, vi, vii (CM, YU, LACM); Moose, Teton Mts., 3 9, vi (LACM); Moran, 3 9 (CM); the Potholes, G. Teton N. P., 8 9, vi (JS, LACM); Signal Mt., Teton Nat'l Park, 2 5 9, vii (LACM); String Lake, Teton Mts., 11 4 9, vi (LACM); Strong Lake, 6750', Grand Teton N. P., 1 9, vi (CIS); Teton Mts., 14 1 9, vii (MCZ, CM); Teton Pass, 8400', 3 9, vii (DG, AM); Teton Trail, Teton Mts., 8 9, vi (LACM); Timber Island, Teton Mts., 1 9 (CAS). Some additional records appear in De Foliart (1956) and Klots (1930).

HOSTS: Eriogonum heracleoides Nutt. var. heracleoides.

IDAHO: Bear Lake Co.: 8 Mile Canyon, S of Soda Springs,
Cache Nat'l For., 6500', 2δ 2φ, vii (AM), adult assoc. (Ellis #1086). NEVADA: Elko Co.: slope ½ air mi. S of Bonanza Gulch, 8000-9500', T46N, R55E, sec. 27, 28, 34, Jarbridge Mts., 14δ 6φ, vii (AM), oviposition (J. F. Emmel #195). Eriogonum umbellatum Torr. var. aureum (Gandg.) Reveal. COLORADO: Pitkin Co.: Aspen (NE end of airport, hill-slope), 1δ 1φ reared from larvae (AM), (Shields #137); the ants Tapinoma sessile (Say) and Formica montana Emery (det. R. R. Snelling) were tending the larvae. NEVADA: Lander Co.: Kingston Canyon, 6600-6800', Toiyabe Range, 10δ 4φ, vi (AM), adult assoc. (Shields #1). Eriogonum umbellatum Torr. var. umbellatum. NEVADA: Nye Co.: 5 rd. mi. W Five Mile Springs on US Hwy. 6, 6400', NW ¼ T3N, R57E, S end Monitor Range, 2δ reared from larvae (AM), (J. F. Emmel #183). UTAH: Grand Co.: Gateway-Castleton Rd., 2 mi. W Polar Mesa turnoff, N side LaSal Mts., 8400', 1δ, vi (AM), adult assoc. (Ellis #1049). Eriogonum umbellatum Torr. var. nevadense Gand. NEVADA: Lander Co.: 4.0 rd. mi. E Carroll Summit, 6700', 9 δ 10φ, vi (AM) adult assoc. (Shields #208). Eriogonum lobbii Torr. & Gray var. robustius (Greene) M. E. Jones. NEVADA: Lyon Co.: 1 mi. N Silver City, 1δ 3φ, vi (AM), adult assoc. (Shields #186). Eriogonum strictum Benth. ssp. proliferum (Torr. & Gray) S. Stokes var. proliferum (Torr. & Gray) Reveal. NEVADA: Elko Co.: Wildhorse Reservoir, Hwy. 51, 64 mi. N Elko, 6500', 9δ 1φ, vi (AM), oviposition (Ellis #1073). Eriogonum ovalifolium Nutt. var. ovalifolium. COLORADO: Mesa Co.: Monument Cyn. trailhead, 5000', Colorado Nat'l Mon., 1δ, iv (AM), adult assoc. (Ellis #1002). See Map 3.

Ssp. ancilla flies from late April to early August.

A small-sized variety of ancilla with light blue males occurs at the following localities: Black Ridge, Austin, Redlands Mesa, Rogers Mesa, and Smith Fork Canyon, Delta Co.; Black Mesa, Curecanti Creek, and Gunnison, Gunnison Co.; Monument Canyon, Mesa Co.; Juniper Mtn. and Plug Hat, Moffat Co.; and Hayden, Routt Co., all in Colorado; Big Spring Wash, Emery Co.; Bennion Creek, Tooele Co.; and Blue Mtn. Plateau, Uintah Co., all in Utah. Superficially these resemble enoptes mojave but appear closest to ancilla. They are probably associated with Eriogonum ovalifolium var. ovalifolium (see host record for Monument Canyon). One dwarf female from a typical ancilla population at Snyderville, Summit Co., Utah, is extraordinarily similar to female mojave on the underside. Perhaps ancilla and mojave are linked by way of this small, light form from Utah.
Map 3.—Distribution of *S. enoptes ancilla.*
and western Colorado. Both subspecies average 13-14 teeth on the valve and have the curved edge bearing the teeth upturned to a 45° angle (also true in dammersi).

Specimens from the vicinity of Burns, Harney Co., Oregon, are typical ancilla, despite the fact that they are geographically close to the range of enoptes columbiae. Several specimens in a series of 26 male columbiae from Mill Creek, Umatilla Co., Oregon, approach ancilla.

A male from Mt. Charleston, 7200', Clark Co., Nevada, VI-26-59 (J. C. Downey, CIS) is nearest ancilla although the black borders are wide (see fig. 3-4); enoptes nr. enoptes also flies in the vicinity.

Although ancilla is usually readily distinguishable from battoides centralis, ancilla resembles centralis on the underside at Grand Lake, Grand Co., and Platte Canyon and Castle Rock, Jefferson Co., Colorado.

Ssp. ancilla approaches the range of battoides glaucon in western Nevada, at Pyramid Lake and Silver City. In Elko Co., Nevada, the two nearly overlap in range, glaucon occurring north of Jarbidge on the Nevada-Idaho border and ancilla flying in the Jarbidge Mts. at Pine Creek near Jarbidge, Jarbidge, 3 mi. S. Jarbidge and Bonanza Gulch. Based on genitalia, two specimens from 8 mi. N. of Jarbidge appear to be hybrids between the two.

Development of the orange auroral band on the lower half of the underside primaries is present in an occasional ancilla specimen from Birch Creek Canyon and Kingston Canyon, Lander Co., Nevada, and about half the females from Black Ridge, Delta Co., Colorado, have a tinge of this primary aurora. One male ancilla from Kingston Canyon is unusually large, about the size of many spaldingi, with some orange on the veins and a partial orange band on the underside of the primaries.

Eriogonum heracleoides var. heracleoides occurs from southeastern Washington south to northeastern California, eastward to Montana, Wyoming, and Colorado, flowering from May to August. E. umbellatum var. umbellatum is common from Washington to northern California eastward to Montana and Colorado, flowering from June to September. Var. aureum is widespread at lower elevations from Nevada to central Colorado, and in scattered locations across Idaho and south-central Wyoming, flowering from June to August. E. lobbii var. robustius is infrequent in extreme west-central Nevada south and west of Reno, flowering from July to August. E. strictum ssp. proliferum
var. *proliferum* ranges from Washington to central California and eastward to western Montana, flowering from June to August. *E. ovalifolium* var. *ovalifolium* is widespread and exceedingly variable, from British Columbia to southern Alberta southward through Washington and eastern Oregon into California along the eastern flank of the Sierra Nevada to northern San Bernardino Co., and southward from Canada along a broad front through Idaho and Montana into Nevada, Utah, Wyoming, and Colorado as far south as northwestern New Mexico and northern Arizona, flowering from April to July. *Shijimiaoides enoptes enoptes* (Boisduval, 1852)

(See discussion in Part IV)

Number of teeth on terminal end (culculus) of the valve = 13 (2), 14 (5), 15 (3), 16 (3), 17 (6), 18 (3), 19 (2), 20 (3), 21 (1), 23 (1); N = 29, average = 16-17, mostly from Lake Spalding and Tehachapi Mts., with ten other localities sampled.

**DISTRIBUTION** (viewed 112$ gen. from 78 localities): CALIFORNIA: Alpine Co.: Brightman Station, 4$ 1$ 2, vii (KH); Ebbetts Pass, 1$ 1$, vi (LACM); Hermit Valley, 2$ 1$, vii (JS); Hope Valley, 2$ 1$, vii (CIS); Sonora Pass Ridge, 9700', 4$ 1$, vi (CAS); Woodfords, Voight Canyon, 1$ 1$, ix (DB). Calaveras Co.: Bloods Crk. at N Fork Stanislaus River, 2$ 2$, vii (AM, LACM); Camp Wolfeboro, 5600-5800', N Fork Stanislaus River, 7$ 1$, vi, vii (LACM, PO, KH); N Fk. Stanislaus R., S Big Meadows, 4$ 1$, vi (CIS); N Fk. Stanislaus R., 2 air mi. E of E end Big Meadow, 1$ 1$, vii (AM). El Dorado Co.: China Flat, 1$ 1$, vii (AM); China Flat Campground from Silver Fork Rd. from Kyburz, 6$ 2$, vi, vii (LACM, AM, NL); Echo Lake, 5$ 1$, vii (LACM); Glen Alpine Creek, 1$ 1$, vii (DB); 6 mi. N Ice House Rd. off Hwy. 50, 1$ 1$, vii (AM); Pilot Creek, 2$ 1$, vii (CIS); 4 mi. N Riverton on Ice House Rd., 5$ 2$, vi (AM); Twin Lakes, 2$ 1$, vi (PO); Wright’s Lake, 1$ 2$, vii (PO). Fresno Co.: Huntington Lake, 1$ 1$, vi (LACM). Glenn Co.: Hull Mtn. Lookout & ridge to E, ca. 6600-6900', W edge Glenn Co., 1$ 1$, vii (AM); Plaskett Mdw., 4$ 1$, vi (AM). Humboldt Co.: Orleans, 1$ 1$, vi (CIS). Inyo Co.: Argus Mts., 1$ 1$, vii (LACM); Brewery Spring, 4880', Surprise Canyon, Panamint Range, 1$ 1$, vi (MCZ); Lone Pine Lake, 8500', 1$ 1$, vi (CIS); near Mono Pass, 10,000-11,900', 5$ 1$, viii (MCZ, PO); Onion Valley Rd., 6800', nr. Tub Springs, 4$ 2$, viii (LACM,
SE); Ruby Lake, 11,500', 1♀, viii (PO); above Ruby L., NW Inyo Co., 1♀, ix (CIS); Whitney Trail, 9000', 1♀, vii (CIS).

Kern Co.: Blackburn Canyon, Tehachapi Mts., 1♂ 1♀, vii (NL); Havilah, 1♂ 1♀, vi (LACM, CM); 4 mi. SE Keene, 1♀, ix (CIS); entrance Kern Co. Park, 5200', Tehachapi Mts., 3♂, vi (NL); up draw NW of jct. Lebec-Frazier Park Rd., 1♂, vii (NL); Pine Tree Mine, 5000', Tehachapi Mts., 4♂, vi (NL). Lake-Glenn Co. lines: 2.0 rd. mi. S Hull Mtn. Lookout turnoff just S of Hull Mtn. summit, 3♂ 6♀, vii (AM); 3 rd. mi. SSE of Hull Mtn. Lookout, along Boardman Ridge, 1♂ 1♀, vi (AM). Lassen Co.: Bridge Crk. Campground, 1♀, vii (CIS); W side Eagle Lake, 1♂, vi (LACM). Los Angeles Co.: Big Rock Crk., nr. Valyermo, 5♂ 10♀, viii (GG); dirt rd. to Horse Flats Campground from Angeles Crest Hwy. (1.0 mi. off hwy.), just N of Chilao Rec. Area, ca. 5900', San Gabriel Mtns., 1♂, vi (AM); 0.7 rd. mi. N Newcomb Ranch Inn, wash bottom off hwy., 5500', San Gabriel Mts., 1♂, vi (AM); Pacifico Mtn., 6400', San Gabriel Mts., 2♂, vii, viii (AM); San Antonio Canyon, 1♂ (CAS); So. Fork Campgd., So. Fork Big Rock Creek, San Gabriel Mts., 5♂ 5♀, ix (JL). Madera Co.: Minaret Ridge, 9265', 1♂ 1♀, vii (AM). Mariposa Co.: Tenaya Canyon, Yosemite, 1♀, vii (LACM). Modoc Co.: .8 rd. mi. E jct. of Hwy. 395 & 299, along Hwy. 299, NE of Alturas, 1♀, vii (AM); 3 rd. mi. E Pine Creek (town), Warner Mts., 2♂, vii (AM); Fandango Pass, 6100', 2♂ 3♀, vii (CIS); Pine Creek, 4800-5100', 1-2 mi. E Pine Creek (town), 6♂ 6♀, vii (AM). Mono Co.: Lake Lundy, 1♂, vi (KH); 1 mi. SE Lake Mary, 1♂, vii (LACM); Lundy Lake, 1♂, vii (PO); Mammoth, 8♂ 3♀, vii (LACM); Mammoth Camp, 3♂ 1♀, vii (LACM); Mammoth Lakes, 5♂ 2♀, vi, vii (LACM, CIS, YU); Minaret Pass, 1♂, vii (LACM); Minaret Summit, Mammoth Lakes, 13♂ 8♀, vii (LACM, AM); Saddlebag Lake, 5♂ 3♀, vii (AM, LACM); Sherwin Summit (old 395), 1♂ 1♀, ix (CIS); Sonora Pass, 1♂, vii (LACM); Tioga Pass, 5♂ 2♀, vii, viii (JL, LACM); W above Tioga Pass, 5♂ 4♀, vii (AM, LACM); 4.9 mi. E Tioga Pass, Hwy. 120, 9400', 1♂ 1♀, vii (AM). Nevada Co.: Bear River nr. Fuller Lake, 3♂ 1♀, vii (CIS); Donner Pass, 1♂, vii (CIS); Donner Summit nr. Truckee, 3♂ 1♀, vi, vii (AM); Truckee, 4♂ 6♀, vii (CM); entrance to Lake Spalding, 17♂ 12♀, vii (AM, CIS). Placer Co.: Big Meadows, 1♂ 2♀, vi, vii (CIS); Cisco, 6000', 2♀, vii (CIS, DB); Donner Summit, 1♂ 4♀, vii (AM); Lake Tahoe, 1♂, viii (UCD). Plumas Co.: Blairsden, 1♀, vii (DB); nr. Chester, 1♂, vi (AM); Keddie,
2♂ 1♀, vi (YU); 4 mi. W Quincy, 1♂, vi (CIS). San Bernardino Co.: Lytle Creek, 7000', San Gabriel Mts., 27♂ 8♀, viii, viii (JL, LACM); Upper Lytle Crk., 20♂ 15♀, vii (KH, PO).
San Luis Obispo Co.: Cottonwood Pass, 2000', 1♂, ix (AM).
Shasta Co.: 3 mi. N Burney, 1♂ 3♀, vii (CIS); between Caieye & Ellery Crks., 15-16 rd. mi. NE of Hwy. 5 (McCloud arm Shasta Res.), 1♂, vi (AM); 2 mi. N Hat Crk., 1♂ 1♀, vii (CIS); Old Station, 1♀, vi (CIS). Sierra Co.: 4 mi. N Camptonville, 1♂ 4♀, vi (PO); 10 mi. W Downieville, 5♂ 3♀, vi (CIS); Glen Alpine Crk., 6500', 1♂, vii (KH); Gold Lake, 3♂ 4♀, vii (AM); Shenanigan Flat, 12 mi. W Downieville, 2♂ 3♀, v, vi (PO); Sierra City, 1♂, vi (CAS); W of Sierra City, 4♀, vi (PO); Sierraville, 1♂, vii (CAS). Siskiyou Co.: Black Butte, 1♀, vii (CIS); Klamath Lodge, Doggett Creek, 1♂, vi (DB); SW entrance to Lava Beds Nat'l Mon. (rd. from McCloud), nr. Mammoth Crater, 5100', 4♂ 2♀, vii (AM); McBride Spgs., 5000-5500', nr. base Mt. Shasta, 4♂ 2♀, vii (GG); McCloud, 1♀, vii (CAS); 5 mi. E McCloud, 2♂ 2♀, vi, vii (CIS); Jct. Mt. Shasta Rd. (Hwy. A-10) & McBride Springs Cmpgd. Rd., 5♂ 5♀, vii (JL, KH); Mt. Shasta City, 3♀, vi, vii (CIS); 2 mi. N Mt. Shasta City, 6♂ 2♀, vi (CIS); Pumice Stone Well, 5♂, vii, (LACM); So. Fork Sacramento River nr. Mt. Shasta, 3800', 1♂ 1♀, vii (CIS); Soda Sprgs., 1♂, vi (CM). Tehama Co.: rocky outcropping on Lassen Trail Rd., 5300', T27N, R3E, S11, nr. Onion Butte, 1♂ (SM). Trinity Co.: Carrville, 2♀, vii (CIS). Tulare Co.: Monarch Lake, 10,000', 1♂, vi (CM). Tuolumne Co.: Big Oak Flat, 2♀, vi (CAS); Big Prater Mdws., N Fork Stanislaus R., 1♂, vii (CAS); Brightman Flat, 2♂ 1♀, vii (PO); Chipmunk Flat nr. Sonora Pass, 1♂ 2♀, vi, vii (CIS); 3¼ mi. SSW Hetch Hetchy Dam, 4800', 1♂ 1♀, ix (AM); Hog Ranch, 4600', 1 mi. E Mather, 1♂ 1♀, vii (CIS); Relief Res., nr. Sonora Pass, 1♂, vi (CIS); Sonora Pass, 1♂, vii (CIS); 5 mi. W Sonora Pass, 3♂ 1♀, vii (CIS); NW above Tioga Pass, 1♀, viii (CIS); Tuolumne Mdws., Yosemite, 3♂ 1♀, vii (CIS, CAS). Ventura Co.: Mt. Pinos, 1♂, viii (LACM). County undetermined: G. Alpine Cr., Tahoe, 1♂, vii (CIS); Sonora Pass, 8000', 2♂, vi (UCD); nr. Sonora Pass, 1♂ 1♀ (CIS); Tamarak L., Tahoe, 1♂, vii (CIS); nr. Vidette Meadows, 2♂, vii (CIS). Erroneous (?): Mt. Baldy, 2♂, viii (CAS). NEVADA: Clark Co.: end Kyle Canyon, Mt. Charleston, 1♀, vii (LACM); Mt. Charleston, 1♂, vii (AM). Douglas Co.: W side Carson Valley, 1♂, ix (DB); SW of Genos, Kingsbury Grade, 5700', 5♂ 1♀, vii (CIS); Glenbrook Creek, 2♂ 1♀,


Ssp. enoptes is on wing from early May to early October.

A southern California form of enoptes enoptes has the broad black borders reduced that are present in males from the Sierra Nevada and northern California and is a lighter blue. This form is found in Kern, Ventura, Los Angeles, and southwest San Bernardino cos. Males from Lytle Creek possess an uppersurface like enoptes dammersi but an underside like enoptes enoptes. A few females from Big Rock Creek, Los Angeles Co., and one from Lytle Creek, have a slight orange band on the underside of the primaries (as in battoides comstocki), one with the lower half predominantly so (in this respect rather similar to rita spaldingi).

Ssp. enoptes enoptes and battoides intermedia are sympatric at Echo Lake and Loon Lake, El Dorado Co.; Donner Summit and Lake Spalding, Nevada Co.; Gold Lake, Sierra Co.; Onion Butte, Tehama Co.; and Carrville, Trinity Co., all in California. A strong tendency in enoptes enoptes to resemble b. intermedia on the underside is manifest at Chester, Plumas Co.; and Donner Summit, and vice versa at Lake Spalding and Onion Butte. An occasional specimen in an enoptes enoptes series from Donner Summit and Truckee, Nevada Co., tends toward enoptes ancilla on the underside. Two specimens from Kyle Canyon and Mt. Charleston, Clark Co., Nevada, are like Sierran enoptes enoptes on the upperside but are smaller and more heavily marked on the underside.

Ssp. enoptes enoptes and battoides battoides are sympatric at Mono Pass and Ruby Lake in Inyo Co., Mammoth Lakes and Tioga Pass in Mono Co., and Gold Lake in Sierra Co. A female from Ruby Lake has the underside heavily spotted as in battoides battoides but the spots are not rectangular.

At Haines Canyon, Douglas Co., Nevada, enoptes enoptes flies in May and again in August.
Map 4.—Distribution of *S. enoptes enoptes* in California.
Eriogonum nudum is widespread from Washington to California and Baja California, eastward into extreme western Nevada. Var. nudum is found from southern Washington southward along the coast to near San Francisco and in the mountains from Washington through Oregon to western Nevada and in California to Tulare Co., flowering from June to September. Var. pubiflorum occurs from southern Oregon, southward to Monterey Co., and in eastern California to Kern and Inyo cos., flowering from July to October. Var. deductum ranges in the Sierra Nevada from Lassen Co., California southward to Inyo Co., and in adjacent extreme western Nevada, flowering from June to September. Var. pauciflorum is found in the mountains of southern California from Los Angeles and San Bernardino cos. southward to northern Baja California to San Pedro Martir, flowering from August to October. E. wrightii var. subscaposum grows in the mountains of eastern and southern California and extreme west-central Nevada, flowering from July to October. E. saxatile extends from San Jacinto and San Bernardino mts. west and north to the San Gabriel, Argus, and Panamint mts., and the southern Sierra Nevada north to Fresno Co., in the Santa Lucia Mts., California, and in Nye and Esmeralda cos., Nevada, flowering from May to July. E. davidsonii occurs in the southern Coast Ranges and mountains of southern California and northern Baja California eastward into western and northern Arizona, southern Utah, and extreme southwestern Colorado, flowering from June to September.

Shijimiaeoides enoptes tildeni (Langston, 1963)


The holotype male was collected at Del Puerto Canyon, 22 mi. W. of Patterson, Stanislaus Co., California, VIII-11-62 (R. L. Langston). This is at best a weakly defined subspecies closely allied to enoptes enoptes and enoptes bayensis. If tildeni deserves a name, no doubt other populations within enoptes enoptes should be so considered, although I prefer to treat highly variable subspecies like enoptes enoptes, enoptes ancilla, battoides glaucon, and battoides ellisi as plastic subspecies for which infra-population names are superfluous. However, tildeni is not hereby reduced to synonymy, to help emphasize its possible evolutionary position between e. bayensis and enoptes
enoptes. Ssp. tildenii is pictured in black-and-white by Langston, who also figures a drawing of the male genitalia, along with some distribution records.

Number of teeth on terminal end (cucullus) of valve = 12, 17, 18 (N = 3), from Del Puerto Canyon.

DISTRIBUTION (viewed 10♂ gen. from 4 localities):
CALIFORNIA: Monterey Co.: 3 mi. SE Parkfield, 1♀, viii (CIS). San Benito Co.: New Idria, 2♀, viii (PO); hills above New Idria, 3200-3600', 2♀, viii (CIS). San Luis Obispo Co.: Cottonwood Pass, 6 mi. NE Cholame, 5♂ 1♀, ix (CIS); Polonio Pass, Hwy. 46, E of Cholame, 1♂, ix (AM); 8 mi. W Simmler, 4♂ 4♀, ix (CIS). Stanislaus Co.: mine, Del Puerto Canyon, ca. 22 mi. W Patterson, 24♂ 2♀, v (AM, GG); 0.3 rd. mi. SSE of mouth of Hideout Canyon, 1550-1600', Del Puerto Cyn. Rd., sec. 16, T6S, R5E, 5♂, vii (AM).


Ssp. tildenii is on wing from mid May to mid September.

In Del Puerto Canyon, Stanislaus Co., California, tildenii uses the annual E. covilleanum in May when E. nudum is just sprouting new growth for the year, then in July to September another flight uses E. nudum blooms. Specimens from the different flights are nearly indistinguishable in appearance, although these may represent two reproductively isolated, single-brooded populations. The population on E. parvifolium var. paynei near Santa Paula, Ventura Co., is intermediate between tildenii and smithi.

E. parvifolium var. paynei is endemic to Santa Paula Canyon, Ventura Co., California. E. covilleanum occurs from Alameda and western Stanislaus cos. southward to Fresno and Kern cos., California (endemic), flowering from April to June.

Shijimiaeoides enoptes smithii (Mattoni, 1954)
The holotype male comes from Burns Creek, State Highway 1, Monterey Co., California, VIII-20-48 (C. I. Smith & R. H. T. Mattoni). Ssp. smithi is distinguishable from its nearest subspecies in geographic proximity, e. bayensis and e. tildeni, by its distinctive underside. Mattoni (1954) lists five characters that in combination distinguish smithi from other subspecies. He thought that its fall flight (actually late summer) and gross appearance suggest that it is closely related to enoptes dammersi. However, in average teeth number on the valve it differs from dammersi and is closer to enoptes tildeni; also there is an intermediate population between the two near Santa Paula. (Ssp. dammersi appears to be more closely related to enoptes mojave and enoptes langstoni than to enoptes enoptes.) Distribution records for smithi are given in Mattoni (1954) and Langston (1963). Ssp. smithi is known only from Monterey Co., chiefly along the coast. Mattoni (1954) figures the upper and lower surface of a male smithi in black-and-white. Langston (1963), after making genitalic preparations from various localities within its range, noted that Mattoni was correct in placing smithi as a subspecies of enoptes.

Number of teeth on terminal end (cucullus) of valve = 13 (1), 14 (1), 15 (2), 16 (3), 17 (6), 18 (7), 19 (2), 20 (4), 21 (3); N = 29, average = 17-18, all from Seaside.

DISTRIBUTION (viewed 45♂ gen. from 6 localities): CALIFORNIA: Monterey Co.: 36 mi. S Big Sur, 6♂ 4♀, vii (GG); Burns Creek, 1♂, viii (KH); ½ mi. N Dolans Creek, 1♂, viii (CIS); 3 mi. S Lucia, 150', 1♂ 1♀, viii (LACM, CIS); 9 mi. NW Lucia, 1♂, viii (CIS); Marina Beach (dunes), 2♀, viii (CIS); Monterey, 10♂ 10♀, vi-viii (CAS); Seaside, 18♂ 22♀, vii (CIS, KH, PO).

HOSTS: Eriogonum parvifolium Sm. in Rees var. parvifolium. CALIFORNIA: Monterey Co.: dunes at NW end Olympia Ave., ca. 25', Seaside, 67♂ 47♀, viii (AM), adult assoc. (Shields #133). Eriogonum latifolium Sm. in Rees. CALIFORNIA: Monterey Co.: dunes W of Marina, 32♂ 20♀, vi (J. Emmel), oviposition (J. F. Emmel #366), no E. parvifolium in the immediate area.

Ssp. smithi flies from June to late August.

Bruce Walsh (in litt.) found a smithi colony at Vasquez Knob, 1600-1800', Carmel Valley, Monterey Co., in association with E. parvifolium; one oviposition was observed.
Shijimiaeoides enoptes bayensis (Langston, 1963)

The holotype male was taken at China Camp, near Point San Pedro, Marin Co., California, VI-17-61 (R. L. Langston). Langston described bayensis from 237 specimens at ten localities. At best, it is a weakly-defined subspecies closely allied to enoptes tildeni although both have significantly different averages in valve teeth numbers. Langston adequately pictures bayensis in black-and-white, figures a drawing of the male genitalia, and gives distribution records. Langston & Comstock (1966) give a life history description of bayensis, unusually rich in ecological details, including the fact that the larvae would not feed on substitute species of Eriogonum furnished them. They note that the foodplant in Solano and Contra Costa counties is Eriogonum latifolium ssp. auriculatum (now placed by Reveal as E. nudum Dougl. ex Benth. var. auriculatum (Benth.) Tracey ex Jeps.). Early records of "Lycaena enoptes" from the hills near Mission Dolores, San Bruno Hills, and Lone Mountain in the San Francisco region (Williams, 1910, p. 39) are perhaps referable to this subspecies.

Number of teeth on terminal end (cucullus) of valve = 17 (1), 19 (5), 20 (2), 21 (2), 23 (4), 24 (1); N = 15, average = 20-21, all from Pt. Richmond.

DISTRIBUTION (viewed 17 $\delta$ gen. from 1 locality):
CALIFORNIA: Contra Costa Co.: Point Richmond, 36 $\delta$ 12 $\varphi$, v, vi, (GG, PO, KH). Humboldt Co.: Fruitland, 7 $\delta$ 14 $\varphi$, vi (CIS, CAS). Sonoma Co.: 2 mi. N Camp Meeker, 1 $\varphi$, vii (CIS).

(Langston, 1970, lists a record for Benecia State Park, Solano Co., vi.)

HOST: Eriogonum nudum Dougl. ex Benth. var. nudum. CALIFORNIA: Sonoma Co.: several miles N & E of Duncan Mills (fide La Due) (Shields #185).

Ssp. bayensis flies from mid May to mid July.

Specimens from Fruitland, Humboldt Co., California, determined as bayensis by Langston, show some tendency toward northern California populations of enoptes enoptes. A close relative of bayensis is no doubt tildeni, which is often similar on the underside to the bayensis population from Point Richmond.

Ssp. bayensis is probably closely related to tildeni but does resemble columbiae in general appearance. In northwestern
California there may be some gene flow in facies towards *enoptes enoptes* as well. It is noteworthy that *smithi* and *bayensis* show no intergradation.

*E. nudum* var. *nudum* is found from southern Washington southward along the coast to near San Francisco and in the mountains from Washington through Oregon to western Nevada and in California to Tulare Co., flowering from June to September.

*Shijimiaeoides enoptes columbiae* (Mattoni, 1954)

The holotype male comes from the Columbia River near Brewster, Okanogan Co., Washington, V-5-47 (D. Frechin). As Mattoni pointed out, it is closely related to *enoptes ancilla* (although readily distinguishable from it in most populations). Ssp. *columbiae* is found in extreme northern Oregon and eastern Washington, while *ancilla* occurs in western Colorado to western Nevada, northward to western Wyoming, extreme western Montana, and extreme southcentral Idaho. (Mattoni noted that a subspecies of *battoides* was sympatric with *columbiae* and was nearly indistinguishable until genitalic separations were made. He said, "This *battoides* form appears close to *P. battoides glaucon.*") Mattoni (1954) made some genitalic dissections of the type series and noted that *columbiae* was a geographic race of *enoptes*, distinguishable from other *enoptes* subspecies by a combination of six characters. He adequately illustrates the upper and lower surface of males from the type series, in black-and-white.

Number of teeth on terminal end (cucullus) of valve = 13 (3), 14 (2), 15 (1), 16 (1), 17 (1); N = 8, average = 13-14, all from Kusshi Creek, Washington.

**DISTRIBUTION** (viewed 51♂ gen. from 26 localities):


**WASHINGTON:** *Douglas Co.::* Rock Isl. Dam, 4♂ 3♀, v (DM). *Kittitas Co.::* 3 mi. W Cle Elum, 1♂ 1♀, vii
(CIS); Easton, 1 $\delta$ (CAS). Klickitat Co.: Kusshi Creek, 32 $\delta$, vi (DB); Satus Creek, 5 $\delta$ 5 $\varphi$, v (DB); Satus Pass, 3200-3500', 4 $\delta$ 3 $\varphi$ v-vii (CIS, AM); Satus Pass Hwy., 4 mi. N Kusshie Creek, 2 $\delta$ 1 $\varphi$, v (DM); Satus Pass Ski Area, 1 $\varphi$, vi (LACM).

Okanogan Co.: Brewster, 4 $\delta$ 7 $\varphi$, v (LACM, CM, YU); Black Canyon, nr. Brewster, 2 $\delta$, v (LACM); Pateros, 2 $\delta$ 2 $\varphi$, vi (YU). Yakima Co.: Ahtanum Creek, 1800-2200', 10 $\delta$ 11 $\varphi$, v (CIS, JS, PO, KH); Bear Canyon off White Pass Hwy., 3000-3200', 10 $\delta$ 5 $\varphi$, v-vii (JS, PO, CIS, AM, DM); Cottonwood Creek, 2000', 1 $\delta$ 1 $\varphi$, vi (CIS); Cowiche Crk. Rr., 1 $\varphi$, vii (DM); Harwood, 1 $\delta$, vi (DM); Kusshi Crk., 2000-3000', 3 $\delta$ 4 $\varphi$, v, vi (AM); Kusssler Crk., 2200', 1 $\delta$, v (CIS); Mill Creek, 1500-1600', 9 $\delta$ 2 $\varphi$, iv, v (KH, JS, CIS, MF); Oak Creek off White Pass Hwy., 3000-3500', 3 $\delta$ 1 $\varphi$, v-vii (DM, PO, CIS); Satus Pass Hwy., ca. 15 mi. S Topp., 1 $\delta$ 2 $\varphi$, v-vii (DM); N of Satus Pass, 1 $\varphi$, v (LACM); 2 mi. W Tieton, 1 $\delta$, vii (DM); White Pass Hwy. 8 mi. E Tieton Ranger St., 1 $\delta$ 1 $\varphi$, vi (DM). County undetermined: "E. of G. Dalles", 1 $\delta$, v (CAS).

HOST: Eriogonum compositum Dougl. ex Benth. in Lindl. var. compositum. OREGON: Malheur Co.: Simmons Gulch at Malheur River, 23 rd. mi. E Juntura, 2 $\delta$ 2 $\varphi$, v (AM), adult assoc. (D. P. Levin, s. n.). See Map 5.

Ssp. Columbieae flies from late April to mid July.

The female of an in copula pair of enoptes taken 8 mi. E of Tieton Ranger Station, Yakima Co., Washington, is like columbieae but the male is similar to enoptes enoptes. One male enoptes (Fig. 12, 13), similar to enoptes enoptes on the underside but otherwise close to columbieae, was taken at Tumwater Canyon, Chelan Co., Washington, V-29-57 (D. L. Bauer, DB).

Although columbieae is so far known only from one location on E. compositum, the closely related ancilla uses E. heracleoides, and battoides glaucon in the vicinity of Brewster, Washington, an area of sympathy with columbieae, uses E. heracleoides var. angustifolium. The range of var. angustifolium corresponds to the range of columbieae and thus may be its principal foodplant.

E. compositum var. compositum is found in southern Washington and western Washington from Mt. Rainier southward to California as far as Lake Co., flowering from April to July. E. heracleoides var. angustifolium ranges along the Columbia River drainage in northern Oregon northward to northeastern Washington and southern British Columbia and eastward into central Idaho where it is local and sporadic, flowering from
Map 5.—Distribution of *S. enoptes columbiae*.
May to July.

*Shijimiaoides battoides* glaucon (Edwards, 1871)

(See discussion of *spaldingi*, in Part IV)

**DISTRIBUTION** (viewed 110 δ gen. from 72 localities):

**CALIFORNIA:** Alpine Co.: Carson Pass, 8573', 1 δ, vi (CIS).
El Dorado Co.: Meyers, 6300', 2 ω, vi (DB); Mt. Tallac, 1 ω, vii (CIS).
Inyo Co.: Andrews Camp, Bishop Creek, 3 δ 6 ω, vi (LACM); Bishop Creek, 3 δ 3 ω, v, vi (LACM); Lone Pine Canyon, 1 δ, vii (LACM); Mahogany Flat, 7500-8000', Panamint Mts., 1 δ 1 ω, vi (DB).
Modoc Co.: Buck Creek, 1 δ, vi (LACM); Fandango Pass, 6100', Hist. Mon. #546, Warner Mts., 1 ω, vi (CIS).
Mono Co.: Bodie, 2 δ, vii (CM); Convict Lake, 1 δ, vi (AM); Cottonwood Canyon, 7000', S of Brodie, 5 δ 3 ω + "10", vi (LACM, CIS); Grant Lake, 7 air mi. S Lee Vining, 4 ω, vi (CIS); Grant Lake, 7500', 5 δ 2 ω, vi, vii (AM); just W of Grant Lake, 3 ω, vi (JL); 2.5 mi. above Grant Lake, 7800', 2 δ 4 ω, vii (AM); June Lake, 1 δ, vi (AM); Lower Rock Creek, 5500', Swall Mead, 1 δ 2 ω, v (DB); Lundy, 1 δ, vii (CM); Mammoth, 4 δ 1 ω, vi, vii (LACM); 4 mi. E Monitor Pass, 2 δ, vi (CIS); Mono Lake, 1 δ 2 ω, vii (CM, LACM); W shore, Mono Lake, 12 δ 1 ω, vi (LACM, AM); Rush Creek, 1 δ, vi (LACM); Silver Lake, 1 δ, vi (LACM); 1½ mi. SE Tom's Place, 48 δ 6 ω, vi (LACM, CIS); Warren Creek, 1 δ, vii (LACM).
Placer Co.: Ward Peak, 8500', 1 ω, vii (LACM).
Shasta Co.: Hat Creek — 3N, 1 δ, vi (CIS); Old Station, 1 ω, vi (CIS).
Siskiyou Co.: Mt. Shasta, 7600', 1 ω, viii (AM); Pumice Stone Well, 1 δ, vii (LACM). **County undetermined:**
Glen Alpine, Tahoe, 1 ω, vi (CAS). IDAHO: Ada Co.: Boise, 4500-7500', 8 δ 12 ω, vii (MCZ). Butte Co.: nr. Craters of Moon Nat. Mon., 7 ω 3 ω, vii (JS); Craters of the Moon Nat. Mon., 4 δ, vii (UI). MONTANA: Sula, 4700', 1 δ, vi (UI). NEVADA: Douglas Co.: Carson Valley, 2 δ 5 ω, vi (NSM). Ormsby Co.: Carson Range, W Stewart, 1 δ 1 ω, vi (DB); Eagle Valley, 9 δ 5 ω, v, vi (NSM); Graphite Cyn., 1 mi. W Carson City, 9 δ 9 ω, vi (GG); Graphite Cyn., ca. 2 mi. S Carson City, 7 δ 5 ω, vi (JS, PO); Kingston Cyn., 5500', 2 δ 8 ω, vi (PO); Lakeview Hill, 12 δ 6 ω, vi (LACM); Voitaire Cyn., 5200', 5 δ 6 ω, vi (DB). Storey Co.: Ophir Grade, 11 δ 5 ω, vi (NSM); Virginia City, 7 mi. Canyon, 5 δ 2 ω, v (DB).
Washoe Co.: Nellie Spgs., S. R. 34, 5 δ 2 ω, v (NSM); Reno, 1 δ 1 ω, vii (CM); Reno,
HOSTS: Eriogonum umbellatum Torr. var. nevadense Gand.

CALIFORNIA: Mono Co.: Cottonwood Canyon, 8200-8300', 2 mi. S Bodie, 4', vi (AM), oviposition (Shields #4); peak slope ca. 1 mi. W Hwy. 395 on Hwy. 89, SW of Topaz Lake,
Fig. 1.—Shijimiaeoides rita, unnamed ssp., ♀ upperside, Uinta Canyon, Duchesne Co., Utah, VIII-4-59 (J. C. Downey).
Fig. 2.—Same, underside.
Fig. 3.—S. enoptes nr. ancilla, ♂ upperside, Mt. Charleston at 7200', Clark Co., Nev., VI-26-59 (J. C. Downey).
Fig. 4.—Same, underside.
Fig. 5.—S. enoptes nr. enoptes, ♂ upperside, Kyle Canyon, 7100', Mt. Charleston, Clark Co., Nev., VII-14-66 (P. H. Arnaud, Jr., CAS).
Fig. 6.—Same, underside.
Fig. 7.—S. enoptes nr. enoptes, So. Cal. population, ♂ upperside, Blackburn Canyon, Tehachapi Mts., Kern Co., Calif., VII-10-64 (N. La Due).
Fig. 8.—Same, underside.
Fig. 9.—Same, ♀ upperside, So. Fk. Campgrd., So. Fork Big Rock Crk., San Gabriel Mts., Los Angeles Co., Calif., IX-9-66 (J. Lane).
Fig. 10.—Same, underside.
Fig. 11.—S. enoptes, unnamed ssp., ♀ underside, Hemet Ridge, 6000', San Jacinto Mts., Riverside Co., Calif., V-24-08 (F. Grinnell, Jr., LACM).
Fig. 12.—S. enoptes nr. columiae, with underside similar to enoptes enoptes, ♂ upperside, Tumwater Canyon, Chelan Co., Wash., V-29-57 (D. L. Bauer).
Fig. 13.—Same, underside.
Fig. 14.—S. battoides nr. glaucon, ♀ underside, Uncompahgre Plateau, 8400', near 25 Mesa Ranger Station, Montrose Co., Colo., VI-22-62 (K. B. Tidwell).
Fig. 15.—S. battoides nr. glaucon (?), ♂ underside, Telescope Mt., Inyo Co., Calif., VII-9-37 (LACM).

Fig. 16.—Same, ♀ underside.
Fig. 17.—S. battoides near ellisi, ♂ underside, Kingston Canyon, Toiyabe Range, Lander Co., Nev., VII-22,23-64 (J. Lane, LACM).
Fig. 18.—S. battoides unnamed ssp., ♂ upperside, Hwy. 89A, 8 mi. ESE of Fredonia, Coconino Co., Ariz., V-18-68 (K. Roever & R. Funk).
Fig. 19.—Same underside.
Fig. 20.—Same, ♀ upperside.
Fig. 21.—Same, underside.
Fig. 22.—S. battoides glaucon X enoptes ancilla hybrid by genitalia, ♂ upperside, Pattee Canyon, 3500', Missoula Co., Montana, VI-23-62 (J. Scott).
Fig. 23.—Same, underside.
Fig. 24.—S. enoptes ancilla, ♀ gynandromorph, Sybille Canyon, 6500', Albany Co., Wyo., VII-4-66 (R. Hardesty).
Fig. 25.—S. enoptes dammersi, ♀ underside, unusual aberrant, Hualapai Mts., Mojave Co., Ariz., IX-4-58 (K. Hughes).
Fig. 26.—S. battoides nr. allyni, ♂ somewhat aberrant, Cedros Island, Mexico, III-18-39 (CAS).
Fig. 27.—S. battoides nr. glaucon, ♀ aberration, Mt. Hood, Ore., VII-20-37 (CM).
Fig. 28.—S. battoides glaucon, ♀ aurora aberrant, 2 mi. NNW Mill Cr. bridge, Warm Spgs. Indian Res., 2500', Wasco Co., Ore., VI-18-66 (B. & S. Perkins, AM).
Fig. 29.—Habitat of S. rita pallescens 8 mi. S of Currant, W. slope Grant Range, Nye Co., Nev., with Eriogonum kearneyi var. kearneyi in foreground.
Fig. 30.—Habitat of S. battoides martini 3 mi. SW Beatty, Nye Co., Nev., with Eriogonum fasciculatum var. polifolium in foreground.
Plate 1
Plate 2

Ssp. glaucon is on wing from early May to mid August. Populations are variable, and distinct segregates may exist.

Ssp. battoides glaucon and enoptes columbicae are sympatric at Juniper Flat, Wasco Co., Oregon; Tumwater Cyn., Chelan Co., and Brewster, Okanogan Co., Washington; and have similar facies at Pateros, Okanogan Co., Washington. One male near Kirk, Klamath Co., Oregon, has an upperside as dark as battoides oregonensis but an underside like glaucon. A female from Fandango Pass, Modoc Co., California, is intermediate between glaucon and intermedia; enoptes enoptes is sympatric there. A ssp. near glaucon is sympatric with enoptes langstoni near Sherwin Summit, Mono Co., California. Specimens of glaucon from Mt. Ashland, Jackson Co., Oregon, are atypical.

A singleton male (gen. det.) from Uncompahgre Plateau, 8400’, near 25 Mesa Ranger Station, Montrose Co., Colorado,
Map 6.—Distribution of *S. battoides* glaucon.
VI-22-62 (KT) is unusual in that it is closer to _glaucon_ than to _centralis_ or _ellisii_ in facies and represents a considerable eastward range extension (See Fig. 14). However, the specimen is not typical _glaucon_.

Female _glaucon_ from Bishop Creek, Inyo Co., and Grant Lake, Mono Co., have some basal blue on the dorsal surface, lacking in other _glaucon_ populations.

_Eriogonum umbellatum_ var. _stellatum_ extends from southeastern Washington and northern Idaho into northern Utah southward to Del Norte, Siskiyou, and Trinity cos., California and along the western flank of the Sierra Nevada to Kern Co., flowering from July to September. Var. _chlorothamnus_ is known from southern Mono Co. s. along the e. side of the Sierra Nevada to s. Inyo Co., California, flowering from late June to September. _E. heracleoides_ var. _angustifolium_ ranges along the Columbia River drainage in northern Oregon northward to northeastern Washington and southern British Columbia and eastward into central Idaho where it is local and sporadic, flowering from May to July. _E. sphaerocaphalum_ var. _halimioides_ is found in central and eastern Oregon south to northern California and northwestern Nevada, then eastward into southwestern Idaho, flowering from May to July. _E. flavum_ var. _piperi_ occurs mainly (but not always) west of the Continental Divide, from south-western Alberta, western Montana, and northwestern Wyoming westward across northern and central Idaho to north-eastern Oregon and eastern Washington and southern British Columbia, flowering from June to August.

_Shijimiaeoides battoides battoides_ (Behr, 1867)

(See discussion in Part IV)

**DISTRIBUTION** (viewed 28° gen. from 16 localities):

**CALIFORNIA:** _Fresno Co._: Bullfrog Lake, 10,634', 1°, viii (LACM); Cartridge Creek Basin, 1°, vii (CIS); Huntington Lake, 4° 3', vi, vii (LACM); Kaiser Crest, 14° 3', vi, vii (AM, LACM, KH); Kaiser Crest, 10,000', 7° 9', vi, vii (KH); Kaiser Pass, 9800-10,100', 5° 2', vii (AM, YU); South Fork, Cartridge Creek, 1°, vii (CIS); Windy Ridge, 1°, vii (CIS). _Inyo Co._: Lone Pine Lake, 8500', 4°, vi (CIS); vic. Mono Pass, 11,500-12,500', 17° 27', viii, ix (PO, CIS, CAS, MCZ, JS, AM); above Ruby Lake, 2° 2', viii, ix (CIS); Whitney Trail, 9000', 2°, vii (CIS). _Madera Co._: Minaret Ridge, 9265' 1° 4', viii (AM). _Mono Co._: Bud Lake, 1°, vii (LACM);
W end Dana Plateau, NE Tioga Pass, 11,000-11,400', 1♂, viii (AM); McLeod Lake, 1♀, vii (AM); Mammoth, 10♂ 3♀, vii (LACM); Mammoth Camp, 7♂ 3♀, vii (LACM); Mammoth Crest, 13♂ 10♀, viii (CIS, CAS); Mammoth Lakes, 3♂ 1♀ + "10", vii, viii (LACM, CIS, CAS, YU); Minaret Summit, Mammoth Lakes, 7♂ 5♀, vii (CIS, LACM, AM); Pilot Knob nr. Tioga Pass, 1♂, viii (JL): Rock Creek, 2♂, viii (LACM); Tioga Pass, 2♂ 2♀, vii, viii (CAS, CIS, LACM); 4.9 mi. E Tioga Pass, 9400', 1♀, vii (AM); E end Tioga Pass, 10,000', 1♂, vii (AM); W above Tioga Pass, 8♂ 8♀, vi-viii (LACM, CIS); Virginia Lakes, 1♂, vii (LACM); Walker River (error ?), 4♂, vii (LACM). Sierra Co.: Gold Lake, 2♂ 4♀, vii (CM). Tulare Co.: Mineral King, 10,500-11,000', 4♂ 4♀, vii (LACM, CAS, CM); Monarch Lake, 10,000', 1♂, vii (CM). Tuolumne Co.: Cockscomb Pk., Yosemite Nat'l Park, 2♂ 2♀, vii (LACM); Helen Lake, Yosemite, 1♀, vii (LACM); May Lake trail, Yosemite, 1♀, vii (PO); Mt. Hoffman, Yosemite, 1♀, vii (LACM); Sonora Peak, 1♂, viii (CIS); Tuolumne Meadows, 1♂ 2♀, vii (LACM); N & NW above Upper Gaylor Lake, 10,600-11,000', NW Tioga Pass, 1♂ 1♀, viii (AM); Vogelsang Pass, 1♀, vii (LACM). County undetermined: Boundary Hill, Yosemite, 1♀, vii (CIS). Some additional records appear in Erik-sen (1962). In mid-August 1963 I took it commonly in French Canyon (Star Lake, Steelhead Lake, 11,700-11,800') and near Wahoo Lakes, 11,500', Fresno Co.


