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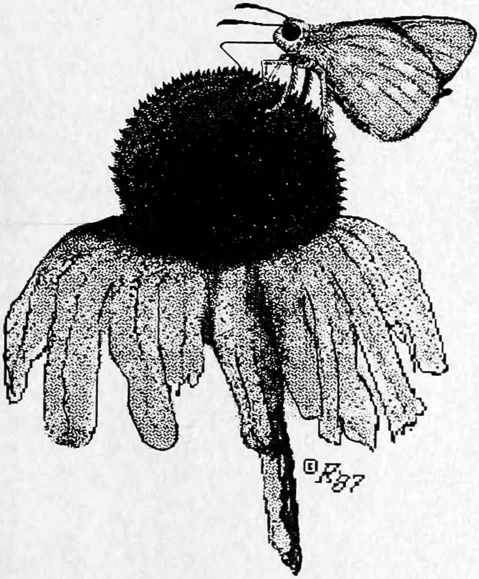

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Cover illustration: Computer-drawn figure of Dakota skipper, *Hesperia dacotae* (Skin.), nectaring on narrow-leaved purple coneflower, *Echinacea angustifolia* DC. Drawing originally executed freehand in the Macintosh application Fullpaint and embellished with FatBits, exported to SuperPaint and further embellished with LaserBits, then produced on a LaserWriter. Cover version is 50% width of LaserWriter version. Submitted by Ronald A. Royer, Division of Science, Minot State University, Minot, North Dakota 58701.

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SPEYERIA ATLANTIS IN COLORADO: REARING STUDIES CONCERNING THE RELATION BETWEEN SILVERED AND UNSILVERED FORMS

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ABSTRACT. *Speyeria atlantis* in the SE Rocky Mts. occurs in two forms, silvered and unsilvered, that could be mere forms or separate species. Nine wild females laid eggs and produced adults in the laboratory. Offspring resembled mothers in most cases, except for two mothers about half silvered and one mother about one-third silvered that produced nearly unsilvered offspring. The two forms have the same courtship, without obvious courtship barriers between them, and male pheromones smell the same. Silvered and unsilvered adults have differently colored larvae. The two forms can differ in habitat, and adults actively select different habitats. The two are probably forms of the same species.

Additional key words: Nymphalidae, habitat selection, polymorphism, courtship.

The relation between silvered and unsilvered forms of *Speyeria atlantis* (Edw.) has puzzled many people (Scott 1986b). Thus Grey et al. (1963) discussed the two forms in the Black Hills of South Dakota, where the silvered form with chocolate ventral hindwing (*a. atlantis*) predominates in wet meadow areas, and the unsilvered form with reddish-brown ventral hindwing (*a. hesperis* Edw. = *a. lurana* dosP. & G.) prevails in drier areas. From a locality with 44% silvered adults, W. Evans (in Grey et al. 1963:146) reared 3 silvered offspring with chocolate ventral hindwing from silvered mothers with chocolate ventral hindwing, and 26 unsilvered plus at least 1 silvered offspring with a reddish-brown ventral hindwing from unsilvered mothers with a reddish-brown ventral hindwing. The exact number of mothers contributing was not known, but was probably one or two for each form. Evans noted that the double dorsal stripes were light brown on *atlantis* larvae, grayish white on *hesperis* larvae, and that *hesperis* pupae have more light-brown shading on the wing case than do *atlantis*. Grey et al. (1963) suggested that the two could be treated as separate species, though they retained them in one species because they seem to intergrade in other western U.S. regions.

A similar situation occurs in SW Manitoba where a dark variety of silvered *a. atlantis* (*a. hollandi* F. & R. Cherm.) with chocolate ventral hindwing flies in mountains and forest, whereas a very pale silvered *a. dennisi* dosP. & G. usually with light-brown ventral hindwing flies on tallgrass prairie. They occur near each other. At Duck Mountain, adjacent populations show no intergradation (J. Troubridge pers. comm.). In this area, they behave as separate species, although westward they intergrade at Meadow Lake Park, Saskatchewan (Hooper 1973).

In Colorado E of the continental divide, the unsilvered form (*a. hesperis*) prevails in the mountain foothills, and as one goes higher in the mountains the silvered form (*a. atlantis*, = *a. electa* Edw.) gradually increases in frequency until it predominates in the Canadian Zone. Silvered forms in Colorado's Front Range usually have a chocolate-brown ventral hindwing, whereas unsilvered forms usually have a reddish-brown ventral hindwing, although this association sometimes breaks down; thus some silvered adults have a red-brown ventral hindwing, and some unsilvered ventral hindwing adults have a darker reddish-brown ventral hindwing. Females have a slightly darker ventral hindwing than males; a bilateral gynandromorph from Critchell, for instance, has a very red-brown ventral hindwing on the male side, a darker red-brown ventral hindwing on the female side.

The silvered or unsilvered color is due to light reflection from individual scales. Silver scales appear transparent through a microscope, but their surfaces reflect a white sheen (evidently due to structural interference of light) which causes the silver appearance. Unsilvered scales are cream in color because they appear to be filled with cream pigment, and their surfaces do not reflect light; their scale structure could be the same as silvered scales if the internal pigment blocks transmission of light through the scale to prevent light interference. So the difference between silvered and unsilvered scales could result solely from absence or presence of internal cream pigment. A given wing spot can be entirely cream (unsilvered), or it can be cream with a few silver scales, or the entire spot can be covered with silver scales. Potentially silvered spots occur in four series on the ventral hindwing: basal, postbasal, postmedian, and submarginal. In the basal series, the dot in the discal cell is more likely to have silver scales than the other spots. The postbasal series of spots is less likely to be silvered than the other series, and the basal and marginal series are most likely to be silvered in the mostly unsilvered forms.

To determine the relation between the forms in Colorado, I reared the eggs of selected females, especially those females of a form rare in their population because these would have the greatest likelihood of mating with a male of the opposite form.

REARING METHODS

To obtain eggs, females were collected from Colorado Front Range localities, brought to the laboratory, and placed in jars with *Viola nephrophylla* Green leaves and fed honey-water once per day. Most females lived about a week and laid several dozen eggs. Eggs hatch readily, but first-stage larvae diapause in nature, so to prevent diapause they were placed under constant light in tiny vials with a slice of green violet leaf. After a few days or weeks some larvae ended diapause and started to feed; these fed steadily until pupation on *V. nephrophylla* leaves. Three months were required to raise offspring of one female. Voucher specimens including larvae, pupal shells, and reared silvered and unsilvered adults are in the National Museum of Natural History, Washington, D.C.

RESULTS

Silvering of Mothers and Offspring

A total of 104 adult offspring were reared from 9 mothers from 6 Colorado sites. Each site is described below.

Tinytown (2120 m), Jefferson Co., is a Transition Zone foothills valley bottom with ponderosa pine, douglasfir, willow, alder, honeysuckle, etc., along the creek; the hostplants *Viola canadensis* L. and *V. adunca* Smith (Scott 1986a) are common on the shaded gulch bottom and the base of the N-facing slope. Here 92% of adults had a reddish-brown ventral hindwing with mostly unsilvered spots, 6% were partly silvered (N = 6 half silvered, N = 1 mostly silvered), and 2% were fully silvered with a chocolate-brown ventral hindwing (N = 117). If the fully silvered mother mated at random, the father was probably unsilvered; yet all offspring were silvered (Table 1).

Corwina Park (2120 m), Jefferson Co., is a Transition Zone foothills wooded gulch draining N; the hostplants *V. adunca* and probably *V. canadensis* are in gulch-bottom shade and E-facing shaded slopes. Here 91% of adults were unsilvered with a red-brown ventral hindwing, 9% silvered with a chocolate-brown ventral hindwing (N = 21). If the completely silvered mother mated at random, the father was probably unsilvered; yet all offspring were fully silvered (Table 1).

O'Fallon Park (2100 m), Jefferson Co., is near Corwina Park, and is also a Transition Zone foothills wooded gulch draining N with the hostplants *V. adunca* and *V. canadensis* in gulch-bottom shade and E-facing shaded slopes. Here 83% were unsilvered with a red-brown ventral hindwing, 13% silvered with a chocolate-brown ventral hind-

TABLE 1. Extent of silvering on ventral hindwing spots, and color of basal two-thirds of ventral hindwing, of mothers and offspring. Numbers are proportions: for example, "1" under "base" means all scales on wing base spots are silvered, "1/5" under "postmedian" means 20% of scales of postmedian spots are silvered, "0" under "submarginal" means no scales of submarginal spots are silvered, etc., "gyn" is bilateral gynandromorph, "f" is female, and "m" is male.