Ssp. battoides is on wing from mid June to September.

Specimens from Kaiser Crest, Fresno Co., are not as boldly square-spotted as they are, e.g., at Mammoth or Tioga Pass, but are closer to battoides battoides than to battoides glaucon. At Gold Lake, Sierra Co., battoides battoides and battoides intermedia are sympatric, with no evidence of intergradation. This ssp. is often abundant at high elevations in the Sierra Nevada.
Map 7.—Distribution of S. battoides battoides.
E. lobbii var. lobbii is widespread in the Coast Ranges from Lake Co. to Siskiyou and Humboldt cos., and in the Sierra Nevada from Plumas Co. southward to Mariposa and Inyo cos., California, and on Mt. Rose and Slide Mountains, Washoe Co., Nevada, flowering from June to August. E. incanum ranges in the Sierra Nevada from Tulare and Inyo cos. northward to Tuolumne and Alpine cos., and infrequently to Nevada Co., California, and isolated on Ashland Peak, Jackson Co., Oregon. E. polypodum occurs in the southern Sierra Nevada in Tulare, Inyo, and Fresno cos., California (endemic), flowering from July to September.

Shijimiaeoides battoides intermedia (Barnes & McDunnough, 1917)


This subspecies was originally described from "Shasta Co., Calif. (presumably the vicinity of Castella in the Upper Sacramento Valley) captured in the third week in July." Barnes & McDunnough (1917) regarded intermedia as so similar to enoptes enoptes in maculation that the two would be inseparable were it not for their striking difference in genitalia. They describe intermedia as having the spots on the underside of the secondaries greatly reduced in size, the aurora broken (±) into lunules, the terminal dark line reduced to a fine hair-line in width, the black border moderately broad in males, and the fringes of the secondaries white and uncheckered. They picture the "types" adequately in black-and-white. Langston (1969) refers to intermedia specimens from Kern and Los Angeles counties taken 30 to 60 years ago. These are probably the newly described battoides comstocki from Tehachapi, Kern Co., and the typical intermedia (possibly erroneous) from Mt. Baldy, Los Angeles County.

DISTRIBUTION (viewed 42♂ gen. from 14 localities): CALIFORNIA: Del Norte Co.: Little Grayback, NE Del Norte Co., 4600', 6♂ , vii (CIS); Little Grayback Pass, 21♂ , vii (CIS). El Dorado Co.: Angora Peak, Tahoe, 1♀ , vii (CIS); Echo Lake, 2♂ , vii (JS, CIS); N ridge of Echo Lake, 7400-7700', 1♂ , vii (LACM); Fallen Leaf Lake, 1♂ 1♀ , vi, vii (CAS, LACM); Tamarak L., 2♂ , vii (CIS). Nevada Co.: Bear River nr. Fuller L., 6♂ 3♀ , vii (CIS); Donner Pass, 1♂ 1♀ , vii, viii (CIS); entrance to Lake Spalding, 10♂ 7♀ , vii (AM, CIS). Placer Co.:
Cisco, 1♀, vii (DB). *Plumas-Sierra Co. line*: Gold Lake, 13♂ 19♀, vii (KH, AM, LACM, CM). *Sierra Co.*: Salmon Lake Lodge, S Gold Lake, 1♀, vii (CIS). *Siskiyou Co.*: Caribou L. & N slope & summit Sawtooth Ridge, Trinity Alps, 6800-7900', 3♂, 4♀, vii (AM); Castle Lake, 79♂ 4♀, vi-viii (CIS, CAS, GG, AM, LACM, DB, PO); Castle L., 5600-6000', 7♂ 3♀, vii (AM); S shore Castle L., 3♂ 2♀, viii (AM); along E side Castle L., 3♂ 2♀, vii (AM); N slope of peak S of Castle L., 5600-6400', 1♂ 3♀, vii (AM); Klamath Lodge, Doggett Creek, 1♂, vi (DB); Little Castle Lake, 5300', 2♀, vii (CIS, GG); Mt. Shasta, 3♂, vii (DB); Mt. Shasta, 7600', 2♂, viii (AM); Trinity Alps, Caribou Mt., 6300-7000', 1♂, vii (CIS). Tehama Co.: rocky outcropping on Lassen Trail Rd., 5300', T27N, R3E, S11, nr. Onion Butte, 10♂ 4♀, vi (SM). *Trinity Co.*: Carrville, 2♂ 1♀, vi (CAS, CIS). Erroneous record (?): Mt. Baldy, 1♂ 1♀ (CAS). OREGON: Morrow Co.: 5♂, vii (NSM).


Ssp. *intermedia* flies from early June to early August.

Ssp. *intermedia* in facies sometimes resembles *enoptes enoptes* (e.g., Lake Spalding, Gold Lake, Castle Lake, and Onion Butte) and on the underside it sometimes resembles *Plebejus lupini* (e.g., Echo Lake and Loon Lake). Both *P. lupini* and ssp. *intermedia* fly over the same *E. marifolium* flowers at Loon Lake, Echo Lake, and Donner Summit. Thus there is perhaps predation pressure selecting for convergence in undersurface pattern. Both *intermedia* and *oregonensis* use *E. marifolium* and are thus perhaps closely related; indeed, both show some affinity to *glaucon*, their probable common ancestor. Material from Ft. Klamath, Oregon, is intermediate among *glaucon, intermedia*, and *oregonensis*. *Eriogonum jamesii*, used by *centralis*, is placed in a section next to *E. marifolium*; both are the most primitive members of their respective sections. Because of this affinity, there may be a relationship between *centralis* and the *intermedia-oregonensis* group. Both *centralis* and *intermedia* on the upper-surface have extensive black borders, and populations from Burns Crk. and Cedar Pass in Modoc Co., California, are nearly
Map 8.—Distribution of S. battoides intermedia.
indistinguishable from centralis. (E. jamesii does not extend to California.)

*E. marifolium* occurs in the Sierra Nevada from Tuolumne Co. northward to Siskiyou and Modoc cos., California, eastward to the Pine Forest Range of Humboldt Co., Nevada, and northward to central and east-central Oregon, flowering from June to August.

*Shijimiaoides battoides oregonensis* (Barnes & McDunnough, 1917)


Barnes and McDunnough originally described *oregonensis* as a subspecies of *battoides* from Crater Lake, Klamath Co., Oregon, from a long series taken during the last two weeks of July. They merely point out that *oregonensis* compared to *battoides battoides* has a broad black border in males, undersurface spots less quadrate and the ground color a “greener hue”, and say that the figures (1-3) on pl. 16 should provide the identification of this subspecies, when compared to *battoides battoides*. Topotypical material I have seen from Crater Lake fits the description and figures, although the underside has a dusky appearance. This is probably a weakly defined subspecies close to *glaucon* and perhaps *intermedia* (see discussions of *glaucon* and *intermedia*), confined to Klamath Co., Oregon. Langston (1969, p. 55) thought that *oregonensis* was a high elevation subspecies in southern Oregon that decreased in altitude with latitude in Washington and British Columbia. However, material I have examined from outside Klamath Co. is *glaucon* (except for one peculiar population from Mt. Hood; see fig. 27).

**DISTRIBUTION** (viewed 4♂ gen. from 4 different localities): **OREGON:** *Klamath Co.*: 2 mi. W of jct. 230 & 97, 1♂, vii (JS); Crater Lake, 4♀, vii, viii (LACM, CM); E Rim Crater Lake, 1♂, vii (AM); S entrance Crater Lake Nat’l Park, 1♀, vi (CAS); 2 mi. W Diamond Lake Hwy. & US 97 Jct., 1♀, vi (CIS); Hillman Peak, 7500’, Crater Lake Nat’l Park, 1♂ 1♀, vii (AM); 1.6 mi. E Hwy. 97, 9 mi. N Kirk, 4650’, 1♂, vii (AM); Miller Creek, 5000’, 1♂ 1♀, vi (CIS).

**HOST:** *Eriogonum marifolium* Torr. & Gray. **OREGON:** *Klamath Co.*: ca. 5 air mi. NE of Chemult, along rd. to Walker Mtn. Lookout, Walker Rim, “3”, vii (AM), adult assoc. (*Shields #107*); .7 mi. SE of jct. Crater Lake N.P. boundary (S) and
Hwy. 62, on Hwy. 62, vii (AM), oviposition (Shields #223); 5 rd. mi. NE Sun Pass, on Hwy 232, vii (AM), adult assoc. (Shields #225); 6 rd. mi. NE Sun Pass, on Hwy. 232, “11”, vii (AM), oviposition (Shields #227).

Ssp. oregonensis flies from late June to early August.

Shjiimiaeoides battoides centralis (Barnes & McDunnough, 1917)


The “types” of centralis were taken at Salida, Chaffee Co., Colorado, July 1-7. Barnes and McDunnough (1917) say that centralis is distinguished by the broad black borders on the upperside in males, a prominent orange shading at the anal angle of the secondaries, a brown underside with spots larger than intermedia and well ringed with white, a continuous aurora, and primaries subterminally with a diffuse smokey shade above the outer angle. It is noteworthy that they felt centralis is very similar to intermedia otherwise (see discussion under intermedia). The ssp. centralis male “type” from Salida is clearly illustrated in black-and-white. Scott, Ellis and Eff (1968) report the foodplant of centralis as Eriogonum umbellatum, but I have found it only in association with E. jamesii.

DISTRIBUTION (viewed 74♂ gen. from 41 localities):

CALIFORNIA: Modoc Co.: nr. Burns Creek Ranger Station, 3♀, vii (LACM); Cedar Pass, 1♂, vi (CIS). COLORADO: Alamosa Co.: Great Sand Dunes Nat’l Mon., 2♂, vii (AM). Chaffee Co.: Maysville, 6♂, vii (CIS, JS, YU); Poncha Creek, 2♂ 2♀, vii (LACM, JS). Conejos Co.: Alamosa Reservoir, 7500’, 2♂ 1♀, viii (MF); ½ mi. N of E end of Alamosa Res., 34♂ 19♀, vii (JS); W end Alamosa Res., 49♂ 1♀, vii (GG, JS); Gato Creek, 8250’ 2♂ 2♀, vii (JS); Schilling’s Spring, 43♂, vii (JS); ½ mi. SE Schilling’s Spring, 85♂ 22♀, vii (JS). Custer Co.: Ben West Hill, 2♂ 1♀, vii (LACM); Hermit Lake Rd., 9000’, W Westcliffe, 2♂, vii (KH); Johnson Gulch, 7700’ 3♂ 2♀, vii (JS); ½ mi. W Rosita, 2♂ 1♀, vii (JS); Sand Gulch, 1 mi. SW Greenwood, 3♂, vii (JS); 2 mi. N Silver Cliff, 1♂ 1♀, vii (JS); Welsh Pony Ranch, W of Hardscrabble Creek, 1♂, vii (JS); Fremont Co.: Box Canyon, 4♂ 1♀, vii (JS); 1 mi. NE Calcite, 14♂ 4♀, vii (JS, SE, LACM); nr. Cotopaxi, 1♀, vii (MF); 3 mi. SW Cotopaxi, 2♀, viii (JS); 1 mi. W Democratic Mtn., 1♂, viii (JS); Falls Culch, 6♂, vii (LACM, JS); South Fork Falls Gulch, 2♂, viii (JS); Fleming Mtn., 1♂, vii (JS); Hayden Creek Campground, 1♂, viii (JS); ½ mi. E. Hillside Cemetery, 1♂, viii (JS); 2 mi. NE Hillside, 1♂, viii (JS); Kiln
Gulch, 4♂ 1♀, vii (LACM, JS); Kuntz Gulch, 1♂, viii (AM); Oak Creek, nr. Cotopaxi, 6500-7000', 2♂ 1♀, vii (MF); Rouch Gulch, 1♂, vii (JS); Spring Creek, 2♂ 1♀, viii (JS); 1 mi. S Wellsville, 1♀, vii (JS). La Plata Co.: 1 mi. S Durango, 7000', 3♂ 2♀, vi (SE). Montezuma Co.: Morefield Cyn., Mesa Verde Nat'l Park, 1♀, vii (AM; Wetherill Mesa, Mesa Verde Nat'l Park, 1♀, vii (AM). Rio Grande Co.: “D” Hill, Del Norte, 32♂ 4♀, vi-viii (SE, MF). Saguache Co.: Cotton Creek, 9000', 11♂, viii (SE); North Crestone Campground, 2♂, viii (SE); Orient Canyon, ESE Villa Grove, 2♂, vii (JS); ca. 5 mi. W Villa Grove, 1♂, vii (JS); 6 mi. W Villa Grove, 11♂ 1♀, vii (JS). San Miguel Co.: Hwy. 141, 3.5 mi. S Hwy. 145, 7800', 7♂ 5♀, vi (SE). NEW MEXICO: Bernalillo Co.: San Embudido Canyon, SW base Sandia Mts., 14♂, vii (JL, KH). Lincoln Co.: 5 mi. N Angus, Hwy. 37, 7050', 1♂, viii (CAS). McKinley Co.: 4 mi. S Fort Wingate, 1♂, vii (CAS). Sandoval Co.: Frijoles Canyon, Bandelier Nat'l Mon., 1♀, viii (AM); Jemez Spgs., 1♂, vii (CM); ca 1 mi. N Sandia Man Cave, Las Huertas Canyon, S of Placitas, 1♂ 1♀, viii (AM). Taos Co.: 4 mi. S Questa, 7800', 1♂, vii (CM). Torrance Co.: Capillo Peak summit, 9200', Manzano Mts., 1♂, vii (CM). County undetermined: ridge NE of Chupidero Canyon, 9100', Sangre del Cristo Range, 1♂, vii (CM).


Ssp. centralis flies from late June to mid August. Some centralis from San Embudido Canyon, Bernalillo Co., New Mexico, show a likeness to battoides ellisii from north-central Arizona in having a narrow aurora and similar markings on the underside. One male from Fort Wingate, N.M., also displays this tendency. Specimens from Hwy. 141, 3.5 mi. S. of Hwy. 145, San Miguel Co., Colorado, are rather atypical centralis and parallel ancilla on the underside; they are not close to ellisii. A singleton female from Alta, Salt Lake Co., Utah, VII-6-43 (MCZ, V. Nabokov) appears to be this phenotype as well. A long series of centralis from Schilling's Spring, Conejos Co., Colorado, is rather similar on the dorsal and ventral surface to rita coloradensis which is not sympatric, and differs consider-
Map 9.—Distribution of *S. battoides centralis*. 
ably from *rita spaldingi* which is sympatric! Both *centralis* and *spaldingi* are also sympatric at Alamosa Reservoir, Conejos Co. Ssp. *centralis* and *r. coloradensis* are sympatric at Great Sand Dunes Nat'l Mon., Alamosa Co.; Ben West Hill and Silver Cliff, Custer Co.; Hillside, Fremont Co.; “D” Hill, Rio Grande Co.; and Villa Grove, Saguache Co., in Colorado.

Of considerable importance are *centralis* records from Modoc Co., California (Burns Creek and Cedar Pass), a dramatic range extension from the southern Colorado-northern New Mexico stronghold. Specimens from Carville, Trinity Co., California, are intermediate between *centralis* and *intermedia* on the underside.

An unusual male specimen from Oak Creek, Fremont Co., Colorado, has exceptionally heavy black borders that encompass the outer half of the upperside.

*Eriogonum jamesii* var. *jamesii* is found from central Arizona, most of New Mexico, and northern Texas, northward into eastern Colorado and western Kansas into southern Wyoming, flowering from June to September.

*Shijimiaeoides battoides bernardino* (Barnes & McDunnough, 1916)


The type locality of *bernardino* is Camp Baldy, “San Bernadino Mts.” [San Gabriel Mts.], San Bernardino Co., California. Originally described only briefly as “a much smaller race” than *battoides battoides* with paler ground and less heavy markings on the underside, the figures of the type (upper and lower surfaces) definitely establish its identity. The statement, “We have other specimens from San Diego, Pasadena and Havilah,” also coincides with the known distribution of *bernardino*. Langston (1965, Map 1) gives a distribution map of *bernardino* in California. This is probably the subspecies referred to as “*Lycaena battoides*” from the Argus Mts. by Riley (1893, p. 244). Comstock and Dammers (1934) give a complete life history description of *bernardino*. They illustrate the last instar and pupa, as do Emmel & Emmel (1973).

**DISTRIBUTION** (viewed 117♂ gen. from 94 localities):

**CALIFORNIA:** Fresno Co.: Parkfield Grade Rd., 4.5 mi. S Hwy. 198, 1♀, v (AM). Inyo Co.: Argus Mts., 1♂, vi (LACM); Big Pine, 1♂ 2♀, vi (CAS); 4 mi. W Big Pine, 1♀, vi (UCD);
Carroll Crk., 9-11 mi. SW Lone Pine, 5 ø, vi (CIS); 8 mi. W Lone Pine, 6200', 3 ø 3 ø, vii (AM); Surprise Cyn., Panamint Mts., 1 ø 1 ø, iv (CIS); Tuttle Crk., 2 mi. SW Lone Pine, 26 ø 8 ø, v (CIS); Wyman Creek Canyon, 6800', White Mts., 1 ø, vii (AM). Kern Co.: Frazier Park, 4 ø 7 ø, vi, vii (CIS, GG, KH); 1 mi. W Jct. Frazier Park Rd., & U.S. Hwy. 99, 1 ø, vi (KH); Hahahahau, 14 ø 6 ø, vi (AM, CM); Keene, 1 ø, vi (CIS); Lebec, 4 ø 1 ø, vi (PO, CIS, GG); nr. summit, road up Mesquite Canyon, 3500', El Paso Mts., 1 ø 3 ø, v (AM); Mojave, 6 ø 1 ø, v (CM); 6 mi. NW Mojave, 1 ø, v (CIS); Mt. Pinos, 3 ø 1 ø, vi (LACM); 4 mi. N Murow, 1 ø, iv (CIS); Randsburg, 2 ø, v (YU); 9 mi. W Randsburg, 1 ø, iv (YU); Tehachapi, 1 ø 1 ø, vii (CM, LACM); Walker Pass, 4200-5250', 18 ø 4 ø, vi, v (KH). Los Angeles Co.: Azusa, 1 ø, iii (LACM); 5 mi. N Beverly Hills, Benedict Canyon, 1 ø, vi (LACM); Bouquet Canyon, 4 ø, vi (LACM, KH); Camp Josepho, Rustic Cyn., 6 ø 3 ø, vi (GG); Cobal Crk. Cyn., Padua Hills, 1 ø, v (KH); Cold Creek Cyn., Santa Monica Mts., 3 ø 2 ø, v (KH); Coldwater Canyon, Santa Monica Mts., 1 ø, vi (LACM); Devils Canyon, 5000', 2 ø 3 ø, vi (AM); Eaton's Wash, Pasadena, 3 ø 1 ø, vi (MCZ, LACM); Encino, 3 ø 5 ø, v (UI); Glendale, 5 ø 3 ø, v, vi (DB); Glendora, 7 ø 2 ø, v, vi (AM, LACM, CAS); Griffith Park, 12 ø 4 ø, iv, vi (CAS, CIS, JL, CM); Horse Trail Campground, Angeles Nat. For., 1 ø, vi (AM); Lake Hughes, 1 ø 2 ø, vi (KH); La Sierra Canyon, 1200', Santa Monica Mts., 1 ø, vi (YU); La Tuna Canyon, 61 ø 13 ø, v-vii (AM, YU); Littlerock, 1 ø + "4", iv (KH, CIS); 1 mi. W Little Rock, 2 ø 1 ø, v (CIS); Long Canyon, 3000', San Gabriel Mts., 1 ø, vi (CM); Los Angeles, 12 ø 7 ø, vi (CAS, LACM); Malibu Lake, Santa Monica Mts., 2 ø 1 ø, v, vi (KH, CIS); Malibu Rd. to Tapia Park, 2 ø 1 ø, vii (JL); Mint Canyon, nr. Acton, 2 ø 1 ø, v, vi (LACM, CM); Mt. Baldy foothills, 1 ø, vi (KH); Mt. Wilson, 1 ø, vi (CM); Pacific Palisades, 1 ø, vii (CAS); Pallatt Creek, 1 ø 1 ø, iv (CIS, AM); Pasadena, 9 ø 3 ø, vi, ix (CM, AM, LACM); Pearblossom, 3 ø, v (GG); 1.1 road mi. E jct. Pine Canyon Rd. & Ridge Route Rd., just NE Sandberg, 2 ø 3 ø, vi (AM); Rancho Santa Ana Botanic Gardens, 1 ø, vi (LACM); Ridge Route nr. Whitaker Peak Rd., Tejon Mts., 3 ø 1 ø, v (KH); Roscoe, 7 ø, v (LACM); San Antonio Canyon, 15 ø 3 ø, vi (CAS, CIS); San Antonio Wash, 2 ø 1 ø, vii (AM); Sandberg, 2 ø 1 ø, vi (KH); 7 mi. NW San Fernando, 1 ø, vii (CIS); San Gabriel Canyon, San Gabriel Mts., 2 ø 2 ø, v, vi (CAS, AM); West Fork, San Gabriel River,
1♂, vi (LACM); San Rafael Hills, Glendale, 1♂, vii (DB);
Santa Anita Canyon, San Gabriel Mts., 2♂, vi (LACM; Santa
Monica Mts., 2♂ 1♀, vi (LACM); Sepulveda Pass, 1♂ 1♀,
vii (KH); Sierra Pelona Rd., Mint Canyon, 2♂, vi (AM);
Soldiers Home, 2♂, vi (CM); Stunt Cyn., Santa Monica Mts.,
3♀, v (JL); Switcher’s Camp, 3♂ 3♀, vii, viii (AM); Switcher’s
Trail, 3500’, San Gabriel Mts., 1♂ 1♀, vi (LACM); Tanbark
Flat, 1♂, vii (CIS); Temescal Cyn., Santa Monica Mts., 4♂,
v (KH); Topanga, 1500’, 25♂ 2♀, v-vii (LACM); Topanga
Cyn., 1♂ 2♀, v (KH); Tujunga, 2♂, v (LACM); 2 mi. NW
Valyermo, 33♂ 23♀, v (CIS); 2 mi. E Valyermo, 12♂ 3♀,
v (CIS). Monterey Co.: Arroyo Seco, 12♂ 4♀, v, vi (CIS, CAS,
LACM); 6 mi. W Greenfield, 1♂, vi (KH); Jamesburg, 1♂ 3♀,
v (KH). Orange Co.: 4 mi. NE Laguna Beach, 1♂, vii (CIS);
Orange Co. Park, 1♂ 1♀, vii (LACM). Riverside Co.: Aguanga,
3♂, vi, vii (CAS); 6 mi. E Anza, 1♂ 3♀, v (CIS); Chino Can¬
yon, nr. Palm Springs, 1♂, iv (AM); Citrus Exp. Sta., 1♂, vi
(CIS); Corona, 1♂, vi (CM); 1 mi. W Cottonwood Spr., Joshua
Tree Nat. Mon., 1♂, iv (CIS); Dripping Springs, 2♀, vi
(LACM); Esperanza Rd., SE Cabazon, 1♀, v (GG); Garnet
Queen Mine, 6000’, Santa Rosa Mts., 1♂, vi (CM); Gavilan
Peak, nr. Lake Matthews, 2♂, iv (KH); Idyllwild, 5♂ 4♀,
vii (YU, CIS); Lee Lake, 7♂ 3♀, v, vi (CAS, LACM); Palm
Springs, 1♂, iv (UCD); near Palm Springs, 1♂ 1♀, iii
(LACM); Palms to Pines Hwy., E slope San Jacinto Mts., 3000’,
3♂, iv (JL); Perris, 4♂ 1♀, vi, vii (LACM); Pinyon Crest, 12
rd. mi. SW Palm Desert, 1♂, iv (CIS); 1 mi. E Pinyon Flat,
1♀, vii (CIS); 3 mi. E Pinyon Flat, Santa Rosa Mts., 1♂, v
(CIS); 4 mi. E Pinyon Flat, 4♂ 1♀, iv (CIS); Railroad Canyon,
3♂ 1♀, v (LACM); hills 3 mi. SW Redlands, 1♂, iv (CIS);
Riverside, 3♂ 3♀, iv-vi (LACM, CAS, CM); 5 mi. W Sage,
4♂ 5♀, vii (CIS); San Jacinto Mt., 1♂ 3♀, vi, vii (LACM);
Santa Ana Mts., 1♂, vi (DB); Snow Creek, 3♂ 1♀, v (CAS,
LACM); 1-2 mi. S Temecula, 13♂ 10♀, v (CIS). San Benito
Co.: 12 mi. S Paicines, 3♂ 4♀, vi (CIS, CAS, LACM); Pin¬
acles Nat. Mon., 1♂ 1♀, v (KH); 4 mi. E Pinnacles Nat. Mon.,
5♂ 6♀, vi (CIS, CAS, LACM); 3 mi. S Tres Pinos, 4♂ 1♀,
vi (CIS, CAS, LACM). San Bernardino Co.: Alta Loma, 1♂,
1♀, vii (AM); Baldy Mesa, nr. Cajon Pass, 5♂ 1♀, vi (LACM);
Barton Flats, 1♂, vi (CAS); Bowen Ranch Rd., Ord Mts., SE
Hesperia, 4♂ 2♀, v (GG); Burns Spring, 10 air mi. NE Yucca
Valley, long series, v (JL); Cactus Flats, 6000’, San Bernardino
Mts., 2♂ 3♀, vii (MCZ); Cajon Pass, 2♂ 3♀, vi (JL); Camp
PHILOTES

Baldy, 1♂, vii (MCZ); 4 mi. SE Devora, 5♂ 1♀, vi (CIS); 9 mi. N Fontana, 1♂, vi (CIS); Granite Mts., nr. Apple Valley, 3♂ 1♀, iv, v (KH); Lucerne Valley, 4♂ 20♀, v (LACM, CM); Hwy. 38 below Marton Pk., 3300', San Bernardino Nat. For., 39♂ 23♀, vii (AM); Morongo, 2♂, v (LACM); Oak Glen, 1♀, vii (CAS); Phelan, 2♂, vi (LACM); 12 mi. ENE Redlands, 3200', 2♂, vi (AM); 16 mi. E Redlands, 1♂ 3♀, vii (GG); Santa Ana Cyn., nr. San Andreas Fault, 3♂, vi (GG); Santa Ana River, 5000', 1♀, vii (AM); 1 mi. SE Sheephole Summit, Sheephole Mts., 2♂ 1♀, iii, iv (CIS, JL); Victorville, 1♂, v (LACM). San Diego Co.: Alpine, 1♂ 1♀, vii (CM); 6 mi. E Banner, 3♂ 5♀, vi (CIS); 2 mi. W Barrett Dam, 1♂, vii (CIS); Bedford Canyon, 1♂, vi (CIS); Black Mtn., 2♂ 2♀, vi (CIS, KH); 2 mi. SE Bonita, 1♂ 2♀, vi (CIS); Box Canyon, 1♂, v (CAS); Buckman Spr., 3♂ 1♀, v, vi (CIS); Calavo Gardens, La Mesa, 19♂, 5♀, v, vi (AM); nr. Camp Ole, Mt. Laguna, 9♂ 15♀, vii (AM, CIS); Cardiff, 1♂, vi (CIS); Challas Hts., 5♂ 2♀, iv (CM); Crest, nr. El Cajon, 5♂ 5♀, vi (GG); Cuyamaca, 1♂, vii (KH); Del Mar, 1♂ 1♀, vi (KH); 1 mi. S Del Mar, 8♂ 18♀, vii (CIS); Dictionary Hill, 1♂, vi (AM); El Cajon, 26♂ 4♀, iv-vi (AM, LACM, GG, YU); Fairmont Cyn., 4♂ 2♀, v, vi (CIS); 4 mi. E Fallbrook, 1♂ 3♀, vii (CIS); Garnet Peak, 5400', Laguna Mts., 3♂, vi (AM); Harbison Cyn., 1♀, vi (CIS); 3 mi. NW Henshaw Dam, 8♂ 9♀, vii (CIS); 5-8 mi. NE Jamul, 2♂ 2♀, vi (CIS); 1 mi. W Julian, 1♀, vii (CIS); Jct. St. Hwy. 76-78, 1♀, vi (KH); Kearney Mesa, 1♂, vi (CM); 2-4 mi. N Laguna Jct., 6♂ 4♀, v, vi (AM, CIS); Laguna Mts., 2♂, v, vi (KH, LACM); La Jolla, 11♂ 11♀, vi (CIS); Lakeside, 2♂, vi (CIS); 2 mi. NE Lakeside, 1♂ 1♀, vi (CIS); La Mesa, 3♂ 1♀, iv, v (CAS, LACM); 1 mi. E Lyons Pk., 4♂ 6♀, vii (CIS); Mason Valley, 6♂ 1♀, iv, v (LACM); Mission Dam, 1♂ 2♀, vi (CIS); Mission Gorge, 10♂ 7♀, vi, vii (KH, PO, CIS); Monument Pk., 1♂, vi (CIS); Mt. Helix, 5♂, v, vii (CIS, CAS); Mt. Laguna, 18♂ 15♀, vi, vii (CIS); Mt. Laguna Jct., 6♂, v (CIS); Mt. Palomar, 8♂ 3♀, vi, vii (CIS); Mt. Soledad, La Jolla, 2♂ 2♀, vi (CIS); 3 mi. NE Poway, 2♂ 1♀, vi (CIS); Powderhouse Cyn., 1♂ 1♀, v (CIS); "S" Mtn., 1♂, v (CIS); San Diego, 7♂ 6♀, v-vii (CM, CIS, LACM); 2 mi. SW Santa Ysabel, 1♂, vii (CIS); Santee, 1♂, vi (KH); Sentenac Cyn., 1♂, iii (UI); Solano Beach, 25♂ 19♀, vi (AM, CIS, UCD); Sorrento Beach, 2♂ 8♀, vii (AM, CIS); Sunnyside, 1♀, vii (CIS); Tecate Mtn., 14♂ 6♀, vi (KH, PO, CIS): Thing
Valley, 1♀, vii (CIS); Warners Hot Springs, 1♂ 4♀, vi, ix (CM); Witch Creek, 2♂ 2♀, vi (CM). San Luis Obispo Co.: 6 mi. S Creston, 1♀, vi (CIS); nr. Pozo, 1♂, vi (KH); 5 mi. E Sta. Margarita, 1♀, vi (CIS). Santa Barbara Co.: 1 mi. S Buellton, 9♂ 7♀, vii (CIS); Green Cyn., 8 air mi. W New Cuyama, 1♂ 1♀, v (CIS); Mission Cyn., Santa Barbara, 4♂ 1♀, v (AM); 6 mi. NW New Cuyama, 15♂ 5♀, v (CIS); 2 mi. E Solvang, 1♀, vi (CIS); 10 mi. E Twitchell Dam, Cuyama River Cyn., 1♂ 1♀, v (CIS). Stanislaus Co.: 7 mi. E Frank Raines Park, Del Puerto Cyn., 1♂, v (J. Mori Coll.) Ventura Co.: Circle X Ranch, B. S. A. Camp, 1500', 3♂ 1♀, iv (CIS); 1 mi. W jct. Frazier Park Rd. & U.S. 99, 3♂ 4♀, vi (KH); Fredalba, 1♂, vii (CM); Nellie, 23♂ 13♀, vii, viii (CM); Ridge Route, Sierra Madre Mts., 1♂ 1♀, vi (LACM). Nevada: Churchill Co.: 7 mi. W Frenchman, 4♂ 5♀, vi (JS); N end Sand Springs Mts., 4♂ 1♀, vi (DB); S end, Stillwater Mts., 5 mi. W Frenchman, 4000', 11♂ 4♀, v, vi (DB). Mexico: Baja California del Norte: Arroyo Seco, Sierra San Pedro Martir, 1♂, v (CAS); 6 mi. NE Arroyo Seco, 1♂, v (CIS); 12 mi. S Ensenada, 1♂, v (CAS); Laguna Hansen, 1♀, vii (LACM); 4 mi. SW La Zapopita, Valle de Trinidad, 1♂, iv (LACM); 9 mi. W Mike’s Sky Ranch, Sierra San Pedro Martir, 2800', 3♂, v (RH); 20 mi. W Mike’s Sky Ranch, Sierra San Pedro Martir, 1800', 3♂, v (RH); 2 mi. W Rancho El Ciprer, Sierra San Pedro Martir, 1800', 5♂ 3♀, iv (RH); 2 mi. E San Telmo, Sierra San Pedro Martir, 1000', 4♂, iv (RH); 2 mi. W Socorro, Sierra San Pedro Martir, 3000', 4♂, v, vi (CIS, CAS).


Ssp. bernardino is on wing from mid March to early August (there are several September records), although not continuously so at any one locality.

Females of bernardino from Pallatt Creek, Los Angeles Co., and Tuttle Creek, Inyo Co., have extensive blue on the underside (as do enoptes langstoni near Lone Pine). A short series from Big Pine, Inyo Co., are very light in color. Material from Solano Beach, San Diego Co., shows a slight tendency toward allyni. One bernardino male (gen. det.) from Chino Canyon, Riverside Co., in April is remarkably like enoptes dammersi on the underside, which flies at this same locality in September and October. The rare September form from the eastern Mojave Desert on E. heermannii varieties appears nearest S. battoides ellisi.

Ssp. bernardino is found in association with Eriogonum fasciculatum var. foliolosum at Arroyo Seco, Monterey Co.; Sage and Temecula, Riverside Co.; Paicines, Pinnacles, and Tres Pinos, San Benito Co.; Bonita, Camp Ole, Fallbrook, Henshaw Dam, Jamul, Lakeside, and Mt. Palomar, San Diego Co.; Buellton, Green Canyon, New Cuyama, and Twitchell Dam, Santa Barbara Co.; and Circle X Ranch, Ventura Co. (Langston records). Var. foliolosum is found in low mountains in southwestern California and northern Baja California.

Ssp. bernardino is also reported for E. fasciculatum var. flavoviride at 1 mi. W Cottonwood Spring, Joshua Tree Nat’l Mon., Riverside Co. (Langston records). Var. flavoviride extends along the northwest margins of the Colorado Desert and adjacent parts of the Mojave Desert, southeastern California.

Eriogonum heermannii var. humilius is found in Inyo and Mono cos., California northward and eastward to Humboldt and Nye cos., Nevada, flowering from June to October (see Reveal, 1970). Var. floccosum occurs in the eastern Mojave Desert in Little San Bernardino, Providence, and Clark Mts., San Bernardino Co., and in southern Clark Co., Nevada, flowering from August to October. Var. sulcatum ranges in Inyo and San Bernardino cos., California, eastward across Clark and southern
Nye cos., Nevada into Washington Co., Utah, and in northern Mohave and Coconino cos., Arizona, flowering from July to September.

*Shijimiaeaoides battoides martini* (Mattoni, 1954)


The holotype male was described from Oatman, Mohave Co., Arizona, IV-17-48 (R. H. T. & D. Mattoni), along with the allotype female and 27 paratypes. The male genital valve indicates that *martini* is a subspecies of *battoides*, according to Mattoni (1954). He found it at Oatman in close association with *E. fasciculatum* var. *polifolium*. It is distinguished from all other subspecies of *battoides* by a combination of light blue cyanic overlay, light grey underside, very wide auroral band, and small macules (?), according to Mattoni (1954). The closest relative of *martini* appears to be *bernardino*, which also uses *E. fasciculatum* (see discussion). Mattoni (1954) gives some distribution records and figures the upper surface of the male holotype and lower surface of the female allotype, in black-and-white (see also Emmel & Emmel, 1973, pl. 8, figs. 4-6).

**DISTRIBUTION** (viewed 25♂ gen. from 14 localities):

**ARIZONA:** Mohave Co.: Goldroades, 1♂ 3♀, v (AM); Kingman, 4♂ 1♀, iv (DB); Oatman, 24♂ 8♀, iv, v (AM, LACM, KH, CAS). Pima Co.: between Quijotoa and Sells, 1♀, v (LACM). Yavapai Co.: Black Canyon, nr. Bumble Bee, 2♂, iii (DB); Hwy. 69, 4 mi. N Canyon, 2600', 11♂ 20♀, iv (CIS, CAS, LACM); nr. Rock Springs, 4♂ 6♀, iv (DB, CIS); Hwy. 69 (now I-17), 4 mi. N Rock Springs, 2♂ 5♀, iv (KR); Hwy. 79, 2 mi. N Rock Springs, 17♂ 13♀, iv (KR). CALIFORNIA: Inyo Co.: Argus Mts., 4♂, v (YU); Homewood Canyon, 3500', Argus Range, 1♂, vi (MCZ). San Bernardino Co.: Bonanza King, Providence Mts., 3♂, iv (LACM); Bonanza King Mine, 1♂ 1♀, iv (PO); 2 mi. N Bonanza King Mine, Providence Mts., 1♂, iv (PO); Clark Mts., 1♂ 1♀, iv (LACM); Gilroy Canyon, Providence Mts., 9♂ 6♀, iv (KH); wash below Gilroy Cyn., 5♂ 6♀, iv (JL); Sunflower Wash, 3200', Old Woman Mts., 11♂, iv (CIS, LACM). NEVADA: Nye Co.: Amargosa Desert, 6 mi. W Beatty, 3♂, v (DB).

**HOST:** *Eriogonum fasciculatum* Benth. var. *polifolium* (Benth. in DC.) Torr. & Gray. CALIFORNIA: San Bernardino Co.: canyon 3/4 air mi. SE Horse Thief Springs, 4400-4700',
Kingston Range, 11 δ, vi (AM), adult assoc. (Shields #2).

NEVADA: Nye Co.: 3 mi. SW Beatty, 5 δ 1 φ, v (AM), adult assoc. (Shields #79). See Map 10.

Ssp. martini is on wing from late March to late June.

Specimens from the vicinity of Beatty, Nevada, appear to be intermediate between martini and bernardino. Also, both martini and bernardino occur in the Argus Mts., California, (although not typical martini). The specimen from between Quijotca and Sells, Pima Co., Arizona, is large, with a partial red band on the underside of the primaries, but is otherwise like martini.

In the Providence Mts. and at Clark Mtn., San Bernardino Co., martini flies in late April, while an unnamed form about the size of bernardino, that is perhaps best described as near ellisi, associated with two varieties of Eriogonum heermannii, is found there in September. This latter form also occurs at Kingston Canyon, Toiyabe Range, Lander Co., Nevada, VII-22 & 23-64, one male (LACM). In the Stillwater Mts., Churchill Co., Nevada, in June, specimens resemble both bernardino and this small form near ellisi, and use a third variety of E. heermannii (see bernardino records).

Material from the Old Woman Mts. is clearly martini, while a short series from the Sheephole Mts. (both in San Bernardino Co.), some 40 miles to the southwest, is bernardino.

Although bernardino is sometimes reported associated with E. fasciculatum var. polifolium, as at Pinyon Crest, Riverside Co., and at Mt. Laguna and 6 mi. E Banner, San Diego Co. (Langston records), martini is exclusively on this variety. Var. polifolium ranges on the deserts of southern California and northern Baja California, southern Nevada, southwestern Utah, and western Arizona.

**DISTRIBUTION SUMMARY**

Subspecies of each Shijimiaoides’ species are mostly allopatric, as are their host Eriogonum species. Some, like ancilla, glaucon, and enoptes enoptes, have a wide range both in elevation and latitude. Others are narrowly restricted to certain plant communities or habitats: spaldingi in ponderosa and pinyon-juniper habitats; bernardino and dammersi to chaparral (and desert); emmeli and ellisi to the Colorado Plateau; pallescens to the Great Basin; battoides battoides to high elevations in the Sierra Nevada; pallescens and emmeli in sandy desert; and allyni, smithi, and bayensis to the seacoast.
Map 10.—Distribution of *S. battoides martini*.
Several "ring", or Rassenkreis, distributions (involving a number of allopatric subspecies of a polytypic species) suggest themselves (although no breeding or genetic evidence is available as yet):

I. 

*rita emmeli*
*rita coloradensis*

**rita rita**

II. 

*enoptes bayensis*  
*enoptes columbiae*

*enoptes enoptes*  
"*rita*" spaldingi  
*enoptes ancilla*

*enoptes langstoni*  
Utah & W. Colo. small  
*enoptes ancilla*

*enoptes mojave*

These rings of related subspecies could be due to re-contact with the parent population from range expansion and subsequent hybridization and suggest that these are still subspecies that have not as yet attained the reproductive isolation of a species.

There are some striking disjunctions within *Shijimiaeoides*. For example, *S. battoides comstocki* is known only from Tehachapi, Kern Co., California, and Park City, Summit Co., Utah. *S. battoides centralis* occurs in northern New Mexico and southern Colorado, with two outlying populations in Modoc Co., California. *S. battoides allyni* is found in the Los Angeles coastal region and on Cedros Island off Baja California. *S. battoides glaucon* occurs in the Northwest from northeastern California, northwestern (and extreme northeastern) Nevada, eastern Oregon, eastern Washington, Idaho, extreme southern British Columbia, and Sula, Montana, with one relict population on the Uncompahgre Plateau in western Colorado. These disjunctions may mean there was a previously wide distribution in the past, with the intervening populations gone due to environmental extinction or competitive displacement.

Two subgenera of *Eriogonum* (*Eucycla* and *Oligogonum*) are widely used by *Shijimiaeoides* and no doubt harbour new, undescribed subspecies. *Eucycla* is common and widespread throughout most of the trans-Mississippi West, from northern Mexico northward into the Great Plains, westward to Baja California, Mexico, and the west coast of the United States (including the islands adjacent to the coast) to southwestern Canada. *Oligogonum* occurs in western United States from northern Mexico into western and northern Texas, westward to Califor-
nia, and northward to southwestern Canada, with outlying populations in east-central Alaska and in Virginia and West Virginia.

ACKNOWLEDGEMENTS

In addition to those people mentioned in Part IV who loaned material, I would like to thank: (AMNH) Frederick H. Rindge, American Museum of Natural History; (UCD) R. O. Schuster, University of California at Davis; (CF) Clifford D. Ferris; (DG) Dennis Groothuis; (UI) D. P. Levin, University of Idaho; (RK) Roy O. Kendall; (BM) Bryant Mather; (DM) David V. McCorkle; (SM) Sterling O. Mattoon; and (CS) Charles A. Sekerman (OS = Oakley Shields, personal collection). John F. Emmel and Richard M. Shields took the photographs. Charles R. Crowe, Ernst J. Dornfeld, and Jon H. Shepard kindly provided many locality records for Oregon and Washington, but these were not used in the present study unless I actually examined the specimens. Drs. Lee D. Miller, J. F. Emmel, N. E. Gary, W. H. Lange, J. L. Reveal, and R. W. Thorp, and Mr. J. Lane, read the paper and offered suggestive criticisms. I thank the two reviewers for their comments. This part completes a series submitted in partial fulfillment of the degree, Doctor of Philosophy, University of California, Davis, California.

BIBLIOGRAPHY


ADDENDA AND ERRATA

Several additional, relevant works have only lately come to my attention. Hemming (1931) recognized three subspecies of *Shijimiaoides divina*: (a) *d. divina* Fixs. (Seoul, Pungking, and Heijo in Korea; July); (b) *barine* Leech (Oiwake, Hokkaido; June-July; Nambu, Honshu); and (c) *asonis* Mats. (Mt. Aso, Kyushu; August).

Waterhouse (1903, p. 211-212) described a small rare blue, *Zizera delospila*, and in 1938 erected a separate genus, *Zetona*, for it. In certain particulars, e.g. small size, wing shape, checkered fringe, white underside, extent of purplish on the upper-side, brown females, etc. it closely approaches *Zizeeria speciosa*, though I reserve judgement on their exact affinity until a detailed morphologic and genitalic comparison can be made. *Zetona delospila* is very rare and flies in June at King’s Sound, Queen’s Islet, and the Ord River, northwestern Australia. “The adults fly close to the ground in open areas amongst grass and low shrubs” (Common & Waterhouse, 1972).


HEMMING, A. F., 1931. On two little-known species of the genus *Scolitan-


Unfortunately in Part IV, figures 29-33 were wrongly numbered. For the captions to be correct, change:

29 to 33
30 to 32
31 to 30
32 to 31
33 to 29
Fig. 31.—Schematic representation of the possible evolutionary development of the Nearctic Shijimiaeoides subspecies, based on comparative adult morphology and host Eriogonum classification.
Fig. 32.—*S. enoptes ancilla X S. battooides glaucon* ♂, possible hybrid, 8 mi. N of Jarbridge, Elko Co., Nev., VI-28-67, leg. J. Lane. Note the intermediate aspect of the valve cucullus. SEM photo, 60X, courtesy R. O. Schuster.
Fig. 33.—Same, showing the teeth regularly arranged and the valve strongly curved though not as bifurcate as in *battoides*. SEM photo, 120X, courtesy R. O. Schuster.
Fig. 34.—*S. enoptes ancilla* X *S. battoides glaucon* ♂ hybrid, Pattee Canyon, 3500', Missoula Co., Montana, VI-23-62, leg. J. Scott. The left valve seen here has a *battoides* aspect though not strongly bifurcate. SEM photo, 58X, courtesy R. O. Schuster.
Fig. 35.—Same, front view of valve showing 10 teeth irregularly arranged as in *battoides*. SEM photo, 73X, courtesy R. O. Schuster.
Fig. 36.—*S. rita spaldingi*, ♂ genitalia, Bee Springs, Kaibab Plateau, Coconino Co., Arizona, VI-30-52, leg. D. L. Bauer. Front view of valve cucullus, showing the aspect of the 14 teeth. SEM photo, 176X, courtesy R. O. Schuster.
Fig. 37.—Same, showing the upraised cristae in the inside of both valvae. SEM photo, 390X, courtesy R. O. Schuster.
I collected the specimen on a patch of virgin prairie where Hesperia dacotae flies. Hundreds of S. idalia were present. Males had been flying for several days, but females were just starting. This aberrant male was not interested in feeding at the numerous coneflowers it passed. It was drifting with the wind and occasionally checking a bunch of grasses in typical female search behavior. In flight, it looked very much like a normal S. idalia, but slightly darker. It was taken, on the wing, about two miles from where it was first sighted.
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THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

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It is with great sadness that we note the death of William Hovanitz on September 14th. His passing is a profound loss to this Journal and to all those involved with Lepidoptera. His contributions in teaching, research, writing and collecting will long be remembered. As a tribute to William Hovanitz, The Lepidoptera Research Foundation will publish a memorial supplement to Volume 16, Number 4 of The Journal of Research on the Lepidoptera. Included will be two of his classic papers, “Ecological Color Variation in a Butterfly and the Problem of ‘Protective Coloration’,” and “Parallel Ecogenotypical Color Variation in Butterflies,” and a complete bibliography of his papers.

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FOODPLANT ECOLOGY OF THE BUTTERFLY

CHLOSYNE LACINIA (GEYER)
(NYMPHALIDAE)

II. ADDITIONAL LARVAL FOODPLANT DATA

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Previously (Neck, 1973) I discussed the larval foodplants of Chlosyne lacinia var. adjutrix (Scudder). Included were extensive personal observations in central and south Texas in addition to previous literature records. The purpose of this publication is to update this previous communication before additional detailed studies are reported in subsequent publications. Several remarks and corrections concerning conclusions of the first paper can be made at this time. Several new foodplant records are available from personal observations. Personal observations were made in central Texas, centering within Austin, Travis County, Texas.

REMARKS ON INITIAL REPORT

Foodplants of Chlosyne lacinia var. adjutrix in central Texas were grouped according to relative importance—major, occasional and rarely utilized foodplants (see table 1). Quantitative data were not available at the time to properly rank the relative importance of the foodplants within each group, however. During 1972, a large, diverse site in the upper part of the old floodplain of the Colorado River (now impounded and re-named Town Lake) in Austin, Travis County, was monitored for foodplant utilization throughout the season (March-October). The total numbers of broods per major foodplant at this site for the entire season were as follows: Helianthus annuus L. — 171, Verbesina encelioides (Cav.) Gray — 119, and Ambrosia trifida.
L. — 71. These three plants are in this same order in the previous publication (Neck, 1973).

The order of the occasional foodplants given in the previous paper appears to represent their relative importance. Actually, the first three species (plant #4 - #6 in table 1) are of approximately equal significance. These plants are of importance under certain seasonal and local conditions. Utilization of these three plants will be discussed in a later article in this series.

*Helianthus debilis* Nutt. var. *cumcumerifolius* (T. & G.) Heiser grows in sandy soils which are somewhat limited in occurrence in the Austin area as much of the alluvial areas have now been inundated as a result of multiple damming of the Colorado River. Additionally, this plant is rapidly replaced in succession by *V. encelioides*, a plant which is persistent in a particular locality from year to year. A site at which *cumcumerifolius* is abundant during one season will quite likely contain no individuals of this sunflower the following season. Such succession has been observed in both the alluvial sands (Quaternary) of the Colorado River in Austin and the Carrizo Sands (Eocene) which outcrop to the east. My personal experience would classify this plant as rarely utilized. However, Kendall (1959) reported a large population of larvae of this plant. Therefore, *cumcumerifolius* is best considered an occasional foodplant, but it is not utilized nearly as widely as the other three plants placed in this category.

The foodplants in group III are only rarely utilized. Many are not known to have become larval foodplants via adult female oviposition; records of several plants are known only from larvae which have crossed-over from another foodplant species. During extensive observations in 1972 only one of these plants were personally observed as a foodplant for *adjutrix*. Several larvae were found on *Heterotheca latifolia* Buck. on 27 June 1972. These larvae, however, had crossed-over from *H. annuus*; oviposition by wild females on this plant is still unknown (see Neck, 1973).

A single final instar larva of *adjutrix* was found on *Calyptocarpus vialis* Less. by R. O. Kendall (pers. comm. 16 Sept. 1972) west of San Antonio in Bexar County. This larva probably crossed-over from *H. annuus* on which a brood was observed in the same general area. Later, I found a single larva on *C. vialis* in Austin in an area devoid of other suitable foodplants. These two additional examples (see first in Neck, 1973) indicate that *C. vialis* is an acceptable but little utilized foodplant.
Previous mention was made of the apparent unsuitability of commercial monocephalic varieties of sunflowers for proper development of *adjutrix* larvae. A recent study of cultivated sunflower plots (Phillips et al., 1973) revealed a peak abundance of 1980 larvae per acre (with 40,000 plants/acre). This figure is only one larva for each 20.2 plants and would involve no more than three to seven egg masses. Of all lepidopteran species collected, *adjutrix* was the least abundant and was not discussed within the text of the report. This unsuitability of a cultivated form when compared to a wild weedy form is opposite that reported for *Papilio polyxenes* (Erickson, 1975).

The "rarely utilized foodplant" initially reported as "Silphium sp." (Neck, 1973) has been identified as *Silphium asperrimum* Hook. (see table 1).

Several publications were omitted from the "Literature Cited" section of the previous paper, i.e. Dethier, 1959; Kendall, 1964; Remington, 1952; Remington and Pease, 1955; Straatman, 1962. These articles are listed in the bibliography at the end of this publication.

NEW LARVAL FOODPLANTS

Four additional plant species are now known to be larval foodplants for *adjutrix*.

R. O. Kendall (pers. comm.) found larvae on *Silphium albi- florum* Gray on 4 April 1968 in Terrell County (14 km W. of Dryden), Texas.

On 20 August 1973 a larval brood was observed feeding on garden grown specimens of the native *Helianthus maximiliani* Schrad. in downtown Austin (two blocks from the state capitol building). Previous years of observation of this plant under natural conditions had revealed no larval infestations. Utilization of these plants apparently resulted from lack of suitable foodplants in an urban environment. Additionally, other foodplants in natural habitats at this time were in dessicated condition due to summer drought; *H. annuus* plants were in poor shape and *V. encelioides* had not yet become lush as yet due to lack of rain.

Infestation of Jerusalem artichoke, *Helianthus tuberosus* L., has been observed in a residential area of Austin. Larvae of two generations (15 June and 14 July 1975) were found on several plants. Other *adjutrix* larvae were located on *H. annuus* concurrently with both instances of *H. tuberosus* infestations (only
ten meters separated the two sites). *H. tuberosus* plants, however, were downwind and visually screened (by an eight-foot privacy fence) from the *H. annuus* plants. Oviposition on *H. tuberosus* by *adjutrix* occurred as the result of "random" flight by *adjutrix* females rather than a directed attraction away from the *H. annuus*. Of further interest was the absence of any *adjutrix* larvae on numerous individuals of *H. maximiliani* which were also present in the same yard as the *H. tuberosus*.

*H. tuberosus* is not native to the Austin area. The nearest native occurrence is in north Texas some 400 kilometers NNE of the Austin area. In a study of *Chlosyne gorgone* (Hüber) in Kansas, O. R. Taylor (personal communication) found that *H. tuberosus* was the third most frequently utilized larval foodplant (after *H. annuus* and *A. trifida*). Possibly, *H. tuberosus* would be a significant larval foodplant of *adjutrix* if it occurred naturally within the resident geographical range of *adjutrix*. Both *tuberosus* and *maximiliani* are members of the section Divaricati, *maximiliani* in Gigantei (see Heiser et al 1969).

*H. petiolaris* is a member of the section Annui which includes the previously reported foodplants *annuus*, *argophyllous* and *cucumerifolius* (Heiser et al, 1969). Members of this section appear to be particularly suitable for *adjutrix* larvae although no adult oviposition has been observed on *H. argophyllous*. The highly pubescent nature of the leaf surfaces of *H. argophyllous* may not provide sufficient ovipositional cues despite the presumed phytochemical resemblance to other related species of *Helianthus*, especially *H. annuus*.

**ADDITIONAL LITERATURE RECORDS**

Several additional literature records of larval foodplants of *adjutrix* have been located (references from California to extreme western Texas refer to the subspecific taxon *crocale* Edwards). Larvae were reported on *Xanthium strumarium* L. (as *X. canadense* Mill.) around Blythe, California (Comstock and Dammers, 1935). Later, Comstock (1946) reported larvae "may be found in the fall throughout the Imperial and Coachella Valleys" on *H. annuus*. Cockerell (1941) reported that "larvae abound on sunflowers" (*H. annuus*) in southern New Mexico and northern Mexico.

Bauer (1975) reported that larvae feed on *Grindelia microcephala* DC. This record originated from an observation by R. O. Kendall (personal communication). Kendall (in litt.) has
informed me that this report is unverified; thus, this species is not accepted as a valid foodplant record at this time. *G. microcephala* is a member of the tribe Astereae (same as *Heterotheca* which is known as *adjutrix* foodplant only by cross-over larvae); therefore, *G. microcephala* is unlikely to be a widely-used foodplant of *adjutrix*.

**ACKNOWLEDGEMENTS**

For personal communication of information utilized in this report, I wish to thank P. Chavez, R. O. Kendall and D. H. Riskind.

**LITERATURE CITED**


TABLE 1.

Larval foodplants of *Chlosyne lacinia* var. *adjutrix* (Scudder) in central Texas with additional data not reported in Neck (1973); Nomenclature from Correll and Johnston (1970).

I. Major Foodplants

1. *Helianthus annuus* L.
2. *Verbesina encelioides* (Cav.) Gray
3. *Ambrosia trifida* L.

II. Occasional Foodplants

4. *Verbesina virginica* L.
5. *Viguiera dentata* (lav.) Spreng.

III. Rarely Utilized Foodplants

8. *Ambrosia artemesiifolia* L.
9. *Parthenium hysterophorous* L.
10. *Helianthus argophyllous* L.
11. *Xanthium strumarium* L.
17. *Helianthus maximiliani* Schrad.
18. *Helianthus tuberosus* L.
DESCRIPTIONS OF A NEW SPECIES OF EUPITHECIA AND THE MALE OF E. COCOATA PEARSALL (GEOMETRIDAE)¹

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ABSTRACT

A new species, Eupithecia peckorum, is described from Missouri belonging to the palpata species group. The male of E. cocoata Pearsall also is described revealing this species to be the first Nearctic representation of its species group.

INTRODUCTION

These findings are the result of a thesis reviewing the Larentiinae of Missouri. Eupithecia cocoata Pearsall (1908) was described from a single female specimen from Plummer’s Island, Maryland. This species has not since been recorded until now. A series of six specimens from Missouri and Arkansas reveals two males with unusual genitalic structure. The laterally bifurcate uncus is unique among the Nearctic fauna introducing a new species group for the region. Its closest ally appears to be E. haworthiata Dbd., a Palearctic species.

The new species is known exclusively from three vernal specimens taken in Independence, Missouri over an eight year period. This is apparently a univoltine species, which is typical for Missouri Eupithecia. It inhabits a sparsely forested environment. The wings and the genitalia show unique characters and cannot be confused with any other species.

Eupithecia cocoata Pearsall

Plate I: Figs. 4,5,6. Plate II: Fig. 8

MALE: Head: Eyes black; vertex heavily gray and brown scaled with slightly raised scales anteriorly, followed by a thin row of erect bristles (chaetosemas) and very small pale scales, and posteriorly with a collar of erect larger scales; frons with closely appressed, gray scales, extending a bit and turning brown at the

¹Contribution from the Missouri Agricultural Experiment Station, Entomology Research Museum, Journal Series No. 7712. Approved by the Director. Received for publication 22 Nov. 1976.
²Research Assistant and Professor of Entomology, respectively.
base of the proboscis; pilifers and proboscis finely pubescent with a few fine hairs, labial palps moderate in length (about diameter of eye), broad and down-curving with thick gray scaling; antennal base gray-scaled, segments as wide as long, with fine ventral and lateral hairs (about one-third length of segment in size), dorsum with gray scales.

Thorax: Patagia with broad, gray scales; tegulae extending beyond base of hindwing, with gray and brown scales and pencils; dorsum covered by small gray and brown scales; venter thickly scaled with white, gray, and brown scales, predominantly light colored; forelegs gray with some tarsal banding with lighter scales, middle and hind legs pale gray.

Abdomen: More thickly scaled and darker, with predominantly gray and some brown scales.

Wings: Length of fore wing: 11 mm. Dorsal surface: Fore wings, ground color gray with some faint, brown, wavy, thin lines; two very obscure premedial lines; medial line leaving costa obliquely into discal spot, continuing faintly and obliquely towards body to inner margin; medial line mirrored by three more identical lines distally; subterminal line thicker but faint. Hind wings, ground color gray with brown, wavy, thicker lines, more prominent than those on forewings but still faint; lines darker toward inner margin; antemedial line present; medial line passing thru discal dot; three more distally located lines present, homologies uncertain. Ventral surface: Identical to dorsum but lines and ground color fainter. Terminal lines of all wings dark; fringe alternating gray and brown hairs.

Genitalia: Uncus laterally bifurcate and well formed; tegumen large and rounded posteriorly, with long setae laterally; transtilla weakly formed; labidal arms and feet normally developed; labidal pads of most common shape, with hairy bases and tips, rest naked; labidal papillae abnormally long and stout (at least one-half size of pads), tipped with fine hairs; juxta normal; saccus normal; valve broad and without processes; costa with setae on its entire length; valvula rather thickly haired and naked proximally; sacculus with a few fine hairs; aedeagus relatively large, thickly spiculate at its opening and pointed, vesica with numerous sclerotizations; ninth segment with hair pencils; ventral plate with base broad and weakly bilobed, tapering at mid-length into two thin arms.

SPECIMENS: Two males from Blue Springs State Park, Washington Co., Arkansas: 3 May 1969 and 4 June 1971 at UV light (R. L. Heitzman); three females from same locality: 29 May
1966, 16 April 1967, and 3 May 1969 at UV light (J. R. Heitzman); one female from Sarcoxie, Jasper Co., Missouri, 16 May 1972 at UV light (J. R. Heitzman).

LOCATION OF SPECIMENS: The described male will be deposited in the United States National Museum, Washington, D. C. where the female type is located, and one female in the Entomology Museum of the University of Missouri, Columbia. The remaining specimens will be retained by the senior author.

*Eupithecia peckorum* sp. nov.

Plate I: Figs. 1,2,3. Plate II: Figs. 7,9,10

**MALE:** Head: Eyes black; vertex heavily brown-scaled, with slightly raised scales anteriorly, followed by thin row of erect bristles (chaetosemas), and posteriorly with a collar of erect, larger scales tipped with dark brown; frons with brown, closely appressed, scales in medial area, scales dark brown and longer near eyes and base of proboscis; pilifers and proboscis finely pubescent, thinly arrayed with longer hairs; labial palps extremely long and up-curving (about twice diameter of eyes), thin but heavily scaled with short and long dark brown tipped scales; antennal base completely scaled, antennae bifasciculate with segments slightly longer than wide, thick patches of fine hairs arising most prominently from two ridges on the ventral surface of each segment (about one-half length of segment in size), dorso-lateral surface covered by dark and light brown scales.

Thorax: Patagia with broad, long, brown scales; tegulae reaching base of hind wing and brown-scaled; dorsum covered with small scales; venter thickly covered with light brown scales and some intermittent darker scales; forelegs light with some dark banding, middle and hind legs evenly light brown.

Abdomen: More darkly and thickly scaled with variations in shading.

Wings: Length of fore wing: 9 mm. Dorsal surface: fore wings, ground color red brown, with dark brown lines; basal line complete and bowing distally; antemedial line arising at one-third length of costa and jutting perpendicular to body for a short distance towards discal dot then abruptly angling down towards body to inner margin; a very obscure medial line arising from inner margin but incomplete and difficult to follow; postmedial line prominent, arising at two-thirds length of costa, curving distally at beginning but quickly straightening and
fading as it nears inner margin; subterminal line represented by weak series of pale dots encased in dark, transverse dashes, final dash near inner margin enlarged and suffused into postmedial line. Hind wings, antemedial and postmedial lines continuing into hind wings but not as dark; basal, medial and subterminal lines vague; discal dot present; ground color same as fore wing but lightened at costal and basal areas. Ventral surface: Fore wings, ground color pale brown; costa dark brown to antemedial; antemedial line very weak; discal dot present; medial line obscure; postmedial line strong and fading before inner margin; subterminal line weak. Hind wings, ground color same as fore wing; antemedial weak; medial obscure; discal dot present; postmedial line strong and complete; subterminal obscure. Terminal lines of all wings dark brown; fringe alternating dark and light brown hairs.

Genitalia: Structures typical of *palpata* group; tegumen with extremely long setae; transtilla thickened centrally; labidal arms and feet well developed; labidal pads regularly haired by minute setae; labidal papillae very small and tipped with small hairs; saccus well developed; costa straight and only slightly thickened medially, displaying several very long setae; valvula with scales on its anterior edge, remainder heavily haired with a long tuft of hairs proximally; sacculus with patch of setae, some very long at its base; aedeagus centrally curved and slightly narrowed in the middle, vesica with an extensive array of complex sclerotizations; ninth segment without pencils; ventral plate with bowed, stout arms recurving distally, tips pointed ventrally and rounded laterally, anterior portion or base well sclerotized with its shape typical of the species group.

FEMALE: Same as male, except antennae not bifasciculate and hairs smaller; fore wing length 10 mm, antemedial line angled more towards body, discal dot very vague; all lines on venter of wings more pronounced.

Genitalia: Ovipositor and apophyses typical of group; ostium narrower than ductus bursae; cervix bursa far removed from ductus seminalis which is atypical for the group; ductus seminalis normally shaped; bursa copulatrix spherical in shape and almost entirely embedded with spines.

ETYMOLOGY: We take pleasure in naming this species for Dr. and Mrs. William B. Peck of Central Missouri State University, Warrensburg. Dr. Peck is a well known araneologist and friend of the authors.

TYPES: Holotype, male, Independence, Jackson Co., Missouri,
19 April 1971 at UV light (R. L. Heitzman); allotype, same locality, 17 April 1963 at UV light (J. R. Heitzman); paratype, one male, data and collector same as allotype.

TYPE LOCALITY: City limits of Independence, Jackson Co., Missouri, in sparsely forested and disturbed habitat.

LOCATION OF TYPES: The holotype and allotype will be deposited in the type collection of the United States National Museum, Washington, D.C. The paratype will remain in the senior author's collection.

DISCUSSION

Only one other Nearctic form, *E. longidens kerrvillaria* Cassino and Swett (1924), approaches *peckorum* in appearance. The former is a light brownish-gray, the lines arise further distally on the fore wings with the subterminal line plain, and the distal dot prominent on the female. The bursa, aedeagus, valve and ventral plate, however, vary quite radically from *peckorum*. The ventral plate of *peckorum* most closely resembles that of *E. pseudotsugata* MacKay, but with the arms bowing more and the apices not so hooked and pointed. The bursa is quite unique and cannot be readily compared with any other species.

ACKNOWLEDGEMENTS

We wish to thank Dr. Douglas C. Ferguson for his comparison of a specimen of *E. cocoata* series with the type in the United States National Museum, Washington, D.C., U.S.A. and his comments on the new species, and also, Dr. Klaus Bolte of the Biosystematics Research Institute, Ottawa, Ontario, Canada and Dr. D. S. Fletcher of the British Museum (Natural History), London, England for comments on and examination of illustrations of the genitalia. Also, thanks are extended to Mr. Paul Szopa of the University of Missouri, School of Forestry, Fisheries and Wildlife for making photographic prints of the adults.

LITERATURE CITED


Figs. 1-3.— *E. peckorum* n.sp. (holotype male). 1, clasping unit; 2, aedeagus; 3, eighth sternite.
Figs. 4-6.— *E. cocoata* Pearsall (male). 4, eighth sternite; 5, aedeagus; 6, clasping unit.
Fig. 7.— *E. peckorum* n.sp. (allotype female), bursa, ventral view.
Fig. 8.— *E. cocoata* Pearsall, male.
Fig. 9.— *E. peckorum* n.sp., holotype.
Fig. 10.— *E. peckorum* n.sp., allotype.
AUTUMNAL FALSE BROODS OF MULTIVOLTINE BUTTERFLIES
AT DONNER PASS, CALIFORNIA

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The phenomenon of autumnal “false broods” produced by multivoltine “weedy” butterflies under warm, settled weather conditions has been documented in the northeastern United States (Shapiro 1962, 1967, 1970) and is well known to local collectors in many parts of North America and Europe. It has not been previously recorded at high elevations in mountainous regions, however. Donner Pass, at roughly 7000 feet in the high montane-subalpine Sierra Nevada of north-central California, would seem an unlikely place to look for it. The climate of the Pass has been vividly described by Emmel and Emmel (1963): “Snowmelt occurs in early June while snow flurries can be expected in early September. Sandwiched between nine months of winter—spring, summer and fall in the Donner Pass area must pass rapidly in succession . . . flight or growth seasons are measured in weeks instead of months.” The Donner Pass winter has earned its place in the history and folklore of the West. The Donner Party arrived at the Pass on 1 November, 1846 and found the snow already five feet deep. Storm after storm added to that total, raising it to eight feet on the level by 13 December (Stewart, 1959). Neither Emmel and Emmel nor Stewart, however, pointed out that Sierran winters vary enormously in their timing and their severity. Since 1972, I have conducted phenological studies of the butterfly faunas of several localities along a transect paralleling Interstate Highway 80, from sea level at Suisun Bay to 7000 feet in Donner Pass (Shapiro, 1975a). From these studies, it has become apparent that the native fauna of the Pass is mostly univoltine and seasonally conservative, but such is not the case with “weedy” species occurring over a wide altitudinal range and characterized by high vagility and developmental flexibility. Under appropriate autumn conditions, these species will continue to emerge and to breed. It is thus not at
all unusual to find butterfly species which do not hibernate as adults flying in Donner Pass in October and in some years into November.

In 1975, 29 species of butterflies were flying in my Donner study area on 30 September. This rather large number reflected the general lateness of the season due to a cold, wet spring and several cold summer storms. The first snow of the season, an inch, fell on 7 October with eight more inches on 10 October and another eighteen inches by the 12th. However, it warmed rapidly, with afternoon highs in the 60s F and lows near freezing, and by 19 October the snow was gone except on north-facing slopes; five species were flying—*Colias eurytheme* and *Pieris rapae*, both “weedy” non-hibernators, and *Nymphalis californica*, *Vanessa virginiensis*, and *Polygonia zephyrus*, all hibernators. In addition, I noted three species of grasshoppers, various Diptera (*Tachinidae*, *Muscidae*, *Syrphidae*) and Hymenoptera, spiders, four species of mammals, three of birds, and two of lizards; the mid-afternoon temperature was 64°F. After a much colder but snowless interval, it warmed again in early November and I returned on 4 November (temperature again 64°F) and saw one individual each of *C. eurytheme*, *P. rapae*, and *Vanessa caraye*.

The 1976 season was very advanced; the snow pack was far below normal and was nearly gone by late April. Most species emerged and disappeared several weeks earlier than in 1975, and by 4 October only 12 species were flying. Continued warm weather produced late emergences of multivoltines and also encouraged altitudinal dispersants, so that 15 species were flying on 15 October with a mid-afternoon temperature of 68°F. On 3 November, in 66° weather, six species were still flying: *Pieris rapae*, *P. protodice*, *Colias eurytheme*, *Plebeius acmon*, and *Pyrgus communis*, all “weedy” non-hibernators, and *Precis coenia*, an immigrant from lower elevations (Shapiro, 1973, 1974). On 10 November, with 60° and variable cloudiness, six species were again recorded: *P. rapae*, *P. protodice*, *C. eurytheme*, *P. acmon*, *P. coenia*, and the hibernator *Vanessa virginiensis*. The butterflies were visiting widely scattered blossoms of *Aster*, *Monardella*, and dandelion (*Taraxacum*). On 14 November a foot of snow fell in the Pass, but immediately thereafter warm, stable conditions returned with daily highs in the 60s and lows in the upper 20s to low 30s. On 20 November, with afternoon temperatures from 63-66°F, snow remained only locally, mostly on north-facing slopes. Five species were recorded: *P. protodice* and *C. eurytheme* (the latter common) and three Nymphalids,
presumably hibernators: *V. virginiensis*, *V. carye*, and *Polygonia zephyrus*. Plants recorded in bloom included species of *Potentilla, Achillea, Aster, Solidago, Tragopogon, Taraxacum, Matricaria, Cirsium, Erodium, Sidalcea, Wyethia, Phacelia, Castilleja*, and *Chrysothemnus*. Two species of grasshoppers, Muscid, Syrphid, and Tachinid flies, bumblebees, spiders, and one species of bird were seen, along with black bear tracks in the snow. *Colias* visited *Aster* and *Taraxacum* and were seen flying from 1220 to 1510 hours. Twenty *C. eurytheme* were collected: 12 males, 4 orange females and 4 white females, of which one white was very worn and the other specimens all more or less fresh; one male was soft-winged. The abundance of *C. eurytheme* was probably an accident of seasonal timing; the first spring records (flyups from the east?) were on 14 May, a month earlier than usual; an entire additional generation may have been reared in the Pass in 1976, providing a large reservoir of hatchable autumn pupae. The "rock garden" habitats of characteristic univoltine spring species such as *Incisalia "fotis" windi*, *Callophrys lemberti*, and *Plebeius lupini* were visited but were devoid of butterfly activity.

The probability of successful reproduction by late-emerging multivoltines at Donner Pass is so low that one must assume natural selection would operate against such "mistakes," constantly perfecting diapause-induction systems. That, however, presupposes the existence of resident overwintering populations there. In the case of *P. protodice* and *P. acmon* that supposition is almost certainly false. *C. eurytheme* seems to overwinter only sporadically. Of the "weedy" multivoltines, only *P. rapae* (Shapiro, 1975b) seems to be a permanent resident, but it also has a temperature-photoperiod system for induction of pupal diapause which would limit the amount of wasted fall development. The occurrence of autumnal "false broods" in so difficult an environment as Donner Pass underscores the poor adaptation of "weedy" multivoltine species to cold climates, the ephemeral nature of their populations there, and their contrast with the native montane, subalpine, and alpine fauna, which is "obligately" univoltine under realistic environmental regimes.

ACKNOWLEDGMENTS

This research was supported in part by grant D-804 from the Committee on Research, U. C. Davis. It has also benefitted from remarks made by students and associates to the effect that
anyone taking a butterfly net to Donner Pass after Labor Day must be crazy, thereby obliging me to do it.

LITERATURE CITED


10. Pinus-Quercus Associes of the Deciduous Woodland

**INDICATOR SPECIES**

- Chlosyne definita (1)
- Callophrys leucania (1)
- Thecla augustula (1)
- Thecla gabatha (1)
- Thecla clarina
- Thecla denarius

**CHARACTERISTIC SPECIES**

- Papilio thoas autocles
- Phoebis agarithe maxima
- Phoebis philea
- Phoebis sennae marcellina
- Eurema d. daira
- Eurema mexicana
- Eurema lisa
- Eurema nise nelphe
- Euptitychia gemma freemani
- Euptitychia mollina
- Euptitychia gigas
- Actinote guatemalena
- Thessalia t. theona
- Junonia evarete
- Euptoieta hegesia hoffmanni
- Mestra amymone

**11. Littoral Woodland**

**INDICATOR SPECIES**

- Anaea morcus boisduvali

**CHARACTERISTIC SPECIES**

- Papilio thoas autocles
- Parides p. polyzelus
- Colias cesonia
- Phoebis sennae marcellina
- Phoebis argante
- Phoebis agarithe maxima
- Eurema albula
- Eurema mexicana
- Eurema lisa
- Eurema nise nelphe
- Eurema proterpia
- Eurema nicippe
- Eurema dina westwoodi

- Strymon melinus
- Hemiargus i. isola (1)
- Baeotes hisbon zonata
- Symmachia tricolor hedemanni
- Isapis agyrtus hera (1)
- Anatole rossi

- Hamadryas februa gudula
- Hamadryas feronia farinulenta
- Hamadryas g. guatemalena
- Limenitis iphicla
- Libytheana carinenta mexicana
- Eumaeus minyas
- Calycopis beon
- Electrostrymon cyphara
- Strymon yojoa
- Thecla bre西亚
- Hemiargus ceraunus zachaeina
- Hemiargus huntingtoni hannoides
- Everes c. comyntas
- Leptotes cassius striata
- Mesene croecela
- Peplia lamis molpe

- Morpho peleides montezuma
- Agraulis vanillae incarnata
- Dryas julia moderata
- Heliconius cleoabae zorcaon
- Heliconius ismenius telchincia
- Heliconius charitoniaz vazquezae
- Heliconius petiveranus
- Anartia jatrophae luteipicta
- Anartia fatima venusta
- Biblis hyperia aganisa
- Hamadryas februa gudula
- Hamadryas ferronia farinulenta

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Ascia m. monuste  Marpesia chiron
Anteos clorinde    Limenitis iphica
Anteos maerula     Limenitis paraeca
Euptychia hesione  Eumaeus minyas
Euptychia hermes sosybius Calycoptis beon
Caligo memnon      Hemiarus ceraunus zachaeina
Melinaea lilis imitata Everes c. comyntas
Mechanitis polynnia lycidice Peplia lamis molpe
Mechanitis egaensis doryssus

12. Swamp Forest

INDICATOR SPECIES
  Thecla ant incus (1)  Eurybia lycisca (2)

CHARACTERISTIC SPECIES
  Dimorphia fortunata  Euptychia metaleuca
  Eurema albula       Euptychia themis
  Eurema dina westwoodi Euptychia hermes sosybius
  Tithorea harmonia salvadoris Euptychia libye
  Melinaea lilis imitata Caligo memnon
  Mechanitis polynnia lycidice Morpho peleides montezuma
  Mechanitis egaensis doryssus Heliconius cleobaea zorcaon
  Mechanitis menapis saturata Heliconius ismenius telchinia
  Hypothyris lycaste dionaea Heliconius petiveranus
  Ithomia patilla     Heliconius charitonius vazquezae
  Oleria paula        Pyrrhogyra hypensor
  Dircenna klugi      Pyrrhogyra otolais neis
  Pteronymia cottyto  Hamadryas februa gudula
  Greta oto           Hamadryas feronia farinulenta
  Greta nero          Hamadryas g. guatemalena
  Taygetes andromeda  Calycoptis beon
  Euptychia hesione   Thecla marysas damo

13. Mangrove Woodland

INDICATOR SPECIES
  None.

CHARACTERISTIC SPECIES
  The same as those for the Swamp Forest.

14. Recently Abandoned Milpas

INDICATOR SPECIES
  Tmolus echion echiolus (1)  Mesene margaretta
  Thecla ares (1)
### CHARACTERISTIC SPECIES

<table>
<thead>
<tr>
<th>Species</th>
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<tr>
<td>Papilio thoas autocles</td>
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<td>Appias drusilla poeyi</td>
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<td>Dryas julia moderata</td>
<td>Hemiargus ceraunus zachaeina</td>
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<td>Euptoieta hegesia hoffmanni</td>
<td>Hemiargus huntingtoni hannahoides</td>
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<td>Chlosyne janais</td>
<td>Everes c. comyntas</td>
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<td>Chlosyne l. lacinia</td>
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<tr>
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<td>Peplia lamis molpe</td>
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15. Pastures

### INDICATOR SPECIES

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<td>Prepona laertes pallantias (2)</td>
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<td>Anaea marthesia (2)</td>
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<td>Callophrys goodsoni (1)</td>
<td>Anatole agave (1)</td>
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<td>Atlides polybe</td>
<td>Theope eleutho</td>
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CHARACTERISTIC SPECIES

Papilio thoas autocles  Phyciodes claudina guatemalena
Appias drusilla poeyi  Phyciodes a. ardys
Ascia m. monuste  Phyciodes myia
Colias cesonia  Phyciodes griseobasolis
Phoebis sennae marcellina  Anartia jatrophae luteipicta
Phoebis philea  Anartia fatima venusta
Phoebis argante  Dynamine mylitta
Phoebis agarithe maxima  Hamadryas februa gudula
Eurema boisduvaliana  Hamadryas g. guatemalena
Eurema mexicana  Marpesia chiron
Eurema proteropia  Limenitis paraeca
Eurema lisa  Anaea aidea
Eurema nise nelphe  Calycopis beon
Eurema dina westwoodi  Strymon yooja
Eurema nicippe  Heterosmaitia palegon
Danaus gilippus strigosus  Thecla marsyas damo
Euptoieta hermes sosybius  Thecla meton
Dryas julia moderata  Thecla tephraeus
Euptoieta hegesia hoffmanni  Hemiargus cerainus zachaeina
Chlosyne janais  Hemiargus huntingtoni
Chlosyne l. lacinia  hannoides
Thessalia t. theona  Everes c. comyntas
Phyciodes vesta  Leptotes cassius striata
Phyciodes frisia tulcis  Peplia lamis molpe

16. Hedgerows

INDICATOR SPECIES

Callophrys miserabilis (2)  Thecla hassan (1)
Panthiades ochus (1)  Thecla hesperitis (1)
Thecla neora (1)  Thecla demonassa (2)
Thecla barajo (2)  Thecla ambrax (1)

CHARACTERISTIC SPECIES

Graphium e. epidaus  Anartia jatrophae luteipicta
Papilio thoas autocles  Anartia fatima venusta
Parides p. polyzelus  Metamorpha stelenes biplagiata
Eurema albula  Biblis hyperia aganisa
Eurema dina westwoodi  Dynamine mylitta
In addition, the data indicate that a second division—less pronounced than the first but nonetheless significant—can be made. A comparison of the formations at relatively low altitudes indicates that the greatest diversity occurs between the species in the Lower Montane Rain Forest and the remaining formations. Indeed, 24 species (13 indicator, 11 characteristic) occur commonly only within the Lower Montane Rain Forest. This “uniqueness” is approached by only one other formation, the Semi-Evergreen Seasonal Forest, which has 25 species (23 indicator, two characteristic) found commonly only within its borders. Thus, a line separating the Lower Montane Rain Forest from all other formations at relatively low elevations can be drawn.

In conclusion, my analysis of the butterfly fauna has led me to the opinion that the classification system employed by Andrle (1964) does not reflect accurately the existing relationships (at least for butterflies) but that the system originally expressed by Goldman (1951) is more applicable. Following the system employed by the latter, I divide the Sierra into two major zones: first, a Lower Tropical Zone, subdivisible into a Humid Lower Tropical Subzone (corresponding to the Humid Tropical Upper Subzone of Andrle), and an Arid Lower Tropical Subzone (corresponding to the Arid Tropical Zone of Andrle); and second, an Upper Tropical Zone, nondivisible and corresponding to
the Humid Tropical Upper Subzone of Andrle. These zones and subzones are defined and characterized in Table III.

**BIOTIC PROVINCE**

The concept of the Biotic Province, originated by Vestal (1914) and developed by Dice (1943), by definition dictates that the entire Sierra de Tuxtla fall within only one category. This, according to Goldman (1951) and Goldman and Moore (1945) is the Veracruz Biotic Province, which "embraces the tropical lowlands from eastern San Luis Potosí, southern Tamaulipas, and northeastern Puebla, southwesterly through Veracruz and Tabasco and small portions of northern Oaxaca and Chiapas." However, I question the validity of including the Sierra within the "tropical lowlands" of Veracruz since the majority of the land surfaces within the range have an average elevation in excess of 1,000 feet and four volcanoes have maximum elevations in excess of 3,000 feet. Furthermore, most of the flora and fauna found at elevations in excess of 2,500 to 3,000 feet seem to have their affinities with forms common farther south. I conclude, therefore, that a new biotic province should be erected for the Sierra de Tuxtla.

**TABLE III**

**LIFE ZONES AND CORRESPONDING PLANT FORMATIONS IN THE SIERRA DE TUXTLA**

I. **Lower Tropical Zone.**—This zone is located from sea level to approximately 2,500 to 3,000 feet in altitude and probably receives an average annual rainfall of less than 150 inches. The zone is divisible into two subzones.

   A. **Humid Lower Tropical Subzone.**—This subzone is found principally on the Gulf slopes of the major volcanoes below 2,500 to 3,000 feet where the average annual rainfall probably averages between 150 and 110 inches. Only one plant formation—Lower Montane Rain Forest—is included in this subzone.

   B. **Arid Lower Tropical Subzone.**—This subzone is found principally along the coast and on the leeward slopes of the
major volcanoes below 2,500 to 3,000 feet, areas in which the average annual rainfall probably is less than 110 to 100 inches. This subzone includes the following plant formations:

- Littoral Woodland
- Mangrove Woodland
- Swamp Forest
- Savanna
- Deciduous Woodland and the *Pinus-Quercus* Associes
- Semi-Evergreen Seasonal Forest and the *Bursera-Sabal-Orbignya* Associes

II. *Upper Tropical Zone.*—This zone is located from approximately 2,500 to 3,000 feet in altitude to the peaks of the principal volcanoes (3,750 feet, 5,250 feet, and 5,450 feet for Volcán San Martín Pajapan, Santa Marta, and San Martín Tuxtla, respectively) where the average annual rainfall probably is in excess of 150 inches. This zone includes the following plant formations:

- Montane Rain Forest (the *Liquidambar-Quercus* Associes being an ecotone)
- Montane Thicket
- Elfin Woodland

Because the “Miscellaneous Formations” (Recently Abandoned Milpas, Pastures, and Hedgerows) occur throughout the Sierra where man has settled, I have not assigned these to any life zone.

AREAL DISTRIBUTION

Faunal-Floral Relationships

A total of 359 species of butterflies representing 133 genera and eight families now have been recorded from the Sierra de Tuxtla. Of these species, 258 (72%) are found primarily in open and relatively open plant formations throughout the range, and for the most part were collected in fields, pastures, and along hedgerows and the margins of forests. In general, members of the Lycaenidae and Riodinidae visit the blossoms of *Cordia spinescens* and *Calliandra grandiflora* very frequently; members of the genera *Hamadryas*, *Historis*, *Smyrna*, *Gynaecia*, *Prepona*, and *Anaea* (*Nymphalidae*) are attracted to fermenting sap oozing from the trunks of citrus trees and to fermenting juices of fallen fruit (principally mangoes); members of the genera *Papilio*, *Graphium* (*Papilionidae*), *Colias*, *Anteos*, *Phoebis*, *Eurema* (*Pieridae*), *Chlosyne*, *Phyciodes*, *Diaethria*, *Dynamine*, *Marpesia* (*Nymphalidae*), *Hemiargus*, *Leptotes*, and *Everes* (*Lycaenidae*) visit flowers (and damp earth) indiscriminately.
The interiors of forests with closed canopies are inhabited by a minority of butterfly species (101 species, 28% of total species). These species belong to 53 genera, 13 subfamilies and eight families and are listed in Table IV. From this table, certain correlations can be made. First, approximately 41% of the butterfly species inhabiting the forests of the Sierra de Tuxtla belong to the families Ithomiidae and Satyridae. Second, all members of the family Ithomiidae and the subfamily Lycoreinae (Danainae) occur within forests. Third, more than half the members of the Pierinae (five species, 55%) and Dismorphiinae (four species, 66%), (Pieridae), Satyrinae (19 species, 83%) and Brassolinae (three species, 60%) (Satyridae), and Amathusinae (two species, 66%) (Nymphalidae) are found within forests. Fourth, relatively few species in the Lycaenidae (10 species, 11%) and the Riodinidae (13 species, 27%) occur within forests.

**TABLE IV**

**GENERAE OF BUTTERFLIES COLLECTED IN THE SIERRA DE TUXTLA WITHIN FORESTS WITH CLOSED CANOPIES**

(Numbers behind genera indicate number of species involved; numbers behind subfamilies indicate total number of species collected.)

A. Genera in which all species occur within forests

- *Catasticta* (1) Pieridae:Pierinae (9)
- *Archonias* (1) Pieridae:Pierinae
- *Itaballia* (3) Pieridae:Pierinae
- *Tithorea* (1) Ithomiidae:Ithomiinae (20)
- *Melininae* (1) Ithomiidae:Ithomiinae
- *Mechanitis* (3) Ithomiidae:Ithomiinae
- *Hypothyris* (1) Ithomiidae:Ithomiinae
- *Napeogenes* (1) Ithomiidae:Ithomiinae
- *Ithomia* (2) Ithomiidae:Ithomiinae
- *Hyposcada* (1) Ithomiidae:Ithomiinae
- *Oleria* (2) Ithomiidae:Ithomiinae
- *Aeria* (1) Ithomiidae:Ithomiinae

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B. Genera in which half or more species occur within forests

Parides (5) Papilionidae:Papilioninae (21)
Dismorphia (4) Pieridae:Dismorphiinae (6)
Taygetes (4) Satyridae:Satyrinae (23)
Euptychia (12) Satyridae:Satyrinae
Morpho (2) Nymphalidae:Amathusiinae (3)
Epiphile (1) Nymphalidae:Nymphalinae (90)
Catonephele (1) Nymphalidae:Nymphalinae
Calycopis (2) Lycaenidae:Lycaeninae (88)
Euselasia (4) Riodinidae:Euselasiinae (6)

C. Genera in which less than half the species occur within forests

Graphium (2) Papilionidae:Papilioninae (21)
Eurema (3) Pieridae:Coliadinae (22)
Heliconius (1) Nymphalidae:Heliconiinae (17)
Chlosyne (1) Nymphalidae:Nymphalinae (90)
Phyciodes (1) Nymphalidae:Nymphalinae
Limenitis (1) Nymphalidae:Nymphalinae
Prepona (2) Nymphalidae: Nymphalinae
Anaea (3) Nymphalidae: Nymphalinae
Thecla (4) Lycaenidae: Lycaeninae (88)
Emesis (1) Riodinidae: Riodininae (42)

Although the species in the previously mentioned families and subfamilies share a common habitat type (tropical forest), they nonetheless have different preferred micro-habitats. The ithomids usually are found in dank ravines in nonspecific butterfly assemblages and in the vicinities of four flowering plants: Tournefortia glabra, Eupatorium macrophyllum, E. pittieri, and Psychotria padifolia. The satyrids are more randomly distributed throughout the forests, Taygetes spp., Dioriste tauropolis, Pediloides pisonia circumducta, Eryphanis aesacus, and Caligo spp. preferring montane formations and Euptychia spp. preferring less dense forest formations. The single species of Lycorea (Danaidae: Danainae) is found in relatively open areas within the Semi-Evergreen Seasonal Forest and the Lower Montane Rain Forest and usually in small butterfly assemblages. The five species (three genera) of Pierinae are found in the Lower Montane Rain Forest and the Semi-Evergreen Seasonal Forest and usually within nonspecific butterfly assemblages—Catisticta n. nimbice preferring less dense areas and Archonias tereas and Itaballia spp. preferring more dense and shaded locales. The four species of Dismorphia (Dismorphiinae: Pieridae) prefer the montane formations—D. praxinoe and D. fortunata the Lower Montane Rain Forest and D. euryope and D. nemesis the Elfin Woodland and Montane Thicket. The two species of Morpho (Ama-thusiinae: Nymphalidae) have very dissimilar ecologies—M. polyphemus luna prefers the montane formations above 3,000 feet and M. peleides montezuma prefers the Lower Montane Rain Forest and other forests at relatively low elevations. The ten species (five genera) of lycaenids and 13 species (eight genera) of riodinids are found in a variety of forests; all seem to prefer the relatively bright sections.

ALTITUDINAL DISTRIBUTION

The maximum altitude of the Sierra is relatively low (5,450 feet) and thus vertical temperature change is not great. It is reasonable to assume that the entire Sierra falls within the normal altitudinal range of most butterfly species. (Indeed,
species that are common in sunny fields along the coast and at relatively low altitudes frequently were seen sailing over the peaks of the highest volcanoes on sunny days.) Yet, as stated previously, the greatest diversity in the butterfly fauna occurs between the Upper and Lower Tropical Zones and so the obvious conclusion is that plant formations with their characteristic plants, some of which probably serve as larval and adult food plants, seem to be the principal factor governing butterfly distributions. In general, the majority of the butterfly species (320 species, 89%) in the Sierra are primarily residents of the plant formations below 2,500 to 3,000 feet (the Lower Tropical Zone); only 39 species (11%) are commonly found in the forests above approximately 3,000 feet in elevation (the Upper Tropical Zone).

Climatic Relationships

SEASONAL VARIATION IN BUTTERFLY POPULATION DENSITIES

Although the climate of the Sierra de Tuxtla is relatively mild and uniform, enough diversity exists to produce a noticeable seasonal fluctuation in butterfly populations. In general, populations reach maximum densities in August, September, and October and minimum densities in January, February, March, and April. In fact, many species virtually disappear during the winter and spring months, even at relatively low elevations. Although many species of butterflies are known to migrate to other areas during the winter months (Williams, 1930, 1958), relatively few of these species (17 species, approximately 5%) occur in the Sierra. These are: Graphium philolaus (Papilionidae), Eurema nicippe, E. albula, E. lisa, Phoebis statira, P. trite, P. philae, P. argante, P. sennae, Anteos maerula, Ascia monuste (Pieridae), Agraulis vanillae, Vanessa virginiensis, Junonia evarete, Marpesia chiron (Nymphalidae), Danaus plexippus, and D. gilippus (Danaidae). The majority (59%) of these belong to the family Pieridae.

During my residence in the Sierra, I saw butterfly movements (which possibly could be termed migrations) in July and August involving principally Phoebis spp. and Marpesia chiron. Each day hundreds of individuals were observed as they flew usually between ten and 30 feet above the ground and in a
northeasterly direction toward the Gulf. In addition, during the fall months populations of *Danaus plexippus* and *Vanessa virginiensis* increased, possibly because of an influx of migrants from the north. Therefore, because of the relatively few migrant species (approximately 5%), and because of a population increase during the fall of at least two species (*Danaus plexippus* and *Vanessa virginiensis*), I conclude that migrations are an insignificant factor in the reduction of the winter butterfly populations in the Sierra de Tuxtla.

An alternative and more plausible explanation is that many species undergo an egg, a larval, or pupal diapause during the winter period, possibly as a result of decreased amounts of daylight, reduced temperatures, and reduced rainfall, or, any combination of these. Unfortunately, there is little data to support this hypothesis for I observed diapause (larval) only in one species—*Anatole rossi* (Riodinidae; Ross, 1966).

Although spring-dry season population minima are the general rule, a few exceptions do exist. The seven species of *Graphium* (Papilionidae:Papilioninae), *Dismorphia jethys* (Pieridae:Dismorphiinae), and *Actinote guatemalena veraecrizis* (Nymphalidae:Acraeinae) have maximum population densities in spring and early summer. All of these species disappear subsequent to the commencement of the summer rains. Also, *Morpho theseus justiciae* (Nymphalidae: Amathusiinae) and *Actinote leucomelas* (Nymphalidae:Acraeinae) are common in March and April but then disappear completely only to reappear in September, October, and November. Thus, these last two species seem either to be double brooded and to have relatively lengthy immature stages or to undergo diapause during some stage in their life cycles. *Philaethria d. dido* is common only in the fall months!