Material	Sex	Ventral hindwing	Base	Postbasal	Postmed.	Submarg.
Tinytown, Jefferson Co., mother caught 20 July 1984						
Mother	1 f	chocolate	1	1	1	1
Offspring	27 m	chocolate	1	1	1	1
Offspring	19 f	chocolate	1	1	1	1
Corwina Park, Jefferson Co., mother caught 13 July 1985						
Mother	1 f	dark choc-brown	1	1	1	1
Offspring	2 m	dark red-brown	1	1	1	1
Offspring	2 f	choc-brown	1	1	1	1
Offspring	1f	dark choc-brown	1	1	1	1
O'Fallon Park, Jefferson Co., mother caught 12 August 1985						
Mother	1 f	red-brown	2/3	1/5	1/2	1/2
Offspring	1 m	very red-brown	0	0	1/4	1/3
Offspring	1 f	very red-brown	0	0	0	1/5
Offspring	1 f	very red-brown	2/3	0	0	1/2
Critchell, Jefferson Co., mother caught 3 August 1985						
Mother	1 f	red-brown	1/2	1/10	1/2	1/2
Offspring	8 f	very red-brown	0	0	0	0
Offspring	6 f	very red-brown	0	0	0	0
Offspring	1 gyn	very red-brown	0	0	0	0
Mt. Judge female B, Clear Creek Co., mother caught 8 August 1985						
Mother	1 f	red-brown	2/3	1/3	1/5	1/3
Offspring	1 m	very red-brown	0	0	0	1/6
Offspring	6 m	very red-brown	0	0	0	1/10
Offspring	1 m	very red-brown	0	0	0	1/5
Offspring	1 m	very red-brown	1/10	0	0	1/5
Offspring	1 m	very red-brown	1/5	0	0	1/10
Offspring	2 f	very red-brown	0	0	0	1/10
Offspring	1 f	very red-brown	0	0	0	0
Cherry Gulch, Jefferson Co., mother caught 17 July 1984						
Mother	1 f	red-brown	2/3	1/5	0	1/3
Offspring	1 f	very red-brown	1/4	0	0	1/3
Mt. Judge female D, Clear Creek Co., mother caught 8 August 1985						
Mother	1 f	dark red-brown	1/5	0	0	1/2
Offspring	2 m	very red-brown	0	0	0	0
Mt. Judge female F, Clear Creek Co., mother caught 8 August 1985						
Mother	1 f	red-brown	1/5	0	0	1/10
Offspring	1 m	very red-brown	0	0	0	1/10
Offspring	1 m	very red-brown	1/10	0	0	1/5
Mt. Judge female A, Clear Creek Co., mother caught 8 August 1985						
Mother	1 f	red-brown	0	0	0	1/5
Offspring	9 m	very red-brown	0	0	0	0
Offspring	3 f	dark red-brown	0	0	0	1/10
Offspring	1 f	dark red-brown	0	0	0	1/6
Offspring	1 f	red-brown	0	0	0	0
Offspring	1 f	red-brown	0	0	0	1/6
Offspring	2 f	very red-brown	0	0	0	0

wing, and 4% intermediate (N = 19). If the nearly half-silvered mother mated at random, the father was probably unsilvered; all offspring were nearly unsilvered (Table 1).

Critchell (2370 m), Jefferson Co., is a shaded E–W streamside in the upper Transition Zone foothills, with ponderosa pine, douglasfir, various shrubs, grassy glades, and *V. canadensis* and *V. adunca*. Here 88% were unsilvered with a reddish brown ventral hindwing, 7% fully silvered, and 5% intermediate (N = 2 half silvered, N = 1 mostly silvered) (N = 53). If the nearly half-silvered mother mated at random, the father probably was unsilvered; all offspring were completely unsilvered (Table 1).

Cherry Gulch (2100 m), Jefferson Co., is a Transition Zone foothills gulch at the base of a N-facing slope covered with douglasfir, *Holodiscus, Physocarpus,* other shrubs, and *Viola canadensis*. Here 97% were unsilvered with a reddish brown ventral hindwing, 3% silvered with a brown ventral hindwing (N = 69). If the mostly unsilvered mother mated at random, the father was probably unsilvered; the single offspring was less silvered than the mother (Table 1).

Mt. Judge (2 km NE, 2770 m), Clear Creek Co., is a Canadian Zone valley bottom, with forest (spruce, pine, douglasfir, some aspen) beside grassy meadows, a tiny creek on the valley bottom, and *V. canadensis* and *V. nephrophylla*. Silvered adults with a chocolate ventral hindwing were most common, with a few silvered adults with a reddish brown ventral hindwing; but unsilvered adults with a red-brown ventral hindwing were also found, a few unsilvered adults with a brown ventral hindwing, and a few variably silvered intermediates. The upperside black lines vary from narrow to wide independent of ventral hindwing variation. Shape of silver spots varies between individuals, as does amount of black at the base of each silver spot, but this variation is also independent of degree of silvering. Four females from this site labeled A, B, D, and F, produced offspring (Table 1). If the Mt. Judge mothers mated at random, they probably mated with silvered males because 74% of males here were silvered (Table 2). However, because of habitat selection at this site (described in next section), and because all four mothers were found in mixed woods away from the creek where only 38% of males were silvered (Table 2), the mothers probably mated with unsilvered fathers. Mother B was about one-third silvered; her offspring were almost completely unsilvered. Mothers A, D, and F, and their offspring, were almost completely unsilvered.

Habitat Selection and Movements

The Mt. Judge site displayed habitat selection by the forms (Table 2). In several meadows along the tiny creek 90% of adults were silvered,

TABLE 2. Frequency of color forms at Mt. Judge site, based on nine visits 1984 to 1987.

	Mixed woods away from creek		Meadows along creek	
Silvering	No. male	No. female	No. male	No. female
Mostly unsilvered	24	13	11	2
Half silvered	1	0	1	0
Completely silvered	15	8	72	53

10% unsilvered. In contrast, at the habitat edge near the head of the valley, away from the creek in mixed woods–tiny meadows edging the large meadow and in the adjacent meadow-edge, one-third (38%) of adults were silvered, and two-thirds (62%) unsilvered.

A small mark-recapture study was conducted at Mt. Judge in 1987 (31 July, 5, 9 Aug.), in which 33 adults were marked and 16 recaptured. Six unsilvered adults were marked (2 male, 4 female), and 3 females recaptured, all in the mixed woods, one after 5 days. Twenty-seven silvered adults were marked (14 male, 13 female), and 13 recaptured (7 male, 6 female), after up to 9 days, including 5 moves completely across the habitat, and 6 halfway across it. I conclude that silvered adults move completely about the habitat, and females probably oviposit in the mixed woods where host violets grow under conifers. But judging from the restricted distribution of unsilvered adults (Table 2), these are more local, and their restricted movement causes the habitat selection difference. In general, unsilvered Colorado adults prefer open woods with violets (N-facing slopes and gulch bottoms in the foothills), whereas silvered adults also occupy more open wet valley bottoms.

Pheromones

Male odor of both forms from Mt. Judge was compared by the author. Males of silvered and unsilvered forms smelled the same: the odor is sweet but has a "hot" or "peppery" sensation, sweet but slightly peppery pungent. Virtually every male had this odor, a few weaker than others. Females lacked an odor. The description of odor is subjective, and different observers might use different words to describe it, but it was the same for both forms. Thus, the male pheromone is probably the same in both forms, although the human nose certainly cannot match the precision of laboratory instruments.

The pheromone system is complex. Males have androconial scales on dorsal wing veins (Scott 1986b:fig. 37) which evidently produce the pheromone odor; pheromone from these scales in the closely related European *Argynnis paphia* L. causes the female to land and accept the male (Magnus 1958). Females have a dorsal gland between abdomen segments 7 and 8 (Scott 1986b:fig. 37). This gland in *A. paphia* produces a pheromone that attracts males: femalelike dummies attract males but do not elicit complete courtship, and freshly killed females are more attractive to males than dried females (Magnus 1958); virgins respond to nearby males by exposing the abdomen gland and aiming the abdomen tip toward the male (Treusch 1967). Males have a paired gland on the abdomen tip (Arnold & Fischer 1977, Scott 1986b) which, by comparison with Heliconiini (Scott 1986b), could possibly transfer pheromone to the female during mating to enable mated females to produce a third pheromone that repels males.