**DAILY VARIATIONS IN BUTTERFLY POPULATION DENSITIES**

During any given season, daily cycles in population densities are evident. Generally, most butterfly species are strongly photopositive and reach maximum activity levels between 10:00 A.M. and noon. However, during the periodic cool spells during the winter and on days of heavy cloud cover, maximum activity periods are delayed from one to two hours.
The notable exceptions to the previous generalization are the two species of *Caligo* (Satyridae:Brassolinae), *Eurybia lycisca* (Riodinidae:Riodininae), and all members of the Ithomiidae. The caligos are decidedly crepuscular and frequently wander out of the forest habitats and into more open areas at dusk; the two specimens of *Eurybia lycisca* were collected as they flew in a very dark, dense thicket at 6:30 P.M.; and members of the Ithomiidae are active under practically all weather conditions (including fog and light rain) in addition to practically all hours of daylight (dawn to dusk).

Faunal Relationships

AFFINITIES AND ORIGINS

Although the Sierra has been open to animal and plant movements from the north and the range is sufficiently near the northern limits of the Neotropical region to permit an influx of Nearctic forms, the fauna and flora have remained essentially tropical. In his avi-faunal investigations, Andrle (1964) states that 43% of the avian species recorded in the Sierra have southern origins as compared to 26% with more northern affinities (the remaining percentage represents species with unknown or uncertain origins). Unfortunately, the science of butterfly zoogeography has not advanced to the state whereby the origins and affinities of most genera and species groups can be defined (see Hovanitz, 1958). However, several generalizations, correlations, and speculations can be made about the Sierra's butterflies.

First, of the 359 species representing 133 genera, only 77 species (21%) representing 45 genera (34%) ever have been recorded from within the borders of the United States (references: dos Passos, 1964; Ehrlich and Ehrlich, 1961). These species, which are listed in Table V, for the most part are found in open, sunny areas throughout the Sierra. Furthermore, of these 77 species, 47 (61%) are known to be breeding residents (reference: Klots, 1951); the remaining species, 30 (39%), enter the United States only as occasional strays. Thus, the majority of the species of butterflies in the Sierra (79%) do not occur even as strays just 500 miles to the north.
TABLE V

SPECIES OF BUTTERFLIES COLLECTED IN THE SIERRA DE TUXTLA KNOWN TO OCCUR WITHIN THE BORDERS OF THE UNITED STATES

Papilionidae (5 species, 25% of represented species)
- Battus polydamas
- Parides arca mylotes
- Papilio polyxenes asterius

Pieridae (20 species, 54% of represented species)
- Appias drusilla poeyi
- Ascia m. monuste
- Colias cesonia
- Anteos clorinde
- Anteos maerula
- Phoebis sennae marcellina
- Phoebis philea
- Phoebis argante
- Phoebis agarithe maxima
- Phoebis statira jada

Pieridae (20 species, 54% of represented species)
- Eurema d. daira
- Eurema boisduvaliana
- Eurema mexicana
- Eurema salome
- Eurema proterpia
- Eurema lisa
- Eurema nise nelphe
- Eurema dina westwoodi
- Eurema nicippe
- Nathalis iole

Danaidae (4 species, 100% of represented species)
- Danaus p. plexippus
- Danaus gilippus strigosus
- Lycorea ceres atergatis

Satyridae (2 species, 8% of represented species)
- Euptychia gemma freemani
- Euptychia hermes sosybius

Nymphalidae (31 species, 29% of represented species)
- Dryadula phaetusa
- Agraulis vanillae incarnata
- Dryas julia moderata
- Heliconius petiveranus
- Heliconius charitonius vazquezae
- Euptoieta hegesia hoffmanni
- Chlosyne janais
- Chlosyne l. lacinia
- Chlosyne definita
- Thessalia t. theona
- Phyciodes vesta
- Phyciodes frisia tulcis
- Vanessa virginiensis
- Junonia evarete

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TABLE V (continued)

Nymphalidae (continued)

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<td>Metamorpha stelenes biplagiata</td>
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<td>Hypanartia lethe</td>
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<td>Biblis hyperia aganisa</td>
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<td>Mestra amymone</td>
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<td>Eunica monima</td>
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<td>Dynamine dyonis</td>
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<td>Hamadryas februa gudula</td>
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Lycaenidae (16 species, 21% of represented species)

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<td>Eumaeus minyas</td>
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<td>Tmolus echion echiolus</td>
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<td>Tmolus azia</td>
</tr>
<tr>
<td>Callophrys miserabilis</td>
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<td>Strymon melinus</td>
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Second, of the 133 genera found in the Sierra, 58 (44%) have been recorded in the United States (reference: dos Passos, 1964). These, in addition to the number of species represented in the Sierra, the United States, and the relative number found within the Neotropical regions, are listed in Table VI. An analysis of the data presented in this table reveals that of the 58 genera, only 19 (33%) are represented by a greater number of species in the United States than in the Sierra, and that of these 19, only four (7%)—Colias (Pieridae), Polygonia (Nymphalidae), Vanessa (Nymphalidae), and Callophrys (Lycaenidae)—have a greater representation in the United States (Nearctic region) than in the entire Neotropical region. Lacking additional information, one may assume with some justification that the center of origin of a genus corresponds to the area containing the greatest number of species (Savage, 1958). Thus, I conclude that at least four genera of the 133 (3%) represented in the Sierra probably have Nearctic origins or at least have their greatest affinities with Nearctic forms and that the remaining genera (129, 97%) probably have Neotropical origins or have their greatest affinities with Neotropical forms.
Third, an analysis of the 37 species (excluding new, endemic species) that have not been recorded from the Sierra according to Hoffmann (1940)—10 range extensions within the state of Veracruz, 18 new state listings, and nine new national listings (Table VII)—reveals that 76% of the new listings (all but the 10 intrastate range extensions) are species with known distributions that are farther south than the Sierra. The remaining

TABLE VI
COMPARISON OF BUTTERFLY GENERA COMMON TO THE SIERRA DE TUXTLA, THE UNITED STATES, AND THE NEOTROPICAL REGIONS

<table>
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<th>No. of species in the Sierra de Tuxtla</th>
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<th>Relative no. of species in the Neotropical regions as compared to the Nearctic regions</th>
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<td>Danaus</td>
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<td>Satyridae</td>
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</tr>
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<tr>
<td>Euptoieta</td>
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<td>Phyciodes</td>
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<td>Polygonia</td>
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<td>Junonia</td>
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<td>Biblis</td>
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<td>Mestra</td>
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<td>Myscelia</td>
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</tr>
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<td>Eunica</td>
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<td>Diaethria</td>
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<td>Dynamine</td>
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</tr>
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<td>Marpesia</td>
<td>4</td>
<td>4</td>
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<td>7</td>
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<td>Chlorippe</td>
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<td>Historis</td>
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<td>Anaea</td>
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**Lycaenidae**

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<td>Tmolus</td>
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<td>Callophrys</td>
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</tr>
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</tr>
<tr>
<td>Pantiades</td>
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<td>1</td>
<td>greater</td>
</tr>
<tr>
<td>Strymon</td>
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<td>12</td>
<td>greater</td>
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<td>Thecla</td>
<td>47</td>
<td>2</td>
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<td>Hemiargus</td>
<td>3</td>
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<tr>
<td>Everes</td>
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<td>1</td>
<td>greater (?)</td>
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<td>Leptotes</td>
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**Riodinidae**

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<td>Calephelis</td>
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<td>9</td>
<td>greater</td>
</tr>
<tr>
<td>Emesis</td>
<td>4</td>
<td>2</td>
<td>greater</td>
</tr>
<tr>
<td>Species</td>
<td>Nearest Previous Recorded Locale</td>
<td>Associated Plant Formations</td>
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</tr>
<tr>
<td>---------</td>
<td>----------------------------------</td>
<td>-----------------------------</td>
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<tr>
<td><strong>I. Intrastate range extensions</strong></td>
<td></td>
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<tr>
<td>Graphium branchus (Papilionidae)</td>
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<td>Semi-Evergreen Seasonal Forest</td>
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<tr>
<td>Graphium belesis (Papilionidae)</td>
<td>Sierra Madre Oriental (Veracruz)</td>
<td>Semi-Evergreen Seasonal Forest</td>
<td></td>
</tr>
<tr>
<td>Graphium agesilaus neosilaus (Papilionidae)</td>
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<td>Dismorphia euryope (Pieridae)</td>
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<td>Montane Thicket, Elfin Woodland</td>
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<td>Prepona brooksiana (Nymphalidae)</td>
<td>Coatepec, Veracruz</td>
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<td>Chlorostrymon s. simaethis (Lycaenidae)</td>
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<td>Hedgerows</td>
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<td>Electrostrymon cyphara (Lycaenidae)</td>
<td>Sierra Madre Oriental (Veracruz)</td>
<td>Lower Montane Rain Forest, Semi-Evergreen Seasonal Forest</td>
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<tr>
<td>Thecla hecate (Lycaenidae)</td>
<td>Sierra Madre Oriental (Veracruz)</td>
<td>Pastures</td>
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<td><strong>II. New state records</strong></td>
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<tr>
<td>Taygetes kerea (Satyridae)</td>
<td>Chiapas, Sierra Madre del Sur (México)</td>
<td>Deciduous Woodland and the <em>Pinus-Quercus</em> Associes</td>
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<td>Phyciodes griseo-basolis (Nymphalidae)</td>
<td>Chiapas (México)</td>
<td>Recently Abandoned Milpas, Pastures</td>
<td></td>
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<tr>
<td>Catagramma lyca (Nymphalidae)</td>
<td>Tabasco, Chiapas, Oaxaca (México)</td>
<td>Lower Montane Rain Forest</td>
<td></td>
</tr>
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<td>Limenitis erotia (Nymphalidae)</td>
<td>Chiapas (México)</td>
<td>Pastures</td>
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<td>Species</td>
<td>Recorded Locale Nearest Previous</td>
<td>Associated Plant Formations</td>
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<tr>
<td>------------------------------</td>
<td>----------------------------------</td>
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<td><em>Limenitis sentia</em> (Nymphalidae)</td>
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<td>Swamp Forest, Pastures</td>
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<td><em>Anaea proserpina</em> (Nymphalidae)</td>
<td>Chiapas (México)</td>
<td>Montane Thicket, Elfin Woodland</td>
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<td><em>Strymon melinus</em> (Lycaenidae)</td>
<td>Oaxaca (México)</td>
<td><em>Pinus-Quercus</em> Associes of the Deciduous Woodland</td>
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</tr>
<tr>
<td><em>Thecla thales</em> (Lycaenidae)</td>
<td>Chiapas (México)</td>
<td><em>Liquidambar-Quercus</em> Associes of the Montane Rain Forest</td>
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<tr>
<td><em>Thecla denarius</em> (Lycaenidae)</td>
<td>Tabasco (México)</td>
<td><em>Pinus-Quercus</em> Associes of the Deciduous Woodland</td>
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<tr>
<td><em>Thecla teta</em> (Lycaenidae)</td>
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<td>Pacific Coast of México</td>
<td>Montane Rain Forest</td>
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<tr>
<td><em>Perophthalma tullius lasius</em> (Riodinidae)</td>
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<td><em>Liquidambar-Quercus</em> Associes of the Montane Rain Forest</td>
<td></td>
</tr>
<tr>
<td><em>Leucochimona v. vestalis</em> (Riodinidae)</td>
<td>Chiapas (México)</td>
<td>Lower Montane Rain Forest, Montane Rain Forest</td>
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<tr>
<td><em>Isapis agyr tus hera</em> (Riodinidae)</td>
<td>Chiapas (México)</td>
<td><em>Pinus-Quercus</em> Associes of the Deciduous Woodland</td>
<td></td>
</tr>
<tr>
<td><em>Celephelis</em> sp. 2 (Riodinidae)</td>
<td>Tabasco (México)</td>
<td>Recently Abandoned Milpas, Pastures, Hedgerows</td>
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<tr>
<td><em>Calydna venusta</em> (Riodinidae)</td>
<td>Oaxaca (México)</td>
<td>Semi-Evergreen Seasonal Forest</td>
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<tr>
<td><em>Emesia lupina</em> (Riodinidae)</td>
<td>Guerrero (México)</td>
<td>Semi-Evergreen Seasonal Forest</td>
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<tr>
<td><em>Polystichtis sudias</em> (Riodinidae)</td>
<td>Tabasco (México)</td>
<td><em>Liquidambar-Quercus</em> Associes of the Montane Rain Forest</td>
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</tr>
</tbody>
</table>

III. New national records

*Epiphile plutonia* (Nymphalidae) Guatemala

*Limenitis oberthuri* (Nymphalidae) Guatemala

Montane Thicket

Lower Montane Rain Forest
percentage (24%) of new listings, representing ten species, are
of species with distributions that are only slightly farther north
than the Sierra. These ten species belong to genera that prob-
ably have had Neotropical origins.

In summary, I conclude that the butterfly fauna of the Sierra
de Tuxtla is essentially tropical.

ENDEMISM

Following the Tertiary uplift of the Sierra de Tuxtla, the
area has been subjected to relatively few physical disturbances.
Other than several volcanic eruptions, ash falls, and lava flows,
the flora has had a considerable span of time in which to develop
and mature. Even during the relatively cool periods of the
Pliocene and Pleistocene the proximity of the Gulf of Mexico
with its warm, moist winds, probably caused a relatively small
decrease in the Sierra’s average yearly temperature (Dorf, 1959).
However, during that period a slight shift in floral (and faunal)
elements conceivably took place; specifically, an extension of
the previously minor subtropical elements (Griscom, 1932, 1950)
and possibly even the establishment of new immigrants from
more northern areas. Subsequent to the Pleistocene, the climate
has ameliorated, which in turn has caused the retreat of the

<table>
<thead>
<tr>
<th>Species</th>
<th>Nearest Previous Recorded Locale</th>
<th>Associated Plant Formations</th>
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</thead>
<tbody>
<tr>
<td>Calycopis pisis</td>
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<td>Liquidambar-Quercus Associated of the Montane Rain Forest</td>
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<tr>
<td>(Lycaenidae)</td>
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<td>Recently Abandoned Milpas</td>
</tr>
<tr>
<td>Thecla ares</td>
<td>Guatemala</td>
<td>Semi-Evergreen Seasonal Forest</td>
</tr>
<tr>
<td>(Lycaenidae)</td>
<td></td>
<td>Hedgerows</td>
</tr>
<tr>
<td>Thecla mulucha</td>
<td>Guatemala</td>
<td>H (Lycaenidae)</td>
</tr>
<tr>
<td>Thecla ambrax</td>
<td>Nicaragua</td>
<td>Montane Rain Forest</td>
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<tr>
<td>(Lycaenidae)</td>
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<td></td>
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<tr>
<td>Thecla dodava</td>
<td>Panamá</td>
<td>Deciduous Woodland, Montane Rain Forest</td>
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<tr>
<td>(Lycaenidae)</td>
<td></td>
<td>Pastures, Pinus-Quercus Associated of the Deciduous Woodland</td>
</tr>
<tr>
<td>Thecla tamos</td>
<td>Costa Rica</td>
<td></td>
</tr>
<tr>
<td>(Lycaenidae)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Theope eleutho</td>
<td>Panamá</td>
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</table>
subtropical floral elements to relatively high elevations of the major volcanoes (and possibly the elimination of some forms) and the expansion once again of the more tropical elements (see Griscom, 1932, 1950). Today these latter predominate. Thus, since the Pleistocene relatively stable conditions have existed in the Sierra and there probably have been no major modifications in the flora and fauna by physical elements except minor volcanic disturbances and hurricanes—both of which have been relatively rare in occurrence. This stability in environment combined with geographic isolation make the area ideally suited for endemism both in flora and fauna. Firschein and Smith (1956) state that at least eight endemic forms of amphibians and reptiles have been reported from the range. Wetmore (1943) listed five birds and Lowery & Newman (1949) one additional bird endemic to the Sierra.

My investigations of the butterfly fauna revealed five endemic forms: three species, one subspecies, and one form (two of the species and the one subspecies still remain undescribed). These endemics are listed in Table VIII. The majority of these forms (four species, 89%) belong to the families Lycaenidae and Riodinidae, many members of which are known to have fairly restricted distributions. Furthermore, of these five endemics two occur in the high montane forests (Upper Tropical Zone) and three in the Lower Tropical Zone (Arid Lower Tropical Subzone). All endemics but one (Callophrys nr. longula) belong to genera that never have been recorded within the United States and which I conclude have had Neotropical origins.

**TABLE VIII**

**BUTTERFLIES ENDEMIC TO THE SIERRA DE TUXTLA**

<table>
<thead>
<tr>
<th>Species</th>
<th>Endemic Form</th>
<th>Associated Plant Formations</th>
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</thead>
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<tr>
<td><em>Morpho theseus</em></td>
<td>Form (but probably good subspecies)</td>
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<tr>
<td><em>justiceae</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>schwezeri</em></td>
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<tr>
<td>(Nymphalidae)</td>
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<tr>
<td><em>Callophrys nr.</em></td>
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<tr>
<td><em>longula</em></td>
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<td>(Lycaenidae)</td>
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<td><em>Thecla nr.</em></td>
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<td>Swamp Forest</td>
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<tr>
<td><em>antincus</em></td>
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<tr>
<td>(Lycaenidae)</td>
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<tr>
<td><em>Anatole rossi</em></td>
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<td>*Pinus-Quercus Assocsies of the Deciduous Woodland</td>
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<tr>
<td>(Riodinidae)</td>
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<td></td>
</tr>
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</table>
Theope eleutho  
(Prodephalinae)  

REFERENCES CITED


APPENDICES

Appendix A

CHECK-LIST OF BUTTERFLY SPECIES COLLECTED
IN THE SIERRA DE TUXTLA

FAMILY PAPILIONIDAE

SUBFAMILY Papilioninae

TRIBE Graphiini

SUBTRIBE Graphiiti
1. Graphium phaon (Boisduval)
2. Graphium branchus (Doubleday)
3. Graphium belesis (Bates)
4. Graphium philolaus (Boisduval)
5. Graphium epidaus epidaus (Doubleday, Westwood, & Hewitson)
6. Graphium agesilaus neosilaus (Hoffer)
7. Graphium calliste calliste (Bates)

TRIBE Troidini

SUBTRIBE Battiti
8. Battus polydamas (Linnaeus)
9. Battus belus varus (Kollar)
10. Battus laodamas copanae (Reakirt)
SUBTRIBE Troiditi

11. *Parides photinus* (Doubleday)
12. *Parides montezuma* (Westwood)
13. *Parides polyzelus polyzelus* (Felder)
14. *Parides sesostris zestos* (Gray)
15. *Parides iphidamas* (Fabricius)
16. *Parides arceus mylotes* (Bates)

TRIBE Papilionini

17. *Papilio polyxenes asterius* Stoll
18. *Papilio thoas autocles* Rothschild & Jordan
19. *Papilio androgeus epidaurus* Godman & Salvin
20. *Papilio anchisiades idaeus* Fabricius
21. *Papilio victorinus victorinus* Doubleday

FAMILY PIERIDAE

SUBFAMILY Dismorphiinae

22. *Dismorphia (Dismorphia) praxinoe* (Doubleday)
23. *Dismorphia (Dismorphia) fortunata* (Lucas)
24. *Dismorphia (Dismorphia) euryope* (Lucas)
25. *Dismorphia (Acmepteron) nemesis* (Latreille)
26. *Dismorphia (Enantia) albania* (Bates)
27. *Dismorphia (Enantia) jethys* (Boisduval)

SUBFAMILY Pierinae

28. *Catasticta nimbice nimbice* (Boisduval)
29. *Archonias (Archonias) tereas* (Hübner)
30. *Appias (Glutophrissa) drusilla poeyi* (Butler)
31. *Leptophobia aripa elodia* (Boisduval)
32. *Itaballia (Itaballia) demophile calydonia* (Boisduval)
33. *Itaballia (Itaballia) pisonis kicaha* (Reakirt)
34. *Itaballia (Pieriballia) viardi viardi* (Boisduval)
35. *Ascia (Ascia) monuste monuste* (Linnaeus)
36. *Melete isandra* (Boisduval)

SUBFAMILY Coliadinae

37. *Colias (Zerene) cesonia* (Stoll)
38. *Anteos clorinde* (Godart)
39. *Anteos maerula* (Fabricius)
40. *Phoebis (Phoebis) sennae marcellina* (Cramer)
41. *Phoebis (Phoebis) philea* (Johansson)
42. *Phoebis (Phoebis) argante* (Fabricius)
43. *Phoebis (Phoebis) agarithe maxima* (Neumoegen)
44. *Phoebis (Phoebis) intermedia* Butler
45. *Phoebis (Rhabdodryas) trite* (Linnaeus)
46. *Phoebis (Aphrissa) statira jada* (Butler)
47. *Eurema (Eurema) albula* (Cramer)
48. *Eurema (Eurema) daira daira* (Godart)
49. *Eurema (Eurema) boisduvaliana* Felder & Felder
50. *Eurema (Eurema) xanthochlora* (Kollar)
51. *Eurema (Eurema) mexicana* (Boisduval)
52. *Eurema (Eurema) salome* (Felder)
53. *Eurema (Pyrisitia) proterpia* (Fabricius)
54. *Eurema (Pyrisitia) lisa* Boisduval & Le Conte
55. *Eurema (Pyrisitia) nise nelphe* (Felder)
56. *Eurema (Pyrisitia) dina westwoodi* (Boisduval)
57. *Eurema (Abaeis) nicippe* (Cramer)
58. *Nathalis iole* Boisduval

**FAMILY ITHOMIIDAE**

**SUBFAMILY Ithomiinae**

**TRIBE Tithoreini**
59. *Tithorea harmonia salvadoris* Staudinger

**TRIBE Melinaeini**
60. *Melinaea lilis imitata* Bates

**TRIBE Mechanitini**
61. *Mechanitis polymnia lycidice* Bates
62. *Mechanitis agaensis doryssus* Bates
63. *Mechanitis menapis saturata* Godman

**TRIBE Napeogenini**
64. *Hypothyris lycaste dionaea* Hewitson
65. *Napeogenes tolosa* (Hewitson)

**TRIBE Ithomiini**
66. *Ithomia leila* Hewitson
67. *Ithomia patilla* Staudinger

**TRIBE Oleriini**
68. *Hyposcada virginiana virginiana* (Hewitson)
69. *Oleria zea* (Hewitson)
70. *Oleria paula* (Weymer)
71. *Aeria pacifica* Godman & Salvin

TRIBE Dirceennini
72. *Dirceenna klugi* (Geyer)
73. *Episcada arlena* (Hewitson)
74. *Pteronymia cottyo* (Guérin)

TRIBE Godyridini
75. *Greta nero* (Hewitson)
76. *Greta oto* (Hewitson)
77. *Greta anetta* (Guérin)
78. *Hypoleria cassotis* (Bates)

FAMILY DANAINAE

SUBFAMILY Danainae
79. *Danaus (Danaus) plexippus plexippus* (Linnaeus)
80. *Danaus (Tasitia) gilippus strigosus* (Bates)
81. *Danaus (Tasitia) eresimus montezuma* Talbot

SUBFAMILY Lycoreinae
82. *Lycorea ceres atergatis* (Doubleday)

FAMILY SATYRIDAE

SUBFAMILY Satyrinae
83. *Pierella luna heracles* Boisduval
84. *Taygetes mermeria excauata* Butler
85. *Taygetes virgilia* (Cramer)
86. *Taygetes andromeda* (Cramer)
87. *Taygetes keneza* Butler
88. *Taygetes kerea* Butler
89. *Euptychia gemma freemani* (Stalings & Turner)
90. *Euptychia hesione* (Sulz)
91. *Euptychia metaleuca* (Boisduval)
92. *Euptychia mollina* Hübner
93. *Euptychia labe* Butler
94. *Euptychia similis* Butler
95. *Euptychia themis* Butler
96. *Euptychia undina* Butler
97. *Euptychia disaffecta* Butler & Druce
98. *Euptychia hermes sosybius* (Fabricius)
99. *Euptychia gigas* Butler
100. *Euptychia libye* (Linnaeus)
101. *Euptychia glaucina* Bates
102. *Euptychia sericella* Bates
103. *Euptychia nr. alcinoe* Felder
104. *Pedaliodes pisonia circumducta* (Thieme)
105. *Dioriste tauropolis* (Doubleday & Hewitson)

**SUBFAMILY Brassolinae**

106. *Opsiphanes (Opsiphanes) boisduvalii* Westwood & Hewitson
107. *Opsiphanes (Opsiphanes) cassiae castaneus* Stichel
108. *Eryphanis aesacus* (Herrich-Schaeffer)
109. *Caligo memnon* (Felder)
110. *Caligo uranus* Herrich-Schaeffer

**FAMILY NYMPHALIDAE**

**SUBFAMILY Amathusiinae**

TRIBE Morphini
111. *Morpho theseus justiciae* Salvin & Godman
112. *Morpho polyphemus luna* Butler
113. *Morpho peleides montezuma* Guénéé

**SUBFAMILY Acraeinae**

TRIBE Acraeini
114. *Actinote leucomelas* (Bates)
115. *Actinote guatemalena veraezeruis* Jordan

**SUBFAMILY Heliconiinae**

116. *Philaethria dido dido* (Clerck)
117. *Dryadula phaetusa* (Linnaeus)
118. *Agraulis vanillae incarnata* (Riley)
119. *Dione junio huascama* (Reakirt)
120. *Dione moneta poeyii* (Butler)
121. *Dryas julia moderata* (Stichel)
122. *Heliconius (Eueides) cleobaea zorcaon* (Reakirt)
123. Heliconius (Semelia) vibilia vialis (Stichel)
124. Heliconius (Semelia) lineata (Salvin & Godman)
125. Heliconius (Semelia) aliphera gracilis (Stichel)
126. Heliconius (Heliconius) ismenius telchinia Doubleday
127. Heliconius (Heliconius) doris transiens Staudinger
128. Heliconius (Heliconius) sapho leuce Doubleday
129. Heliconius (Heliconius) sara veraepacis Bates
130. Heliconius (Heliconius) petiveranus Doubleday
131. Heliconius (Heliconius) charitonius vazquezae Comstock & Brown
132. Heliconius (Heliconius) hortense Guérin

SUBFAMILY Nymphalinae

TRIBE Argynididi
133. Euptoieta hegesia hoffmanni Comstock
134. Chlosyne janais (Drury)
135. Chlosyne hippodrome (Geyer)
136. Chlosyne lacinia lacinia (Geyer)
137. Chlosyne erodyle (Bates)
138. Chlosyne definita Aaron
139. Thessalia theona theona (Ménétriers)
140. Phyciodes (Phyciodes) vesta (Edwards)
141. Phyciodes (Eresia) frisia tulcis (Bates)
142. Phyciodes (Eresia) claudina guatemalena (Bates)
143. Phyciodes (Eresia) phillyra (Hewitson)
144. Phyciodes (Tritanassa) atronia (Bates)
145. Phyciodes (Tritanassa) ardyss ardyss Hewitson
146. Phyciodes (Tritanassa) eranites mejicana (Roeber)
147. Phyciodes (Tritanassa) myia (Hewitson)
148. Phyciodes (Tritanassa) griseobasolis Roeber
149. Phyciodes (Tritanassa) clara (Bates)

TRIBE Nymphalini
150. Polygonia g-argenteum (Doubleday & Hewitson)
151. Vanessa virginiensis (Drury)
152. Junonia evarete evarete (Cramer)
153. Anartia jatrophae luteipicta Fruhstorfer
154. Anartia fatima venusta Fruhstorfer
155. Metamorpha stelenebi plagiata (Fruhstorfer)
156. Metamorpha epaphus (Latreille)
157. Hypanartia lethe (Fabricius)
158. Hypanartia dione Latreille
TRIBE Biblini
159. Biblis hyperia aganisa Boisduval

TRIBE Eunicidi
160. Mestra amymone (Ménétrixé)
161. Pyrrhogyra hypensor Godman & Salvin
162. Pyrrhogyra edocla aenaria Fruhstorfer
163. Pyrrhogyra otolais neis Felder
164. Pseudonica flavilla canthara (Doubleday)
165. Temenis laothoe liberia (Fabricius)
166. Epiphile adrasta bandusia Fruhstorfer
167. Epiphile plutonia Bates
168. Catonephele nyctimus (Westwood)
169. Catonephele numilia esite (Felder)
170. Nessaea aglaura (Westwood & Hewitson)
171. Myscelia cyaniris Doubleday & Hewitson
172. Myscelia rogenhoferi Felder
173. Eunica monima (Stoll)
174. Eunica alcmena alcmena Doubleday & Hewitson
175. Catagramma lyca Doubleday & Hewitson
176. Catagramma titaia Salvin
177. Catagramma casta Salvin
178. Diaethria anna (Guérin)
179. Diaethria astala (Guérin)
180. Dynamine mylitta (Cramer)
181. Dynamine dyonis Geyer

TRIBE Ageroniidi
182. Hamadryas februa gudula (Fruhstorfer)
183. Hamadryas feronia farinulenta (Fruhstorfer)
184. Hamadryas guatemalena guatemalena (Bates)
185. Hamadryas ipthime (Bates)
186. Hamadryas amphinome mexicana (Lucas)
187. Hamadryas laodamia laodamia (Cramer)

TRIBE Marplesiidi
188. Marpesia chiron (Fabricius)
189. Marpesia harmonia (Klug)
190. Marpesia corita (Westwood)
191. Marpesia petreus (Cramer)
TRIBE Liminitidi

192. Limenitis (Adelpha) melanthe (Bates)
193. Limenitis (Adelpha) leuceria (Druce)
194. Limenitis (Adelpha) erotia (Hewitson)
195. Limenitis (Adelpha) oberthuri (Boisduval)
196. Limenitis (Adelpha) iphiclæ (Linnaeus)
197. Limenitis (Adelpha) basiloides (Bates)
198. Limenitis (Adelpha) felderi (Boisduval)
199. Limenitis (Adelpha) sentia (Godman & Salvin)
200. Limenitis (Adelpha) paraeca (Bates)

TRIBE Apaturidi

201. Chlorippe cherubina (Felder)
202. Chlorippe paeon (Latreille)
203. Chlorippe lauræ (Drury)
204. Historis odius (Fabricius)
205. Smyrna blomfildia datis Fruhstorfer
206. Gynaecia dirce (Linnaeus)

TRIBE Charaxidi

207. Prepona demophon centralis Fruhstorfer
208. Prepona antimache gulina Fruhstorfer
209. Prepona amphimachus (Fabricius)
210. Prepona laertes pallantias Fruhstorfer
211. Prepona brooksiana Godman & Salvin
212. Anaea (Siderone) marthesia (Cramer)
213. Anaea (Zaretis) itys (Cramer)
214. Anaea (Zaretis) callidryas (Felder)
215. Anaea (Anaea) aidea Guérin-Ménéville
216. Anaea (Consul) fabius (Cramer)
217. Anaea (Consul) electra (Westwood)
218. Anaea (Memphis) eurypyle confusa Hall
219. Anaea (Memphis) artacæna (Hewitson)
220. Anaea (Memphis) pithyusa (Felder)
221. Anaea (Memphis) proserpina (Salvin)
222. Anaea (Memphis) morvus boisduvali W. P. Comstock
SUBFAMILY Libytheinae

223. *Libytheana carinenta mexicana* Michener

FAMILY LYCAENIDAE

SUBFAMILY Lycaeninae

TRIBE Theclini

SUBTRIBE Strymoniti

224. *Eumaeus minyas* Hübner
225. *Eumaeus debora* Hübner
226. *Theorema eumenia* Hewitson
227. *Chlorostrymon simaethis simaethis* (Drury)
228. *Chlorostrymon telea* (Hewitson)
229. *Calycopis beon* (Cramer)
230. *Calycopis trebula* (Hewitson)
231. *Calycopis pisis* (Godman & Salvin)
232. *Calycopis* sp. “C”
233. *Tmolus echion echiolus* (Draudt)
234. *Tmolus crolinus* (Butler & Druce)
235. *Tmolus azia* (Hewitson)
236. *Oenomaus ortygynus* (Cramer)
237. *Callaphrys (Cyanophrys) amyntor distractus* Clench
238. *Callaphrys (Cyanophrys) herodotus* (Fabricius)
239. *Callaphrys (Cyanophrys) leucania* (Hewitson)
240. *Callaphrys (Cyanophrys) miserabilis* (Clench)
241. *Callaphrys (Cyanophrys) goodsoni* Clench
242. *Callaphrys (Cyanophrys) agricolor agricolor* (Butler & Druce)
243. *Callaphrys (Cyanophrys)* nr. *longula* (Hewitson)
244. *Atlides polybe* (Linnaeus)
245. *Panthiades ochus* (Godman & Salvin)
246. *Strymon melinus* Hubner
247. *Strymon yojoa* (Reakirt)
248. *Strymon columella istapa* (Reakirt)
249. *Strymon bazochii* (Godart)
250. *Strymon albata sedecia* (Hewitson)
251. *Strymon serapio* (Godman & Salvin)
252. *Electrostrymon cyphara* (Hewitson)
253. *Cycnus battus jalal* (Reakirt)
254. *Arawacus aetolus togarna* (Hewitson)
255. *Arawacus sito* (Boisduval)
256. *Heterosmaitia palegon* (Cramer)
257. *Allosmaitia pion* (Godman & Salvin)
258. *Evenus regalis* (Cramer)
259. *Thecla cypria* (Geyer)
260. *Thecla marsyas damo* (Druce)
261. *Thecla augustula* Kirby
262. *Thecla lisus* Stoll
263. *Thecla mavors* (Hubner)
264. *Thecla inachus carpophora* Hewitson
265. *Thecla neora* Hewitson
266. *Thecla laothoe* Godman & Salvin
267. *Thecla barajo* Reakirt
268. *Thecla janias* (Cramer)
269. *Thecla hassan* (Stoll)
270. *Thecla meton* (Cramer)
271. *Thecla janthina janthodonia* Dyar
272. *Thecla nr. polibites* (Cramer)
273. *Thecla vibidia* Hewitson
274. *Thecla hecate* Godman & Salvin
275. *Thecla jebus* (Godart)
276. *Thecla brescia* Hewitson
277. *Thecla ligurina* Hewitson
278. *Thecla mycon* Godman & Salvin
279. *Thecla thales* (Fabricius)
280. *Thecla tephraeus* (Geyer)
281. *Thecla syncellus syncellus* (Cramer)
282. *Thecla minthe* Godman & Salvin
283. *Thecla empusa* Hewitson
284. *Thecla ares* Godman & Salvin
285. *Thecla ahiola* Hewitson
286. *Thecla gabatha* Hewitson
287. *Thecla tarpa* Godman & Salvin
288. *Thecla maeonis* Godman & Salvin
289. *Thecla hesperitis* (Butler & Druce)
290. *Thecla denarius* (Butler & Druce)
291. *Thecla plusios* Godman & Salvin
292. *Thecla clarina* Hewitson
293. *Thecla demonassa* Hewitson
294. *Thecla tera* Hewitson
295. *Thecla coronata* Hewitson
296. *Thecla scopas* Godman & Salvin
297. *Thecla mathewi* Hewitson
298. *Thecla politus* Druce
299. *Thecla basalides* (Geyer)
300. *Thecla mulucha* Hewitson
301. *Thecla ambrax* Westwood & Hewitson
302. *Thecla dodava* Hewitson
303. *Thecla kalikimaka* Clench
304. *Thecla tamos* Godman & Salvin
305. *Thecla nr. antincus* Felder

**TRIBE Plebejini**
306. *Hemiargus (Hemiargus) ceraunus zachaeina* (Butler & Druce)
307. *Hemiargus (Echinargus) huntingtoni hannoides* Clench
308. *Hemiargus (Echinargus) isola isola* (Reakirt)
309. *Everes comyntas comyntas* (Godart)
310. *Leptotes cassius striata* (Edwards)
311. *Celastrina argiolus gozora* (Boisduval)

**FAMILY RIODINIDAE**

**SUBFAMILY Euselasiinae**

**TRIBE Euselasiini**
312. *Euselasia sergia* (Godman & Salvin)
313. *Euselasia hieronymi* (Godman & Salvin)
314. *Euselasia cheles aurantiaca* (Godman & Salvin)
315. *Euselasia cataleuca* (Felder)
316. *Euselasia pusilla* (Felder)
317. *Euselasia eubule* (Felder)
TRIBE Riodinini

318. *Hades noctula* Westwood
319. *Perophthalma tullius lasius* Stichel
320. *Leucochimona philemon nivalis* (Godman & Salvin)
321. *Leucochimona vestalis vestalis* (Bates)
322. *Mesosemia tetrica* Stichel
323. *Mesosemia gaudiolus* Bates
324. *Eurybia lycisca* Westwood
325. *Cremna umbra* (Boisduval)
326. *Ancylusis jurgensenii* (Saunders)
327. *Rhetus arcius thia* (Morisse)
328. *Isapis agyr tus her a* Godman & Salvin
329. *Notheme eumeus diadema* Stichel
330. *Calephelis fulmen* (Stichel)
331. *Calephelis sp. 1*
332. *Calephelis sp. 2*
333. *Charis velutina* (Godman & Salvin)
334. *Charis myrtea* (Godman & Salvin)
335. *Charis psaros* (Godman & Salvin)
336. *Charmona gynaea zama* (Bates)
337. *Baeotis hisbon zonata* Felder
338. *Lymnas pixe pixe* Boisduval
339. *Mesene margaretta* (White)
340. *Mesene croceela* Bates
341. *Symmachia rubina* Bates
342. *Symmachia accustrix* Westwood
343. *Symmachia tricolor hedemanni* (Felder)
344. *Phaenochitonia sagaris tyriotes* (Godman & Salvin)
345. *Anteros carausius carausius* Westwood
346. *Calydna venusta* Godman & Salvin
347. *Emesis liodes* Godman & Salvin
348. *Emesis mandana mandana* (Cramer)
349. *Emesis tenedia* Felder
350. *Emesis lupina* Godman & Salvin
351. *Tharops menander isthmi ae* Godman & Salvin
352. *Thisbe irenea belides* Stichel
353. *Polystichtis sudius* (Hewitson)
354. *Anatole agave* (Godman & Salvin)
355. *Anatole rossi* Clench
356. *Peplia lamis molpe* (Hübner)
357. *Nymula calice mycone* (Hewitson)
358. *Calociasma lilina* (Butler)

TRIBE Theopini
359. *Theope eleutho* Godman & Salvin

Appendix B

PLANTS IDENTIFIED FROM THE SIERRA DE TUXTLA

Acanthaceae
   *Aphelandra aurantiaca* (Schiedw.) Lindl.
   *Odontonema callistachyum* (S. & C.) Kuntze
   *Ruellia fluviatilis* Leonard

Amaryllidaceae
   *Agave* sp.

Anacardiaceae
   *Spondias mombin* L.

Annonaceae
   *Annona muricata* L.
   *Annona reticulata* L.
   *Annona* sp.

Apocynaceae
   *Stemmadenia galeottiana* (A. Rich.) Miers.
   *Tabernaemontana citrifolia* L.

Aristolochiaceae
   *Aristolochia asclepiadifolia* T. S. Brandeg.

Asclepiadaceae
   *Asclepias woodsoniana* Standl. & Steyerm.
   *Asclepias tuberosa* L.

Aspidiaceae
   *Didymochlaena truncatula* (Swartz) J. Smith
Bombacaceae
   *Bomboullia flammea* Oliver
   *Ceiba pentandra* (L.) Gaertn.
   *Pachira aquatica* Aubl.

Boraginaceae
   *Cordia alliodora* (R. & P.) Cham.
   *Cordia spinescens* L.
   *Heliotropium indicum* L.
   *Tournefortia glabra* L.

Burseraceae
   *Bursera simaruba* (L.) Sarg. sens. lat.

Campanulaceae
   *Centropogon affine* Mart. & Gal.

Caprifoliaceae
   *Viburnum acutifolium* Benth.

Clethraceae
   *Clethra macrophylla* M. & G.
   *Clethra suaveolens* Turcz.

Combretaceae
   *Terminalia amazonia* (Gmel.) Exell.

Compositae
   *Ageratum conyzoides* L.
   *Baltimora recta* L.
   *Bidens pilosa* L. var. *bimucronata* (Turcz.) Schultz
   *Calea cacosmoides* Less. (tentative)
   *Calea longipedicellata* R. & G.
   *Calea zacatechichi* Schlecht.
   *Conyza chilensis* Spreng.
   *Eupatorium incomptum* DC.
   *Eupatorium macrophyllum* L.
   *Eupatorium pittieri* Klatt
   *Eupatorium tuerckheimii* Klatt, vel aff. (tentative)
   *Hidalgoa ternata* Llave
   *Liabum dimidium* Blake (tentative)
   *Liabum* sp.
   *Melampodium divaricatum* (Rich.) DC.
   *Melampodium kunthianum* DC.
   *Melanthera angustifolia* A. Rich.
   *Polymnia maculata* Cav.
   *Schistocarpha* sp.
   *Senecio* sp.
   *Stevia rhombifolia* (H.B.K.)
Vernonia argyropappa Buek.
Vernonia leiocarpa DC.

Convolvulaceae
  Ipomoea pes-caprae (L.) Sweet
  Ipomoea stolonifera (Cyr.) Gmel.

Corylaceae
  Carpinus caroliniana Walt.

Cucurbitaceae
  Anguria tabascensis Donn. Sm., vel aff.

Cycadaceae
  Ceratozamia mexicana Brong. sens. lat.
  Zamia loddigesii var. angustifolia (Regel) Schuster

Cyatheaceae
  Alsophila schiedeana Presl.
  Cyathea sp.

Cyperaceae
  Bulbostylis papillosa Kukenth. (tentative)
  Cyperus articulatus L.
  Cyperus ligularis L.
  Dichromena ciliata Vah.
  Rhynchospora globosa (H.B.K.) R. & S.
  Rhynchospora tuerckheimii Clarke

Dilleniaceae
  Curatella americana L.
  Saurauia sp.

Elaeocarpaceae
  Sloanea sp.

Ericaceae
  Gaultheria sp. (tentative)

Erythroxylaceae
  Erythroxylon tabascense Britton

Euphorbiaceae
  Acalypha diversifolia Jacq. var. carpinifolia (Poepp. & Endl.)
    Muell.-Arg.
  Acalypha unibracteata Muell.-Arg., vel aff.
  Alchornea latifolia Sw.
  Croton glabellus L.
  Croton repens Schlecht.
  Croton soliman Schlecht. & Cham.
  Gymnanthes actinostemoides Muell.-Arg.
  Jatropha curcas L., vel aff.
  Rondelitia galeottii Standl., vel aff.
Fabaceae
   *Dussia mexicana* (Standl.) Harms
   *Erythrina americana* Mill.
   *Gliricidia sepium* (Jacq.) Steud.

Fagaceae
   *Quercus conspersa* Benth.
   *Quercus ghiesbreghtii* Mart. & Gal., vel aff.
   *Quercus oleoides* S. & C.
   *Quercus peduncularis* Née, vel aff.
   *Quercus skinneri* Benth.

Flacourtiaceae
   *Casearia nitida* (L.) Jacq.
   *Casearia sylvestris* Sw.
   *Pleuranthodendron mexicana* (A. Gray) L. Wms.
   *Xylosma* sp.

Gleicheniaceae
   *Gleichenia palmata* (Schaffner) Moore

Gramineae
   *Aulonemia* sp.
   *Cenchrus incertus* M. A. Curtis
   *Chloris petraea* Swartz
   *Distichlis spicata* (L.) Greene (tentative)
   *Eragrostis* sp.
   *Isachne arundinacea* (Sw.) Griseb.
   *Paspalum pectinatum* Nees
   *Paspalum plicatum* Michx.
   *Sporobolus cubensis* Hetchc.

Guttiferae
   *Clusia salvinii* Donn. Sm.
   *Rheedia edulis* (Seem.) Tr. & Pl.
   *Vismia mexicana* Schlecht.

Hamamelidaceae
   *Liquidambar styraciflua* L.

Icacinaceae
   *Calatola* sp.

Juglandaceae
   *Engelhardtia guatemalensis* Standl.
   *Engelhardtia mexicana* Standl.

Labiatae
   *Salvia Shannonii* Donn. Sm.

Lauraceae
   *Persea longipes* (Schlecht.) Meissn.
Phoebe bourgeauviana Mez
Phoebe mexicana Meissn.
Phoebe psychotrioides (Nees) Mez (tentative)

Leguminosae
Albizia idiopoda (Blake) B. & R.
Albizia sp.
Calliandra grandiflora (L'Her.) Benth.
Cassia fruticosa Mill. (tentative)
Cassia hispidula Vahl
Cassia occidentalis L.
Cassia spectabilis DC., vel aff.
Crotalaria vitellina Ker
Dalbergia sp. (tentative)
Erythrina mexicana Krukoff
Inga leptoloba Schlecht.
Inga spuria Humb. & Bonpl.
Pithecolobium arboreum (L.) Urb.
Vigna luteola (Jacq.) Benth. (tentative)

Magnoliaceae
Talauma mexicana (DC.) G. Don

Malpighiaceae
Byrsonima crassifolia (L.) DC.

Malvaceae
Hibiscus tiliaceus L.

Melastomaceae
Conostegia xalapensis (Bonpl.) DC.
Miconia argentea (Sw.) DC.
Miconia glaberrima (Schlecht.) Naud.

Melioceae
Guarea sp. (tentative)

Meteoriaceae
Pilotrichella flexilis (Hedw.) Jaeg.

Monimiaceae
Siparuna andina (Tul.) A. DC.

Moraceae
Cecropia mexicana Hemsl.
Ficus cotinifolia H.B.K.
Ficus glaucescens (Liebm.) Miq.
Ficus obtusifolia H.B.K.
Ficus padifolia H.B.K.
Ficus spp.
Pseudolmedia oxyphyllaria Donn. Sm.
Musaceae
   *Heliconia latispatha* Benth.
Myricaceae
   *Myrica cerifera* L.
   *Myrica splendens* (Sw.) DC.
Myristicaceae
   *Virola guatemalensis* (Hemsl.) Warb.
Myrsinaceae
   *Ardisia* sp. (tentative)
   *Deherainia smaragdina* (Planch.) Decaisne
Myrtaceae
   *Eugenia* sp. (tentative)
Orchidaceae
   *Elleanthus capitatus* (R. Br.) Reichb.
Oxalidaceae
   *Oxalis neaei* DC. sens lat.
Palmae
   *Astrocaryum mexicanum* Liebm.
   *Chamaedorea elegans* Mart. (tentative)
   *Chamaedorea ernesti-augustii* Wendl. (tentative)
   *Chamaedorea tepejilote* Liebm.
   *Chamaedorea* sp.
   *Orbignya* sp.
   *Sabal* sp.
Passifloriaceae
   *Passiflora ambigua* Hemsl.
   *Passiflora biflora* Lam.
   *Passiflora coriacea* Juss.
   *Passiflora serratifolia* L.
Pinaceae
   *Pinus oocarpa* Schiede
Piperaceae
   *Piper auritum* H.B.K., vel aff.
   *Piper cordovan* C. DC., vel aff.
   *Piper* spp.
Podocarpaceae
   *Podocarpus oleifolius* D. Don
Polypodiaceae
   *Dryopteris* sp.
   *Pteridium aquilinum var. caudatum* (L.) Sadele
Proteaceae
   *Roupala borealis* Hemsl.
Pterobryaceae
  *Pterobryum densum* (Schwaegr.) Hornsch.