Courtship

Courtship of *Speyeria atlantis,* which is nearly identical to that of *Argynnis paphia* (Magnus 1950), was described by Scott (1986b) based mainly on unsilvered form courtships in Jefferson Co., Colorado. In addition, a completed courtship between silvered male and female forms was seen at Mt. Judge: female on flower when male sighted her and landed; she fluttered her mostly spread wings with small amplitude for 1 s, he flicked his nearly closed wings behind her for 1–2 s; she rotated around flower top 1 revolution with her wings still spread while he rotated after her and flicked his nearly closed wings once during turn; she stopped, closed her wings, tilted forward so that her abdomen was raised slightly but lowered from between hindwings; he spread his wings partway; they joined.

Four courtships were seen at Mt. Judge between unsilvered males and silvered females, as follows.

1) Male patrolled near female (prior mating status unknown) on flower, landed, flicked wings (wingtips vibrating 0 to 1 cm apart about twice per s) for 10 s, curved abdomen laterally to attempt joining (meanwhile female, wings closed, leaned forward with abdomen lowered from between closed hindwings and abdomen raised above horizontal about 60°); wind blew them and he flew, fluttered over her for 1 s, landed, flicked beside her 10 s, curved his abdomen but was too close and his abdomen tip missed (during his bending she kept abdomen exposed), then he flew away. Female was evidently receptive because she exposed her abdomen and did not perform rejection dance (fluttering wings vigorously).

2) Male patrolled near silvered virgin (later found to have no spermatophores) on flower, landed, flicked his wings, she crawled away with closed wings, he crawled after her for 5 min while flicking and bending his abdomen, she stopped and spread wings partly while he flicked and curved abdomen to attempt mating for 5 min, he flew away (evidently she did not extrude genitalia, so he could not join). She was unreceptive even though she did not flutter her wings, perhaps because, as judged from weak flight, she was too young.

3) He pursued her in flight, they landed, she fluttered slightly and crawled away while he flicked his wings and crawled behind, she got farther away, he flew up a short distance but did not find her and flew away.

4) She raised her wings and slightly lowered and partly extruded her abdomen while he flicked his nearly closed wings behind her, he flew away after about 30 s.

Data on courtship between forms are too few to be conclusive, but no obvious courtship barriers to mating occur. Releases of reared virgins are needed. Grey et al. (1963) inconclusively report abnormal courtship of a few laboratory adults.

Larval Differences
(Figs. 1–14)

Color photographic slides were made of larvae and pupae from each study site except larvae from Corwina, and some larvae and pupae were preserved to correlate their color pattern with adult appearance.

From a distance, older larvae producing silvered adults (Figs. 5, 7–9) appear mottled black with orangish tan spines and two middorsal white lines, whereas older larvae producing unsilvered adults (Figs. 10–14) appear solid black with orange spines. Viewed more closely, larvae of both forms are basically black, with a pair of middorsal whitish lines 1 mm apart, and three rows of scoli (lateral to middorsal lines, supraspiracular, and subspiracular) which are tan or orange with black tips. The head of both forms is black with the dorsal half of the rear half of the head orangish.

Larvae of the silvered form (based on larvae from Tinytown, Figs. 5, 7–9) have the middorsal whitish lines conspicuous and mostly continuous, though alternately wider and narrower. Because Corwina pupae had less conspicuous lines than Tinytown pupae, Corwina larvae may not have had the lines this conspicuous. Scoli of the silvered form are orangish tan with black tips. Ground color is not as black as in the unsilvered form so three rows of black bands with very sinuous narrowly white edges are recognizable: along the dorsalmost scoli (edging middorsal white lines), along the supraspiracular scoli, and in between these (Figs. 8, 9). A light gray-brown transverse band circles the rear of each segment except middorsally, a remnant of the pale transverse stripes of *Speyeria nokomis* (Edw.) larvae (Scott & Mattoon 1981).

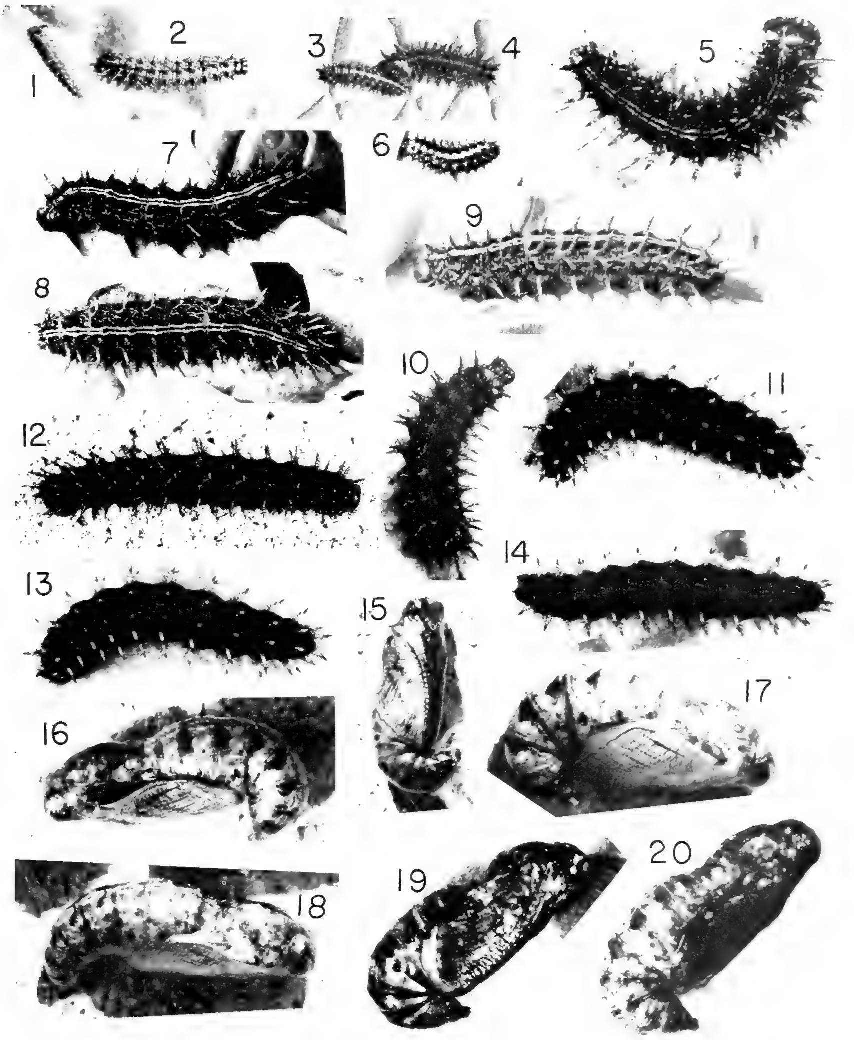
Larvae of the unsilvered form (from O'Fallon, Critchell, Cherry Gulch, Mt. Judge) are a little darker black and the pattern is obscured, so the black sinuous bands are unrecognizable without a microscope, and the middorsal two lines are fainter and broken into two dashed lines (Figs. 10–14). Scoli are orange with black tips. The only variation between localities among unsilvered larvae involves the single Cherry Creek larva which had slightly less orangish scoli. Edwards' (1888b) description of the unsilvered form is very similar.

The above descriptions of larvae do not correspond with descriptions of larvae of the silvered and unsilvered forms in the Black Hills of South Dakota (Grey et al. 1963). Both are described as identically black with orange spine shafts, the two middorsal lines grayish white in the unsilvered form, light brown in the silvered form. Thus the two middorsal lines are described as whiter in the unsilvered form in South Dakota, whereas they are whiter in the silvered form in Colorado. My descriptions are based on 104 larvae and dozens of color slides from many sites, whereas the South Dakota data are fewer.

Width of the two pale middorsal lines of the larva is apparently not closely linked to degree of silvering of the adult; among larvae producing silvered adults, the whiteness differed somewhat between the Tinytown and Corwina sites in Colorado as noted above, and differed between Colorado and South Dakota adults.

Thus, both larvae and adults of the unsilvered form have more pigment—more cream in adult scales, more orange on larval spines, more black on larval body—so one can guess that the gene responsible for the unsilvered form causes an increased deposition of some dark pigment such as melanin.

Larvae and pupae of silvered ventral-hindwing *S. atlantis* from NE



FIGS. 1–20. **1,** First-stage larva, silvered form, Tinytown; **2,** Second-stage larva, silvered form, Tinytown; **3,** Third-stage larva, silvered form, Tinytown; **4,** Fourth-stage larva, silvered form, Tinytown; **5,** Fourth-stage larva, silvered form, Tinytown; **6,** Third-stage larva, silvered form, Tinytown; **7,** Mature larva, silvered form, Tinytown; **8,** Mature larva, silvered form, Tinytown; **9,** Mature larva, silvered form, Tinytown; **10,** Third-stage larva, unsilvered form, O'Fallon female C; **11,** Mature larva, unsilvered form, O'Fallon female C; **12,** Mature larva, unsilvered form, Cherry Gulch; **13,** Mature larva, unsilvered form, Mt. Judge female F; **14,** Mature larva, unsilvered form, Mt. Judge female A; **15,** Pupa (orange-brown wings), silvered form, Tinytown; **16,** Pupa (orange-brown wings), silvered form, Tinytown; **17,** Pupa (orange-brown wings), silvered form, Tinytown; **18,** Pupa (orange-brown wings), silvered form, Tinytown; **19,** Pupa (partly orange-brown wings), unsilvered form, O'Fallon female C; **20,** Pupa (black wings), unsilvered form, Mt. Judge female F.

U.S. (Edwards 1888a) are grayer than Colorado-South Dakota *S. atlantis*; larvae and pupae evidently show geographic variation as do adults.

Pupal Differences
(Figs. 15–20)

Pupae from localities with sufficient numbers show great individual variation, but there is no obvious important difference between silvered and unsilvered forms. The pupa resembles *S. nokomis* (Scott & Mattoon 1981) in general, but is darker (orange-brown), and the posterior half of each abdominal segment is darker because it is mottled with tiny black dots and dashes. The anterior half of each abdominal segment is not uniformly black as in *nokomis*: some pupae have a broad black irregular band, but most have the black areas broken into spots, including triangular spots just beside the anterior-pointing orange-brown middorsal triangles on segments 5–7. Pupae from Tinytown have two sinuous tan middorsal abdominal lines, but pupae from Corwina (both sites produced silvered adults) and the other sites had weak tan middorsal lines. Pupal wing color varies from mostly black to almost wholly orange-brown, but most are mostly orange-brown, a few black-winged.

Grey et al. (1963) describe the pupal wing cases of silvered forms as darker with less light brown mottling than those of unsilvered forms in the Black Hills. However, they reared only three silvered adults, so the difference is probably due to small sample size because all Colorado sites with large samples show considerable variation in pupal wing color. Pupae producing silvered adults are not darker in Colorado.

DISCUSSION

There are several reasons why *S. a. atlantis* and *S. a. hesperis* could be treated as distinct species: they often fly together, they prefer different microhabitats, amount of silvering seems usually linked with ventral hindwing color, mothers usually produce offspring resembling themselves, and their larvae differ. If scientists were aware only of Black Hills populations, the two would certainly be treated as separate species because they are so distinct there. Some anecdotes (coincidences?) also fit the two-species theory. For instance, six unsilvered males and one silvered pair were found in the Mt. Judge mixed woods 28 July 1987, the silvered pair in copula.

There are several reasons why *S. a. atlantis* and *S. a. hesperis* could be treated as one species:

1) Silvered and unsilvered forms are linked by a complete series of intermediate adults, from slightly to partly to half to mostly silvered, although only slightly silvered intermediates are common.

2) Unsilvered mothers sometimes produce silvered offspring (Grey et al. 1963:146), and half-silvered mothers often produce unsilvered offspring (Table 1).

3) In many populations, silvered forms are rare (<5%) as in the lower foothills of the Colorado Front Range, rarity a true species might have difficulty surviving. The reverse is also true, in which unsilvered forms are rare within silvered populations, as in the wet center of the Black Hills (Grey et al. 1963). However, *S. coronis* (Behr) is just as rare and it survives.

4) Frequencies of the forms show clinal trends, both altitudinally in the Colorado Front Range, and along habitat gradients. For instance, in the Black Hills (Grey et al. 1963), *atlantis* is common in wet meadow habitats on poorly drained granite, and is rarer away from these areas. Similarly, in S Colorado (Scott & Scott 1980) *hesperis* predominates in the lower foothills, both forms occur in dry areas at higher altitude, and *atlantis* predominates in three wet meadow enclave habitats at middle altitudes: Coaldale in Arkansas Canyon, Fremont Co.; SW of Westcliffe on Wet Mountain Valley floor, Custer Co.; Stonewall in upper Purgatoire River valley, Las Animas Co. Such enclaves have not been found in the Front Range W of Denver, where silvered forms are rare in the foothills and increase in frequency with altitude until they predominate in the upper Canadian Zone.

5) When attempts are made to divide *S. atlantis* into silvered and unsilvered "species", their distributions are incongruous because unsilvered forms cut an E–W swath through the range of silvered forms, replacing them in the process (Scott 1986b).

The silvered-unsilvered division also fails to solve the problem of sympatry of *S. a. dennisi* and *S. a. atlantis* (*hollandi*), both of which are silvered, in Manitoba. A species *S. dennisi* could include *S. atlantis ratonensis* Scott from NE New Mexico and *S. a. greyi* from NE Nevada, but *dennisi* is said to intergrade W to *atlantis* in Saskatchewan-Alberta, and *greyi* intergrades with *dodgei* in S Idaho (P. C. Hammond pers. comm.), and at least *greyi* seems independently evolved toward similar pallidity.

6) Other *S. atlantis* subspecies have polymorphisms of silvered-unsilvered adults: *wasatchia* dosP. & G. (=*tetonia* dosP. & G.) in W Wyoming-Utah is usually unsilvered, *chitone* (Edw.) in S Utah and *schellbachi* Garth in N Arizona are usually silvered.

7) Other species of *Speyeria* have silvered-unsilvered polymorphisms: *zerene* (Bdv.) in California and S Oregon, *callippe* (Bdv.) in N California and the Sierra Nevada, *egleis* (Behr) in the Sierra and Utah, *hydaspe* (Bdv.) in British Columbia. These polymorphisms are accepted by lepidopterists. Boggs (1987) hypothesized that rare unsilvered *S. mormonia* are homozygous recessives that fail to reproduce, which is dubious because *S. mormonia artonis* (Edw.) are nearly always unsilvered.

8) Association between ventral hindwing color and silvering and larval color pattern breaks down geographically. In the Black Hills and E of the continental divide in the Colorado mountains, silvered adults have a chocolate-brown ventral hindwing (darker in the Black Hills), and unsilvered adults usually have a reddish brown ventral hindwing. However, in N-central New Mexico, 98% of adults ($N = 60$) are silvered but the ventral hindwing varies from chocolate- to reddish brown. In SW Manitoba *S. atlantis dennisi* and *S. a. atlantis* (*a. hollandi*) are 100% silvered but the ventral hindwing is usually light brown in the former and chocolate-brown in the latter. And silvered adults have the ventral hindwing browner in the Black Hills than in the Colorado Front Range. Larval differences in Colorado are partially reversed in the Black Hills, and larvae are grayer in E North America.

The conclusion that silvered and unsilvered adults are polymorphic forms of one species seems preferable.

Paleogeography

The current geographic distribution of wing characters suggests that the dark silvered form (*S. a. atlantis*) occupied the coniferous forest in N U.S. and the Rocky Mountain foothills during the Ice Age; afterwards it moved higher in altitude and latitude. The unsilvered form with reddish brown ventral hindwing (now *S. a. hesperis, a. wasatchia, a. irene* [Bdv.]) occupied open forest in the southern Great Basin lowlands; after the Ice Age it spread N into the mountains, E through lowland S Wyoming to the Black Hills, and S along the Colorado mountain foothills. The silvered form with narrower black lines and a pale brown ventral hindwing (now *S. atlantis dennisi* and *a. ratonensis*) occupied aspen parkland in the current S Great Plains or central Texas; after the Ice Age it spread, respectively, N to Canada, and upward to a mountain mesa. The forms became sympatric after the Ice Age.

Mechanism of Inheritance

The inheritance mechanism of silvering is unknown. Rarity of half-silvered adults suggests dominance, but some broods with half the offspring silvered and half unsilvered should occur but did not. If half-silvered adults were heterozygotes, they would not produce all-unsilvered broods as at Critchell. If silvered is dominant, rare silvered mothers would be likely to produce silvered offspring, as at Tinytown and Corwina. O'Fallon and Cherry Gulch broods perhaps suggest modifier genes that cause part-silvering.

Maternal inheritance seems the best guess now, and fits all the reared broods; offspring would resemble the mother, the father having no effect or perhaps merely modifying partly silvered offspring. Sterling O. Mattoon (pers. comm.) states that *Speyeria* offspring generally resemble their mother very closely, although some silvered offspring have been reared from unsilvered mothers and vice versa.