Rhizophoraceae
  *Rhizophora mangle* L.

Rosaceae
  *Hirtella racemosa* Lam.

Rubiaceae
  *Borreria suaveolens* Mey.
  *Cephaelis elata* Sw.
  *Crusea calcocephala* DC.
  *Deppea excelsa* (H.B.K.) Standl., vel aff.
  *Hamelia longipes* Standl.
  *Hamelia patens* Jacq.
  *Hoffmannia lenticillata* Hemsl.
  *Lindenia rivalis* Benth.
  *Machaonia* sp., vel aff. (tentative)
  *Psychotria padifolia* H. & B. (tentative)
  *Psychotria* sp.
  *Rondeletia strigosa* (Benth.) Hemsl.

Rutaceae
  *Zanthoxylum elephantiasis* Macf.

Sapindaceae
  *Thouinidium decandrum* (H. & B.) Radlk.

Saxifragaceae
  *Weinmannia pinnata* L.

Schrophulariaceae
  *Escobedia laevis* C. & S.
  *Lamourouxia viscosa* H.B.K.
  *Stemodia durantifolia* Sw., vel aff. (tentative)

Simaroubaceae
  *Picramnia andicola* Tul., vel aff. (tentative)

Solanaceae
  *Solanum ochraceo-ferrugineum* (Dunal) Fernald
  *Solanum schlechtendalianum* Walp.
  *Solanum* spp.

Theaceae
  *Saurauia* sp. (tentative)

Tiliaceae
  *Apeiba tibourbous* Aubl.
  *Belotia* sp.
  *Luehea speciosa* Willd.
Turneraceae
   *Turnera ulmifolia* L.

Ulmaceae
   *Mirandaceltis monoica* (Hemsl.) Sharp

Urticaceae
   *Boehmeria* sp. (tentative)
   *Myriocarpa bifurca* Liebm. (tentative)
   *Myriocarpa longipes* Liebm.
   *Trema micrantha* (L.) Blume
   *Urera elata* (Sw.) Griseb.

Verbenaceae
   *Aegiphila costaricensis* Moldenke
   *Lantana camara* L.

Violaceae
   *Rinorea guatemalensis* (Wats.) Bartlett
The distribution of *Paratrytone melane* (Edwards, 1869) in California has been treated recently by Heppner (1973). He noted a large distribution gap in the Coast Ranges from the Santa Ynez River in Santa Barbara County north to Big Sur in Monterey County. Heppner suggested that this gap might indicate an allopatric distribution, with “a northern population concentrated in the San Francisco Bay area and a southern population in most of coastal southern California.” However, the present author has located several specimens from San Luis Obispo County which fill in this prominent distributional gap.

A specimen from Lopez Canyon, collected “2-9-[19]64” by Richard Hart, is present in the Santa Barbara Museum of Natural History collection. Two specimens from Atascadero, collected “5-10-1932” by Victor L. Clemence, have been located in the Clemence collection. One of these is now in the author’s collection, while the other remains in the Clemence collection.

These previously unpublished records show that *P. melane* is indeed distributed throughout the Coast Ranges of California. The records also demonstrate the need for additional study of the lepidopterous fauna of this region. The author is indebted to Mrs. Grace Clemence and Mr. Nelson W. Baker for their assistance.

**LITERATURE CITED**


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THE JOURNAL OF RESEARCH
ON THE LEPIDOPTERA

published by
The Lepidoptera Research Foundation, Inc.
at
2559 Puesta Del Sol Road, Santa Barbara, California 93105

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CHARIDRYAS FLAVULA
BARNES AND McDUNNOUGH
(NYMPHALIDAE):
A QUESTION OF IDENTITY

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Laramie, Wyoming 82071

and

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INTRODUCTION

The Palla boisduval complex of species in the Melitaeinae
has been referred to a number of genera including: Lemonias
Hübner, 1806 [not Felder and Felder, 1859] by Dyar, 1902;
Melitaea Fabricius, 1807 by Barnes and McDunnough, 1918;
Chlosyne Butler, 1870 by Higgins, 1960; Microtia Bates, 1864 by
dos Passos, 1964; Charidryas Scudder, 1872, 1875 by Bauer in
Howe, 1975. The Bauer treatment seems reasonable and recog¬
nizes nine species in Charidryas [Type Species Melitaea nycteis
Doubleday] composed of a six-species western (palla) group
which lacks the dorsal postmedian series of black spots on the
hindwings found in the three-species eastern (harrisi Scudder)
group. In addition to the maculation, there are differences be¬
tween the two groups in pupal morphology. Because of pheno¬
typic differences in the imagines between the northern
Charidryas and southern Chlosyne, we choose to treat the former as
a full genus, rather than a subgenus as did Bauer.

The taxonomic status of C. flavula Barnes and McDunnough,
1918 has been clouded since its original description. McDun-
M. S. FISHER

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nough (1938), Higgins (1960), and dos Passos (1964, 1969) offered divergent opinions concerning its position relative to *C. palla* (Boisduval) and *C. acastus* (W. H. Edwards). Apparently some further study is indicated concerning the affinity of *flavula* to these two species. The purpose of this paper is to review the past treatment of the taxon and to assign it to what we feel is its proper position for permanent reference in the nomenclature.

**TAXONOMIC CHARACTERS**

Barnes and McDunnough (1918) indicated, before formally describing *flavula* as a full species, that it might prove to be a form of *palla*. McDunnough (1938) retained *flavula* as a full species. Higgins (1960) extensively revised the *palla* group and placed *flavula* as a subspecies of *gabhii* Behr. dos Passos (1964) listed it under its original status, but later (1969) placed it as a form of *acastus*.

The Barnes and McDunnough description does clearly compare the differences between *flavula* and *acastus*, but their study material was limited and generally incompletely labeled. Based upon the stated localities from which they had specimens, they apparently worked with Colorado material from both east and west of the Continental Divide. The type series contained 13 males, 11 of which were labeled simply “Colorado”, and were probably collected by David Bruce. Two specimens were labeled respectively “Glenwood Spgs., [Garfield Co.] Colo.” and “Hall Valley, [Park Co.] Colo.” Brown (1957) observed on page 79: “Since no other specimens of *flavula* have been found on the eastern slope, I assume that the Hall Valley label was inadvertently attached to a Glenwood Springs specimen. On this basis I believe it best to designate Glenwood Springs as the type locality of *flavula*.”

In the original description, *flavula* was compared with California and Colorado *palla*, and *acastus* from Glenwood Springs. Reference was also made to Utah and Wyoming specimens, but no conclusions were drawn. An examination of an extensive series of the *flavula* phenotype from western Colorado, where *flavula* and *acastus* are sympatric, indicates that there are distinct characters which place *flavula* in the *C. palla* complex.

There are several characters that reliably separate *flavula* from *acastus*. As noted by Barnes and McDunnough, *flavula* is smaller than *acastus*, but it is also much darker. The brownish-
black areas of the wings are more extensive, producing, in most specimens, a reduction in the checkered maculation. This maculation is distinctly more contrastingly bi-colored, reddish-to-yellowish dorsally than in *acastus*. Ventrally, the checkered maculation on the hindwings is buff-white, separated by fine black lines along the veins. By comparison, *acastus* is clearly flat white to pearly-white, with broader black lines. The basal area of both wings is more solid reddish in *flavula*, while in *acastus* it is mottled extensively with white and black on the hindwings and orange-buff on the forewings. On the whole, *C. palla flavula* differs from its congener, *C. palla calydon* (Holland) by its smaller size, brighter colors above, and larger spot-bands on the hindwings beneath. The differences are illustrated in Figures 1-14.

**DISTRIBUTION**

*C. palla flavula* occupies a fairly narrow geographic zone in the plateau country of western Colorado and eastern Utah with an extension into southern Wyoming. It is locally common in dry habitats at an altitude range from 6000-8000' (1830-2440m) where Sagebrush (*Artemisia tridentata* Nutt.) is the dominant plant species. It does occur, however, in similar habitat up to 9500' (2895m). The larval foodplant is probably Indian Paintbrush (*Castilleja* species) as it is for *calydon*. *C. acastus* occurs in semi-arid lowlands in this same region and meets *flavula* in and around Glenwood Springs. *C. p. flavula* is the more montane of the two insects and replaces *acastus* completely in similar habitats at higher elevation.

The *flavula* phenotype should also occur in northwestern New Mexico since it occurs in adjacent areas in Colorado. Barnes and McDunnough stated: “We have it from Utah (Provo, Salt Lake) and also from the Yellowstone Park region.” The Yellowstone citation undoubtedly refers to *calydon* based upon specimens that we have examined from western Wyoming. Holland did not describe *calydon* until 1931. We have also examined a short series of *palla* collected north of Salt Lake City in Cache Co.; these do not match the *flavula* characters defined above. The same is true of material from Emigration Canyon and Lamb's Canyon in Salt Lake Co., Utah. This material is more unicolorous above, and in terms of maculation, similar to *acastus*. Figure 15 indicates the presently known distribution for *flavula*.

Brown (1957) discussed the type material of *flavula* as noted above. Contrary to Bauer in Howe (1975), the specimen figured
Fig. 1.—C. p. flavula, male upper, nr. Snowmass, Pitkin Co., Colorado, 13-vi-74.
Fig. 2.—C. p. flavula, female upper, Rabbit Ears Pass area, Routt Co., Colorado, 12-vii-74.
Fig. 3.—C. p. calydon, male upper, nr. Nederland, Boulder Co., Colorado, 22-vi-74.
Fig. 4.—C. p. calydon, female upper, same data as male in Fig. 3.
Fig. 5.—C. p. calydon, male upper, South Turkey Creek Canyon, Jefferson Co., Colorado, 2-vii-68 (Topotype).
Fig. 6.—C. acastus, male upper, Coalmine Point, Black Ridge Breaks, Mesa Co., Colorado, 26-v-71.
Fig. 7.—C. acastus, female upper, same locality as male, 29-v-70.
Figures 8-14 respectively are the undersides of the specimens shown in Figs. 1-7.
Fig. 15.—Known distribution of *C. palla flavula*. Locality data appear in the Appendix.
as *flavula* by Brown is good *flavula*, although his discussion of the differences between it and *calydon* is somewhat confused. Brown did not figure *acastus* and it was not included in the Colorado species list, although Barnes and McDunnough (1918, Pl. 11, f. 13) illustrated a specimen from Glenwood Springs. It is possible that some of the material that Brown used for comparison represented *acastus* from *flavula* localities, thus furthering the confusion. The male *flavula* figured in Howe (1975, Pl. 72, f. 11) is a poor representation of this subspecies, but does represent the Utah population previously mentioned.

**SUMMARY**

The Barnes and McDunnough name *flavula* is presented here as a valid subspecies assigned to the Charidryas *palla* complex. The distinctiveness of *flavula* is supported by specific differences in color, maculation, distribution, and especially by its sympatric occurrence with *acastus* at and near the Glenwood Springs type locality. At Basalt, Eagle Co., Colorado, *acastus* and *flavula* occur sympatrically with no indication of intergradation between the two species.

**LITERATURE CITED**


APPENDIX

Distribution data for the points indicated on the map (Figure 15) are given below. We would like to thank Scott Ellis, Ft. Collins, Colorado and R. E. Stanford, Denver, Colorado for supplying data. The localities listed on page 79 of Brown (1957) are also included.


Scott Ellis has reported that _flavula_ and _acastus_ are sympatric at Mesa Verde in Montezuma Co., Colorado. He has collected one specimen that appears to be a hybrid between the two species.
ConSIDERABLE VARIATION EXISTS between the size and position of the elliptical hyaline area of the forewing. It is this area, when surrounded with darkly pigmented scales that constitutes the postdiscal ocellus. The discal ocellus is triangular in shape and situated nearer to the basal area of the forewing. Some specimens of this species show the complete absence of this first, elliptical hyaline area (fig. 4), whereas in other specimens enlargement of this area results in the fusion of the postdiscal ocellus with the discal ocellus (fig. 3). By chance, the author when comparing these forms noticed that the form exhibiting 'fusion' also had a considerably larger wingspan than the average for its sex. It was this observation that prompted the author to investigate further, and try to provide an answer to the question “... is there a relationship between wingspan and postdiscal ocellus variation?...”

A sample of four hundred and ninety set specimens of A. atlas Linn., were used for the study, all being bred in India. For each separate individual the length of the elliptical hyaline area was measured, as well as the distance between the apices of the forewings. The gross sample was segregated into two divisions, that of male and female specimens. Once this was completed scattergrams were prepared illustrating 'Wingspan vs Ocellus length' in millimetres. One for the sample of 146 male specimens, and a second for the sample of 344 female specimens.
Fig. 1.—Forewing maculation of *A. atlas*. Typical male.

Fig. 3.—Forewing maculation of *A. atlas*. Female showing fusion of hyaline areas, discal and postdiscal.
Fig. 2.—Forewing maculation of *A. atlas*. Typical female.

Fig. 4.—Forewing maculation of *A. atlas*. Female showing absence of post-discal hyaline area.
RESULTS. (table 1.)

<table>
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Greatest recorded wingspan = 221 mm
Smallest recorded wingspan = 175 mm
Mean value for wingspan = 196 mm
Greatest length of elliptical hyaline area of forewing = 14 mm
Smallest length of elliptical hyaline area of forewing = 1 mm
Mean value for elliptical hyaline area of forewing = 7.56 mm
Correlation was calculated between the length of the elliptical hyaline area and wingspan, the value obtained was found to be -0.707

Greatest recorded wingspan = 247 mm
Smallest recorded wingspan = 166 mm
Mean value for wingspan = 202 mm
Greatest length of elliptical hyaline area of forewing = 18 mm
Smallest length of elliptical hyaline area of forewing = 0 mm
Mean value for elliptical hyaline area of forewing = 10.23 mm
Correlation was calculated between the length of the elliptical hyaline area and wingspan, the value obtained was found to be +0.252

DISCUSSION

The correlation value between the wingspan of a female and the length of the elliptical hyaline area was found to be 0.252 which shows that there is a weak, but nevertheless significant relationship between wingspan and ocellus. Furthermore, as the figure obtained is positive the relationship is a direct one. Thus, a specimen with a small wingspan would show a greater tendency towards the small ocellus size. This relationship is indeed verified. From the three specimens in the sample exhibiting the absence of the ocellus the wingspans were 166, 182 and 184 millimetres, these figures are well below the mean for the sample which was calculated at 202 mm. Alternatively, we can look at the incidence of fusion within the sample. Two examples of the fused condition were found with wingspans of 221 and 211 mm, both were above the mean for wingspan, this suggests strongly that the relationship is direct.

We can thus predict that the specimens with unusually small wingspans will show a reduction in ocellus size with complete deletion of the area in extreme examples. In specimens showing
unusually large wingspans we can predict that the two hyaline areas of the forewing will increase in size and ultimately fuse.

In the sample of males, the correlation figure was found to be -0.707, this forcibly shows that there is a 'strong' relationship and good correlation. From the knowledge that the figure is negative we can arrive at the conclusion, that unlike the case of the females the relationship within the male population is indirect. Thus specimens with large wingspans would have small reduced ocelli on the forewings, while specimens with smaller than average wingspans would have larger than average ocelli. This point cannot be illustrated by reference in the sample to fused or absent areas as none were found. The females therefore in this sample exhibited the extreme variations, within the male population these extremities were not shown.

ACKNOWLEDGEMENTS

The author would like to express his thanks to Mr. Minet of Hastings College of Further Education for providing the statistical approach to the data and generally helping with the mathematical aspect. My thanks are also due to Mr. Perrie who furnished the specimens for the study.

LITERATURE CITED


FOODPLANT ECOLOGY OF THE BUTTERFLY
CHLOSYNE LACINIA (GEYER)
(NYMPHALIDAE)

III. ADULT RESOURCES

RAYMOND W. NECK
Texas Parks and Wildlife Department
4200 Smith School Road
Austin, Texas 78744

Much data exists for many rhopalocera species concerning larval foodplants. Such information is of obvious importance in the study of the ecology and evolution of any particular species. For many years, however, another important aspect of rhopaloceran biology has been generally ignored—the importance of adult energy sources. Some moth species have dispensed with adult feeding, thus depending entirely upon the larval stage for acquisition of energy stores. This evolutionary event has not been observed in rhopalocerans, however; much important data remain to be collected on various butterfly species. Norris (1936) produced an early review of the topic but little more was published on this topic until the 1970's.

Recently, this aspect of rhopaloceran biology has received more attention by various workers. Shields (1972) reviewed literature references and added personal records but little synthesis was attempted. An extreme example of butterfly-plant mutualism involving the coevolution of Heliconius butterflies and Anguria/Guranea pollen and nectar plants has been studied by Gilbert (1975). Gilbert (1972) earlier reported the assimilation of pollen proteins by Heliconius. Pollen-fed Heliconius ethilla lay more than five times as many eggs as those without pollen. Obviously, adult resources are a possible topic of much discussion and importance. Not all adult resources of lepidoptera are supplied by plant products; Downes (1973) discussed mud puddles, dung and carion in this respect.

During the process of collecting data concerning the larval foodplant ecology of Chlosyne lacinia var. adjutrix Scudder
(Nymphalidae: Melitaeinae), observations were made concerning adult acquisition of energy and/or water resources. These data are not as comprehensive as the larval foodplant data, but what is available is presented here. All observations occurred in central Texas centering in Austin, Travis County.

ADULT RESOURCES

Verbesina encelioides (Cav.) Gray. This plant is the major source of nectar for adjutrix during the fall months when V. encelioides serves as a primary nectar source for all butterflies. Quite possibly, adjutrix has some advantage over other butterfly species in utilization of this plant as a nectar source because females do not have to leave the area to oviposit on the proper foodplant. V. encelioides is the second most commonly utilized foodplant of adjutrix; during the fall months V. encelioides is by far the major foodplant of this butterfly.

Helianthus annuus L. Nectar of this plant is utilized at times, but generally it is not very acceptable to adult adjutrix. H. annuus can be best classified as a “bee plant” in reference to flower visitation; honey bees and bumble bees are the most frequent visitors to this plant. This is the primary larval foodplant of adjutrix, particularly during the spring and early summer months. The general unsuitability of this plant as a nectar source for adjutrix does not affect its utilization as a larval foodplant because various annuals associated with stands of sunflowers are prime nectar sources.

Heterotheca latifolia Buckl. This species is a prime nectar source for adjutrix especially in association with H. annuus over which H. latifolia is utilized. H. latifolia tends to be ignored in the presence of V. encelioides.

Verbesina virginica L. This plant does not bloom until the fall; at this time it may serve as a temporary prime nectar source. This plant is probably utilized to a lesser extent by adjutrix than other butterflies because V. virginica occurs in wooded areas of central Texas; adjutrix tends to avoid such shaded areas.

Zexmenia hispida (H.B.K.) Gray. The small inflorescences of this species are utilized by adjutrix during the lengthy blooming period (late spring to fall). This plant is classified as an “occasional” larval foodplant (Neck, 1973).

Viguiera dentata (Cav.) Spreng. This plant, also an “occasional” larval foodplant, is utilized by adult adjutrix during blooming season which is restricted to the fall months.
Gaillardia pulchella Foug. The colorful inflorescences of this species may supply nectar to adjutrix adults during spring and early summer. H. latifolia appears to be preferable to G. pulchella which has "rarely" been utilized as an adjutrix larval foodplant (Neck, 1973).

Eysenhardtia texana Scheele. This plant is an important periodic source of nectar. Flowers generally appear in late spring and fall but react mainly to rainfall.

Lantana horrida H.B.K. and Lantana macropoda Torr. Adult adjutrix have been observed at the flowers of these species but the plants generally appear to be ignored. These two species are major nectar sources for swallowtail and heliconian butterflies. Possible factors involved in the low utilization of Lantana by adjutrix will be discussed later in this article.

Rubus trivialis Michx. The blossoms of dewberry are utilized as nectar sources in early spring, particularly if alternate sources are uncommon. Such is often the case during a dry early spring which follows a dry winter; few annuals germinate and produce blossoms early in the season. When other suitable flowers begin to appear, R. trivialis is ignored by adjutrix.

Several plants common in areas frequented by adjutrix are apparently ignored by this species although not necessarily by other butterflies. Verbena bipinnatifida Nutt. is frequently visited by Battus philenor (L.), for example. Lupinus texensis Hook. is primarily visited by bees. Phlox drummondii Hook. is apparently ignored by adjutrix although the major pollinators of plants of this genus are butterflies of the genus Colias (see e.g. Levin, 1969).

Non-floral adult resources are also known for adjutrix. Adults in predominantly male groups may be seen congregated at water holes (as previously reported by Bauer, 1953, in Arizona), especially under high adult density conditions when the nectar supply may be insufficient. After reviewing the literature of lepidoptera visits to dung, carrion and puddles, Downes (1973) concluded that these visits functioned to obtain some unidentified nutrient. Studies by Arms et al. (1974) revealed that male Papilio glaucus were attracted to sand soaked with sodium salts. These results were interpreted as adult supplement of a larval diet deficient in sodium. Male adjutrix have been observed to feed on carrion and feces when sufficiently moist. Several other melitaeine butterflies have been reported as feeding at mud puddles and carrion (Voss, 1954, Payne and King, 1969). Dur-
ing a summer picnic a single male *adjutrix* was observed to feed on a piece of fresh watermelon rind for approximately thirty minutes.

**DISCUSSION**

Nectar sources heavily utilized by *adjutrix* are, for the most part, general "butterfly flowers" as far as flower visitors are concerned. Faegri and van der Pijl (1966) remark that butterflies, generally speaking, "seem to prefer sucking nectar out of narrow tubes, frequently florets of Compositae." Nine of the eleven plants listed above have tubular flowers; seven are Compositae.

Blossom color preference has been shown in several butterfly species (Dronamraju and Spurway, 1960). The blossom colors of the most important nectar sources of *adjutrix* are yellow (*V. encelioides*, *H. annuus*, *H. latifolia*, *Z. hispida* and *V. dentata*), white (*V. virginica*, *E. texana* and *R. trivialis*) and red/yellow (*G. pulchella*). Blossom color of those common plants which were noted as being ignored are purple, blue and pink. Detailed quantitative field data will be required to determine whether these color differences between utilized (yellow-white) and non-utilized (blue-pink) are truly significant but a strong tendency has been demonstrated. Levin (1969) reported that both corolla color and outline influence the number of visits by butterflies to *Phlox* blossom. Work with *Heliconius charitonius* has revealed results that were interpreted as "spontaneous" color preferences (Swihart and Swihart, 1970) which may be modified by "conditioning" (Swihart, 1971). These reported "spontaneous" color preferences may have been due to conditioning, however, because wild-caught specimens were utilized in the original experiments. One would expect a preference for a particular flower or group of similarly shaped and/or colored flowers to occur through experience or "conditioning". Exceptions concerning instinctual, i.e. genetic, preferences will occur in highly co-evolved butterfly-plant systems (e.g. Gilbert, 1975).

Studies by Knoll (1926) and Ilse (1928) as reviewed by Norris (1936) has revealed variation in methods utilized by rhopalocera to locate nectar sources. Certain butterflies, e.g. *Papilio* and various pierids, appear to be attached to blossoms entirely by visual cues. Other species, e.g. charaxine nymphalid species, are guided to food sources entirely by olfactory cues. Ilse (1928) reports that most butterflies, however, utilize both classes of cues and therefore comprise an intermediate group in
continuum. Odor is probably largely utilized by \textit{adjutrix} to locate feces, carrion and puddles. Flowers may be located by a combination of the senses. Restriction of the major nectar sources to blossoms of white or yellow color classes indicates that vision is important. The near lack of utilization by \textit{adjutrix} of \textit{Lantana}, which is widely used by such visually-oriented butterflies as \textit{Papilio}, would tend to indicate that vision is not of prime importance. Alternately, the pigments present in \textit{Lantana} corollas may be quite different from the pigments present in corollas of the prime nectar sources.

There is no necessarily direct relationship between larval foodplant and adult nectar plants. However, observations of \textit{adjutrix} populations suggest that subtle interacting influences may exist between these energy sources for the two active phases of its life cycle.

Previously (Neck, 1973), I stated, “pure, isolated” stands of \textit{A. trifida} had never been observed to be infested by \textit{adjutrix}. Since that statement was published, a few broods have been found in isolated stands of giant ragweed. Such utilization is of uncommon occurrence. The important factor does not appear to be lack of adult female oviposition stimulation by either \textit{H. annuus} or \textit{V. encelioides} as previously suggested (Neck, 1973). Lack of concentration of adults due to absence of sufficient nectar sources for adult energy requirements seems to be the significant factor (See Neck, ms.) \textit{V. encelioides} is a prime source for \textit{adjutrix} and many other insects. \textit{H. annuus} is only a minor nectar source for \textit{adjutrix}, but plants associated with sunflower are important nectar sources. \textit{A. trifida} produces little, if any, nectar, being anemophilous (wind-pollinated). Therefore, adult \textit{adjutrix} are not as attracted to ragweed as to other larval foodplants because of lack of nourishment source. Larval infestations on giant ragweed tend to be heavier in areas where disturbance of the soil has allowed colonization by other annuals which are a nectar source for this butterfly.

Both \textit{Zermenia hispida} (H.B.K.) Gray and \textit{Viguiera dentata} (Cav.) Spreng. are rated as “occasional” larval foodplants of \textit{adjutrix} (Neck, 1973, ms.). \textit{Z. hispida} appears to be preferred to \textit{V. dentata} as a larval foodplant. (unpub. data). Such a preference is somewhat surprising as the genus \textit{Viguiera} is very closely related to \textit{Helianthus} (Heiser, 1969). The smell of crushed leaves of \textit{V. dentata}, to the human nose, is very similar to the smell of crushed leaves of \textit{Helianthus annuus}, the primary
larval foodplant of *adjutrix* in central Texas. One possible factor favoring utilization of *Z. hispida* is the lengthy blooming season (late spring to fall) of this species in contrast to the restricted blooming season (fall) of *V. dentata*. An adult female *adjutrix* which is attracted to flowers of *Z. hispida* is more likely to detect individuals of this species as acceptable ovipositional substrates than individuals of *V. dentata* which supplies no such visual attraction during much of the year.

Utilization of *Verbesina virginica* as a larval foodplant is quite limited but is more likely to occur during the fall months (unpub. data). As this period of the year is also the blooming period of this species, adult attraction to flowers for nectar could increase the utilization of this plant.

Adult resources are of such importance that they represent a potential limiting factor in the growth of *adjutrix* populations. While the presence of various sugars in nectar (Wykes, 1952; Van Handel et al., 1972) has long been known and/or assumed, recent work has revealed that nectar of many species contain amino acids (Baker and Baker, 1973) which could be utilized by butterfly visitors. Initial investigations have revealed that butterfly-pollinated blossoms tend to be richer in amino acids than bee-pollinated flowers (Baker and Baker, 1973b). The lack of protein supplied by nectar may limit the reproduction of *adjutrix* even if moderate amounts of larval foodplant material are available.

The effect of nectar shortage is not likely to be as dramatic in *adjutrix* populations as in populations of *Heliconius ethilla* which has intensively co-evolved with its pollen sources (Ehrlich and Gilbert, 1973). However, observations of natural populations of *adjutrix* indicate that nectar is extremely important, at times, as a limiting factor. Early 1970 was a time of abundant larval foodplant material, but very low population levels of *adjutrix* were present. As a result of deficient rainfall, a greatly reduced amount of nectar was available because few individual plants were blooming. A similar situation was observed in spring 1976.

**SUMMARY**

Adult resources (nectar, dung, carrion and mud puddles) of *Chlosyne lacinia* var. *adjutrix* as observed in central Texas are discussed. Numerous plants supply nectar to *adjutrix* but flowers with white or yellow corollas are favored. Primarily males are
attracted to dung, carrion and mud puddles. Relative roles of visual and olfactory cues in location of resources are discussed. An indirect relationship between larval foodplant utilization and adult resource utilization is postulated. At times adult resources are believed to be a limiting factor in the growth of populations of *adjutrix*.

**LITERATURE CITED**


———. ms. Ibid. II Additional larval foodplant data.


A NEW SUBSPECIES OF COLIAS PALAENO (LINNAEUS) FROM BAFFIN ISLAND, N.W.T., CANADA (PIERIDAE)\textsuperscript{1}

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In 1973, the senior author received a small number of dark Colias palaeno (Linnaeus) from the vicinity of Frobisher Bay, Baffin Island, Northwest Territories. In 1975 and again in 1976, additional specimens were received from the same locality. When examination specimens were sent to C. F. dos Passos, C. D. Ferris and the late Colin Wyatt, all agreed that the Frobisher Colias were indeed a new form of palaeno as described below.

Although dos Passos cited nominate palaeno in his 1964 Checklist, it is a European species as noted by Klots 1951, 1975 (in Howe). To date, all North American palaeno have been referred to subspecies chippewa Edwards [TL Restricted by F. M. Brown, 1973 to west end of Great Slave Lake, Northwest Territory, Canada]. The species is Holarctic and the range of chippewa in North America extends from Alaska across arctic and subarctic Canada to Labrador. Baffin Island, in which Frobisher Bay is situated, is of significant size and is physically removed from mainland North America. It is not surprising, then, that an isolated race of palaeno should develop under such conditions. The new subspecies is now described.

\textsuperscript{1} Published with the approval of the Director, Wyoming Agricultural Experiment Station as Journal Article no. JA 896.

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Colias palaeno baffinensis Ebner and Ferris, new subspecies


The holotype and allotype will be placed in the collection of the American Museum of Natural History, New York, N.Y.
Paratypes: 17 specimens, 9-12-viii-73; 54 males and 38 females 7-31-vii-75; 13 males and 4 females 26-vii-19-viii-76, all from Frobisher Bay, Baffin Island, N.W.T., Canada. All material is from the vicinity of the town of Frobisher Bay.

Paratypes are being distributed to the National Museum of Natural History, Washington, D.C. and the Canadian National Collection, Ottawa, Ontario, Canada. Additional paratypes are placed in the collections of the authors, C. F. dos Passos, Oscar Dorfmann, Gerald Hilchie and others. The Colin Wyatt collection contains examples of the new subspecies.

Figures 1 - 4

Diagnosis: The new subspecies differs from chippewa and the European and Japanese subspecies in the very narrow black borders of the males. This character is consistent and unvarying. The ratio of the wing width (measurement along the FW costal margin) to the border width at vein Cu2 is 7.4:1 in the male holotype of baffinensis; in the specimen of chippewa illustrated (Fig. 5), this ratio is 6.1:1. These values are typical of the two subspecies. The white ground color of the females is generally a more greenish white than in chippewa and the dark markings tend to be more intense. Ventrally the hindwings in both sexes exhibit much more dark suffusion than is found in chippewa or the European and Japanese races, and the HW discocellular spot is strongly rimmed with dark pink scales not found in the other subspecies. This melanic condition appears to be genetic and not related to thermo-regulation, as the melanism exhibited does not occur in chippewa taken in other localities at the same or higher latitude. The ventral surfaces are much darker than the specimen of chippewa figured by Howe (1975, Pl. 73, f. 15).

Two subspecies are recorded from western Europe: palaeno Linnaeus and europome Esper (Higgins & Riley, 1975). The latter is more brightly colored and the black border in the males is usually slightly wider than in typical palaeno. Specimens are shown in Figures 7-8. Nominate palaeno occurs in Fennoscandia, while europome ranges through portions of France and Germany.
EXPLANATION OF FIGURES

Figure 1.—Holotype male, *Colias palaeno baffinensis* Ebner and Ferris, Frobisher Bay (town), N.W.T., 10-viii-73, upper side. Label is red imprinted with black ink.

Figure 2.—Holotype male, underside. Label is white imprinted with black ink.

Figure 3.—Allotype female, *C. p. baffinensis*, Frobisher Bay (town), N.W.T., 19-xiii-76, upper side. Label is green imprinted with black ink.

Figure 4.—Allotype female, under side. Label is white imprinted with black ink.
Figure 5.—*C. p. chippewa*, male, Churchill, Manitoba, 11-vii-73, upper and under sides. Figure 6.—*C. p. chippewa*, female, same data as male in Fig. 5, upper and under sides. Fig 7.—*C. p. palaeno*, male, Les Fonts, H.A., France 2000 m, 20-vii-68, upper and under sides. Fig 8.—*C. p. palaeno*, female, same data as male in Fig. 7, upper and under sides. Figure 9.—*C. p. aias*, male, Asama Mts., Nagano, Japan, 2200 m, 24-vii-74, upper and under sides. Figure 10.—*C. p. aias*, female, Mt. Asama, Nagano, Japan, 2200 m, 23-vii-56, upper and under sides.
to Rumania. Various forms have been described which have been elevated to subspecific status by some workers. Petersen (1947) has discussed the variation that occurs in Scandinavian populations. Two *palaeno* subspecies are known from Japan. The larger and more heavily marked *aias* Fruhstorfer (Figures 9-10) occurs in the mountains of central Honshu, while *sugitani* Esaki is found in the Japanese Alps in the western portion of central Honshu. The differences between these two subspecies are slight.

Description: Male. DFW: uniformly dull yellow, discal spot usually absent, but sometimes faintly indicated; narrow dark borders widest at apex and uniformly black to inner margin; variable in breadth, and sometimes lightly invaded by light streaks along veins. Fringes pink with costal margin thinly outlined in gray-black, occasionally pink. Basal area near thorax dark.

DFW: dull yellow, tending to be more greenish than FW. Dorsal discocellular spot always evident and pronounced as a cream colored spot; black borders uniformly dark, always less in breadth than primaries and occasionally interrupted with lighter streaks along veins. Fringes pink, more pronounced along inner margin and adjoining outer margin. Basal area darkly suffused and radiating discally more extensively than in primaries.

VFW: less yellow than above, tending toward white along tornus to inner margin; dorsal margins apparent. Pink fringes more contrasted; pink costal margin with inward dark suffusion. Discal cell spot occasionally present; macular spots rare.

VHW: strongly contrasting with ground color of FW, dark olive green with intense dark suffusion throughout. Discal cell spot always well-developed, usually strongly rimmed with dark pink to brownish-red, occasionally dagger-shaped as in *C. hecla* Lefèbre. Discocellular spot much larger than in *chippewa*, more angular. Fringes pink.

Antennae red-brown above and beneath, pink with club bright yellow. Eyes brown to brownish-black.

Expanse: base of primary-to-apex: 17-21 mm.

Female. Dimorphic: white form prevalent (3.75:1 ratio) with some specimens intermediate between white and yellow. Of 43 females examined, 30 were white, 8 were yellow and 5 were intermediate.

DFW: white form: uniformly gray-white. Discal cell spot absent or inconspicuously present. Dark marginal border always
widest at apex, but variable in breadth, sometimes containing several light markings, either enclosed partially or completely by a dark band. Fringes pink. Basal area dark brown at thorax. Costal margin thinly lined with pink edge and sometimes suffused lightly with dark scales.

DHW: white form: contrasts slightly with FW, usually a more bluish-gray. Discal spot always evident and cream colored. Outer marginal black border narrow and always slightly developed. Fringes pink.

VFW: white form: more glossy white than DFW; apical area conspicuously tinged with greenish-yellow. Costal margin lined thinly in pink; fringes pink.


Antennae and eyes as in males. Thoracic hairs at base of FW strongly pink.

Expanse: 19-23 mm.

The yellow form is essentially identical to the white form, but with all of the white areas replaced by pale yellow.

Variation: Geographic variation cannot be considered, as all of the specimens have been taken in the same locality. Except for sexual dimorphism, the subspecies shows remarkably little variation. The observed variation relates to the shape of the VHW discocellular spot as noted above and the dorsal coloration in the males, which in a very few examples is a dark yellow. A female Colias specimen from Frobisher Bay appeared to reflect a hybrid between hecla and palaeno. The ground color was quite orange, but the dark markings were characteristic of palaeno.

Some specimens of palaeno from both Coppermine and Baker Lake, N.W.T. appear to be intermediate between chippewa and baffinensis. The dark rimming of the VHW discocellular spot is more prominent than in chippewa.

Baffin Island is one of the few areas in North America where pelidne Boisduval & LeConte and palaeno come into contact. Hovanitz (1950) discussed Baffin Island pelidne but palaeno was not recorded from the area. The dot on his distribution map (Figure 4) occurs in the vicinity of Lake Harbour which is west of both the town of Frobisher Bay and the body of water bearing the same name. Rare examples of pelidne phenotypes occur
in the vicinity of the town of Frobisher Bay and may represent migrants from a colony elsewhere on the island. In one character, the strongly rimmed discocellular spot, *baffinensis* is intermediate between the two species. In all other characters, however, it is clearly *palaeno*. Perhaps weak introgressive hybridization in the past has contributed to the discocellular spot character.

Bionomic Notes: The life history of *baffinensis* is unknown. Because of its swift and low flight, the butterflies are difficult to capture. It appears restricted to the lower elevations of the hills which surround Frobisher Bay. The butterflies occur in mixed dry-wet areas on slopes ranging from 300-500 feet (100-160 m) in elevation. They are absent from the hill tops and the dry lower regions of the slopes.

Arctic Cotton (*Eriophorum* sp., Cyperaceae), Fire Weed and Willow Herb (*Epilobium* sp., Onagraceae) grow in the general areas where *baffinensis* flies. It is sympatric with *C. nastes* Boisduval & LeConte and *hecla*. Five species of *Boloria* occur in the region along with *Lycaena phlaeas feildeni* (M'Lachlan) and *Plebejus aquilo* (Boisduval). In the higher and drier areas where *baffinensis* does not occur, *Erebia rossii* (Curtis) and two species of *Oeneis* may be taken.

LITERATURE CITED


DISTRIBUTION OF *SHIJIMIAEOIDES RITA*, ESPECIALLY S. R. *RITA* AND S. R. *COLORADENSIS* (LYCAENIDAE)

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From a study of *Shijimiaeoides* (=*Philotes*) recently completed (Shields, 1975, and in press), there are a series of fairly discrete, allopatric *S. rita* (Barnes & McDunnough) subspecies that appear to gradually intergrade into one another at the perimeter of their ranges. This cline is expressed through phenotype, valve teeth counts, and foodplant preferences. I.e., *S. rita emmeli* Shields grades into *S. r. coloradensis* (Mattoni) and *S. r. rita* on the east and south and *S. r. pallescens* (Tilden & Downey) on the west, and *S. r. pallescens* grades into *S. r. elvirae* (Mattoni) on the west (see Fig. 1). *S. r. rita* and *S. r. elvirae*, although separated by only 200 miles, are at opposite ends of this spectrum. Likewise, *S. r. pallescens* and *S. r. spaldingi* (Barnes & McDunnough) in the Stansbury Mts., Utah, are very distinct. Preliminary data on chromosome counts of *S. rita* are variable: *S. rita emmeli* has $n = 33$, and *S. rita pallescens* has $n = 34$ (2 localities) and $n = 25$ (2 localities) (T. C. Emmel & O. Shields, unpublished).

In Shields (1975), I move *spaldingi* to the position of a *rita* subspecies since it possesses cristae on the valves. In that paper, possible ties of *spaldingi* with *r. rita* and *r. coloradensis* are assumed on morphological and foodplant similarities. *S. r. emmeli* flies only in areas of Triassic-Jurassic age sands, while *S. r. spaldingi* occupies regions of Upper Cretaceous-Cenozoic age mostly, at higher, wetter elevations.

*S. r. pallescens* probably occurs in the little-collected region of central and southern Nevada to western Utah and north-
Fig. 1.—Distribution of *Shijimiaeoides rita* subspecies. 1 = *S. r. elvirae*, 2 = *S.r. pallescens*, 3 = *S.r. mattonii*, 4 = *S.r. emmeli*, 5 = *S.r. spaldingi* (from Shields, 1975, and in press). Black triangles = *S.r. rita*, black circles = *S.r. coloradensis*, half-shaded circles = intergrade populations. Arrows denote presumed evolutionary trends.
western Arizona, where *E. kearneyi* Tidest. is found on sandy soils. *E. plumatella* Dur. & Hilg. grows in southeastern California to Mohave Co., Arizona, but so far *S. r. elvirae* has failed to turn up there.

*Shijimiaeoides rita coloradensis* (Mattoni)

Number of teeth on terminal end (cucullus) of valve = 23 (1), 24 (3), 25 (2), 26 (4), 27 (3), 28 (3), 29 (2), 30 (2), 35 (1); N = 21, average = 26-27, from Kendrick and Silver Cliff. For distribution, see appendix.

HOST: *Eriogonum effusum* Nutt. var. *effusum*. COLORADO: Chaffee Co.: Chalk Creek Trout Farm, viii-11-65, 1♂ (J. Scott, JS), adult association (*Shields #138*), Scott, Ellis, & Eff (1968) report oviposition on *E. effusum* in Fremont and Lincoln Cos., and adults on this species in Saguache Co. At the Lowry Bombing Range, Arapahoe Co., Colorado, *r. coloradensis* averages small and is in association with an annual *Eriogonum* species on overgrazed range land (fide Shapiro).

*Eriogonum effusum* var. *effusum* (see Fig. 2) is found in Pennington Co., South Dakota, southward into Converse and southern Niobrana Cos., Wyoming, southward in southeastern Wyoming and adjacent extreme western Nebraska to central and east-central Colorado in the Front Ranges and on the Great Plains to northern New Mexico from eastern San Juan County eastward to Union County and with an outlying population in Socorro County, New Mexico, flowering from June to September (Reveal, 1971).

*S. r. coloradensis* is on wing from early July to late August.

*S. r. coloradensis* may be found in W. Kansas, SE Wyoming, and possibly W. Nebraska, as suitable habitats occur there or once did, although isolated and hard to locate in the farming areas according to Mike Fisher (*in litt.*). Scott, Ellis, & Eff (1968) give some records for *coloradensis*, repeated here.

Mattoni (1965) described *coloradensis* in detail for the first time and compared it with "rather similar" *rita rita*. From the results of this study, *coloradensis* and *r. rita* are distinguishable but closely related subspecies that intergrade in north-central New Mexico. Mattoni (1965) gives some distribution records for both.

*Shijimiaeoides rita rita* (Barnes & McDunnough)

Number of teeth on terminal end (cucullus) of valve = 21 (1), 22 (1), 23 (1), 24 (3), 25 (1), 26 (3), 27 (1), 28 (3), 29 (1), 31 (1); N = 16, average = 26, all from Ramsey Canyon.
Fig. 2.—Distribution of *Eriogonum effusum* var. *effusum* (from Reveal, 1971).
For distribution and hosts, see appendix.

Kendall (in litt.) says he found larvae of *rita rita* on *E. wrightii* in the flats below Panther Canyon, Big Bend National Park, Brewster Co., Texas, in 1971. In 1972, he found one larva on this plant in Green Gulch, and one larva and two adults on this plant in the approach to Pine Canyon, both in Big Bend N. P. Comstock (1953) described the egg of *rita rita* and compared it with *enoptes dammersi* (Comstock & Henne).

*E. wrightii* var. *wrightii* is found in southeastern California eastward to western Texas southward to northern Mexico, flowering from July to September. *E. polycladon* occurs from extreme south-central Utah and Arizona across New Mexico to western Texas southward to northern Mexico, flowering from July to October. *E. rotundifolium* ranges from northern New Mexico southward to Chihuahua, Mexico, eastward into central Texas and Coahuila, Mexico, flowering from April to October. (The above information was drawn from Reveal, 1969.) *E. corymbosum* var. *velutinum* is probably only casually used by *rita*, as varieties of the species *corymbosum* are widely used by *battoides ellisii* Shields on the Colorado Plateau (Shields, 1975).

Ssp. *r. rita* is on wing from mid August to late September.

*S. r. rita* may range into northern Mexico on *E. wrightii*, but in southeastern California, extreme southern Nevada, and central Arizona it is replaced by *S. enoptes dammersi*. In the vicinity of Cherry and Hillside, Yavapai Co., Arizona, both are sympatric and synchronic. North, west, and east of the range of *S. r. rita* in the vicinity of Prescott, *S. enoptes dammersi* flies over *E. wrightii* at Stanton, Jerome, Mingus Mtn., Sycamore Canyon, Poland Jct., Montezuma Well, Verde Hot Spgs., Tonto Natural Bridge, East Verde River nr. Payson, and Sunflower.

Clench (1967) mentions the Silver City, Grant Co., N. M., record and the Rio Verde Mts. being NE of Phoenix, for *rita rita*.

A specimen of *r. rita* from the Huachuca Mts., Cochise Co., Arizona, no date (AMNH) labelled "*P. rita* B. & McD., identified by Barnes & McDunnough," one male, bears a red label "Metatype"; also from this locality at AMNH are 1♂ 1♀ "ex Barnes Collection," the female bearing the date VIII-16-23. For a discussion of the taxonomy of *rita rita*, see Mattoni (1965) and Shields (1975).

The "*Philotes rita*" reported by Garth (1944) from the southern slopes of the Ajo Mts., Pima Co., Arizona, in April on
Eriogonum fasciculatum Benth. is most likely S. battoides martini (Mattoni).

Populations in Sandoval and Santa Fe Cos., New Mexico, are best characterized as clinal between r. rita and r. coloradensis. At 13 mi. N. Lemitar, Socorro Co., N. M., the majority of specimens are typical rita rita but some trend toward r. coloradensis. A short series from SW of Cuba, Sandoval Co., tends smallish and appears to be a mixture of rita rita, r. coloradensis, and r. emmeli. A large female S. rita ssp. from Uinta Canyon, Duchesne Co., Utah, viii-4-59 (J. C. Downey, CIS) is probably near emmeli or coloradensis although it is not readily classed in either category.