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POPULATION FLUCTUATIONS OF *AZETA VERSICOLOR* (FABRICIUS) (NOCTUIDAE) ON *GLIRICIDIA SEPIUM* (JACQ.) (FABACEAE) IN NORTHEASTERN COSTA RICA

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ABSTRACT. Counts of early stages, especially caterpillars, of *Azeta versicolor* on the host tree *Gliricidia sepium* planted as shade cover in a vanilla plantation were made intermittently during five years. Based on field observations and rearings, the mature caterpillar and pupa were described, noting two distinct color morphs in the former. Tachinid parasites were also noted. Caterpillar abundance was analyzed and interpreted in relation to monthly rainfall and leaf-flushing in the host tree, since caterpillars feed preferentially on new (flush) leaves. Numbers of caterpillars were highly correlated with monthly rainfall. It is concluded that population cycles of the moth are regulated by seasonal patterns of leaf-flushing in the host.

Additional key words: immature stages, leaf flushing, population dynamics.

Impact of seasonal fluctuations in rainfall on leaf-flushing of semi or fully deciduous host trees is a major environmental factor molding population dynamics of noctuids and other Lepidoptera in the tropics (Vaishampayan & Veda 1980, Blair 1982, Tucker & Pedgley 1983). Fabaceous legume crops in the tropics are especially preferred hosts of noctuid and pyralid defoliators, with seasonal patterns of population outbreaks typical for several of these host species (Bradley & Carter 1982, Panchabhavi & Holihosur 1982). In many species, caterpillars preferentially defoliate immature leaves or other most nutritious tissues of the host, which are often only seasonally available (Futuyma & Wasserman 1980, Bracken 1984). Here I report seasonal abundance pattern of immature stages for the noctuid moth *Azeta versicolor* (Fabricius) on leaves of the fabaceous legume tree *Gliricidia sepium* (Jacq.) planted as shade cover in a vanilla plantation.

METHODS

Counts of life stages of *Azeta versicolor* were obtained on 16 dates between March 1982 and June 1987 at "Finca La Tirimbina," near La Virgen (10°23'N; 84°07"W; 200 m elev.), Sarapiqui District, Heredia Province. Within a ca. 1600 m^2 plot containing about 900 trees of *Gliricidia sepium* planted a few years earlier to shade vanilla plants, 30 arbitrarily selected trees (canopy height ca. 3 m) were censused for *Azeta versicolor* caterpillars at various times. The medium-sized (40 mm wingspan) adults and caterpillars were readily recognizable in field censuses: adult moths are drab greenish brown with striking red abdominal coloration, and yellowish mature caterpillars usually rest close to the base of host trees, typically on stems and leaves of vanilla orchid vines and other epiphytes under the trees.

On a given caterpillar census, as many as 100 samples of both mature or immature leaves and stems on each tree (usually up to height of 1.5 m) were searched for "young" caterpillars (mixed early instars) and eggs. Condition of canopy foliage of *Gliricidia sepium* was also noted (such as presence or absence of flush leaves), providing a qualitative picture of local timing of peak flushing periods in relation to seasonality. A total of 30 caterpillars (later instars) were placed in clear-plastic bags containing fresh cuttings of *G. sepium* and kept tightly shut for rearing. Parasitism of caterpillars and pupae was noted from this sample.

RESULTS

Natural history. In both of two color morphs of the final stage caterpillar, roughly equal in abundance and not sexual dimorphism, the head is pinkish white with black dots. Thoracic and abdominal regions of the mature caterpillar (40 mm long by 5 mm wide) have eight lengthwise narrow bands, which, in the dark form are as follows, dorso medial to latero ventral: (1) deep yellow; (2) faintly yellow edged in black; (3) pale bluish streaked with tiny black lines and a single round black dot on each segment; (4) pale bluish yellow; (5) wide pale blue; (6) lateral (spiracular) stripe pale blue with thin black line medially and reddish spiracle openings, each with a black dot dorsoanteriorly and yellow dot ventroposteriorly; (7) yellow with black edging ventrally; (8) grayish with raised black dot, one per segment. Prolegs pinkish, each with yellow dot laterally, ringed with black. Glossy black elongate setae on profuse raised areas of cuticle. Anal clasper faintly pinkish; true legs reddish. In the light form, there are no black stripes bordering other stripes.

The reddish brown pupa (20–22 mm long by 5–6 mm wide) occurs in a loosely constructed cocoon of host leaves pulled together and anchored with light brown silk. Both caterpillar and pupa thrash about vigorously when picked up. Adults are active throughout the day, and are skittish and difficult to capture with an insect net. The spherical, glossy yellow eggs are placed singly on the undersides of *G. sepium* leaves. Of 257 eggs discovered in the field, ca. 70% were on immature (meristem) leaves. As noted above, mature caterpillars rest on vanilla vines and other epiphytic debris on host trunks during daytime, and are chiefly nocturnal feeders, crawling into the *G. sepium* canopy to feed. Each of 3 pupae (out of 30 reared from collected caterpillars) yielded 1 tachinid parasite.

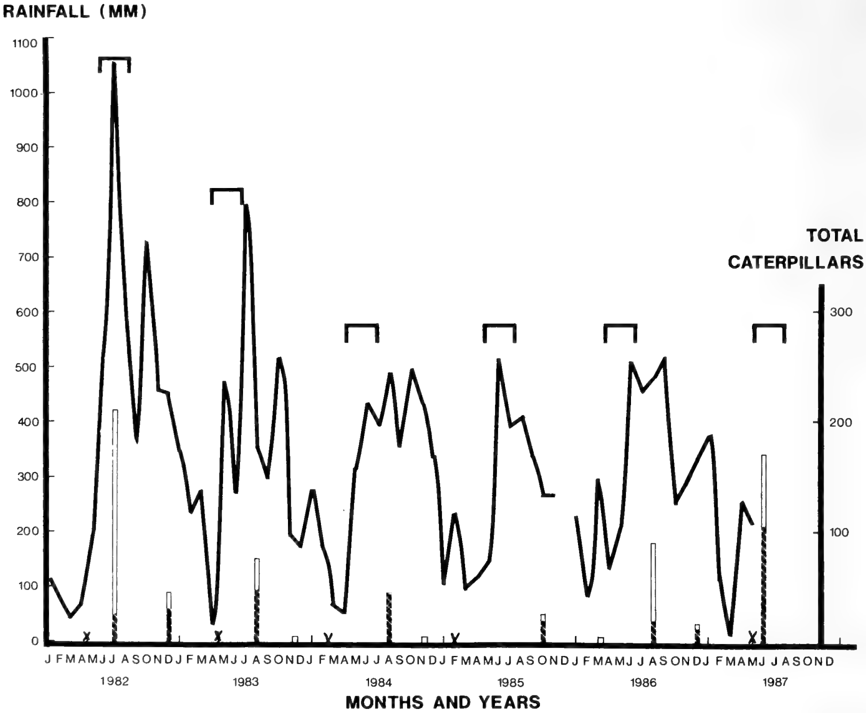

FIG. 1. Monthly total rainfall (line), total numbers of *Azeta versicolor* caterpillars (vertical bars, 5th instars represented by hatching), timing of leaf-flushing (brackets), and periods of caterpillar absenses (x), in the 36-tree subplot of *Gliricidia sepium* at "Finca La Tirimbina." Rainfall data courtesy of Finca La Tirimbina.

Seasonal population fluctuations and leaf-flushing. Abundance of *Azeta versicolor* caterpillars on sampled *Gliridia sepium* trees varied greatly among census dates (Fig. 1). Aside from an occasional hesperiid and limacodid caterpillar, I did not observe other herbivores abundant on these trees. When the data are examined relative to rainy and dry season periods at La Tirimbina, two patterns become apparent: (1) the highest numbers of mature and partly grown caterpillars occurred in the rainy season, especially June–August, approximately during the first half of the lengthy rainy season characteristic of this locality; (2) caterpillars are absent during the dry season (February–March) (Fig. 1). A high positive correlation resulted between numbers of caterpillars and monthly rainfall ($r = 0.81$, $P < 0.01$).

Also during July–August, as many as 500 adults were counted within a 600 m^2 strip of low vegetation bordering one side of the vanilla grove during a 2 morning census (0800–1000 h). As many as 100 eggs were counted within the 36-tree subplot on a single day in July or August, and none were found in February or March. During dry months, host trees are partly deciduous, and only mature leaves are present. Flowering in *G. sepium* at La Tirimbina is most intense during March and early April. During the first three months of the rainy season, *G. sepium* exhibits intensive leaf flushing (Fig. 1).

The highest population density of *Azeta versicolor* at La Tirimbina follows intense flushing of new leaves on larval host trees. The increased availability of immature (flush) leaves during the beginning of the rainy season provides an abundant food resource for larvae. Population build-up can be so intense in the rainy season as to result in 80–100% defoliation of *G. sepium* on some plots. I conclude that the breeding population of this Neotropical noctuid fluctuates in size throughout the year at La Tirimbina in a consistent manner, and in response to the seasonal leaf-flushing cycle of *G. sepium*.

DISCUSSION

Some tropical legume crops attacked by host-specific noctuids and other moths undergo severe defoliation at certain times of year (Singh & Budhraja 1980). Legume tree species typically planted as a permanent shade over perennial crops in the tropics such as cacao, coffee, and vanilla, including *G. sepium* (Inostrosa & Fournier 1982), and others such as *Erythrina* (Borchert 1980) undergo pronounced seasonal cycles in leaf-flushing in direct response to water-stress and rehydration (Reich & Borchert 1982). The complete absence of *Azeta versicolor* caterpillars on *Gliricidia sepium* in the dry season at La Tirimbina is due to absence of immature (newly flushed) leaves. Thus, availability of edible leaf tissues, a consequence of seasonally regulated hostplant leaf-flushing, determines temporal pattern of population build-up in this noctuid. The degree to which *A. versicolor* exploits other larval host plants at La Tirimbina is unknown.

Skittish behavior of the diurnally active adults, and their vivid red abdominal colors, suggest aposematism, perhaps a consequence of larval feeding on *G. sepium,* a species well known for high concentrations of courmarin compounds in its leaves (Allen & Allen 1981). Marked build-up of the adult population in the first half of the rainy season at La Tirimbina suggests a population structure in which biotic regulation of the herbivore may be minimal.

Gliricidia sepium is capable of producing a new flush of leaves following a period of intense herbivory by (J. R. Hunter & A. M. Young pers. obs.). The ability of *G. sepium* to recover rapidly from intense defoliation may be mediated in large part by the tree's capacity to fix nitrogen in the soil.

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BUTTERFLIES OF NORTHEAST TENNESSEE

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ABSTRACT. Here we give results of a 10-year survey of butterflies in a seven-county, 7000 km^2 area of NE Tennessee. Ninety-one species are listed and their seasonal occurrence tabulated on a 10-day basis. Twenty-seven species are judged to be univoltine, twenty-nine bivoltine, and twenty-one multivoltine. The remainder are thought to be migrants or strays that do not overwinter in NE Tennessee. Comparison of our species list with that of SW Virginia and N Georgia indicates the fauna lacks a number of lowland species that occur in N Georgia, and some typically northern species in SW Virginia. Ten species known to occur in both comparison areas, but not recorded here, will probably be found in the future.

Additional key words: Appalachians, biogeography, survey, Georgia, Virginia.

There is little published information on the butterfly fauna of Tennessee (Field et al. 1974). Osburn (1895a, 1895b) lists 70 species occurring around Nashville. Richards (1932) provides some Tennessee records. Watson (1946) and Snyder (1957) list some species occurring in the Smoky Mountains. The best source for the State as a whole is Opler (1983) which contains county distribution maps for all species occurring in the eastern U.S.

We have collected extensively in NE Tennessee for more than 10 years. Here we summarize results of our collecting, make comparisons with other areas in the S Appalachian region, and list additional species likely to occur in NE Tennessee.

STUDY AREA

The area encompasses seven counties in NE Tennessee with a total area of 7000 km^2 (Fig. 1). Two physiographic subdivisions of the S Appalachian region are represented. The SE portion of the area lies within the Blue Ridge Province, the remainder in the Ridge and Valley Province.

The peaks of the Blue Ridge are known locally as the Unaka Mountains. They are characterized by rugged terrain and heavily forested slopes. Elevations vary from 450–600 m in the narrow valleys to 750–1900 m on the peaks. Underlying sedimentary and metamorphic rocks are Cambrian and Pre-Cambrian in age. Soils tend to be sandy and acidic. Most of this portion of the area lies within the Cherokee National Forest (Miller 1974, USDA 1953, 1956, 1985).

The Ridge and Valley portion is underlain by strongly folded sedimentary rocks of Ordovician and Cambrian age. Differential weathering has resulted in long, narrow sandstone ridges trending NE to SW, alternating with valleys developed on less resistant limestone and shale. The easternmost valley is broad and part of a series of connecting valleys extending from Pennsylvania to Alabama commonly called the Great Valley

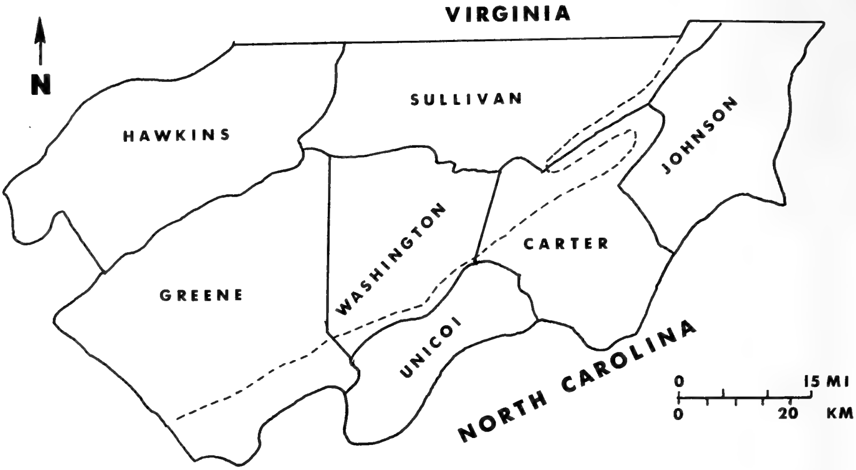

FIG. 1. Study area in NE Tennessee, showing county boundaries. Dashed line is approximate boundary separating Blue Ridge Province (Unaka Mts., SE) from Ridge and Valley Province (NW).

Within it there is local relief in the form of shale knobs and entrenched streams. To the NW, straddling the border of Greene and Hawkins counties, and extending into SW Sullivan Co., are a group of ridges collectively called Bays Mountain. Another prominent feature, Clinch Mountain, runs through NW Hawkins Co. Elevations average lower in the Ridge and Valley Province, ranging from 300 m in the valleys to 600–900 m on ridges. Ridge soils are generally sandy, shallow, and unproductive while valley soils developed on limestone are rich and fertile (Fenneman 1938, Miller 1974, U.S. Dep. Agric. 1953b, 1958a, 1958b, 1979, 1985).

The entire area is drained by the Holston River and its tributaries, part of the Tennessee River drainage system. The rivers have been extensively impounded for flood control and power generation (Hunt 1967).

Climate is characterized by mild winters and warm summers. Average annual precipitation is 100–150 cm except at highest elevations where it may exceed 200 cm. Topography and altitudinal differences cause much local variation in climate. As a rule, S- and W-facing slopes are drier than those facing N and E. Average frost-free season varies from 190 days in NW valleys to 150 days in the Unaka mountains (Walker 1969, U.S. Dep. Agric. 1953, 1979).

Before European settlement, the area was covered with oak-chestnut forest. Clearing of valleys for agriculture, logging in the mountains, and chestnut blight decimated primary forests, especially in the Ridge and Valley. Today forests are concentrated in the Unaka Mountains and on the NW ridges. At lower elevations, oaks (*Quercus* spp.), hickories (*Carya* spp.), yellow poplar (*Liriodendron tulipfera* L.) and other hardwoods are common, often mixed with hemlock (*Tsuga* spp.), and several pines (*Pinus* spp.). The Unaka Mountains are high enough to show altitudinal zonation. Above 900 m, northern forest types such as sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britton) are common. Above 1500 m, red spruce (*Picea rubens* Sarg.), and fraser fir (*Abies fraseri* [Pursh.] Poir) predominate. Treeless, dome-shaped summits called balds occur on some peaks. In the Ridge and Valley, stands of red cedar (*Juniperus virginiana* L.) are common in old fields on limestone soils. Marshes and canebrakes are rare throughout, most having been drained, cleared, or inundated by reservoirs (Braun 1950, Walker 1969, U.S. Dep. Agric. 1953a, 1953b, 1956, 1958a, 1958b, 1979, 1985).