The S. rita complex is chiefly confined to the primitive species of the Eriogonum subgenus Eucycla, ranked as the most primitive subgenus by Reveal (1969). The Colorado Plateau in southeastern Utah is likely the place of origin of Eucycla by virtue of its concentration of endemic species, evolving in the Triassic-Jurassic sand-dune deserts (Shields, 1975). Following the phylogenetic Eriogonum classification of Reveal (1969, 1971), S. r. emmeli on primitive E. leptocladon Torr. & Gray would be the presumed originator of the S. rita complex, giving rise to S. r. pallescens on E. kearneyi and S. r. coloradensis on E. effusum (Fig. 1 & Table 1). In turn, S. r. pallescens produced S. r. elvirae on E. plumatella and S. r. mattonii Shields on E. microthecum Nutt., and S. r. coloradensis gave rise to S. r. rita on E. wrightii. The derivation of S. r. spaldingi on E. racemosum Nutt. from S. r. coloradensis would have occurred latest in the sequence, in Late Cretaceous or Early Tertiary times.

ACKNOWLEDGEMENTS

I wish to thank the following people for loaning material used in this study: (AM) Allyn Museum of Entomology, Lee D. Miller; (AMNH) American Museum of Natural History, Frederick H. Rindge; (RB) Richard Bailowitz; (CAS) California Academy of Sciences, Paul Arnaud and Thomas W. Davies; (CIS) California Insect Survey, Robert L. Langston and Jerry A. Powell; (CM) Carnegie Museum, Harry K. Clench; (SE) Scott Ellis; (CF) Clifford Ferris; (MF) Michael Fisher; Paul Grey; (KH) Keith Hughes; (RK) Roy Kendall; (NL) Noel La Due; (LACM) Los Angeles County Museum of Natural History, Julian P. Donahue; (MCZ) Museum of Comparative Zoology, Harvard, John Burns; (PO) Paul A. Opler; (KR)
Kilian Roever; (JS) James A. Scott; (CS) Charles Sekerman; Arthur M. Shapiro; and (YU) Yale University, Douglas C. Ferguson and Charles L. Remington. Mike Fisher assisted in constructing the distribution map of \textit{S. r. coloradensis}. Dr. James L. Reveal of the University of Maryland kindly identified all the \textit{Eriogonum} species and deposited voucher specimens at the National Arboretum in Washington, D.C. I thank John Lane for reviewing the manuscript and offering helpful suggestions. This work was supported in part by a grant from the Allyn Museum of Entomology (Arthur Allyn) and an N. S. F. Graduate Traineeship.

**LITERATURE CITED**


**TABLE 1.**

Variation in teeth number on terminal end (cucullus) of male valve in \textit{Shijimiaoides rita} subspecies (Shields, 1975, and in press).

<table>
<thead>
<tr>
<th>Subspecies</th>
<th>Average</th>
<th>Range</th>
<th>Sample Size</th>
</tr>
</thead>
<tbody>
<tr>
<td>\textit{S. rita coloradensis}</td>
<td>26-27</td>
<td>23-35</td>
<td>21</td>
</tr>
<tr>
<td>&quot; &quot; spaldingi</td>
<td>13-15</td>
<td>11-18</td>
<td>35</td>
</tr>
<tr>
<td>&quot; &quot; rita</td>
<td>26</td>
<td>21-31</td>
<td>16</td>
</tr>
<tr>
<td>&quot; &quot; emmelii</td>
<td>20-22</td>
<td>20-26</td>
<td>18</td>
</tr>
<tr>
<td>&quot; &quot; pallescens</td>
<td>17-19</td>
<td>11-24</td>
<td>41</td>
</tr>
<tr>
<td>&quot; &quot; mattonii</td>
<td>—</td>
<td>15-19</td>
<td>3</td>
</tr>
<tr>
<td>&quot; &quot; elvirae</td>
<td>16</td>
<td>13-19</td>
<td>10</td>
</tr>
</tbody>
</table>
Shijimiaeoides rita coloradensis (Mattoni)

**DISTRIBUTION** (viewed 27♂ gen. from 13 localities):

**COLORADO:**
- **Adams Co.**: 1 mi. E Bennett, 5750', viii (MF).
- **Alamosa Co.**: entrance to Great Sand Dunes Nat'l Mon., viii-17-64, 1♂ (J. F. Emmel, AM).
- **Arapahoe Co.**: 0.4 mi. E Boxelder Crk., 6000', ca. 20 mi. SE Denver, viii (MF);
- **Lowry Bombing Range, 6000', viii-5-73, 3♂ 1♀** (A. M. Shapiro, AM).
- **Chaffee Co.**: Salida, vii-29-67, 2♂ (J. Scott, JS).
- **Cheyenne Co.**: Aroya (spelled "Arroyo"), viii-21-34, 1♀ (C. L. Remington, YU).
- **Custer Co.**: 1/4 mi. NW Ben West Hill, vii-25-65, 5♂ (J. Scott, JS, PO); 1/2-1 mi. S Silver Cliff, viii-7 & 8-65, 15♂ 2♀ (J. Scott, JS, LACM); 2 mi. N Silver Cliff, vii-18-65, 1♂ 1♀ (J. Scott, JS); 1.5 mi. NW Westcliff, vii-25-65, 1♂ 1♀ (J. Scott, JS).
- **Elbert Co.**: 5-6 mi. E Kiowa, 6300', viii (MF).
- **El Paso Co.**: 10 mi. E. Colorado Springs, Hwy. 94, 6000' (MF); Fountain Valley School & vicinity east (F. M. Brown, MF); along Hwy. 94 E. of #14, including nr. Ellicott, Rush, Yoder (MF); locals between Hwy. 94 & north to Hwy. 24 (Rush to Ramah) along the "Ramah" Hwy. and west to Peyton and north on county road toward Elbert, slightly into Elbert Co., distribution fairly continuous from Hwy. 94 north to near Kiowa, first week of August 1973 (MF).
- **Fremont Co.**: nr. Cotopaxi, vii-5-69, 1♂ 1♀ (MF); 1/2 mi. NW to 1 mi. W Democratic Mtn., viii-20-65, 1♂ 1♀ (J. Scott, JS); 2 mi. N Hillside, viii-24-68, 1♂ 3♀ (J. Scott, JS);
- **Hillside Cemetery, viii-17-65, 5♂ 2♀** (J. Scott, JS, LACM); 1/2 mi. E Hillside Cemetery, viii-17-65,
1♀ (J. Scott, JS); Hillside School, viii-17 & 23-65, 1♂ 8♀
(J. Scott, JS, LACM); Kuntz Gulch, 1 mi. W Cotopaxi, viii-16-65,
2♂ 2♀ (D. Eff, JS, LACM); mouth of Kuntz Gulch, viii-15-65,
12♂ 17♀ (J. Scott, JS, PO, LACM); McCoy Gulch, 6800',
 viii-16-65, 2♂ 4♀, (J. Scott, JS, PO, LACM).
Lincoln Co.: nr. Jct. 94 & 71 on Hwy. 94 (MF); 2-5 mi. E Arriba & I-70 east
of there in Kit Carson Co., 5000-5100', viii (MF).
Rio Grande Co.: "D" Hill, Del Norte, vii-6-68, 1♀ (S. Ellis, SE).
Saguache Co.: 2 mi. SW Villa Grove, vii-18-66, 5♂ 6♀
(J. Scott, PO, JS); 4 mi. S Villa Grove, vii-22-69, 6♂ 13♀,
(J. Scott, JS). Washington Co.: 5 mi. W Last Chance, 5500',
 viii (MF). Weld Co.: Hilltop along I-80S (now I-76) 2 mi.
S. of Empire Resvr., 5000' (MF); IBP site, E. of Nunn, vii,
and vic. of Pawnee Buttes (International Biome Project,
Research Facility, fide Fisher).
WYOMING: Albany Co.: T.15N., R.73W., 7500', vii-9 &
S Bitter Creek, vii-15 & viii-1-42, 2♂ 2♀ (CM).

Shijimiaeoides rita rita (Barnes and McDunnough)

DISTRIBUTION (viewed 43♂ gen. from 15 localities):
ARIZONA: Cochise Co.: Huachuca Mts., viii-16-23, 2♂ 1♀ (AMNH);
Ramsey Canyon, Huachuca Mts., viii, ix, 106♂ 68♀ (CIS, NL, LACM,
 AMNH, AM, PO, JS); Ramsey Canyon, 2 mi. SW of Route 92, 5300',
Huachuca Mts., ix-7-59, 3♂ 1♀ (K. Roever, KR). Maricopa Co.:
Cherry, viii-19-53, 2♂ 1♀ (J. W. Tilden, AMNH); Cleator, viii-24-74,
1♂ (R. Bailowitz, RB); 1 mi. N. Granite Dells, viii-16-76,
1♂ 1♀ (R. Bailowitz, RB); 1 mi. S Hillside, ix-20-71, 2♂
Peeples Valley, viii-24-76, 1♂1♀ (R. Bailowitz, RB); 6 mi. NW Prescott, vili-21-76, 1♀ R. Bailowitz, RB);
(C. Goodpasture, AM); Humboldt, viii-26-53, 3♀ (J. W. Tilden, AMNH);
Yarnell, viii-21-60, 7♂4♀ (K. C. Hughes, KH, PO, CIS).
ca. 11 rd. mi. NW Cloverdale, ca. 5500', Coronado Nat'l For.,
Peloncillo Mts., viii-24-70, 1♀ (S. L. Ellis, O. Shields, & M. E.
Toliver, AM). Grant Co.: Silver City, viii-13-?, 1♂
(J. B. Wallis, CM). TEXAS: Brewster Co.: 21 mi. S Alpine,
ix-20-70, 2♀ (J. Scott, JS); Big Bend Nat'l Park, ix-25 & 27-71,
ex larvae, 1♂1♀ (R. O. & C. A. Kendall, RK); Panther Canyon,
Big Bend Nat'l Park, ix-25-71, 1♀ (R. O. & C. A. Kendall, RK);
Pine Canyon, Big Bend Nat'l Park, ix-27-72, 1♂1♀ (R. O. &
C. A. Kendall, RK).
HOSTS AND DISTRIBUTION: Eriogonum wrightii Torr. ex
Benth. in Dc. var. wrightii. ARIZONA: Cochise Co.: jct. of
Ramsey Canyon Rd. & Hwy. 92, 6.0 mi. S of jct. of Hwys. 90 & 92,
SE of Ft. Huachuca, vii-28-70, one larva on flowers, adults
taken commonly here in past (O. Shields) (Shields #125).
Yavapai Co.: Mayer, viii-26-70, 1♂2♀ (C. A. Sekerman, CS),
adult assoc., (area visited with L. Martin) (Shields #181).
NEW MEXICO: Catron Co.: 1/2 mi. S Alma, 5600', ix-11-72,
1♂ (O. Shields, AM), adult assoc. (Shields #246). Hidalgo Co.:
22.0 rd. mi. S Animas, ca. 4900', along Hwy. 338, Animas Valley,
viii-24-70, 5♂1♀ (S. L. Ellis, O. Shields, M. E. Toliver, AM),
adult assoc. (Shields #153); ca. 13-14 rd. mi. NE Lordsburg, along
Hwy. 90, viii-25-70, 31♂ 22♀ (S. L. Ellis, O. Shields, M. E. Toliver, AM), adult assoc. (Shields #155), although most adults at this locality were roosting on Eriogonum polycladon (Shields #154).

Eriogonum polycladon Benth. in DC. NEW MEXICO: Grant Co.: W edge of city limit of Central, along Hwy. 180, viii-26-70, 3♀ (O. Shields, M. E. Toliver, AM), oviposition (Shields #157); 18 rd. mi. WNW of Silver City, along Hwy. 180, viii-26-70, 2♂ 1♀ (O. Shields, M. E. Toliver, AM), adult assoc. (Shields #158).

(Clinal populations between rita rita and rita coloradensis):

Eriogonum effusum Nutt. var. effusum. NEW MEXICO: Sandoval Co.: 2.0 rd. mi. SW of jct. 44 & 85, ca. 5000', along Hwy. 85 (SW of Bernalillo), viii-19-70, 4♂ 2♀ (S. L. Ellis, O. Shields, M. E. Toliver, AM), adult assoc. (Shields #150); 8.0 rd. mi. SW of jct. of 197 & 44 (SW of Cuba), along Hwy. 197, viii-18-70, 4♂ 2♀ (S. L. Ellis, O. Shields, AM), adult assoc. (Shields #149); 18 rd. mi. NW San Ysidro, along Hwy. 44, viii-18-70, 1♂ (S. L. Ellis, O. Shields, AM), adult assoc. (Shields #148).

Santa Fe Co.: 8.4 rd. mi. NE of Cerrillos, ca. 6100', along Hwy. 10, viii-17-70, 1♂ 1♀ (S. L. Ellis, O. Shields, AM), adult assoc. (Shields #144); 10.8 rd. mi. NE of Cerrillos, ca. 6200', along Hwy. 10, viii-17-70, 1♂ 1♀ (S. L. Ellis, O. Shields, AM), adult assoc. (Shields #143). Socorro Co.: 13 rd. mi. N of Lemitar, ca. 5000', at La Joya State Game Refuge exit of Hwy. 25, viii-21-70, 25♂ 6♀ (S. L. Ellis, O. Shields, M. E. Toliver, AM), oviposition (Shields #151), and adults also in association with Eriogonum rotundifolium Benth. in DC. (Shields #152). Eriogonum corymbosum Benth. in DC. var. velutinum Reveal. NEW MEXICO: Santa Fe Co.: 1.1 rd. mi. SW of Cerrillos, ca. 5800', along Hwy. 10, viii-17-70, 1♂ (S. L. Ellis, O. Shields, AM), adult assoc. (Shields #145).
The Sedge-Feeding Marsh Butterfly and skipper fauna of eastern and central North America shows many interesting distributional phenomena which were analyzed in an earlier paper (Shapiro, 1971). That investigation grew out of the observation that the Broad-Winged Skipper, Poanes viator (Edwards), was distributed in a variant of the Coastal Plain — Great Lakes pattern familiar to plant geographers. At that time there were no confirmed records in the Mississippi Valley from northern Iowa, Illinois and Indiana (all within the glaciated area) to west-central Mississippi (in the Mississippi Embayment, part of the Coastal Plain province). Many experienced collectors were contacted in the search for such records. In their absence it was inferred that P. viator, like Euphyes bimacula (Grote & Robinson), had dispersed northward along the Atlantic Coastal Plain from a glacial refugium in the Deep South and subsequently colonized the Great Lakes region from the east, perhaps via the Hudson-Mohawk connective across New York State. At the conclusion of that study I stated that “new information may well require the re-evaluation of many of the ranges discussed in this paper.” Such information is now at hand for P. viator. The critical new records are:

IOWA: Muskrat Slough, Jones County, 5 July 1971, leg. S. Miller (Miller, 1972). This is at the terminal moraine in east-central Iowa.

MISSISSIPPI: Bluff Lake, Oktibbeha County, 19 August 1972, and 9.3 mi E Louisville, Winston County, 12 September 1972, both leg. C. T. Bryson (Bryson, *in litt.*)


When these records are added to the map of the range of *P. viator* given in Shapiro (1971), they provide a strong case for the northward postglacial dispersal of *P. viator* on both sides of the Appalachians (but not in them, as in *Speyeria idalia* (Dru-ry)).

The sharp phenotypic and biological disjunction between *viator* populations across the well-documented distributional break in New York State led to the naming of a subspecies, *zizaniae* Shapiro — the larger Coastal Plain entity. Now that a few relict Mississippi Valley populations are known it is possible that the subspecies will be found to intergrade clinally from north to south in this part of the range. All of the records reported here are based on short series, and nothing can yet be said in any statistical sense. However, the opportunity is now present to test the alternative hypotheses for the origin of the Great Lakes populations, both of which are possible. If *viator* entered the Great Lakes from the south and then dispersed eastward to its present limit in central New York and north-central Pennsylvania, the easternmost populations — being the most recent and farthest removed from the source — might be expected to differ the most from *zizaniae*. If *viator* entered the Great Lakes from the east and then spread south — and westward, the southern-most Great Lakes populations might be expected to be the most differentiated from *zizaniae*.

If the Great Lakes - Coastal Plain pattern is potentially explicable in this species by double migration (with the two groups of populations never coming into contact across New York), the same may be true for many or most of the species discussed in Shapiro, 1971. The best evidence will always be extant relict populations. Many populations of marsh species might have been eradicated in the Mississippi Valley during the Xerothermic interval, giving rise to the present pattern of apparent disjunction. All range extensions for the species discussed in the 1971 paper are of potential biogeographic interest and deserve wide publicity.
LITERATURE CITED


Fig. 1. — Distribution of Poanes viator (Shapiro, 1971), with new records shown by large dots. Dotted line in northeast indicates distributional break between coastal subspecies zizaniae Shapiro and nominate viator.
THE BUTTERFLIES OF
CRATER LAKE NATIONAL PARK, OREGON
J. W. TILDEN\(^1\) and DAVID H. HUNTZINGER\(^2\)

ABSTRACT

Seventy-eight species of Rhopalocera are recorded for Crater Lake National Park, Oregon. The list is presented in annotated form, with a discussion of conditions in the Park, and of certain of the records.

INTRODUCTION

Most of the specimens on which this paper is based were collected in 1957-1962 inclusive. Most of the field work was done by Huntzinger. Tilden collected in the area in June, 1960, and in August, 1962, adding a number of previously unrecorded species. The original intent had been to do considerably more field work before writing the results, but Huntzinger received another assignment, and other commitments prevented Tilden from doing further research in the area. It seems best to present the results now, so that such work as has been done will not be lost. It seems certain that this list includes the major number of butterfly species to be found in the Park. Others will no doubt be added in time, but it is hoped that the present list will provide a basis for future work.

In Crater Lake National Park, most of the butterfly species are concentrated in a relatively few favored areas. Experience taught that large parts of the Park are depauperate in butterfly fauna.

The dry area north and west of the lake yielded very few species or specimens. The peaks (unlike similar areas in many other mountain masses) support few species not also found at more moderate levels. Emergence dates, however, are naturally later for the same species at higher elevations.

The least collected area of Crater Lake National Park is the

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\(^2\) National Park Service
extreme southwest corner. This lies at a lower elevation than the rest of the Park, and if new records are sought, this should be a likely area. One only record is admitted of a species not actually taken or seen anywhere in the Park. This is *Habrodais grunus* (Bdv.), taken just outside the West Entrance. This species should occur inside the Park, where oaks are found.

Because of the policy of the National Park Service, large series of most species were not collected. There are also several species that were taken only one to a few times. This may reflect either scarcity of the species, or incomplete collecting. Relative abundance was estimated from the number of times a species was seen in the field. Many localities were explored, from which no specimens were taken. Such localities are not mentioned by name. In those cases in which a species was found in a number of localities, and seems to be well-distributed in the Park, this is mentioned under the species annotation.

The senior author has checked all specimens that he could examine. Only a few were unavailable for study. The physical basis for this list is housed in four collections, at least for the present: The Collection of Crater Lake National Park, located at Park Headquarters; The Collection of San Jose State University, San Jose, California; the small private collection of David H. Huntzinger; and the collection of J. W. Tilden. The most of the Crater Lake specimens now in this latter collection will later be placed in the California Academy of Science's collection.

The sequence of families and species is primarily that of dos Passos, 1964. The determinations are those of the senior author, who assumes responsibility for them. Some populations seem to merit confidence at the subspecific level, others do not. Mention is made in each case where the population does not seem to fit any usual named entity.

**PREVIOUS WORK**

The first specimens retained in the collection of Crater Lake National Park were taken by H. A. Scullen in 1930-1931. Ten of these specimens remain. It is not known if there were originally more. There is also one specimen taken in 1931 by F. Lyle Wynd.

Crater Lake Nature Notes for 1951 has a two-page article (pp. 10-11) on Crater Lake Butterflies, and lists 18 species, some of which were not taken by the present authors. No specimens were found as a basis for this list, which is by Donald C.
J. W. TILDEN and D. H. HUNTZINGER

Lowrie. Therefore the determinations cannot be checked, but there seems to be no good reason to doubt them. The article also describes outbreaks of the California Tortoise-shell (*Nymphalis californica*) for 1930-1931, and for 1951. The bulk of the specimens in the collection of Crater Lake National Park were placed there by the junior author during the years 1957-1960.

**BUTTERFLY HABITATS OF THE PARK**

Crater Lake National Park is situated in Klamath County, Oregon. Elevations within the Park range from 4500 ft. at the South Boundary and 5956 ft. at the North Entrance, to 8938 ft. at the summit of Mt. Scott, located in the northeast part of the Park. The high points around the Rim of the Lake exceed 8000 ft. The greater part of the Park lies between 6000 and 7000 ft. in elevation.

In spite of its name, Crater Lake is not in fact a crater, but a caldera, caused by the collapse inwardly of Mt. Mazama. Portions of the present Rim have been glaciated. Much of the entire Park has been covered deeply by pumice and scoria, ejected at the time of the collapse. On such soils the flora is sparse and lacking in variety, with few butterfly food plants present. As a result, the butterfly fauna of such areas is correspondingly poor. However, certain butterfly species, the food plants of which are present, reach good populations in these areas.

It is believed that much of the flora was destroyed by the glowing avalanche of pumice and scoria at the time of the collapse. This has been discussed by Tilden (1963b). The flora that has regrown is uneven in distribution and its density seems to depend inversely on the depth to which pumice covered the surface. Areas of light pumice fall recovered more rapidly and more completely, and now have the densest and most varied flora, and the greatest variety of butterfly species as well.

The Park is drained by several small streams, which run down the slope and out of the Park. Sand Creek, running east out of the Park at the now unused South Entrance, runs through an area of heavy pumice fall, and supports along its course a rather meager number of plant species. Annie Creek, running south out of the Park, flows through an area that has largely recovered, especially where it reaches the South Boundary. The canyon of Annie Creek is at times rather spectacular, and there are small meadows and groves of stream-side trees. This area, which lies slightly east of the road on which one enters from the south, and which extends from Annie Creek Station south
out of the Park, is the most favored part of the Park for butter-
flies, and several species were taken only here.

On the South Boundary on the margin of Annie Creek there
are meadows and forest glades, mixed with sagebrush and
_Eriogonum_, where fly several species that barely enter the Park
at this point. The dirt road that runs east across Annie Creek at
the South Boundary leads into an area of mixed coniferous
forest, meadow, streamside vegetation, aspen grove, and sage-
brush, offering the greatest number of habitats in the Park, and
showing at present little effect of pumice fall.

Small montane meadows occur at several localities in the
Park. Among these are Pole Creek Meadows, the meadows
below Vidae Falls, and those in the vicinity of Kerr Notch.
These meadows support populations of certain butterflies. Other
favored localities are near Park Headquarters, and on the
glaciated portions of the Rim, where pumice is absent or less
evident.

The Pumice Desert supports very few butterflies, and these
appear to originate elsewhere. Few if any seem to develop there.

The higher points around the Rim of the Lake may be
considered subalpine in nature. The butterfly species in these
localities are few, but some species occur in fair numbers.
_Speyeria egleis_ is found here more commonly than it is else-
where in the Park.

An annotated list of the butterfly species so far known to
occur in Crater Lake National Park follows. Collectors’ names
are given in parentheses. References to Lowrie’s 1951 paper are
cited as Lowrie (1951). As stated above, no specimens are
known to support these records. For the collections, the follow-
ing abbreviations are used: Crater Lake National Park Collec-
tion, CLNP; San Jose State University Collection, SJSU; J. W.
Tilden, JWT; David H. Huntzinger, DHH.

Hesperiidae

1. _Ochlodes sylvanoides_ (Bdv.)
   South Boundary, 11.VIII.62 (Tilden) (JWT). Very com-
   mon, both sexes, though apparently not previously reported
   in the Park.

2. _Polites sabuleti_ (Bdv.)
   South Boundary, 11.VIII.62 (Tilden); Pole Creek, 25.VII.59;
   Annie Springs, 16.VII.57, 30.VII.58, 3.VIII.59; Park Head-
   quarters, 28.VII.57; “C. L. N. P.”, 27.VIII.58 (all Hunt-
zinger); East Boundary, 11.VIII.62 (Tilden). MacNeill, who examined all of the skippers for this study, noted that these specimens represent an unnamed population of *Polites sabuleti*. However, considering the variability of this species, it seems unnecessary to add any more names. The senior author has specimens of three other populations of *P. sabuleti* that he has for many years been reluctant to name.

3. *Polites sonora* (Scud.)
South Utility Area, 1.VII.59 (Huntzinger, JWT). So far as known, these fresh specimens (2♂♂) are the only ones so far examined from the Park. MacNeill notes that they seem to represent a blend zone between *P. sonora sonora*, and *P. sonora siris*, being darker below than usual *sonora*, but by no means as dark as *siris*.

4. *Hesperia harpalus oregonia* (Edw.)
Well-distributed throughout the Park in the meadows. Greatly attracted to flowers. All records are for late July and August. Determination by MacNeill.

5. *Hesperia juba* (Scud.)
South Boundary, 11.VI.59 (♂); Annie Springs, 18.VI.59 (♀), (both Huntzinger, JWT), both much worn. The apparent scarcity of this species may be an artifact of collecting. It may fly earlier than most of the collecting was done.

6. *Carterocephalus palaemon* (Pallas)
South Boundary, 11.VI.59 (Huntzinger). Taken within the Park only the one time. The location of this specimen is in doubt; it was not seen in any of the collections.

7. *Pyrgus ruralis* (Bdv.)
South Utility Area, 11.VI.59 (♂), 14.VI.59 (♂); Vidae Falls, 25.VI.58 (♂) (all Huntzinger) (CLNP); South Boundary, 22.VI.60 (♂) (Tilden, JWT). Found sitting on the ground in openings.

8. *Erynnis icelus* (Scud. & Burg.)
South Boundary, 11.VI.59 (♂♂) (Huntzinger); same, 22-23.VI.60 (3♂♂) (Tilden); Annie Creek Road, 9.VII.64 (♀) (Tilden); all JWT. Found streamside, in vicinity of willows and *Populus*. Determination by J. M. Burns.

9. *Erynnis persius* (Scud.)
South Boundary, 11.VI.59 (♂) (Huntzinger); same, 22-23. VI.60 (4♂♂) (Tilden) (all JWT). Found together with *Erynnis icelus*. In New England, Scudder found that *E.
persius larvae ate willow and Populus. The food plants for this Oregon population are unknown. Burns labelled these as E. persius complex.

10. *Erynnis pacuvius lilius* (Dyar)
Annie Springs 4.VIII.58 (♂); South Boundary, 11.VI.59 (♂) (both Huntzinger); same, 22-23.VI.60 (♂ ♀) (Tilden) (all JWT). Found in the lower southern part of the Park where its presumed food plant, Ceanothus velutinus, is common and forms an understory in the Ponderosa Pine forest.

11. *Thorybes mexicana nevada* (Scud.)
Pole Creek, 6.VII.59 (♂); Park Headquarters, 17.VII.59 (♀) (both Huntzinger, both JWT). This species appears to be quite scarce in the Park. These specimens were taken at an intermediate elevation. Why it should seem to be absent from higher elevations is not clear.

Papilionidae

12. *Parnassius clodius claudianus* Stichel
Fairly common, especially around the Rim, where in places may be found quantities of its food plant, *Dicentra*. Two species of *Dicentra*, *D. formosa* and *D. uniflora*, occur in the Park; *D. formosa* is the larger and more common species. At the time this work was done in Crater Lake NP, the life history of *P. clodius* was not known. In the Sierra Nevada of California, at intermediate levels, the larvae, which are purplish black with yellow markings (and look a good deal like certain millipedes), may be found in the day time under the leaves at the base of the plants. The subspecies there is usually considered to be *P. c. sol*.

Lowrie (1951) called the Crater Lake *Parnassius*, *baldur*, but they seem closer to *claudianus*.

13. *Papilio zelicaon* Lucas
Reported by Lowrie (1951). Seen, but not taken, by Huntzinger. There is no specimen in the CLNP collection.

14. *Papilio rutulus* Lucas
South Boundary, 20.VII.58 (Huntzinger, CLNP); same, 22.VI.60 (♂) (Tilden, JWT).

15. *Papilio eurymedon* Lucas
South Boundary, 20.VII.58 (Huntzinger, CLNP). The Papilios are not as scarce as the few records would imply. Much of the Park is steep and offers few opportunities to take these soaring butterflies.
Pieridae

Whitehorse Camp, 25.VIII.30 (H. A. Scullen) (CLNP); “C. L. N. P.”, 22.VIII.58 (Huntzinger, CLNP); listed by Lowrie (1951). This late species is probably more common after most of the summer collectors have gone.

17. *Pieris beckerii beckerii* Edw.
Listed by Lowrie (1951). The specimen does not seem to be in the Park collection. However, there seems to be no reason why the species should not occur in the Park, since it has been found in the lower Sand Creek Area outside the Park.

The Watchman, 13.VII.59 (Huntzinger, CLNP). The single record may be late for this usually early species.

Sun Notch, 8.X.53 (R. C. Wood, CLNP); Kerr Notch, 11.VIII.62 (Tilden, JWT); Lowrie, 1951, lists *Pieris protodice vernalis* Edw.

Near Union Peak, 13.VII.59; Park Headquarters, 10.VII.59 (both Huntzinger). Normal-looking *P. occidentalis*, not form *calyce* Edw.

North Junction, 10.VII.68 (Huntzinger). This species should be more easily found earlier in the season.

22. *Pieris rapae* (L.).
Park Headquarters, 20.VII.59 (Huntzinger); Kerr Notch, 11.VIII.62 (worn) (Tilden) (both JWT). It is evident that this introduced pest has invaded the Park.

Taken by Scullen, Park Headquarters, 2.IX.30 and East Entrance, 28.VIII.30. Listed also by Lowrie, 1951. Taken several times and seen frequently during the present study. Found throughout the Park. All specimens seen were the summer form *amphidusa* Bdv.

24. *Anthocharis sara flora* Wright
Sun Creek, 23.VI.60 (♀) (P. A. Fosterla); Park Headquarters, 15.VI.60 (♂) (Huntzinger) (both JWT). Others were seen but not taken.
Lycaenidae

25. *Habrodais grunus herri* Field
Two miles west of Crater Lake National Park, Rogue River National Forest, 1.IX.59 (1♂ 2♀, worn) (JWT). This species, the larvae of which feed on oaks, especially *Quercus chrysolepis*, may occur in the southwest corner of the Park. For this reason, these specimens from just outside the Park are included here.

26. *Satyrium behrii behrii* (Edw.)

27. *Satyrium saepium* (Bdv.)
Park Headquarters, 31.VII.59 (Huntzinger, CLNP). This species, the larvae of which feed on various species of *Ceanothus*, should be more prevalent than this one record would indicate.

28. *Satyrium californicum* (Bdv.)
South Boundary, 11.VIII.62, common but worn (Tilden, CLNP, JWT). Should be common in its proper season, along the southern part of the Park.

29. *Incisalia augustinus iroides* (Bdv.)
South Boundary, 11.VI.59, South Utility Area, 14.VI.59 (both Huntzinger, CLNP). These two records, from the southern limits of the Park, are all for this species. It should be more widely distributed.

30. *Incisalia eryphon eryphon* (Bdv.)
This pine-feeding species is the most generally distributed hairstreak in the Park. It is very unobtrusive, sitting on pine foliage or visiting flowers of Pussy Paws (*Calytridium umbellatum*).

31. *Mitoura spinetorum* (Hew.)
South Boundary, 22-23.VI.60 (Huntzinger & Tilden, CLNP, JWT). Several specimens, at flowers of *Calytridium*. All were worn. The food plants, species of Dwarf Mistletoe (*Arceuthobium*) are common, but the butterfly is quite irregular in distribution.

32. *Mitoura nelsoni* (Bdv.)
South Boundary, 23.VI.60 (Tilden, JWT). One only, a ♂ in good condition, at flowers of *Calytridium*. A close examination of the area yielded no others. Associated with Incense Cedar, the presumptive food plant.

33. *Callophrys lemberti* Tilden
Arent Peak, 3.VII.58 (Huntzinger, CLNP); The Watchman, 12.VII.59 (Huntzinger, JWT); South Boundary, 22.VII.60 (Tilden, JWT). This recently recognized species seems not to be abundant anywhere in its known range. It should be looked for at high elevations. The South Boundary specimen is unexpected, and is badly worn. It may be referable to some other species, but its condition makes identification uncertain. It is left here since no other species of the genus than *lemberti* is found in the Park.

34. *Lycaena heteronea gravenotata* Klots
South Boundary, 11.VIII.62 (Tilden, JWT). A single ♀, worn but recognizable. The heavy spotting UNH indicates that it represents *gravenotata* Klots, which has been taken at Diamond Lake, just north of Crater Lake. Collecting in July should locate fresh material in the Park.

35. *Lycaena editha* (Mead), near *montana* Field
South Boundary, 22.VI.60 (Tilden, CLNP); same, 11.VIII.62 (Tilden, JWT). Both males, at flowers of Pussy Paws (*Calyptridium*). Widely distributed in the West, this species should occur more commonly and at higher elevations than these two specimens indicate.

The most common copper in the Park, often found at flowers in the meadows of the Annie Creek drainage, flying from late June to August. The specimens from the park are not entirely typical *mariposa*, but show darkening, especially of the outer edge both above and below, and are somewhat intermediate to *penrosae* Field.

37. *Lycaena nivalis nivalis* (Bdv.)
Park Headquarters, 31.VII.59 (Huntzinger, DHH); Vidae Falls, 28.VIII.59 (Huntzinger, JWT); Kerr Notch, 8.VIII.58 (Huntzinger, CLNP); same, 10.VII.59 (Huntzinger, DHH); same, 11.VIII.62 (Tilden, JWT); also listed by Lowrie, 1951. The few records are clustered on the south and east shoulders of Mt. Mazama, from Park Headquarters to Kerr Notch, at median elevations. These localities show less effect from the pumice fall. These are nearer to *nivalis* from the Sierra Nevada, than they are to *brownii* dos Passos, which occurs further north and east.

38. *Lycaena helloides helloides* (Bdv.)
South Boundary, 20.VII.58 (Huntzinger, CLNP, JWT); same, 11.VI.59 (Huntzinger, JWT); same, 22-24.VI.60 (Huntzinger & Tilden, JWT); Lost Creek, 11.VI.59 (Huntzinger,
DHH); North Entrance, 9.VII.58 (Huntzinger, CLNP). Common along the southern edge of the Park.

39. *Lycaena cupreus cupreus* (Edw.)
South Boundary, 22-23.VI.60 (3♂♂ 1♀) (Tilden, JWT). The finding of this species, usually associated with high elevations, at a moderate elevation and in one locality only, is a bit puzzling. All were found on a small sandy stream-side flat, visiting flowers of *Calyptridium*. Others were seen but not taken.

40. *Lycaenides argyrognomon ricei* (Cross)
This large showy Blue is one of the characteristic species of the Park, and apparently of the Cascades in general. It flies from late June to at least mid-August, and may be found along roadsides as well as in the meadows. The subspecific name *ricei* is used, following Nabokov (1949), but the late F. Chermock informed me (in Litt.) that he had seen the type of *ricei* Cross, and that in his estimation it was a specimen of some subspecies of *Plebejus icarioides*, and for that reason, he had proposed the name *fretchini* Chermock for the Oregon population of *argyrognomon*.

41. *Plebejus saepiolus* (Bdv.)
Common in the moist meadows on the south and east shoulders of the mountain. These appear to represent an unrecognized population. The males are large and brightly colored; the females are completely brown, and have the submarginal lunules of the hind wing developed in most individuals. However, there are so many recognizably different populations of *saepiolus* that it seems useless to propose more names at present.

42. *Plebejus icarioides* (Bdv.)
In Crater Lake National Park, as in many parts of the western states, this is the commonest and the most ecologically tolerant of the larger “Blues”. It is always associated with perennial lupines, and is usually found wherever these grow. The males of the Crater Lake population have wider dark borders than most, and look most like the Arizona subspecies, *P. i. buchholzi* dos Passos.

43. *Plebejus lupini* (Bdv.)
Annie Springs, 4-6.VIII.58 (Huntzinger, CLNP); Kerr Notch, 8.VIII.58 (Huntzinger, JWT); The Watchman, 13.VII.59 (Huntzinger, JWT); South Boundary, 23.VI.60 (Tilden, JWT). Lowrie (1951) lists *Plebejus acmon* (West. & Hew.), which may occur in the Park, or he may have referred to
the insect here treated as *lupini* Bdv. Without specimens, this point cannot be settled. The females from Crater Lake are unusually large and dark.

44. **Agriades aquilo podarce** (F. & F.)
Boundary Springs, 5.VII.57 (Huntzinger, JWT); Pole Creek, 8.VIII.58 (Huntzinger, CLNP); same, 6.VII.59 (Huntzinger, JWT, DHH); same, 23.VII.59 (Huntzinger, DHH); Annie Springs, 6.VII.58. This species is found only in very wet or marshy meadows, and so far has been taken in the Park only in the Annie Creek drainage. The Crater Lake population resembles *podarce* from the Sierra Nevada of California, much more closely than it does *megalo* McDunnough from further north.

45. **Everes amyntula** (Bdv.)
South Boundary, 23.VI.60 (2♀♂) (Tilden, JWT); South Utility Area, 23.VI.60 (♂) (Huntzinger, JWT). The male from the South Utility Area is much larger than the two females from the South Boundary.

46. **Shijimiaeoides battoides oregonensis** (B. & McD.)
Generally distributed in the Park, flying in June at the South Boundary, and in August on the slopes of Mt. Scott. It is fairly common, but inconspicuous, staying close to its food plants, which in the Park seem to include several species of perennial *Eriogonum*.

47. **Glaucopsyche piasus piasus** (Bdv.)
Pole Creek, 23.VI.59 (Huntzinger); South Boundary, 23.VI.60 (2♂♂) (Tilden, JWT). This is seldom a common species.

48. **Glaucopsyche lygdamus columbia** Skin.
Rather common; a number taken and others seen. It flies a little earlier than the other large blues, and is worn by mid-July. Found flying along trails as well as over the meadows.

49. **Celastrina argiolus echo** (Edw.)
Fairly common, flying early in the year for this elevation, the records mostly in early and mid-June; no records after early July, and these worn. This usually multivoltine species would appear to be one-brooded in the higher mountains of the west.

**Nymphalidae**

50. **Limentitis lorquini** (Bdv.)
Annie Springs, 19.VI.58 (Huntzinger, CLNP); Vidae Falls, 29.VII.59 (Huntzinger, CLNP); Pole Creek, 11.VIII.62 (Tilden, JWT). Reported by Lowrie (1951). More common than these few records indicate. The brick red of the wing tips is reduced, approaching the subspecies (or form) *burrisonii* Maynard.

51. *Adelpha bredowii californica* (Butler)
South Boundary, 20.VI.58 (Huntzinger, CLNP); The Watchman, 14.VIII.59 (Huntzinger, CLNP). This species would not be expected to occur commonly in the Park, because of the absence from much of the region, of the oaks with which it is associated. However, it is a wide-ranging species that sometimes occurs as a straggler far from its point of origin. It should be found regularly in the southwest corner of the Park.

52. *Vanessa atalanta rubria* (Fruhst.)
Park Headquarters, 10.VIII.60 (Huntzinger, CLNP, 2 specimens). The single record of this conspicuous butterfly may indicate actual scarcity in the Park.

53. *Cynthia virginiensis* (Drury)
Listed by Lowrie (1951). No specimens seem to exist for Crater Lake National Park. Lowrie (p. 10, second paragraph, line 4) mentions the "Painted Lady," but *Cynthia cardui* does not appear on Lowrie's list on p. 11.

54. *Cynthia cardui* (L.)
North Entrance, 30.VII.57 (Huntzinger, JWT); same, 17.VII.58 (Huntzinger, CLNP); Annie Springs, 10.VIII.58 (Huntzinger, JWT). Reported by Huntzinger to be very common in Crater Lake National Park during the summer of 1958. This was an outbreak year, and a migration year for this species over the southwestern United States. The Painted Lady is commoner in the Park than the few records show.

55. *Cynthia anabella* Field
Huntzinger reports seeing this species several times when he was not collecting. He also has seen a colored slide taken by Richard Brown when Brown was an Assistant Park Naturalist in 1957. It is also reported by Lowrie (1951). However, to date no actual specimen for the Park is known to exist.

56. *Junonia coenia* (Hbn.)
Huntzinger has seen a colored slide of this species, taken in the Park. No specimen seems to exist. It is entirely possible
that this and the two previous doubtful species may occur within Crater Lake National Park, but evidence in the form of specimens would be desirable.

57. *Nymphalis californica californica* (Bdv.)
Huntzinger found this species in outbreak numbers everywhere in the Park in 1958. Tilden found similar outbreak numbers in all parts of the Park that he visited in 1962. The *Ceanothus* was nearly defoliated in many places. Lowrie (1951) describes similar outbreaks for 1930 and for 1951. It appears that Crater Lake National Park is subject to outbreaks of the California Tortoise-shell, as are so many other places in the Pacific States. These outbreaks are in irregular cycles (gradations) and the number of years from peak to peak is not predictable.

58. *Nymphalis milberti furcillata* (Say)
Near Park Headquarters, 22.VIII.30 (Scullen, CLNP); Sleepy Hollow, 15.VI.58 (Huntzinger, CLNP); Top of Wineglass, 5.VII.57 (Huntzinger, JWT); reported by Lowrie (1951) (as *Aglais milberti* Godt.). *N. milberti* occurs in all the western states in the mountains. Overwintering adults appear as soon as the snow is melted.

59. *Nymphalis antiopa* (L.)
Annie Springs, 18.VI.59 (Huntzinger, CLNP). Reported by Lowrie (1951) (as *Aglais antiopa* Linn.). This species must be more common in the Park than records show.

60. *Polygonia faunas rusticus* (Edw.)
Near Park Headquarters, 29.VIII.30 (Scullen, CLNP); South Boundary, 23.VI.60 (Tilden, JWT). Reported by Lowrie, 1951. The South Boundary specimen is much worn, and may be overwintered. The small numbers may reflect the type of collecting. It should be more common, especially along the Annie Creek drainage.

61. *Polygonia zephyrus* (Edw.)
The common Anglewing of the Park, found in forest openings and along trails, often in the vicinity of its food plants, *Ribes* spp. (Currant, Gooseberry). An August specimen is freshly emerged. Individuals noted in June and July are worn, and probably overwintered.

62. *Chlosyne palla* (Bdv.)
South Boundary, 20.VII.58 (Huntzinger, CLNP); same, 23.VI.60 (4♂♂1♀) (Tilden, JWT). So far taken in an area of small extent, in the immediate vicinity of Annie Creek where it runs out of the Park. The habitat is moist
and overgrown. These specimens are not referred to any subspecies. They resemble whitneyi Behr, from the Sierra Nevada of California, more than they do nominate palla.

63. *Chlosyne hoffmanni segregata* (B. & McD.)
Quite generally distributed in the Park, the common checker-spot, from South Boundary to near the Rim at Kerr Notch. It flies in meadows and forest glades, and a wide range of dates indicates a rather long flight period, with later emergence at higher elevations. Since segregata was described from the vicinity of Crater Lake National Park, these specimens should be quite typical.

64. *Phyciodes campestris* (Behr)
Park Headquarters, 31.VII.59 (Huntzinger, CLNP); Meadow just below Vidae Falls, 13.VII.59 (Huntzinger, CLNP). This seems to be an uncommon species in the Park. The few specimens appear closest to montana Behr.

65. *Phyciodes mylitta* (Edw.)
Union Peak, 13.VII.59 (Huntzinger, CLNP); Park Headquarters, 17.VII.59 & 26.VIII.59 (Huntzinger, CLNP). Rather oddly, these records are for localities well within the Park and at fair elevations, not from the lower levels.

Arent Peak, 3.VII.58 (Huntzinger, CLNP); East Rim, near base of Mt. Scott, 11.VIII.62 (Tilden, JWT, 1♂). The meager records suggest that this is not a common insect in the Park. Both captures are for high elevations and late in the season. While these are here referred to lawrencei Gund, there is some question as to whether they may be remingtoni Burdick. There may even be some doubt that remingtoni Burdick is distinct from lawrencei.

South Utility Area, 22.VI.59 (♂) (Huntzinger, JWT); Pole Creek, 22.VI.59 (2♂♂) (Huntzinger, JWT); same, 11.VIII.62 (♀) (Tilden, JWT); South Boundary, 23.VI.60 (2♀♀) (Tilden, JWT). So far this species has been taken in the Park only in the Annie Creek drainage. It has been found only in lush streamside situations, but is locally common. A specimen exists in the CLNP collection, data unknown.

68. *Speyeria coronis* (Behr)
Pole Creek, 24.VII.57 (♀) (Huntzinger, JWT); South Boundary, 24.VI.60 (♀) (Tilden, JWT). These are the only records for the Park, and S. coronis must be considered
rather uncommon in the area. Outside the Park, along Sand Creek, specimens were taken by Tilden in 1957 and in 1962 (June). All specimens resemble *snyderi* Skinner very closely, and might be referred to this subspecies.

69. *Speyeria zerene* (Bdv.)
South Utility Area, 12.VII.59 (Huntzinger, CLNP); Park Headquarters, 31.VII.59 (Huntzinger, CLNP); South Boundary, 23.VI.60 & 11.VIII.62 (2♂♀ 2♂♀) (Tilden, JWT); Vidae Falls, 10.VIII.62 (♂) (Tilden, JWT); Kerr Notch, 11.VIII.62 (♀) (Tilden, JWT). The several specimens show great variation. Some closely resemble subspecies *conchyliatus* from northern California; others are as light as some specimens from eastern Oregon. This species typifies the range of variation seen in certain *Speyeria* populations in the Crater Lake region, as noted by Tilden (1963).

70. *Speyeria callippee* (Bdv.)
Stewart Falls, 17.VII.57 (♂) (brown disc) (Huntzinger, JWT); North Gate, 9.VII.57 (♂) (green disc) (Huntzinger, JWT). The only two so far found within the boundaries of the Park. This species is quite common east out of the Park in the Sand Creek Basin. The Stewart Falls specimen would fit a series of *liliana* H. Edw. from Lake Co., CA. The North Gate specimen has a dull green disc with the ground color showing through, and resembles the dull green population of the arid Oregon interior. Such variation in two specimens of *S. callippee* shows the futility of attempting subspecific determinations of *Speyeria* from regions inhabited by unstabilized populations, such as are found in the volcanic regions of interior Oregon.

71. *Speyeria egleis* (Behr)
The most common *Speyeria* in the Park, and the only one found in numbers at higher elevations. *S. egleis* from the Sand Creek basin east out of the Park are quite variable, but those taken inside the Park are quite uniform in appearance, and seem referable to *oweni* (Edw.), closely resembling specimens from Mt. Shasta.

72. *Speyeria atlantis dodgei* (Gunder)
North Entrance, 30.VII.57 (♀) (Huntzinger, JWT); Vidae Falls, 28.VII.59 (Huntzinger, CLNP); same, 11.VIII.62 (♀) (Tilden, JWT); South Boundary, 23.VII.60 (♂) (Tilden, JWT); same, 11.VIII.62 (♂♀) (Tilden, JWT). Found in suitable habitats here and there in the Park. Several seen and not taken.
73. *Speyeria hydaspe* (Bdv.)
Pole Creek, 24.VII.59 (♂) (Huntzinger, JWT); Vidae Falls, 28.VII.59 (Huntzinger, CLNP). These seem to be the only records for the Park. The specimens are a bit lighter than *purpurascens* H. Edw. from northern California.

**Danaidae**

74. *Danaus plexippus plexippus* (L.)
There is a specimen in the CLNP collection. This butterfly must occur in the Park. It has most likely been neglected in the search for less conspicuous species.

**Satyridae**

75. *Coenonympha california eryngii* H. Edw.
Annie Springs, 18.VI.59 (Huntzinger, CLNP); South Boundary, 22.VI.60 (Tilden, SJSU, JWT). The small numbers probably indicate, not scarcity, but that this insect flies earlier, before most collectors arrive for the summer. It seems to be absent from higher elevations.

76. *Cercyonis pegala hoepis* (Behr)
Pole Creek Meadow, 15.VIII.30 (Scullen, CLNP); South Rim Crater Lake National Park, 6.VIII.30 (Scullen, CLNP); reported by Lowrie, 1951. Not taken by Tilden & Huntzinger. Lowrie’s inclusion may be on the basis of Scullen’s specimens, which are listed in the Crater Lake NP Collection, and in Lowrie, as *alope* Fab.

77. *Cercyonis oeta oeta* (Bdv.)
The most common and widely distributed satyr in the Park. It flies from late June into August, in almost all of the more open and arid habitats.

78. *Oeneis nevadensis nevadensis* (F. & F.)
South Utility Area, 14.VI.59 (Huntzinger, JWT); South Boundary, 20.VII.58, worn (Huntzinger, CLNP); same, 22-24.VI.60, common (Tilden & Huntzinger, SJSU, JWT); Vidae Falls, 10.VIII.62, badly worn (Tilden, JWT). Except for the one record from Vidae Falls, this species seems to be found in the Park only along the southern limits, where it flies in openings and glades in coniferous forest. It is known to have a two year cycle. In the Crater Lake area its periods of abundance are on the even-numbered years.
ACKNOWLEDGEMENTS

The senior author wishes to thank the National Park Service for collecting permits which made a part of this study possible. He also wishes to thank Bruce W. Black, Chief Park Naturalist at the time that the last of the field work was done, for his help and cooperation.

REFERENCES


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THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

published by
The Lepidoptera Research Foundation, Inc.
at
2559 Puesta Del Sol Road, Santa Barbara, California 93105

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PHOTOPERIOD AND TEMPERATURE IN PHENOTYPE DETERMINATION OF PACIFIC SLOPE PIERINI: BIOSYSTEMATIC IMPLICATIONS

ARTHUR M. SHAPIRO
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FOR THE PAST DOZEN YEARS I have been studying seasonal phenotype determination in the family Pieridae. As you all know, many butterflies and moths which have several generations a year display seasonal “forms” or phenotypes, often so different in appearance that they were described as different species; their conspecificity was proven only by breeding them, one from the other, or preferably by split-brood experiments in which different rearing conditions elicited different phenotypes in the progeny of single females. From the earliest days of evolutionary biology down almost to the present, such seasonal variation was subsumed by the familiar Victorian word “polymorphism.” In the past decade, however, particularly since the advent of “electrophoretic genetics” — in which allelic frequencies are estimated by examining the mobility of enzymes in an electric field for a suitably large sample of the population in question — the word “polymorphism” has been increasingly appropriated by geneticists to refer specifically to variation which has a genetic, rather than an environmental, basis. This restriction can be traced to E. B. Ford’s now classic definition of polymorphism as the occurrence in a population of more than one allele at a locus, such that the rarest allele is too common to be maintained solely by recurrent mutation. What, then, are we to call seasonal phenotypic variation which is under en-

1 Read by John H. Lane at the 23rd annual meeting of the Pacific Slope section of the Lepidopterists’ Society, Nevada State Museum, Carson City, Nevada, July 2, 1976.
environmental control? We can call it just that; or we can use Ernst Mayr's convenient word *polyphenism*, coined in parallel to polymorphism, and defined as "the occurrence of several phenotypes in a population, the differences between which are not the result of genetic differences." Studies in various laboratories — H. J. Muller's and Rolf Reinhardt's in East Germany, Ward Watt's at Stanford, and our own — are establishing how widespread and complex a phenomenon seasonal polyphenism is in the Lepidoptera. We are finding, much as the great developmental geneticist C. H. Waddington foresaw twenty-some years ago, that developmental plasticity provides an alternative to genetic polymorphism which allows natural populations to cope with a variable environment in an economical, adaptive way. We are also finding that studies of the physiological mechanisms determining phenotype allow us to interpret the history of a specific group's climatic and geographic adaptation — and this in turn gives us clues bearing on the perennial problems of species diversity and community stability.

Mayr pointed out in 1961 that any adaptation can be studied from the standpoint of *proximate* or *ultimate* causality. Any time we ask a "why" question in biology, we are really asking several questions at different levels all at once. Let us consider the familiar Gray-Veined White, *Pieris napi* (sens. lat. — if you buy B. C. S. Warren's single-character taxonomy you can leave the room now). Everyone knows, or thinks he knows, that Californian *napi* are seasonally diphenic — they have a spring phenotype with black veins, known as *venosa*, and a summer one without black veins, called *castoria*. I'll show in a minute or three that you don't really know that, but first let's ask "Why does *Pieris napi* have two seasonal phenotypes?" There are several possible answers. At the proximate, or immediate, level we have physiological mechanisms which translate from some environmental cue to an eventual phenotype by affecting melanin pigment synthesis and deposition. The most complete studies of such systems have been done not on *Pieris napi* but on the Nymphalid *Polygonia c-aureum* in Japan by Hidaka, Aida, Fukuda, Endo, and Takahashi. Their papers, beginning 13 years ago, are not well known in this country; most English-speakers are still laboring under the misapprehension fostered by E. B. Ford in a casual remark in *Butterflies*, that the seasonal forms of *Polygonia* are food-determined. Actually *P. c-aureum* is broadly representative of seasonally polyphic butterflies in
that the primary factor controlling adult phenotype is larval exposure to daylength (photoperiod), with some input from temperature. That shouldn’t be too surprising. In middle latitudes photoperiod is a much more reliable predictor of season than temperature is: the daylength is essentially the same on every June 25, but the temperature may be wildly different. These Japanese workers have shown with painstaking thoroughness that long days interacting with high temperatures stimulate certain cells in the larval brain to produce a hormone, which travels through the nerves to the corpora cardiaca of the pupa, whence it is released into the hemolymph (blood) where it induces development of the summer adult phenotype. But that is not the end of the story: the dark, summer animals breed immediately, but light, winter animals are quite uninterested in sex — and Endo wanted to know why. It turns out that ovarian maturation and female pheromone (sex-stimulant chemical) production are also under neurosecretory control — the relevant hormone being daylength-dependent. In *Pieris napi*, unlike *Polygonia* species, there is no adult hibernation and sexual behavior is not at issue. But the hormonal regulation of adult phenotype is probably very similar.

We have now studied about a dozen *napi* populations from the Yukon to central New Mexico, including a variety of Californian ones. It appears that adult phenotype in the Gray-Veined White is under the control of photoperiod, temperature, and certain genes, interacting in complex — and immensely interesting — ways. The basic situation in nature is that pupae which go into programmed dormancy — “diapause” as it is known to physiologists — produce dark-veined, i.e. spring phenotypes, and those which develop directly, without diapause, produce light-veined, or summer ones. This applies even to populations which are normally single-brooded in nature, with “obligate” diapause — we can prevent diapause by appropriate rearing conditions, which lie outside the range of real environments the animals would encounter afield. Since the primary control of diapause is photoperiodic, until quite recently it was assumed that phenotype was physiologically coupled to development — that the hormonal control of diapause also affected pigment synthesis and deposition. But I now no longer believe that — at least, not quite. The blame for my disillusionment lies with August Weismann.
You may remember Weismann’s name from your genetics classes; he first enunciated the dogma of the isolation of the germ cells from environmental influences — the critical repudiation of Lamarckian heredity, the inheritance of acquired characteristics. He was one of the greatest of the early Darwinians, and until his failing eyesight forced him to become a theoretician, he worked on Leps, including *Pieris napi*. Now, Weismann was a monstrous clever fellow: 70 years before Mayr he talked about multiple levels of causality, and he even discussed seasonal polyphenism from that standpoint. When he bred *napi*, biological photoperiodism hadn’t been thought of yet; the influence of daylength on insect development remained to be discovered in the 1940s by Danilyevskiy in Russia. So Weismann figured temperature was the environmental cue, and designed experiments accordingly; and he got ambiguous results, at least with Pierids. Since we now know these critters to be strongly photoperiodic, I felt it necessary to repeat Weismann’s experiments under controlled daylengths to determine whether there really might be a temperature effect. Not having central European *napi*, I settled for coastal central Californian.

It turned out that certain chilling treatment applied to *non-diapause* pupae quite unambiguously produced the spring phenotype! The identical treatment was much less effective on Inner Coast Range material. This difference among stocks underscores the rather obvious fact that physiological mechanisms have a genetic basis — the interface between Mayr’s proximate and ultimate levels of causality. But how is one to account for the apparent redundancy of photoperiodic and temperature mechanisms? The fact is that the photoperiodic mechanism has never been unambiguously demonstrated at all! Diapausing pupae will never eclose unless chilled for a number of weeks. Although we know that temperature treatment has no effect on adult pigmentation when the pupa is in deep diapause, what if diapause intensity gradually decreases, allowing for increasing sensitivity to environmental cues? This is precisely the clinical picture of diapause being advanced by Tauber and Tauber at Cornell (see their recent review in *Annual Review of Entomology*). We are currently testing this hypothesis by monitoring the day-to-day metabolism of diapausing *napi* pupae and subjecting them to various temperature regimes when they begin to wake up.
Underlying whatever proximate, i.e. physiological, answers to our “why” question are genetic answers, and these reflect a history of natural selection. The ecological basis of selection — the adaptive value — is the ultimate level of causality. Ward Watt at Stanford, formerly at Yale, followed up on Leigh and Smith’s work and demonstrated the efficacy of seasonal phenotypes in body-temperature regulation of the Orange Sulphur, *Colias eurytheme*. Our work points in the same direction for *Pieris napi*. One striking aspect is the consistent sexual difference in *napi* — in all populations and in both seasonal phenotypes, males are more heavily marked than females. Field studies suggest that this confers an adaptive advantage in that the darkest males can become active at lower temperatures in the morning, giving them first crack at newly-emerged virgin females. (*Pieris napi*, like most butterflies, has a diel periodicity of emergence, with most eclosions occurring shortly after sunrise even at low temperatures.)

I hope the preceding remarks have given you some feel for the directions in which polyphenism studies are going. But I’d like to wind up with some comments on their biosystematic implications for *Pieris napi*, because I have a petition in to the International Commission on Zoological Nomenclature that is apt to raise some eyebrows when it appears in the Bulletin. I might add, with no snobbery intended, that I commit taxonomy only when dragged into it kicking and screaming by the biology.

I said several minutes ago that everyone “knew” that Californian *napi* had two seasonal phenotypes, *venosa* and *castoria*. Last year Bob Langston suggested at these meetings that they might be two different species; our work dispels that notion. Clearly, they are seasonal phenotypes produced by the same genome responding to different environmental cues. The problem — as Langston first pointed out to me — is that what we have been calling “castoria” isn’t what Reakirt described as *castoria* in 1867! Here is Reakirt’s O.D.:

Size and form of *Pieris oleracea*, Harris.
*Male*, upper side pure white, inner half of costa of primaries, and base of both wings, strewn with a few dark atoms; a rounded black spot in the medio-superior interspace of the fore wings... no other markings; fringes white, expanse 2-2.12 inches.
Underneath immaculate white; a faint yellowish tinge on the apex of the primaries, and along the costa of the secondaries.

Body black, with whitish hairs below; antennae black, with incomplete white annulations interrupted above. Club yellowish, or yellowish brown at tip.


Herman Strecker, in 1877, was the first to consider *castoria* as the second brood phenotype of double-brooded California *napi*; in this he was followed by W. H. Edwards in his (1881) revision of the *napi* group, and by most authors since. Yet very, very few specimens collected in the wild from double-brooded populations come near to this description. Almost all of them have some dark scaling on the veins beneath, at the apex of the fore- or hindwing above, or whatever. When it turned out that the so-called type of *castoria* at the Field Museum was a pseudotype (in fact it is a typical second brood specimen from a coastal population, matching Strecker's sense but not Reakirt's description of *castoria!*), it was exceedingly difficult to find prospective neotypes that matched the O.D. Now, as it happens the O.D. matches *perfectly* the normal phenotype produced by non-diapause pupae of interior, single-brooded California *napi*. Confused? Let's backtrack a bit.

Our experiments concur with field data in suggesting that there are two subspecies of *napi* in central California. Subspecies *venosa* is found on and near the coast, in places subject to summer fog; it is best developed from San Francisco south. It is at least partially double-brooded, with the two seasonal phenotypes. In the hot, dry, fogless Inner Coast Range and on the west slope of the Sierra Nevada occurs a single-brooded subspecies, showing only a spring phenotype in nature. The oldest available name for this population is usually considered to be *microstria* Comstock, 1925. The spring phenotype of *microstria* is lighter than that of *venosa* reared under identical conditions. When diapause is artificially prevented, *microstria* will make a summer phenotype in the lab, and it matches perfectly Reakirt's O.D. of *castoria* — being lighter than the summer phenotype produced by *venosa*. Recently we have found a couple of places, in cold canyons, where *microstria* is naturally double-brooded and makes a summer phenotype just like our lab one. This raises an uncomfortable taxonomic specter.
Suppose it could be shown that what Reakirt had was not a second brood coastal specimen at all, as everyone has now assumed for 99 years, but one of the very rare interior ones? Then the oldest valid name for the inland subspecies would be *castoria*, and we would be obliged to use it; the familiar usage for the second-brood phenotype of *venosa* would be scrapped, and the name *microstriata* would sink into oblivion.

And everyone would hate me.

Where did Reakirt's type come from? "California," says the O.D. But F. Martin Brown has shown that Reakirt never collected in California; he got his stuff from Lorquin. Where did Lorquin get it? Unfortunately there is still too little evidence at hand to reconstruct his itineraries very well; we know he collected in both *venosa* and *microstriata* country, though. I was wrestling with this when I noticed that, in the same paper as he describes *castoria*, Reakirt also describes *Pieris yreka*. Now, this is rather an infamous description since it can only apply to *rapae* — and the type, at the Field Museum, is a spring *rapae* — thus implying that *rapae* was in California before 1867, which is inconsistent with the idea of a single introduction in southern Canada about 1860 — but we wander. The point is that, although the type locality of *yreka* is not specified, it's a good bet it was the town of Yreka. I checked this out in that invaluable resource, Gudde's *California Place Names*, and found that Yreka was named in 1852. Well, if Yreka was the type locality of *Pieris yreka*, was Castoria the type locality of *Pieris castoria*? Here's what Gudde says about the town of Castoria: Castoria = French Camp, San Joaquin County . . . known as Castoria (Latin for beaver) from 1850-59 . . . formerly the headquarters of French beaver trappers on the San Joaquin River . . . ! Could Lorquin, a Francophone, stay away from such a place?

Alas, there are to be no toptotypes. 125 years ago French Camp was in a maze of riparian woodland and marshland; today it has been thoroughly civilized, and there are no *napi* there. In fact, there are no *napi* currently known anywhere on the floor of the Great Central Valley. Still, on climatic and biogeographic grounds we can infer that any population at French Camp must have been of the interior subspecies — thus our taxonomic nightmare becomes real.

So I have asked the Commission to do something very odd. I have asked them to suppress the name *castoria* under the
Plenary Powers for synonymy but not homonymy. If they do, it will be unavailable for use at the subspecific (or specific) level, but can continue to be used informally, as a seasonal phenotype name, the way it is now and has been for 99 years. It was necessary to take this roundabout route because *microstriata* hasn’t been used often enough in the literature to qualify for conservation under Article 79 — yet common sense demands that nearly a century of usage of *castoria* not be upset just because some dingbat at Davis finds that there’s more to *napi* than meets the eye. Like I said, I do taxonomy only under compulsion.

Now do you see why I’m not here?
ANTENNAL SENSILLA OF SOME CRAMBINAE

J. A. KAMM

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ABSTRACT

When the antennal sensilla of several common species of Crambinae were studied with the scanning electron microscope, trichoid sensilla were dominant; the primary function of Crambinae antennae may therefore be detection of semiochemicals. Sensilla chaetica (mechanoreceptors) were well represented and would be useful to the moths for orienting within the grass canopy. Sensilla coeloconica and styloconica were present, but sensilla auricillicum were absent. The sensilla of Crambinae are simple and functional relative to those of many Lepidoptera and appear to be designed for orientation within grassland habitat.

Many Lepidoptera explore a large habitat (e.g., a forest) and make relatively long flights in response to various stimuli that are perceived by antennal sensilla of various sizes, arrangements, densities, and sculpturing (Callahan, 1975). Adult Crambinae (the grass-feeding larvae are commonly referred to as sod webworms), in contrast, make short, erratic flights (3-5 meters) within or slightly above the canopy of grass and also explore the interior of the canopy by walking. The male perceives and orients to the sex pheromone of females during flight (Banerjee and Decker, 1966; Kamm, 1974). Both sexes, particularly females heavy with eggs, often fall to the ground in response to mechanical stimuli and feign death rather than attempt escape by flight. Since information about the antennal sensilla of the Crambinae would help to understand the mechanism by which adults perceive their environment, a study was made to determine the types of sensilla on the antennae of several common species of Crambinae and to relate the types with known functions to the behavior of the moths.

1 Contribution of the Agric. Res. Serv. USDA in cooperation with the Agric. Exp. St., Oregon State Univ. Technical Paper No. 4492 of the latter.

2 Mailing address: Department of Entomology, Oregon State University, Corvallis, OR 97331.
MATERIALS AND METHODS
Study moths were reared in the laboratory from insects collected near Corvallis, Ore. (Kamm 1970). The antennae of five species of both sexes were excised from newly emerged adults, cut into pieces of several segments, and mounted on a specimen stub with fast drying silver paint. The mounted antennal segments were then coated with a thin layer of gold-palladium alloy and observed with the scanning electron microscope. In this way, the entire circumference of the flagellum of females could be scanned by using a single segment, but two segments had to be used in observing both sides of the male sensilla since they surround most of the flagellum. Segments from five antennae of each sex were examined for each species. Measurements of sensilla were made at random locations on the antennae but sensilla that arose from or were adjacent to the scale area of the flagellum were avoided because they were often of atypical shape and size. The terminology of Schneider (1964) was used to classify the sensilla described herein. The species studied were: Crambus tutillus McDunnough, Chrysoteuchia topiaria (Zeller), Pediasia trisecta (Walker), Crambus leachellus cypri dalis Hulst, and Tahama bonifatella (Hulst) all of which are commonly found in the grasslands in the Willamette Valley of Oregon.

OBSERVATIONS
The antennae of all five species were typical setiform and had a scape, pedicel, and variable number (45-72) of flagellar segments. Also, the spine-like Bohm bristles were present in groups on the scape and pedicel of all species. In general, the number of sensilla on each flagellum decreased toward the distal end of the antenna. The shape of the flagellum was variable and different among species and sexes. Males always had more sensilla per flagellum, and they covered an estimated 75 percent or more of the surface area of the flagellum; the remaining area on all species except P. trisecta was covered with scales, but P. trisecta had some scales among the field of the sensilla. The sensilla on females covered 50 percent or less of the surface area of a typical segment. This difference between sexes was just discernible on the high power (45 x) of a binocular microscope with good resolution. The net-like sculpturing on the flagellum was similar among species but lacked the rough textured terrain common on the antennae of some Lepidoptera (Jefferson et al., 1970). The range in size (μ) of sensilla is given in Table 1.
Table 1. Range in size (µ) of 10 randomly selected sensilla on the antennae of five species of Crambinae.

<table>
<thead>
<tr>
<th>Type of sensilla</th>
<th>C. topiaria</th>
<th>C. tutillus</th>
<th>C. l. cyprientalis</th>
<th>T. bonifatella</th>
<th>P. trisecta</th>
</tr>
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<tr>
<td>Trichoid I</td>
<td>27 - 32</td>
<td>25 - 34</td>
<td>27 - 35</td>
<td>24 - 30</td>
<td>29 - 32</td>
</tr>
<tr>
<td>Trichoid II</td>
<td>12 - 21</td>
<td>15 - 25</td>
<td>11 - 18</td>
<td>11 - 20</td>
<td>11 - 20</td>
</tr>
<tr>
<td>Coeloconica (width of pit)</td>
<td>7 - 8.5</td>
<td>5 - 7</td>
<td>6 - 7</td>
<td>8 - 10</td>
<td>9 - 11</td>
</tr>
<tr>
<td>Styloconica² (elevation from base flagellum)</td>
<td>10 - 12</td>
<td>7 - 9</td>
<td>7 - 10</td>
<td>11 - 14</td>
<td>7 - 12</td>
</tr>
</tbody>
</table>

1 Measurements made with millimeter rule from micrographs.
2 Reliable measurements of the sensory cone not possible.
Two types of trichoid sensilla were distinguished: type I (T-I) was curved and sharply hooked at the tip; type II (T-II) was shorter than type I, was slightly curved though it lacked the pronounced hook at the tip, and was almost always adjacent to type I sensilla (Fig. 1-A). Type I was the most abundant sensilla on the antennae of both sexes. Neither type had any discernible longitudinal or annular striations on the surface (Fig. 1-B).

Sensilla chaetica (Ch) were present on most flagellar segments on all species (Fig. 1-C). High magnification revealed some with longitudinal or annual striations (Fig. 1-D) but most had a smooth surface. No constant pattern or distribution on the flagellar segments was apparent, but the terminal segments of both sexes often had several sensilla chaetica that extended beyond the apices which suggested a tactile function.

Sensilla coeloconica (Co) occurred in clusters of 2-3 sensilla on most flagella (Fig. 1-E) and were nearly always located away from the scales of the flagellum. However, the peg is corrugated longitudinally in C. topiaria and arises from a shallow pit surrounded by slanting spines (Fig. 1-F).

Sensilla styloconia (St) were present on the distal margin of most flagellar segments of all species but occasionally were absent from some segments (Fig. 1-C). The elevation of the cuticle that ends in these sensory cones varied among species (Table 1). In general, only one sensilla styloconica was present on a flagellar segment but there were exceptions. Females of T. bonifatella often had a flagellar segment with a single sensilla followed by a segment with two sensilla. The tip of the terminal segment had what appeared to be a modification of sensilla styloconica that appeared in clusters of 2-4 sensilla (Fig. 1-D) and were probably specialized for close range perception of stimuli.

DISCUSSION

The species investigated had the types of sensilla found commonly on the antennae of many Lepidoptera. However, the trichoid sensillum was dominant which suggests that the primary function of the antennae is to detect semiochemicals. Since the trichoid sensilla of male Lepidoptera are known to respond to the sex attractant of females (Schneider, 1962), they probably have a similar function in the Crambinae. The sensilla coeloconica are olfactory in some insects but in Lepidoptera they also respond to warm humid air (Schneider and Steinbrecht,
Fig. 1.—A. *C. topiaria* ♀, 700x Sensilla trichodea (T-I); Sensilla trichodea (T-II). B. *C. topiaria* ♂, 3000x (note smooth surface texturing of sensilla). C. *C. topiaria* ♀, 1000x Sensilla chaetica (Ch), Sensilla styloconica (St). D. *T. bonifatella* ♀, 5000x; cluster of sensory cones on distal end of terminal segment.
E. C. *topiaria* ♂, 700x Sensilla coeloconica (Co). F. C. *topiaria* ♀, 15,000x; grooved peg of sensil coeloconica.
1968), which would be useful to the insect in identifying oviposition sites. The sensilla chaetica are known mechanoreceptors (Schneider, 1964) and are well represented in the Crambinae. Since these adults explore the leaves and culms of grasses by walking, these sensilla are probably essential for orientation within the grass canopy. Females, which have more sensilla chaetica, probably rely more on these receptors than males since flight is difficult and impractical for females heavily laden with eggs.

Relative to many Lepidoptera, the Crambinae have fewer sensilla and some types are conspicuously absent. For example, the auricillicum sensilla (shoe horn sensilla) probably provide directional perception of stimuli as the insect orients to the source but these sensilla were absent in the study species. The Crambinae also lacked the various types of surface texturing on olfactory sensilla that may permit the insect to distinguish several types of odors with a single sensilla (Callahan, 1975). Thus, the sensilla of the study species were simpler and had a more functional design that those of many Lepidoptera. However, they are well adapted to orientation within the limited habitat of the grass canopy that adult Crambinae explore.

LITERATURE CITED


INFORMATION ON
AVAILABILITY OF HOLOTYPES
OF THE DESCRIBED
TAXONS AT A PUBLIC INSTITUTION (RHOPALOCERA)

DALIBOR WEISS
Bruselská 3, 120 00 Praha 2, Czechoslovakia

I WOULD LIKE TO ANNOUNCE that holotypes of the described geographical races Clossiana angarensis sedychi Weiss (1964), Colias cocandica sidonia Weiss (1968) and Parnassius eversmanni magadana Weiss (1970) have been transferred from my private collection to the National Museum collections in Prague in order to comply with the stipulation of the International Commission for Zoological Nomenclature that new taxons are invalid in the case that they are not deposited in a public institution.

LITERATURE CITED


GYNANDROMORPHIC POLITES SKIPPERS
(HESPERIIDAE)

M. C. NIELSEN
3415 Overlea Drive, Lansing, Michigan 48917

During the past 30 years of field collecting Michigan lepidoptera, the family Hesperiidae has been one of my favorites. Therefore, it was unique that during this period only two gynandromorph Hesperiinae skippers were collected: Polites mystic (Scudder), Otsego County, 17 June 1962, and P. origines (Fabricius), Monroe County, 1 July 1965. The colored plates reveal most of the unusual characteristics; however, the following comments will further describe the two specimens.

Polites mystic

The female pattern on the left side of the forewing is slightly atypical. The costal area, extending from the basal area to just beyond the apical spots, is tawny, instead of the predominantly fuscous on typical females. Otherwise, the female portion is within the range of normal patterns found in this locality.

The male right side of the forewing is slightly deformed with a pronounced curve in the basal half of the costal edge, and a more rounded anal angle. There is a slight interruption of the tawny costal area just basal of the apical spots. The hindwings, dorsally, are not noticeably different as compared to normal specimens; nor are there appreciable differences on the ventral surfaces. Dissection of the genitalia revealed that it is a female.

Polites origines

At first glance, in most respects the specimen appears to be a male. The left dorsal surface of the forewing exhibits more fuscous scaling than the right side, especially pronounced in the costal area. Also, the left stigma is broken (best seen under magnification) at the CU₂ vein, and the stigmal patch is reduced in area. There are no differences on the hindwing dorsal surfaces, nor on the ventral surfaces. It was the thick, heavy abdomen that called my attention to the specimen in the field. Dissection of the genitalia has since indicated that it is a female, filled with ova, with some abnormal development of the post-vaginalis as compared to a normal female.
A review of the literature discloses that the gynandromorph phenomenon in lepidoptera is apparently uncommon. Scudder (1889) cited a report by Dr. Hagen of 31 gynandromorph species, mostly European, in the Papilionidae, Pieridae, Lycaenidae, Nymphalidae and Satyridae in which most showed complete bilateral distinction. He suggested that the left side is usually female, and in a few cases, one side will have mixed sexual differences. Ford (1945) illustrated two butterfly species, bilateral gynandromorphs, in which the female is expressed on the left dorsal surfaces, and two species that had traces of the other sex. Both Emmel (1964) and Opler (1966) figured a *Colias* and *Lycaena*, respectively, in which the female is on the right dorsal surfaces. There have been fewer reports of gynandromorphs in the moths. Bilateral gynandromorph moths have recently been reported by Hessel (1964), Muller (1966) and Blanchard (1969) in which the specimens exhibit female characteristics on the right dorsal surfaces. In most of the above references, these authors did not report the dissection of the genitalia to confirm the sex.

It would appear that these two skippers may be the first reported Hesperiidae gynandromorphs. Unfortunately, amateur lepidopterists do not usually favor skippers in their field activities, which may account of the paucity of records. As one can see, these skipper gynandromorphs are not as striking in appearance as compared to some of the other gynandromorphs figured in the above references. Hopefully, other collectors will be alerted by this experience and report their findings.

**LITERATURE CITED**


SPECIAL THANKS

I should like to take this opportunity to express deep and sincere gratitude to Karen Nielson Hovanitz, who will be continuing as assistant editor, Rudi Mattoni, acting editor and Scott Miller, assistant editor (elect). Without the unselfish and unfailing support they have given, the journal could not be continuing.

Our plans for continuing the journal are, we believe and hope, innovative and forward looking. We welcome comments from our subscribers and were greatly encouraged by the large number of spontaneous requests to continue the journal, as well as offers to help do so in any way possible.

To the many friends who sent cards and letters expressing sympathy to myself and family in the loss of Bill, a very heartfelt thank you.

Barbara Hovanitz
STUDIES ON THE EXCRETORY SYSTEM

OF THE FULLY GROWN LARVA OF

CALOGRAMMA FESTIVA DONOV.

(NOCTUIDE)

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Kampala, Uganda

ABSTRACT

Fully grown larvae of Calogramma festiva Donov., possesses six malpighian tubules, three on either side of the gut arising from a common duct. The proximal portion remains suspended in the haemolymph as a free tubule while the distal convoluted portion of the nephric tubules in association with the rectum form the nephro-rectal complex. On the basis of histological details three regions are distinguishable in the free tubule whereas the nephric tubule is divisible into proximal and distal regions. The nephro-rectal complex is formed of nephric tubules and components from the gut wall. The pronephric epithelium and the longitudinal muscles form a cover for the nephric tubules.

INTRODUCTION

Very little is known about the excretory system of lepidopterous larvae. Ishimori (1924) has described the distribution of malpighian tubules of certain larval form of Lepidoptera. Except for the study of Mathur (1966) in noctuid caterpillars, Prodenia litura and Trichoplusia ni, no attempt has been made to investigate the structural details of malpighian tubules of lepidopterous larvae. Studies on the development of tubules in Pieris brassicaceae (Henson, 1932), Venessa urticae (Henson, 1937) and Philosamia ricini (Srivastava and Khare, 1966) give only inadequate informations on the histology of the malpighian tubules. The present work therefore, has been undertaken to describe the anatomical details of the excretory system of fully grown larva of Calogramma festiva D.
MATERIALS AND METHODS

Adults were collected from the field and reared in the laboratory. The fully grown larvae were anaesthetised with ether vapour and dissected in Ringer’s solution under binocular microscope. For histological purposes, malpighian tubules were fixed in Bouin’s fluid. Sections were obtained at 5-6 \( \mu \) and staining was done with haematoxylin and eosin.

RESULTS

The excretory system of the larva of *Calogramma festiva* D., is in the form of six malpighian tubules, three on either sides of the gut. The three tubules on each side actually arise from a common duct (Fig. 1). Major portion of each tubule remains suspended in the haemolymph as free tubule while the distal portion called nephric tubule in association with the rectum forms a nephro-rectal complex.

A. Free Tubule

Immediately after its origin from the common duct each tubule runs towards anterior side of the gut as ascending limb (AMal) and on reaching the stomodeum, it turns backwards and runs posteriorly as descending limb (DMal). The ascending limb of the malpighian tubule is translucent whereas, the two thirds of the length of descending limb is dull white in colour. The remaining portion of the descending limb is characterised by the presence of small diverticulae on the wall of the tubule.

On the basis of histological details, three regions are distinguished in the free portion of malpighian tubule. In the first region (Fig. 2) peritoneal layer (Pl) is not distinct and the basement membrane (BMb) holds a ring of epithelial cells. The infoldings of the cell membrane (FcMb) in the basal zone of the cell are loosely packed and are fewer in number. In the central zone, cytoplasm is coarsely fine and contains elongated nucleus (N) measuring 5-7 \( \mu \) x 2 \( \mu \), but in certain cells more elongated nuclei of 26-29 \( \mu \) in size are observed. Border zone is formed of short filaments (sb) which are free towards the lumen. The second region (Fig. 3) is distinct from the first region in that the infoldings of the cell membrane (FcMb) are thickly packed in the basal zone of the cell and the reticulate cytoplasm in the central zone lodges variously shaped nucleus (N). The nucleus may be dumb-bell shaped, branched or semilunar. The cytoplasm presents scattered granules around nucleus. Border zone is formed of elongated free filaments (sb). An outer peri-
Fig. 1.—Diagrammatic representation of hind gut of *C. festiva* to show the arrangement of malpighian tubules.
Fig. 2.—Section passing through the first region of malpighian tubule of *C. festiva*.

**ABBREVIATIONS**
AInt, anterior intestine; AMal, ascending limb of malpighian tubule; ANt, anterior portion of nephric tubule; BMb, basement membrane; CD, common duct; DMal, descending limb of malpighian tubule; FcMb, infoldings of the cell membrane; GR, granules; In, intima; iPE, inner pronephric epithelium; Lum, lumen; mcl, muscle layer; MG, midgut; N, nucleus; oPE, outer pronephric epithelium; Pl, peritoneal layer; PNt, posterior portion of nephric tubule; RE, rectal epithelium; Rect, rectum; sb, striated border; Tra, tracheole.
Fig. 3.—Section passing through the second region of malpighian tubule of *C. festiva*.

Fig. 4.—Section passing through the third region of malpighian tubule of *C. festiva*. 
The peritoneal layer (Pl) is present. In the third region (Fig. 4) the basal zone is highly reduced. The reticulate non-granular cytoplasm contains variously shaped nucleus (N) in the central zone. The border zone is formed of many long filaments (sb) which are free towards the lumen (Lum).

The common duct (Fig. 5) differs in histological details from the tubule. The peritoneal layer is indistinct and a tough basement membrane holds a ring of epithelial cells whose boundaries are not clear. The basal zone is highly reduced. The central zone contains dense cytoplasm. Some of the nuclei (N) present in this region are much elongated. The border zone shows elongated free filaments (sb).

B. Nephro-rectal complex

The nephric tubule in association with the rectum forms the nephro-rectal complex (Fig. 6) which includes the nephric tubule (Nt), pronephric epithelium (PE) and the muscle layer (mcl). The pronephric epithelium takes its origin from the gut epithelium. Immediately after its emergence from the latter, it divides into two strata, the inner pronephric epithelium (ipE) and outer pronephric epithelium (opE) both of which are formed of single layer of cells. The outer pronephric epithelium is very thin and weakly developed. The inner pronephric epithelium is well developed and formed of elongated cells. Both the layers form a loose cover over the rectal wall. Due to the provision of two epithelial layers the pronephric chamber is divided into an inner and outer chamber. Each nephric tubule after its entry into the outer chamber runs up to the posterior limit of the rectum. Thereafter it pierces the inner pronephric epithelium and enters into the inner chamber. The nephric tubule within the inner chamber takes an anteriorly directed course up to the middle of the rectum where each tubule ends blindly.

The proximal portion of the nephric tubule (ANt) lying within the outer chamber is very narrow having very thin wall. Peritoneal layer and the basal zone are indistinct. The dense cytoplasm of the central zone lodges the nucleus. The border zone is highly reduced. In the distal portion of the nephric tubule (PNt) the basal zone is formed of loosely packed infoldings of the cell membrane (FcMb). Oval nucleus is found in the reticulate cytoplasm of the central zone. The border zone is formed of long filaments (sb) which are free at their distal ends. A longitudinal muscle layer taking its origin from the gut wall surrounds the outer pronephric epithelium.
Fig. 5.—Section passing through the common duct of malpighian tubule of *C. festiva*.

Fig. 6.—Longitudinal section passing through the nephro-rectal complex of *C. festiva*.
DISCUSSION

In Lepidoptera there are six tubules in both larvae and adults (Henson, 1931; Mathur, 1966) with perhaps only exception of Tiniedae in which the six typical tubules of the larvae are reduced to only one pair in the adults (Snodgrass, 1935).

The malpighian tubules of insects are invested by a peritoneal coat having abundant supply of tracheoles (Wigglesworth, 1965). The tubules of *P. litura* and *T. ni* (Mathur, 1966) are surrounded by a peritoneal layer of very thin squamous cells with widely separated nuclei. Since there are significant variations in its structure at various levels of the tubules, it seems that these cells perhaps play a role in the tubule physiology. The nuclei of malpighian tubule differ in size, location and shape not only in various insects but also in different regions of the tubule of the same insects (Mohamed, 1974). Bertheau (1963) distinguishes five regions in the anterior part and seven regions in the posterior part of the tubule of *Carausius morosus* based on the relation between nucleus and cytoplasm. But the well marked differences between the nuclei of upper and lower segments of *Rhodnius* observed so clearly under light microscope (Wigglesworth, 1931) have not been reported in electron microscopic study (Wigglesworth and Salpeter, 1962). The size of the nucleus varies greatly in different regions of the tubule of certain aquatic bugs and many terrestrial plant feeding bugs (Bahadur, 1961; 1964). In *Forficula*, the diameter of the nuclei of the tubule at certain ecdysis become almost doubled possibly because of incomplete mitosis (Henson, 1946). The increase in the size of nucleus in *Pieris brassicae* (Henson, 1932) is accompanied by lobulation and ramification as well. So it seems evident that variously shaped elongated nuclei of *C. festiva* are either due to difference in increase of size or incomplete mitosis.

Ishimori (1924) has described the arrangement of nephric tubules in many lepidopterous larvae. The arrangement of the tubules in larval *C. festiva* is similar to that described by Henson (1931) in *V. urticae* except that instead of loops a number of convolutions are formed. In *C. festiva* the distal portion of the nephric tubule which is lodged in the inner chamber of the nephro-rectal complex extends only upto the middle of the latter as it is in the case of *Bombyx, Gastropacha* and *Spilosoma* (SAINI, 1964).
Ishimori (1924) described the 'cryptonephric envelope' of lepidopterous larvae as composed of three layers, the outer muscle layer, middle epithelial layer and inner membranous layer. The present observations agree with that of Ishimori (1924) in the number of layers but differ in the nature of pronephric epithelial layers. In the larval Calogramma the outer pronephric epithelial layer is very thin and weakly developed whereas, the inner pronephric epithelial layer is thick and is formed of elongated cells. It also extends firm support to the view of Srivastava and Khare (1966) that the two layers of the cells of the cryptonephric envelope originate from the epithelial layer of the gut wall.

ACKNOWLEDGEMENTS

The present work has been carried out at the Aligarh Muslim University, India and the authors are grateful to the Head of Zoology Department for providing necessary laboratory facilities. One of us (U.V.K.M.) is thankful to Prof. K. J. Joseph of the University of Calicut for enabling him to take up this work at Aligarh.

LITERATURE CITED


RECTIFICATION OF A RECENT PAPER ON

LEUCANELLA MEMUSAE GARDINERI

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In Vol. 15 Of This Journal, Gardiner (1976) has described and figured the early stages of Leucanella memusae gardineri Lemaire and compared these to what he said is the nominate subspecies, L. memusae memusae (Walker). However, Gardiner’s figures of what he says represent the nominate subspecies are actually of L. viridescens (Walker.) The two species have long been confused in the literature. Because the source locality of the L. viridescens stock is not given, I am unable to say which subspecies of L. viridescens it is. The aforementioned remarks result from reference to an excellent and recent revision by Lemaire (1973).

It is stated in the original description of L. m. gardineri that the type series consisted of wild specimens supplied to Lemaire by F. Plaumann of Brazil. Gardiner states that the type series was reared by himself in England.

Gardiner’s paper is valuable for confirming that L. memusae and L. viridescens are not conspecific by showing differences between the larvae.

LITERATURE CITED


1Attacidae=Saturniidae
THE SCOLITANTIDINI

I: TWO NEW GENERA AND A GENERIC REARRANGEMENT. (LYCAENIDAE)

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Although I have been working with “Philotes” for over thirty years, it was apparent after the first few months of casual study that the then available arrangements of circumscribed species was incorrect. At the time, the McDunnough (1938) list of North American species included Philotes battoides (Behr) 1867, P. glaucon (Edw.) 1871, P. enoptes (Bois.) 1852, P. mojave (Watson & Comstock) 1920, P. spaldingi B. & McD. 1917, P. rita B. & McD. 1916, P. speciosa (Henry Edwards) 1876, P. sonorensis F. & F. 1865. Lycaena regia, Bois. (1869), a synonym of P. sonorensis, was the type species Scudder (1876) designated in erecting the genus. The arrangement of species concepts has been maintained by most recent workers, incorporating the recognition of glaucon as a subspecies of battoides following my diagnosis (1945).

Based upon criteria of facies, habit, and male genitalia, P. sonorensis appeared widely separated from P. speciosa, with both quite clearly differentiated from the remaining group of battoides, enoptes, mojave, spaldingi, and rita. In 1945, I mistakenly believed the above group of species were closely related to the Palearctic vicrama, baton, abencerragus group on the basis of my incomplete knowledge of the work of Hemming (1929). This led me to also suggest they were in Turanana, a massive error (Mattoni, 1954b). Hemming (1932), unknown to me, had placed the group in Philotes, where they remained through Forsters (1938) revision until the work of Henry Beuret. Beuret (1958, 1959) illuminated several relationships by examining most members of the tribe using a taxonomy based on male genitalia and androconia. He erected the new genus Pseudophilotes, type species baton (Bergstrasser) 1779, to include vicrama (Moore) 1865, abencerragus (Pierret) 1837, and bavius (Evers-
mann) 1832. He also erected *Shijimiaeoides*, type species *divina* (Fixsen) 1887, which included the Tibetan species *lanty* (Oberthür) 1886 and North American *enoptes*.

Forster (1940) had in the meantime (and unknown to Beuret in 1958) corrected the earlier misidentification of *Shijimia moorei* (leech) (*Everini*) with the new entity *Sinia leechi*, Forster, 1940 and included *lanty* and *divina* in *Sinia*.

The Beuret diagnosis of *enoptes* in *Shijimiaeoides* was unnoticed until Shields commenced his comprehensive study on the biology, distribution and variation of North American *Philotes*. Shields (1974) noted Beuret’s conclusion and applied *Shijimiaeoides* to the North American *enoptes* and *rita*, later including *battoides* (Shields, 1975).

Heretofore I have hesitated to erect new genera without exploring possible relationships within the whole tribe *Scolitantidini* Tutt 1909 (syn. *Glaucopsychini* Hemming 1932, see Beuret 1959). Sufficient morphological data are available which indicate the propriety of doing so now.

Although *S. divina* shares certain morphological features with *enoptes et al.*, and may in fact be the closest relative to the North American group, I believe it quite distinct.

**EUPHILOTES MATTONI, NEW GENUS**
Type Species: *Lycaena enoptes* Boisduval 1852, Ann. Ent. Soc. France 2 (10) :298

**Adult** (Table 1, Plates 1, 2, 5, 9, 12)

Head. Antenna 28 segments in male, 30 in female; Club 14-15 segments, nudum 12. Eyes smooth, round in frontal aspect. Frontal ratio eyes to head coverage 69%. Labial pulps erect, densely covered with white scales dorsally and caudally, black hairscales ventrally. Ratio of segments 1 : 3.4 : 1.1, third segment with a terminal notch about half the length.

Wing shape and venation commonplace for the tribe. Venation of forewing radial vein system ratio unique (rf. Plate 10): A/B 0.75, B/C 1.50.

Males with dense androconial scales with average length of .210 mm, width of .149 mm (Ratio 1.4) with 15 striae. Flavone present as the underside ground pigment.

Legs robust L/W Ratio 4.2, pro- and mesothoracic legs with large tibial process and two pairs of short, fine calcaria in both sexes. Ungual edont lobes absent.
Male Genitalia. Tegumen heavy, vinculum light in lateral aspect, relatively compressed cephalo-caudally. Saccus very long. Labides not produced, flat, somewhat broad in caudal aspect (L/W Ratio 2.0). Falces short, relatively fine, tapered, not touching. Aedeagus simple with well developed pair of basal lopes, seminal duct entering dorso-cephalad. Zone almost terminal. Cornuti spines short, coarse, numerous, borne on a single dorsal plate.

Female Genitalia. Papillae anales subtriangular. Posterior aeophyses short, straight, not tapered, attached to papillae anales subdorsally. Lodix large subcuboid formed as a single apparent sclerite. Deeply invaginated into the seventh segment. Corpus bursa simple, elongate, without cervix or signa.

DIAGNOSIS: Euphilotes can be differentiated at once from all numbers of the tribe by the single character of venation of R (Table 1). The combination of robust legs, large tibial process, paired calcaria, and antennal segment number of both sexes; and single cornutus plate, absence of Chapmans process on the aedeagus, and short falces in the male are also of generic value.

The conformation of the valves in the male genitalia and lodix and ovipositor in the female, though of highly significant taxonomic value, appear for the most part limited to specific differentiation. In our projected study these and other internal characters will be subject to multivariate analysis to more exactly define phenetic relationships.

The specific sets of characters which serve to define Euphilotes and differentiate it from related genera are given in Table I and the cited plates. These data compare E. enoptes and its congeners which have been examined, to all other genera in the “red maculed” section of the tribe. In several cases it should be recognized that the evaluations are based on single specimens. Accordingly further study may show several individual aberrant traits. The trends, nevertheless, are fairly clear.

Euphilotes is confined to western North America and includes the species enoptes, rita, mojave, spaldingi, and battoides. Contrary to the diagnosis of Shields (1975) there is adequate evidence regarding E. spaldingi as a distinct species on morphological and biological grounds and E. mojave on the basis of several instances of sympatry and cryptic morphological differentiation. These points will be expanded in a forthcoming paper. Pending outcome of a long term project Shields and I are com-
mencing, more complex relationships may be revealed in the future.

The assignment of other related species in this section is fairly straightforward. Both Philotes and Scolitantides are monospecific. Pseudophilotes as a homogeneous set of species clearly defined by the produced labides of the male genitalia. The genus includes P. baton, P. vicrama, P. abencerragus and the newly described P. sinaicus Nakamura 1974 plus other possible included cryptic species as panoptes. (Hbn.) 1808. I have placed bavius in Sinia on the basis of many shared morphological traits in spite of a somewhat divergent facies (rf. Figs. 2 & 3). Higgins (1975) clearly perceived bavius did not belong with Pseudophilotes, placing it in Scolitantides. Shijimiaeoides lanty has been retained with S. divina. Although there are several important divergences, both far eastern species appear more closely related than to any others. Based upon limited data S. divina is close to Maculinea and may exemplify the link of the "red macule" species to the Glaucopsyche section.