METHODS

Most records come from collections and fields notes made by the authors from 1975 through 1986. Additional records were obtained from participants in a Southern Lepidopterist Society field meeting in the area in 1980, and from collections made by students at Sullivan (County) High School during fall 1977 and 1978. Collections at the U.S. National Museum (USNM) and the Carnegie Museum of Natural History (CMNH) were examined, but no additional records were found. Most specimens are retained in the authors' collections; others have been placed in USNM and CMNH. Some identifications were confirmed by C. V. Covell Jr., University of Louisville, and by R. K. Robbins and J. M. Burns (USNM). Butterfly nomenclature follows Hodges et al. (1983).

To facilitate comparison with NE Tennessee, we define SW Virginia as Giles, Montgomery, and Floyd counties and those counties to the SW entirely or predominantly within the transition zone of Clark and Clark (1951). North Georgia is defined as those counties entirely or predominantly within the mountain region of the State as defined by Harris (1972). Species records for these regions were obtained from Opler (1983), Clark and Clark (1951), and Harris (1972).

RESULTS AND DISCUSSION

We recorded 91 species of butterflies and skippers from NE Tennessee (Table 1). In addition, specimens of *Celastrina ladon* form *neglecta-major* Tutt, considered by some to be a distinct species (Opler & Krizek 1984), have been collected in May and early June. An old sight record for *Anaea andria* Scudder for which we do not have a precise date is not included in the table but is discussed below.

The species found in NE Tennessee can be considered as falling into two categories: residents, which overwinter in the area; and migrants or strays, which do not normally overwinter in the area, although many regularly occur in summer and fall.

A number of resident species are rare or local in distribution, but only one appears limited to a particular part of the study area. *Speyeria aphrodite* (F.) has been collected only in the Blue Ridge, where it is often common at elevations above 600 m.

Analysis of flight-period data in Table 1 to determine number of broods for resident species is complicated by the fact that the flight period of a species at any particular locality may vary from year to year due to climatic and biological factors. Flight periods are also affected by elevation, beginning and ending one to three weeks later at high elevations in the Blue Ridge than in the Ridge and Valley. For example, summer brood *Erynnis horatius* (Scudder & Burgess) has been collected at Bays Mountain Park (600 m) in Sullivan Co. from late June through mid-August, but a fresh specimen was collected in Carter Co. at 1200 m on 8 September.

We believe the following residents are univoltine in NE Tennessee:

Thorybes bathyllus (J. E. Smith)
T. pylades (Scudder)
Erynnis icelus (Scudder & Burgess)
E. brizo (Bdv. & Leconte)
E. juvenalis (F.)
Wallengrenia egremet (Scudder)

TABLE 1. Temporal distribution of butterfly species adults in NE Tennessee.

	Mar.		Apr.			May		
Species	11–20	21–31	1–10	11–20	21–30	1–10	11–20	21–31
Hesperiidae								
Epargyreus clarus				X	X	X	X	X
Autochton cellus								X
Achalarus lyciades								X
Thorybes bathyllus								
T. pylades								X
Staphylus hayhurstii								
Erynnis icelus				X	X	X		
E. brizo			X	X	X			
E. juvenalis			X	X	X	X	X	X
E. horatius								
E. baptisiae								
Pyrgus communis					X			
Pholisora catullus								
Nastra lherminier								X
Ancyloxypha numitor								X
Thymelicus lineola								
Hylephila phyleus								
Polites coras							X	X
P. themistocles								X
P. origenes						X		
Wallengrenia egeremet								
Pompeius verna							X	X
Atalopedes campestris								X
Atrytone delaware								X
Poanes hobomok							X	X
P. zabulon					X	X	X	X
Euphyes ruricola metacomet								X
Amblyscirtes hegon					X		X	
A. aesculapius							X	X
A. vialis				X		X		
Papilionidae								
Battus philenor			X	X	X	X	X	X
Papilio polyxenes asterius			X		X	X	X	
P. cresphontes								
P. glaucus		X	X	X	X	X	X	X
P. troilus			X	X	X	X	X	X
Eurytides marcellus		X	X	X	X	X	X	X
Pieridae								
Pontia protodice								
Artogeia virginiensis			X	X	X	X	X	X
A. rapae	X	X	X	X		X	X	X
Euchloe olympia		X	X	X		X		
Falcapica midea		X	X	X	X	X	X	
Colias philodice	X		X	X	X	X		X
C. eurytheme	X	X	X	X	X		X	
Phoebis sennae eubule								
Eurema lisa								
E. nicippe								

TABLE 1. Continued.

June			July			Aug.			Sept.			Oct.			Nov.	
1–10	11–20	21–30	1–10	11–20	21–31	1–10	11–20	21–31	1–10	11–20	21–30	1–10	11–20	21–31	1–10	11–20
X	X	X	X	X	X	X	X									
X			X	X												
X	X				X	X			X							
	X															
X	X	X														
		X														
X		X														
X																
		X			X		X		X							
			X	X	X	X										
												X	X	X		
							X									
						X	X	X		X						
X	X	X	X	X	X	X	X	X	X	X						
							X									
													X	X		
X	X			X	X	X	X	X		X						
X	X				X	X	X	X	X	X						
			X			X	X	X	X	X						
X	X		X						X							
X	X	X	X				X	X		X						
			X		X	X	X	X	X	X	X	X	X	X	X	X
	X	X	X			X	X	X	X	X						
X	X															
X	X				X	X	X	X	X	X						
X		X	X		X											
X	X															
X			X	X	X	X	X	X	X	X	X		X	X		
		X			X		X	X	X	X	X			X		
									X							
X		X		X	X	X	X	X	X	X						
X		X			X	X	X	X		X						
X	X	X							X	X						
													X			
X		X			X	X	X	X		X	X	X	X	X	X	X
X	X	X	X			X	X	X	X	X	X	X	X	X	X	X
X	X	X				X	X	X	X		X	X	X	X	X	X
									X							X
								X	X	X				X		
		X						X		X		X	X	X	X	

TABLE 1. Continued.

Species	Mar.		Apr.			May		
	11–20	21–31	1–10	11–20	21–30	1–10	11–20	21–31
Lycaenidae								
Feniseca tarquinius						X		
Lycaena phlaeas americana					X	X		
Harkenclenus titus mopsus								
Satyrium calanus falacer								X
S. caryaevorum								
S. liparops strigosum								
Calycopis cecrops					X		X	
Mitoura grynea					X	X	X	
Incisalia augustus croesioides				X				
I. henrici		X	X	X	X	X	X	
I. niphon		X	X	X	X	X	X	
Parrhasius m-album								
Strymon melinus			X	X	X	X		
Erora laeta				X	X	X		
Everes comyntas			X	X	X	X		
Celastrina ladon		X	X	X	X		X	X
C. ebenina				X	X	X		
Glaucopsyche lygdamus				X	X	X		
Libytheidae								
Libytheana bachmanii								
Nymphalidae								
Polygonia interrogationis	X					X		X
P. comma	X	X	X					X
Nymphalis antiopa	X	X	X	X	X	X		X
Vanessa virginiensis				X	X		X	
V. cardui						X		
V. atalanta								X
Junonia evarete								
Euptoieta claudia								
Speyeria diana								
S. cybele						X		X
S. aphrodite								
Clossiana bellona toddi			X	X	X	X		X
Phyciodes tharos					X	X	X	X
Charidryas nycteis							X	X
Euphydryas phaeton								
Basilarchia arthemis astyanax								X
B. archippus								X
Apaturidae								
Asterocampa celtis							X	X
A. clyton								X
Satyridae								
Enodia anthedon								X
E. creola								
Cyllopsis gemma				X		X	X	
Hermeuptychia sosybius								X
Megisto cymela								X
Cercyonis pegala								
Danaidae								
Danaus plexippus					X			

TABLE 1. Continued.