The relationships of speciosa are not well defined. Although it is not close to P. sonorensis, it is also not congeneric with Euphilotes. Shields (1974) recognized this fact and placed speciosa in Zizeeria (Zizeerini) based upon features of the male genitalia and early stages. Although the Scolitantidini and Zizeerini appear phenetically close, speciosa clearly belongs in the former tribe by virtue of gross structure of genitalia, legs, androconia, and probably other factors.

Since Forster (1938) erected Praephilotes for anthracias and Paleophilotes for triphysina, claiming these as primitive forms, it appeared fruitful to include the duo in an analysis as possible relatives of speciosa. P. anthracias is a common butterfly in the Karakum Desert, P. triphysina a virtually unknown inhabitant of the Sikiang steppes. Neither appears close to speciosa, nor, based on the data given, to any other members of the group, including one another. P. triphysina is particularly bizarre (Table I and Figures) with regard to venation; male genitalia with the laterally bent aedeagus and deeply involuted ductus entry, strongly produced labides, heavy long bent tegumen, a complex bifurcate juxta, and a definative sclerite surrounding the anal opening. In particulars of the male genitalia there are some suggestions of relationship to Pseudophilotes. The facies of both P. triphysina and P. anthracias are decidedly Zizeerine. P. anthracias otherwise appears closer to the Scolitantidid groups. I have concluded accordingly, that speciosa requires a new genus.
PHILOTIELLA MATTONI, NEW GENUS


Adult (Table 1, Plates 3, 4, 5, 10, 12)

Head; antenna 29 segments in male, 30 in female; Club 13 segments, nudum 10. Eyes smooth, round in frontal aspect. Frontal ratio of eyes to head coverage 64%. Labial palps erect, densely covered with hairscales ventrally and scales dorsally. Both scale types white basally and black proximally. Ratio of segments 1 : 2.5 : 0.8, third with small terminal notch.

Forewing. Shape commonplace Scolitantiidid but slightly more elongate (L/W 1.85 vs 1.75 for. Euphilotes enoptes). Venation commonplace, except branch of R₄₊₅ from R₃ more distad than any other genera in the group excepting P. triphy-sina.

Hindwing. Shape and venation commonplace for the tribe. Males possess abundant androconial scales with an average length of .178 mm, width of .126 mm and 13 striae, ratio 1.4). Flavones present as underside ground pigment.

Legs unique for the tribe, femur more robust than any of the tribe with L/W ratio 3.0. Proleg with very large tibial process and one pair of short fine calcaria in both sexes. Tibial processes absent on meso- and metathoracic legs. Ungual edont lobes absent.

Male genitalia unique for the tribe. Tegumen and vinculum heavy in lateral aspect, saccus absent, labides not produced, flat, suboval in caudal aspect (L/W Ratio 1.3). Falces short, heavy except distally terminating in fine apical processes bending posteriad and ventrad and parallel with one another. Juxta straight in lateral aspect, relatively short. Aedeagus unique in possessing a quadrilobed base. Seminal duct entering dorso-cephalad. Zone almost terminal. Vesica slender bearing few small blunt, coarse cornuti spines.

Female genitalia. Papillae anales subquadrate with the membranous setal caudal portion almost exactly bisecting the quadrate form. Posterior apophyses short, tapered and bent, jointing the papillae anales subdorsally. Lodix subcylindrilar in caudal view, formed of two sclerites, the ventral appearing the smaller
PLATE 1

PLATE 2
Undersides of PLATE 1.
PLATE 3
Uppersides. Top Row, Philotiella speciosa speciosa, Male, Randsburgh, Calif., 4 May, 1954, leg. R. Ford; Female, Mojave Desert, Calif., 12 May, 1924, leg. J. A. Comstock; Philotiella speciosa bohartorum, Briceburg, Calif., 10 May, 1969, leg. J. Lane. Second Row, Paleophilotes triphysina, Male and Female, Altyn Tag, China, Turkestan, no date (ZSB). Third Row, Praephilotes anthracias, both males, Repetek, Transcaspian, 4 April, 1966 (ZSB); Kuldaha, Thien-Shan, 1885 (ZSB).

PLATE 4
Undersides of PLATE 3.
of the two. The lodix is only slightly invaginated into the seventh segment. Corpus bursa simple, elongate, without cervix or signa. DIAGNOSIS: Philotiella can be distinguished from other closely related genera by the single character of venation of R (Table I). The extremely heavy proleg femur is also unique. Although the ratio is given for the male (Table I) the female is virtually identical. The large tibial process of the prothoracic legs in contrast to a small process on the mesothoracic legs is also unique. The aedegus likewise exhibits characters found only in this genus: the relative overall length and the four lobed base.

The pattern of variation in the Scolitantidini is complex, probably because of an evolutionary history with both substantial radiation and convergence. Monophyletic (monophenetic) lines are difficult to recognize at this time. With data on more characters, including early stages, we hope to perform multivariate analysis in order to quantitate possible phenetic distances.

It is intriguing to speculate that the center of origins of the tribe lies in the vicinity of the North Eastern Tibetan plateau. In the area of western Szechwan the following genera are represented: Glaucopsyche, Sinia, Shijimiacoides, Maculinea, Phengaris, Caerulia and Scolitantides. Within a distance of 2000 km to the west and north, all remaining Palearctic genera are to be found: Paleophilotes, Praephilotes, Pseudophilotes, Turanana, and Iolana. Included with the latter group is Lycaena panope, Eversmann 1851, which cannot be generically assigned at this time; and a new genus and species from the Koh-I-Baba Mountains of Afghanistan which appears close to Turanana. Pseudophilotes and Euphilotes appear to represent a case of convergence in facies following adaptive responses towards the Mediterranean west and east into North America. Both genera appear actively evolving in adapting to the conditions of their respective habitats to this day. Such a situation would account for the taxonomic dynamism of the genera at this point in the biological history of the earth.

ACKNOWLEDGEMENTS

My special thanks to Drs. Walter Forster and Wolfgang Dierl of the Zoologische Sammlung Des Bayerischen Staates (ZSB) for the loan of key specimens, to Mssrs. Boris Izenbek of Akmene, Lithuania and J. C. Weiss of Hagondage, France for generously providing much other Eurasian Material, to Dr.
Takashi Shirozu of Kyushu University, Japan for donating a beautiful series of S. divina, to John Lane, University of California, Davis, for providing the P. speciosa bohartorum specimen used, to John Sorensen for providing the manuscript of his invaluable morphological study, to Julian Donahue of the Los Angeles Museum of Natural History by always making their collection and library completely available, and last but not least, to my colleague Oakley Shields for the many discussions on this group we are so deeply committed to study.

Location of Figured Material: (ZSB) from the Zoologische Sammlung Des Bayerischen Staates, Munich, Germany. All others from the Los Angeles Museum of Natural History. Prepared material will accompany their specimens.

LITERATURE CITED


PLATE 5
Labial palps of eleven species as labelled, scale indicated.

All illustrations, with exception of the venation diagram, to the same scale. Execution using a Wild M5 Microscope with the Wild Drawing Attachment, by R. H. T. Mattoni.
PLATE 6

Male genitalia of *Scolitantiides orion* (above); *Philotes sonorensis* (below).
Upper left figures: Aedeagus, lateral view (above); dorsal view (below).
Upper right figures: entire genitalia with valves not shown, caudal view showing relative shape or labides and falces.
Lower left figures: entire genitalia lateral view.
Lower right figures: entire genitalia with valves not shown, dorsal view, caudally oriented to bottom of plate.
PLATE 7
Male genitalia of *Pseudophilotes vicrama* (above) and *Sinia bavius* (below) orientation as PLATE 6.
PLATE 8
Male genitalia of Shijimiaoides lanty (above) and Sinia leechi (below) orientation as PLATE 6.
PLATE 9
Male genitalia of *Shijimaeoides divina* (above) and *Euphilotes enoptes* (below).
PLATE 10
Male genitalia of *Philotiella speciosa* (above), *Praephilotes anthracias* (second row) and *Paleophilotes triphysina* (third row). Aedeagus lateral and dorsal views to left, entire genitalia next, entire genitalia without valves shown caudal view, and lastly, entire genitalia without valves, dorsal view. Lower figures giving (left) forewing venation of *S. orion* to show measurement for relative distance ratio determinations of R to R₃, base of R₃ to margin, and distal length R₄ + s to margin. Lower figure (right) caudal view of male genitalia of *E. enoptes*, not showing valves, indicating areas measured to describe the labides. In this paper only the ratio of A/B is given.
PLATE 11

Female genitalia of S. orion, P. sonorensis, P. vicrama, S. bavius, and S. lanty. Upper figure of each depicts the papilla anale and posterior apophysis in lateral view. Middle figure shows the lodix in lateral view oriented with the ostium vaginalis to the right. The course of the ductus bursa indicated by broken lines. The lower figure shows the lodix from the ventral view. The specimen of S. lanty had lost its lodix.
PLATE 12

Female genitalia of *S. leechi*, *S. divina*, *E. enoptes*, *P. speciosa*, and *P. triphysina*. Orientation as in PLATE 11.
### Table 1

**Morphological Data for Related Type Species and Some Other Species in the Scolitantidini**

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<th>SCOLITANTIDES</th>
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<th>PSEUDOPHILOTES</th>
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<td>1.05/1.75</td>
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<tr>
<td><strong>Ratio Proleg Femur:Tibia:Tarsus</strong></td>
<td>1.0:0.9:1.0</td>
<td>1.0:0.8:0.9</td>
<td>1.0:0.8:0.9</td>
<td>1.0:0.9:1.1</td>
<td>1.0:0.8:0.7</td>
<td>1.0:0.8:0.9</td>
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<td>5.6</td>
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<td>0.66/1.13</td>
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<td>Minute/Minute</td>
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<td>None/None</td>
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<tr>
<td><strong>Calcaria Shape</strong></td>
<td>Short/coarse</td>
<td>Short/fine</td>
<td>Long/fine</td>
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<td>Short/fine</td>
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<tr>
<td><strong>Endodent Lobes</strong></td>
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<td>0</td>
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<td>0</td>
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<td>7.1:3.1</td>
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<td>3.7:2.4</td>
<td>5.6:2.5</td>
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<td><strong>(Expanded) L/W shaft/w base</strong></td>
<td>Chapman Process</td>
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<td>Well dev.</td>
<td>Poor</td>
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<td>Saccus</td>
<td>Labides L/W&lt;sup&gt;1&lt;/sup&gt;</td>
<td>Falces Form &amp; Relationship</td>
<td>Shape Corpus Bursa</td>
<td>Sigma Bursa</td>
<td>Posterior Apophyses</td>
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<tr>
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<td>1.7 blunt</td>
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<tr>
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</tr>
<tr>
<td></td>
<td>1.9 blunt</td>
<td>long / parallel</td>
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<td>0</td>
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<td>0</td>
</tr>
<tr>
<td></td>
<td>1.3 blunt</td>
<td>long / parallel</td>
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1. See Plate 10
2. 0 straight, 1 slight curve, 2 strong s curve
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<th>Species</th>
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<th>Labial Paips</th>
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<th>Ratio Proleg Femur/Tibia</th>
<th>Ratio Proleg Tibia/Metatarsus</th>
<th>Ratio Tarsus/Propodeum</th>
<th>Tarsal Process Pro &amp; Meta Legs</th>
<th>Capitulum Fovea</th>
<th>Posterior Apex</th>
<th>Antennal Club</th>
<th>Palpi</th>
<th>Palpi &amp; Proboscis</th>
<th>Shape Palpae Analues</th>
<th>Attachment to Palpae Analues</th>
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<td>0.80/1.11</td>
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<td>Anthracion</td>
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<td>1.5</td>
<td>Straight/taperd, no data</td>
<td></td>
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</table>
EDITORIAL

Since the death of Dr. Hovanitz, I have assumed the role of acting editor of this Journal as directed by the trustees of the Lepidoptera Research Foundation. We are seeking someone who will take the position permanently, but are faced with numerous problems in so doing. No small consideration is the physical one of having our entire publishing facility, technical editing, and business location in one place. Another is the sheer responsibility of the job description, an item well expanded upon by Stan Nicolay in his presidential message to the Lepidopterists' Society (1977 Jr. Lep. Soc. 31:217-222). In the meantime, the mechanics of publishing so well established by Bill Hovanitz are well oiled. The JRL has the financial prospects and will continue as long as appropriate manuscripts need a home.

Although short papers, reviews, habitat descriptions, etc. will be accepted, the value of the JRL lies in the longer, well illustrated articles we prefer. These articles should emphasize research on environmentally and genetically induced variation, patterns of distribution, population structure, behavior, comparative morphology, phylogenetic and phenetic systematics and comparative physiology. In a word, on evolution as the central theme of biology as applied to Lepidoptera.

The liberal use of color plates has been an important adjunct, made possible by Bill's ability to coordinate a printer in Pasadena and a color separation firm in Missouri. Thus an apparent extravagance is permitted on our very limited budget. We are studying setting up typesetting with our own automatic composing equipment. This step would be undertaken jointly with other societies who also must find alternatives to the high costs from "turn key" publishers. Such a move would also ease editorial work both by propinquity and elimination of more layout efforts.

The basic policy of the Foundation will continue to be the publication of the JRL with few minor changes. Bill had intended to standardize formats of all papers, and this will be done in Volume 17. Changes will include providing more information in the space available. Instructions to authors will be specified on the back inside cover. The notice section will be separately printed in a "newsletter" form which will permit and encourage increased communication among members. The notices section
is open to all members; we hope you will feel free to more extensively use the service. Lastly, if we receive sufficient favorable comment we will start a section of abstracts of papers of more than usual interest which have not appeared in the regular Lepidoptera press. Accordingly, we should solicit your aid in providing reprints or notices of such papers. Our objective is to increase both membership and member participation to both better serve you and ease the load on us. The latter will occur with being able to purchase outside help. We will have publication up to date before the end of 1978 (Volume 17 completed). We invite your comments, criticisms, and help.

Barbara Hovanitz will continue to give generously of her time in the position of secretary-treasurer. She will handle all business matters including subscriptions and memberships. Karen Nielson Hovanitz as assistant editor is responsible for formatting, layout, coordination of printing, illustrations, publications, and mailing. Scott Miller has become a second competent assistant editor and colleague. Serendipity has provided an able team. Bill would be proud of us.

R. H. T. Mattoni
THE USE OF \( \alpha \)-ECDYSONE
TO BREAK PERMANENT DIAPAUSE
OF FEMALE HYBRIDS BETWEEN
PAPILIO GLAUCUS L. FEMALE AND
PAPILIO RUTULUS LUCAS MALE

C. A. CLARKE
Department of Genetics, University of Liverpool, England

AXEL WILLIG
Department of Biochemistry, University of Oldenburg, Germany

Previously we have shown that both males and females can be produced by the cross female P. rutulus X male P. glaucus (Clarke and Sheppard, 1955) but the reciprocal cross only produces males, the females remaining in permanent diapause until they die.

In order to examine the phenotype of the F1 females for genetic purposes we attempted to use ecdysone (Clarke, Sheppard and Willig, 1972) in order to get the female adults to eclose. Although a number started to develop only one was sufficiently advanced to score the phenotype, and that did not emerge. The present paper reports the successful use of \( \alpha \)-ecdysone and describes the phenotype of the F1 females when the female glaucus parent was the black form.

METHOD

\( \alpha \)-Ecdysone was purchased from Simes, Milan. The hormone was dissolved in ethanol and diluted with distilled water to give a final concentration of 7.0 \( \mu \)g/ml in 10% ethanol-water. The pupae (1.4 g) were injected with 20 \( \mu \)l each of this solution (100 ng \( \alpha \)-ecdysone/g w.w) through the intersegmental membrane of the abdomen, avoiding piercing the pupal gut, nervous system or spiracles. The injections were repeated every second day, each pupa receiving six in all. The butterflies emerged 24 days after the first injection.

RESULTS

Two female insects which were similar to one another were
produced from the two pupae injected. It will be seen from the plate (bottom right) that they are intermediate between the black and yellow forms in that the normal yellow pattern is present but heavily suffused with black scales. The suffusion is almost complete in a triangular area at the base of the forewing, extending out as far as the proximal black bar in normal yellow *rutulus*. A corresponding black area is to be found in the hind-wing extending from the inner margin to the proximal black line running through the cell towards the anal angle.

A similar female, together with a number of others showing less yellow, right through to black *glaucus*, was obtained by back crossing males of the F₁ to black *glaucus*.

On the ventral surface the F₁ females are also suffused with black but to a much lesser degree, so that the general appearance is rather like a sooty yellow form.

**DISCUSSION**

The use of α-ecdysone opens up the possibility of studying the genetics of species differences. In the case of the present cross this seems particularly likely as the F₁ hybrid females had their full complement of developed ova.

The black and yellow female forms of *P. glaucus* are controlled by a locus on the Y chromosome, apparently associated with a cytological marker (Clarke, Sheppard and Mittwoch, 1976). The inheritance of the black form is therefore maternal since the female is the heterogametic sex. The presence of an intermediate F₁, plus similar insects in the back cross using male hybrids, demonstrates conclusively that *rutulus* carries an autosomal or perhaps X-linked gene (or genes) which modifies the effect of the Y-linked allelomorph controlling black. This finding has interesting implications with respect to the evolution of the black form, which mimics *Battus philenor*. *P. rutulus*, although it flies with *B. philenor* in a number of places, including the coastal range of California, has never evolved a mimetic form. It seems possible that in the *rutulus* gene complex the Y-linked black allelomorph if it arose would be so suppressed (the F₁s having only half the *rutulus* gene complex) that it would not produce a phenotype sufficiently close to *Battus* to have any advantage.

With the new technique we hope to get a series of back crosses to *rutulus* to test this hypothesis.
TEXT FOR PLATE
LITERATURE CITED


THE ROLE OF INTRA- AND INTERSPECIFIC MALE: MALE INTERACTIONS IN POLYOMMATUS ICARUS ROTT. AND SOME OTHER SPECIES OF BLUES (LYCAENIDAE)
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University of Goteborg
S-431 33 Molndal, Sweden

INTRODUCTION

The males of Polyommatus icarus start to emerge and fly before the females. The males show a greater flight activity than the females. In addition, they mostly fly higher above the ground vegetation and are more easily observed. The more or less zigzag-formed patrol flight of the males has in other butterflies (e.g. Argynnus paphia L., Magnus 1956) been interpreted as a typical appetite behaviour, a sexual search flight which brings the male into contact with the stimuli of females. A complete courtship is seldom observed. It is most often the vigorous mate refusal behaviour of the female or sometimes a pair in copula that catches the sight. In fact it was the astonishing frequency of male: male interactions that first struck me when I started to study this species. During the patrolling the males perpetually meet, whirl around and often pursue each other in a straight fast flight. Such “male chases” of more than 25 meters are not rare.

The aim of this paper is to discuss the role of the intra- and interspecific male: male interactions in the light of our present knowledge of natural regulation of number in populations. A survey of theories in this field is given by Dajoz (1974).

The investigation of the approach reaction of the males was performed in 1963 and in 1964, some complementary experiments in 1966.

The field observations brought about the following questions:
1. Are all butterflies visually equally attractive to the P. icarus males?
2. Is the approach reaction of the P. icarus males released to the same extent by conspecific males and females?
3. How attractive are the blue males of other species of blues compared to P. icarus females and P. icarus males?
MATERIAL AND METHODS

Spanned and dried butterflies were used as dummies to release the approach reaction of the males. The dummies were hanging freely close over the vegetation in a thin black thread from 1 meter long hazelrods obliquely stuck in the ground. The position of the dummies was randomized by arranging the "angle rods" in a Latin square. A simultaneous testing of e.g. 5 types of dummies required consequently 5 x 5 rods placed at a distance of 1 meter from each other. A moderate clearing of the area was made to remove tall plants which could conceal a dummy. Further details about the experiments are summarized in Tables I - IV.

The responses of the males were classified as approach-reactions and fluttering around reactions. The approach reactions were recorded as a "D", alluding to the fact that the response often was a fast dip movement against the dummy. It was in practice hard to distinguish between D and F reactions (fluttering around) though two observers were always recording the responses. D was much more frequent than F. The experimental method was best suited to comparing the approach tendency of the males to various visual dummies. At the compilation of the results the D and F reactions were put together.

If the same male when flying through the square responded to more than one dummy, this was recorded as well as the order of the approaches. The proportions of the results were not changed when the repeated responses were excluded.

RESULTS

The field observations showed that butterflies are strikingly more attractive to the males of Polyommatus icarus than other insects are. This preference has in other species been explained by the typical way of movement of butterflies.

1. Are all butterflies visually equally attractive to the P. icarus males?

In five experiments (Table I) 4 dummies were various blue-winged blues but the 5th alternative was another type of butterfly also occurring in the habitat. The choice of species was partly determined by the supply of spanned and dried butter-
flies. It is obvious that the *P. icarus* males did approach blue colored blues far more often than other butterflies. The greater attractiveness of the copper, *Palaeochrysophanus hippothoe* L. (Lycaenidae) and the fewer approaches to the brown lycaenid females (*Cyaniris semiargus* Rott.) can also be noted.

2. Is the approach reaction of *P. icarus* males released to the same extent by conspecific males and females?

The experiments show (Table II) that the males are as easily attracted to specimens of their own sex. The brown females of this species are more or less flushed with blue scales. The dummy females used were intermediate blue. Out of 156 females collected on Öland in 1965, 10 were classified as blue-shimmering at the wing base, 55 were blue almost to submarginal lunules, and 91 were blue almost to the black marginal line. No completely brown females with or without orange lunules were caught. The blue females are of course over-represented as they can be more easily seen.

3. How attractive are the blue males of other species of blues to the *P. icarus* males as compared to *P. icarus* females and *P. icarus* males?

The answer to that question is that the males of the tested species (*Cyaniris semiargus* Rott., *Lysandra icarus* Esp. and *Lysandra argester* Bgstr.) successfully compete with *P. icarus* butterflies of both sexes about the approach reactions of the *P. icarus* males (Table II).

Even if the experimental method only tested the initial approach stage of the male chase, the experiments have shown that intra- and interspecific male:male interactions are two characteristic ways of behaviour in *Polyommatus icarus*. Table III illustrates the same behaviour in *Plebejus argus* L.

4. What stimuli release the approach responses of the males?

The experimental squares were set up in wind-protected parts of the habitat. As a rule only the upper side of the dummy wings was exposed to the males. In the first experiment the spanned butterflies were first hanged 30 centimeters above the vegetation. Most of the males flew below the dummies. Between 9:20 a.m. and 2 p.m. 19 nonresponses and 8 approaches were registered. The dummies were then lowered to hang close over the vegetation. Between 2 and 5:10 p.m. only 2 out of 37 males passed through the area without taking notice of the dum-
mies. This behaviour indicates that colour signals from the upper side of the wings are the active stimuli. An objection is that the under side of the dummy wings is shaded. This was not the case when a spanned and dried male was rotated around the body axis. The rotating dummies were fixed to a thin steel axis running through a 2 m long hollow spinning rod. The rotational velocity could be varied with the spinning reel which drives the axis. The alternating flashes of upperside and underside colour from a male dummy with a "fluttering speed" which seems normal to our eyes did not increase the attractiveness of the male as compared to when presented not rotating.

To examine the reaction of the male to a larger blue wing surface "giant males" (3 x) were made by covering a butterfly silhouette of stiff paper with the wings from 3 males. The giant males got almost as many responses as the normal *P. icarus* males (Table II). As similar experiments have already been made (Tinbergen 1942; Magnus 1956) no further experiments were made to see if the ordinary size of the male is optimal. The reactions to deformed males suggest that the shape of the coloured object is unimportant to the males as in other species of butterflies which have been investigated in this respect.

In many species of blues e.g. *Polyommatus icarus* and *Lysandra icarius* the ground colour of the females varies from brown to more or less blue. The readiness of the males to approach blue objects ought to lead to a selection in favour of the blue colour genes. The grey-green mutant colour form valesina of *Argynnis paphia* is hereditary dominant expressed only in females. Magnus (1956) has shown that one explanation of its rareness is a sexual preference by the males for the normal yellow-brown colour of the female.

The two species *Plebejus argus* and *Lycaeidias idas* are very similar and often hard to distinguish without examination of the genitalia. The *P. argus* females are brown but the *L. idas* females more or less blue and rarely completely brown. The square experiments have confirmed (Table III) the existence of interspecific male approaches between these species.

*P. argus* and *L. idas* are consequently suited objects for an investigation of the female colour preference of the males. Fortunately, I had in my possession some blue and some brown spanned female specimens of *L. idas*. The most eligible locality found in the neighbourhood was an area in a pine forest clear-cut some years ago, with *Calluna vulgaris* as a dominant in the
herb layer. 60 males were caught and released again, 28 were *P. idas* and 32 were *P. argus*. As it is impossible to determine with certainty to which species the approaching males belong without catching the butterflies a pure population of *L. idas* would have been better.

The supply of spanned females permitted only a 3 x 3 square with: 1 *L. idas* brown female, 2 *L. idas* blue female and 3 *L. idas* male. The result (Table IV A) is very interesting. Males of both species respond to the dummies which was verified by catching some of the reacting males. The experiment indicates a visual preference selection of blue *L. idas* females. Even the *P. argus* males are more easily attracted to the blue *L. idas* females than to their own brown females. This remarkable fact was further supported by two experiments in a locality where only *Plebejus argus* were flying (Table IV B).

A similar visual interspecific female preference has earlier been found in other species. According to Petersen et al. (1952, 1954, 1963) the white males of *Pieris bryoniae* Hübner prefer the white females of *P. napi* L. to their own yellow females. This may be a secondary effect of intra- and interspecific male:male interactions released by the white male colour of *Pieris*. The *P. bryoniae* males do more often approach each other than their own females. Males of *Papilio rutulus* Boisduval are in the beginning of the courtship more often attracted to female *P. multicaudus* Kirby than to their own females (Brower, 1959). In this case the explanation can be quantitative differences. To human vision the females have the same yellow colour, but the yellow area on the wings of *P. multicaudus* is larger.

Sign stimuli are mostly qualitatively optimal. One of the phenomena which the dummy experiments have revealed to the ethologists is the existence of supernormal stimuli. Various selection pressures often prevent the realization of quantitatively optimal stimuli in the organism. It must yet be considered as remarkable that in two sympatric species or two allopatric species with a contact zone the females of one of the species have got supernormal sign stimuli to the approach reaction of the males of the other species. It is necessary to ask for the compensating isolating mechanisms. Brower found a partial season isolation and a difference in altitude preference in *Papilio multicaudus* and *P. rutulis*. Petersen established that where *Pieris bryoniae* and *P. napi* appear as different species habitat
isolation and a bad hybrid vitality were active. An understanding of the isolation of *P. argus* and *L. idas* needs further investigations. Although they morphologically are very similar species the male genitalia are strikingly different (according to Chapman the most different in tribus *Plebejini*). Sengün (1944) showed that curtailed males without the whole copulation apparatus including aedeagus are capable of fertilizing the females. As Petersen (unpubl.) has pointed out such experiments are only indicating. Small quantitative differences in male copulation success can have a considerable isolating importance. *Plebejini* is characterized by female genitalia deviating from those of the main part of *Rhopalocera*. The vaginal orifice is situated on the tip of an extrudable organ (hypostema + heina) behind the 7th sternite. As I have failed to handpair these butterflies it seems that the female copulation apparatus is not extruded reflexably when the valves of the male grip the abdomen tip. It may function as an effective refusal apparatus against males which do not present the right stimuli.

5. Are the male:male interactions the defence part of a territorial behaviour?

Gently following males of *Polyommatinus icarus* in various localities did not indicate that the male:male interactions are concerned with the defence of an area through chasing or leading the intruder away from a domain to which the male returns. Every male was followed until it was lost. The most frequent reason was interference with another male. The males were frequently lost during the flight chase or it was impossible to identify the traced male afterwards.

During observations of another species I spent some whole days on a 200 meters long rectangular meadow. In this locality the first *icarus* males emerged on the 11th June in the year 1966. The male resided all the day in a well defined area in the east part of the meadow. The size of the domain was estimated to 1/3 of the length and 1/8 of the width of the meadow. On the 13th June male No. 2 appeared. The first male was still flying in the same area as before. Male No. 2 spent the whole day in a less well-defined domain west of the flight area of No. 1. In the afternoon a sustained "fluttering around" was observed near the ground in the contact zone between the domains followed by a fast chase to the west end of the meadow. Later on both males were again observed in their respective areas. On
the next day several males were flying. The population was in constant restlessness. The male chases were frequent.

Without individual marking one cannot be absolutely sure that defended territories do not exist but my field observations indicate that the *P. icarus* males locate their mates by patrolling according to the terminology of Scott (1972). Tendencies to perching are observed at low population densities but male: male interactions not attributable to the defence of a defined area to which the defender returns are much more frequent.

A 16 mm colour film on the biology of *Cupido minimus* L., *Maculinea arion* L., *Lycaenides argyrognomon* Bgstr., *Aricia allous* H-Gbg., *Cyaniris semiargus* Rott., *Polyommatus icarus* Rott., *Lysandra icarius* Esp. and *L. argester* Bgstr. has been made and it is filed in the Department of Entomology at the Institute of Zoology, at Uppsala university, together with a scenario in English. In this film (1,5 hrs) male: male interactions as well as feeding behaviour, courtship and egglaying are documented.

**DISCUSSION**

I find it very unsatisfying to explain the male: male interactions as the result of a poorly characterized releasing mechanism for the sexual appetite flight. There ought to have been a selection against unnecessary approaches as indicated by the few approaches to other butterflies. The selective disadvantage of "timewaste" during the search for females measured as reduced fertilization rate has been demonstrated (Parker, 1970) in a dung fly (*Scatophaga stercoraria* L.)

What evolutionary advantages have maintained the high level of intra- and interspecific interactions between blue males? There must also have been a selection for epigamic recognition. That is why the males' chasing of each other seems too sustained only to be a mate recognition behaviour. The explanation can be that the male: male interactions are aggression concerned with the defence of an area. Perching behaviour is defined by Scott (1972) as a mate-locating method in which males sit at characteristic sites and dart out at passing objects in search of females. This type of behaviour is frequent in butterflies but I know of only two investigations focused on the return of the male to the same area, the defended territory. A comparison between these is made in Table V.

According to Baker (1972) the benefit of the territorial be-
haviour of the nymphalid butterflies, *Aglais urticae* L. and *Inachis io* L. is an increased female quota for a territory-occupying male. The optimum territories have an edge or corner site where the stream of females is more intense. The study area is not more closely described but the localities seem not to be isolated. Both species are migrant. Voluntary male displacement occurs between the territorial periods. The distance covered during a fine day is about 1 km in *Aglais urticae* and 0.5 km in *Inachis io*. Without physically injuring the intruders the territorial defence is rather elaborate involving in *I. io* defence by the very presence of a male in the territory, chasing or leading the intruder away, and demonstration of better manoeuverability and thus as a consequence seemingly potential superiority in a coming courtship contest about the same female. A low territory: male ratio, i.e. the ratio of suitable territories to the number of males, is suggested to select for a break-down of the territorial system. Tendencies in that direction are shown by *A. urticae* through the increasing readiness of the incoming males to share a territory with males already established rather than to continue to search for an unoccupied territory.

Douwes (1975 b) has investigated the territorial behaviour in *Heodes virgaureae* L. as a part of a detailed study of the ecology and ethology of the adult stages of this species. The study area was a well isolated, fairly small locality of the species with a low migration and a low territory: male ratio. Only a few males defend a couple of optimal territorial sites (perching areas). Douwes’ results indicate that territorial *H. virgaureae males* are inferior to non-territorial ones in the competition for females and nectar resources, since females and suitable flowers occur principally in the open field at some distance from the male territories. The selective advantages of this territorial behaviour is hard to understand but Douwes suggests it might be that it makes the males cover the habitat better in their search for females. Tendencies to territorial behaviour occur also outside the territories preferred. The few males which occupy the preferred territorial sites due to their superiority in competition seem to “sacrifice” themselves for the best of the population. The consequence ought to be a lower female quota and a negative selection which work to eliminate this behaviour. A solution of these difficulties might be to look upon the preferred territorial sites as located not “at a distance from” but
"on the route to" feeding and oviposition sites. According to the description they can be edge territories similar to the ones in *I. ino* and *A. urticae*. That only one female was observed in the territories could perhaps be explained by the more unobtrusive behaviour of the females and by the fact that the territorial study was performed before the peak of the female number. The distribution study (Douwes, 1975 a, Fig. 5) shows that the territorial sites lie at intense traffic routes. In addition they lie close to two of the three most loco-climatically favourable sites and two places with abundant Tubuliflorae flowers. Douwes also studied thoroughly another population which virtually lacked territorial sites and territorial males at least with the characteristics defined from the other locality. Such a habitat-adapted behavioural polymorphism is conceivable. Chitty (1967) writes about intraspecific competition: "If we can expect that interference has severe effects on survival and reproduction it is less reasonable to assume that all genotypes suffer equally than to assume that they are affected non-randomly". Through the work of Gilbert and Singer (1973) we know that in the butterfly *Euphydryas editha* "the longstained selection pressure associated with the detailed ecology of each population can produce intraspecific genetic differentiation in dispersal tendency such that even populations with abundant resources may differ in dispersal behaviour". Douwes (1976 a) found that also in the non-territorial population the colour responsible for the attraction of the male to the female is less strongly expressed in the female than in the male. This means that the male: male interactions must be frequent also in the non-territorial population.

Breakdown of territorialism at least in the butterfly species discussed here does not lead to breakdown of the male: male interactions. The intraspecific competition seems to have different expressions at different population densities in the same way as has been found in e.g. *Mus musculus* (Anderson, 1961) with the exception that when territorialism breaks down when the population density rises, no social hierarchy is established in the butterflies in absence of ability to individual recognizing.

The male: male interaction are truely density-dependent. If the variations in behaviour as a function of population density are summarized (Table VI), it seems highly probable that the male: male interactions are the feed-back part of the natural regulation of population density. All females are initially unwill-
ing. Small differences in persistance are aimed to affect fecundity.

According to Magnus (1963) performing of "mistake" approachflights in *Argynnis paphia* gives a lowered stimulus threshold and a sexual over-excitement. The males' chasing of each other may contribute to maintain the sexual mood especially in the beginning of the flight period when females are rare as the males begin to hatch earlier than the females.

Why are the male butterflies more brilliantly coloured? This problem has been discussed by many authors, e.g. Scott (1972) and Douwes (1976 a). Is it because sexual selection is more important in the males whereas in the females there is a counter selection against predation? On the other hand male colour is not exposed during the decisive stages of the courtship. The existence of polymorphism mainly restricted to the females speaks for sexual differences in selection. One suggested explanation is genetic (Magnus, 1963). If male:male interactions have the vital importance for population regulation, which is suggested in this paper, male colour is meant for other males. This may also include chemical male signals. Douwes (1975 b) found a gap between the male response to conspecific males in *H. virgaureae* and to other butterflies which cannot only be explained by differences in visual stimuli. In the Latin square experiments with *P. icarus* odor-males painted with a chloroform extract of fresh males got more approach responses than non-odor males (Table I). These results may indicate that male odor is a signal in the male:male interactions.

Color similarity and color unimportance at the end of the courtship mean selection for chemical and tactile specificity. The main components of the male wing volatiles have been identified (Lundgren & Bergstrom, 1975) only in one species of blues (*Lycaeides argyrognomon*). Since then the methods for isolation and concentration of the odor substances as well as the sensivity of the GLC-MS instrument have been improved. A GLC of the volatiles from the male wings of the same species (Fig. 1) shows a very complicated peak pattern, representing more than 120 components with rich possibilities of species specificity of the male scents. *Polyommatus icarus*, *Lysandra icarius*, *L. argester* and *Cyaniris semiargus* have partly overlapping spectra of larval host plants. They also share the nectar resources. Nectar is continually produced but Wynn-Edwards (1970) emphasizes correctly that all supplies of food are finite
Fig. 1.
Capillary gas chromatogram of the volatiles from the wings of two males of *Lycaenides argyrognomon*. Ionization at 70 eV electron energy and 200μA electron voltage. Temperature programmed with 5°C/min from 80 up to 230°C. More than 120 components are separated. Scot column 65 m, SE-30.
in terms of their yield per unit area and time. Changes in the population structure of *Euphydryas editha* (Gilbert and Singer, 1973) indicate that the number of butterflies per unite of volume of nectar is the operative density index. The distribution of the lycaenid *Heodes virgaureae* (Douwes, 1975 a) shows a positive correlation with the distribution of Tubifloral nectar plants.

It is hard to explain the high frequency of interspecific male:male interactions between blue males compared to the number of responses to males of other butterfly species unless it involves some kind of group advantage. It is difficult to show that the resource overlap is important enough to select for interspecific male color similarity and male:male interactions capable of regulating dispersion and population density within the group in the same way as this behaviour obviously does within the species. This remains a fascinating possibility. Such an ecological relationship between species does not conflict with the niche concept as long as this is not misinterpreted as spatial. On the contrary the interspecific male:male interactions may be an important part of the niching of the resources.

**SUMMARY**

An high frequency of male:male interactions was observed in *Polyommatus icarus*. The approach reactions of the males were investigated using spanned and dried butterflies as dummies arranged in Latin squares. All butterflies are visually not equally attractive for the *P. icarus* males. Other butterflies ("non-blues") got only a few responses. Males in flight are as easily attracted to specimens of their own sex as to females. Males of other species of blues compete successfully with *P. icarus* females about the approach reactions of the *P. icarus males*. The blue wing colour of the upper side of the wings is an important stimuli for the approach reaction. A visual preference for blue females was found in *Lycaeides idas* where the female colour varies from blue to brown. Also males of *Plejebus argus* preferred visually the blue *L. idas* females to their own brown females. The female genitalia of these species which have to be extruded before the males succeed in copulation may be a compensating mate refusal apparatus. *Polyommatus icarus* was in the studied habitats found to be a patrolling species with tendencies to perching. The male:male interactions cannot be merely "mistake" approaches meant for females. True territorial behaviour occurs in butterflies but male:male interference persists after the breakdown of territorial behaviour at low ter-
ritory: male ratios. The following suggestions are made: The male: male interactions are the feedback part of the natural regulation of population density. The more brilliant male colours and perhaps also the male scents are primarily directed to other males. Colour similarity of males and interspecific male: male interactions may be adaptive within species complexes by adjusting the fecundity to overlapping resources.

ACKNOWLEDGEMENTS

I am grateful to Dr. Björn Petersen for focusing my interest on the lycaenids, a neglected butterfly group in behaviour research. I should like to thank Professor Bertil Kullenberg for providing stimulating working facilities at the Ecological Station on Öland. My thanks are due to my wife for her help with the field observations. I am also indebted to Gunnar Stenhagen for making the GLC-analyses of the wing volatiles. Research support from the National Swedish Environment Protection Board and the Knut and Alice Wallenberg Foundation are gratefully acknowledged.
Table I

*Polyommatus icarus.* Male approach responses to some other butterfly species compared to responses to blues of the species *P. icarus* (P.i.), *Cyaniris semiargus* (C.s.), *Lysandra icarius* (L.i.) and *L. argester* (L.a.). Dried and spanned butterflies. Latin square 5 x 5. The odor dummies were painted with a chloroform extract from 5 fresh male or female specimens.

<table>
<thead>
<tr>
<th>Dummies</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>Other butterfly species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Exp. No.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.i. ♀</td>
<td>12</td>
<td>27</td>
<td>37</td>
<td>44</td>
<td>Argynnys paphia ♀ 2</td>
</tr>
<tr>
<td>P.i. ♂ (odor)</td>
<td>16</td>
<td>20</td>
<td>18</td>
<td>30</td>
<td>Brenthis ino ♀ 2</td>
</tr>
<tr>
<td>P.i. ♂</td>
<td>39</td>
<td>49</td>
<td>57</td>
<td>63</td>
<td>Palaeochrysopanus ♂ 17</td>
</tr>
<tr>
<td>Exp. No.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.i. ♀</td>
<td>20</td>
<td>19</td>
<td>16</td>
<td>14</td>
<td>Coenonympha ♂ 0</td>
</tr>
<tr>
<td>P.i. ♂ (odor)</td>
<td>22</td>
<td>14</td>
<td>18</td>
<td>18</td>
<td>Pamphilus ♂</td>
</tr>
<tr>
<td>P.i. ♂</td>
<td>46</td>
<td>21</td>
<td>33</td>
<td>27</td>
<td>Cyaniris semiargus ♀ (brown) 2</td>
</tr>
</tbody>
</table>

Table II

*Polyommatus icarus.* Interspecific male responses to males of other species of blues compared to conspecific butterflies of both sexes. Dried and spanned butterflies. Latin Square 3 x 3 and 5 x 5. Species name abbreviations the same as in Table I.

<table>
<thead>
<tr>
<th>Dummies</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Exp. No.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.i. ♀</td>
<td>8</td>
<td>23</td>
<td>12</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.i. ♂ (odor)</td>
<td>22</td>
<td>49</td>
<td>29</td>
<td>30</td>
<td>28</td>
</tr>
<tr>
<td>P.i. ♂</td>
<td>14</td>
<td>18</td>
<td>19</td>
<td>18</td>
<td>8</td>
</tr>
<tr>
<td>P.i. ♂</td>
<td>21</td>
<td>20</td>
<td>17</td>
<td>18</td>
<td>9</td>
</tr>
<tr>
<td>Sum (exp. 2-5)</td>
<td>61</td>
<td>87</td>
<td>73</td>
<td>65</td>
<td>70</td>
</tr>
</tbody>
</table>

Table III


<table>
<thead>
<tr>
<th>Dummies</th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Exp. No.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plebejus ♀</td>
<td>10</td>
<td>23</td>
<td>19</td>
</tr>
<tr>
<td>Plebejus ♂</td>
<td>20</td>
<td>42</td>
<td>27</td>
</tr>
<tr>
<td>Cyaniris semiarigus ♂</td>
<td>30</td>
<td>65</td>
<td>46</td>
</tr>
</tbody>
</table>

Table IV

*Plebejus argus and Lycaeides idas.* Male approaches to brown and blue females respectively. A. experiments with a mixed population of *P. argus* and *Lycaeides idas.* Males of both species respond to the dummies. B. Only *P. argus* occurred in the locality. Dried and spanned butterflies. Latin square 3 x 3.

A.

<table>
<thead>
<tr>
<th>Exp. No.</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Lycaeides idas ♀</td>
<td>17</td>
<td>81</td>
<td>96</td>
</tr>
<tr>
<td>Lycaeides idas ♂</td>
<td>19</td>
<td>27</td>
<td>46</td>
</tr>
</tbody>
</table>

B.

<table>
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<tr>
<th>Exp. No.</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Plebejus ♀</td>
<td>0</td>
<td>10</td>
<td>6</td>
</tr>
<tr>
<td>Lycaeides idas ♀</td>
<td>7</td>
<td>48</td>
<td>18</td>
</tr>
</tbody>
</table>
### Table V

**Comparison between the territorial behaviour in *Inachios io*, *Aglais urticae*, and *Heodes virgaureae*.**

<table>
<thead>
<tr>
<th>Behaviour characteristics</th>
<th>I. io (Baker, 1972)</th>
<th>A. urticae (Baker, 1972)</th>
<th>H. virgaureae (Douwes, 1975b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>site of the territories</td>
<td>en route to oviposition sites</td>
<td>at the oviposition sites</td>
<td>at some distance from feeding and oviposition sites</td>
</tr>
<tr>
<td>territory: male ratio</td>
<td>high</td>
<td>low</td>
<td>low</td>
</tr>
<tr>
<td>number of males per territory</td>
<td>1</td>
<td>4</td>
<td>1 - 2</td>
</tr>
<tr>
<td>mating place</td>
<td>at roosting place to which the female is followed</td>
<td>at the territory</td>
<td>at feeding places</td>
</tr>
<tr>
<td>time for holding a territory</td>
<td>240 min</td>
<td>90 min</td>
<td>1 - 2 days</td>
</tr>
<tr>
<td>time for setting up a territory</td>
<td>midday earlier than A.u.</td>
<td>midday</td>
<td>morning</td>
</tr>
<tr>
<td>number of territories per male and day</td>
<td>1</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>voluntary displacement</td>
<td>before midday until settling down in a territory</td>
<td>before and between the territorial periods</td>
<td>after the territorial period</td>
</tr>
<tr>
<td>types of male: male interactions</td>
<td>deterring through presence, chasing (leading) away, contest of manoeuvrability</td>
<td>chasing or leading away</td>
<td>chasing or leading away</td>
</tr>
<tr>
<td>territorial: nonterritorial male ratio</td>
<td>high</td>
<td>high</td>
<td>low</td>
</tr>
<tr>
<td>suggested selective advantages</td>
<td>increased female quota, proximity of roosting sites</td>
<td>increased female quota, containing roosting sites</td>
<td>spacing out the males, increased chances for the females to be fertilized, decreased female quota for territorial males</td>
</tr>
</tbody>
</table>

### Table VI

**Variations in behaviour as a function of population density.**

<table>
<thead>
<tr>
<th>Increasing population density</th>
</tr>
</thead>
<tbody>
<tr>
<td>Increasing</td>
</tr>
<tr>
<td>male: male interactions</td>
</tr>
<tr>
<td>disturbances of egglaying females</td>
</tr>
<tr>
<td>physiological stress</td>
</tr>
<tr>
<td>net emigration</td>
</tr>
</tbody>
</table>
LITERATURE CITED


NEW ADDRESS: The address of the Journal is now: c/o Santa Barbara Museum of Natural History, 2559 Puesta Del Sol Road, Santa Barbara, California 93105.

MAILING DATES: As of this issue, the mailing date of each number of the Journal will be listed in the Notice column, Volume 16, Number 3: December, 1977.

NEW BOOKS: Available from Entomological Reprint Specialists, P.O. Box 77224, Dockweiler Station, Los Angeles, California 90007, USA:
- Allan, P. B. M. Leaves from a Moth Hunter's Notebook, 1977. $9.00.
- Goater, Barry. The Butterflies and Moths of Hampshire and the Isle of Wright. 1975. $15.00.

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WANTED: Correspondence with members interested in trading or selling North American Lepidoptera. Send list of offers to: Marc Grocoff, 1950 Cottrill Lane, Westland, MI 48185.

MANUSCRIPTS: May be sent to the Acting Editor at the Journal address.

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WANTED TO BUY: Comstock's Butterflies of California. Also, any other out-of-print books on North American Lepidoptera. J. G. Manesis, M.D., Fargo Clinic, Fargo, North Dakota 58102.

The note "Type locality for Calosaturnia walterorum Johnson (Saturniidae)", which appeared in this journal (15(4): 214, 1977) was published by mistake, having been formally withdrawn from consideration by the Journal of Research on the Lepidoptera prior to its acceptance and publication in the Journal of the Lepidopterists' Society (29(3): 191, 1975). We regret this error.
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