June			July			Aug.			Sept.			Oct.			Nov.	
1–10	11–20	21–30	1–10	11–20	21–31	1–10	11–20	21–31	1–10	11–20	21–30	1–10	11–20	21–31	1–10	11–20
	X	X			X	X	X									
X	X	X	X			X										
	X	X	X													
X	X	X	X	X	X											
	X															
X	X		X													
					X		X									
		X			X											
X		X														
					X	X										
		X	X		X	X	X	X	X	X	X			X		
		X			X	X		X		X				X	X	
X	X	X		X	X	X		X		X						
	X	X	X		X		X									
	X	X	X		X	X	X	X	X	X					X	
X		X			X	X	X	X	X	X			X			
X						X		X				X		X		
		X	X	X	X		X	X		X				X	X	
						X				X			X	X	X	
X	X	X	X	X	X		X			X						
			X	X	X			X	X	X		X		X	X	
X		X		X			X			X		X	X	X	X	
		X	X	X	X	X		X	X	X						
X	X	X	X	X	X	X	X	X	X	X	X					
		X	X	X	X											
X		X	X	X	X		X	X	X	X		X		X		
X		X		X	X		X	X		X	X	X	X	X		
X	X	X			X	X										
X		X														
X		X			X	X	X	X	X	X				X	X	
X		X			X	X	X	X	X	X	X	X			X	
X					X	X	X	X	X							
X		X			X		X	X	X							
X		X			X		X			X	X					
X							X									
X								X	X							
X					X	X		X	X							
X	X	X		X												
		X	X	X	X	X	X	X	X							
					X	X	X	X		X	X	X	X	X	X	

Poanes hobomok (Harr.)
Euphyes ruricola metacomet (Harr.)
Amblyscirtes hegon (Scudder)
Artogeia virginiensis (Edw.)
Euchloe olympia (Edw.)
Falcapica midea (Hbn.)
Harkenclenus titus mopsus (Hbn.)
Satyrium calanus falacer (Godt.)
S. caryaevorum (McD.)
S. liparops strigosum (Harr.)
Incisalia augustus croesioides (Scudder)
I. henrici (G. & R.)
I. niphon (G. & R.)
Celastrina ebenina Clench
Glaucopsyche lygdamus (Doubleday)
Speyeria diana (Cram.)
S. aphrodite
Euphydryas phaeton (Drury)
Megisto cymela (Cram.)
Cercyonis pegala (F.)

Speyeria cybele (F.) flies from May through September and would appear to be multivoltine, but the long flight period is caused by staggered emergence of a single brood (Opler & Krizek 1984, Scott 1986).

The following are bivoltine:

Autochon cellus (Bdv. & Leconte)
Achalarus lyciades (Gey.)
Nastra lherminier (Latr.)
Polites coras (Cram.)
P. themistocles (Latr.)
P. origenes (F.)
Pompeius verna (Edw.)
Atrytone delaware (Edw.)
Poanes zabulon (Bdv. & Leconte)
Lycaena phleas americana (Harr.)
Calycopis cecrops (F.)
Mitoura grynea (Hbn.)
Nymphalis antiopa (L.)
Charidryas nycteis (Doubleday)
Basilarchia arthemis astyanax (F.)
B. archippus (Cram.)
Asterocampa celtis (Bdv. & Leconte)
A. clyton (Bdv. & Leconte)
Enodia anthedon A. H. Clark
E. creola (Skin.)
Cyllopsis gemma (Hbn.)
Hermeuptychia sosybius (F.)

Fresh *Basilarchia archippus* and *B. arthemis astyanax* taken in October and early November indicate that partial third broods are produced when mild weather persists well into fall.

Additional species are probably bivoltine, though not apparent from our data. *Erynnis horatius* (Scudder & Burgess) and *E. baptisae* (Fbs.) should have spring broods on the wing in April and May. They have likely been overlooked amid large numbers of *E. juvenalis* flying at that time. *Pholisora catullus* (F.) is also likely to have a spring brood, and is probably more common than our records suggest. *Erora laeta* (Edw.), *Amblyscirtes aesculapius* (F.), *A. vialis* (Edw.), and *Staphylus hayhurstii* (Edw.) have been taken only in spring or early summer. All four species probably have second broods in summer overlooked due to very local occurrence.

Another group of resident species are multivoltine, with three or more broods per year:

Epargyreus clarus (Cram.)
Ancyloxypha numitor (F.)
Battus philenor (L.)
Papilio polyxenes asterius Stoll
P. glaucus L.
P. troilus L.
Eurytides marcellus (Cram.)
Artogeia rapae (L.)
Colias philodice Godt.
C. eurytheme Bdv.
Feniseca tarquinius (F.)
Strymon melinus Hbn.
Everes comyntas (Godt.)
Celastrina ladon (Cram.)

Polygonia interrogationis (F.)
P. comma (Harr.)
Vanessa virginiensis (Drury)
V. atalanta (L.)
Clossiana bellona toddi (Holl.)
Phyciodes tharos (Drury)

One additional species, *Parrhasius m-album* (Bdv. & Leconte), is probably multiple brooded. We have taken a worn specimen in SW Virginia near the Tennessee line in early May, and sources indicate that a third brood in late August–September is likely (Opler & Krizek 1984, Scott 1986).

We consider the following species to be migrants or strays:

Pyrgus communis (Grt.)
Hylephila phyleus (Drury)
Atalopedes campestris (Bdv.)
Papilio cresphontes (Cram.)
Pontia protodice (Bdv. & Leconte)
Phoebis sennae eubule (L.)
Eurema lisa (Bdv. & Leconte)
E. nicippe (Cram.)
Libytheana bachmanii (Kirtland)
Vanessa cardui (L.)
Junonia coenia (Hbn.)
Euptoieta claudia (Cram.)
Danaus plexippus (L.)

Most of these species overwinter in the SE coastal plain where they are multivoltine. As their populations expand during the summer, they move N and W, often penetrating into the Appalachians. Although they may reproduce during summer and fall, they generally cannot survive winter in NE Tennessee. There are exceptions, as evidenced by an April record for *Pyrgus communis*. In NE Tennessee, migrants are most likely to be found from mid-August through October. During this period *Atalopedes campestris* is one of the most common butterflies in gardens and disturbed areas. At the other extreme, *Papilio cresphontes*, *Pontia protodice*, and *Hylephila phyleus* are known from only one or two records. Remaining species are usually present every year in varying numbers. *Libytheana bachmanii* differs from the usual migrant pattern of occurrence in that it has been found from mid-June through mid-August. It is regularly present, but usually only as one or two individuals at a given time and place. We include it as a migrant because we have never collected overwintered individuals in spring.

We are not certain of the status of *Thymelicus lineola* (Ochs.) in NE Tennessee. It has been taken only once, near a campground in Sullivan Co. adjacent to a N-S interstate highway. This European species has spread rapidly southward since it was accidently introduced into Canada around 1910 (Scott 1986), and there are records from SE Kentucky and SW Virginia (Opler 1983). If not already a resident, it is likely to become one soon.

While walking in the late 50's or early 60's, the senior author saw a single *Anaea andria* flying in a clover field in Sullivan Co. Without a net he could not capture it, but followed it for a distance and was certain of the identification. This species is resident around Center Hill

Lake, 130 km E of Nashville, and the junior author recently captured several overwintered individuals in Lee Co., SW Virginia. While we have not seen *A. andria* in NE Tennessee during the past 10 years, it is somewhat migratory (Scott 1986), and should be expected on occasion.

Southwest Virginia and N Georgia have more species than NE Tennessee, 120 and 108, respectively. This disparity is at least partly due to the fact that Virginia and Georgia have been collected longer than NE Tennessee.

Amblyscirtes aesculapius was the only species found in NE Tennessee that has not been recorded from SW Virginia. The Clarks (1951) recorded it only from the coastal plain of Virginia, but there are records from E Kentucky, and it probably occurs locally along rivers in SW Virginia. *Euchloe olympia* and *Clossiana bellona toddi* are resident in NE Tennessee, but are not known to occur in N Georgia. These species are at or near the limits of their ranges in NE Tennessee.

The 39 species recorded from SW Virginia and/or N Georgia not collected in NE Tennessee are listed in Table 2. Sixteen of these species are known only from SW Virginia, nine from N Georgia only, and fourteen occur in both regions.

Many species recorded from SW Virginia but not from NE Tennessee are northern species whose ranges extend southward in the Appalachian region. Southwest Virginia includes the entire breadth of the mountainous Blue Ridge Province, and elevations in the Valley and Ridge Province exceed 1200 m in places (Fenneman 1938). More extensive areas of high elevation coupled with higher latitude make SW Virginia more hospitible for some northern species than NE Tennessee.

Species recorded from N Georgia but not NE Tennessee include *Satyrium kingi* (Klots & Clench), *Amblyscirtes carolina* (Skin.), *Agraulis vanillae* (L.), and other species more typical of the lowland Piedmont and Coastal Plain provinces. Relative to NE Tennessee, the Appalachian region of N Georgia is lower in elevation and has a milder climate. In particular, the prominent ridges that characterize the Ridge and Valley further N are absent (Fenneman 1938). Broad valleys open onto the Piedmont, while the oak-pine forest association and red-yellow podzolic soils characteristic of the Piedmont extend into the Georgia portion of the Ridge and Valley (Braun 1950, Walker 1969). These climatic and topographic factors create favorable habitats for some lowland species, and provide easy access for migrants.

We predict that the following species in SW Virginia and N Georgia will eventually be found resident in NE Tennessee:

Thorybes confusis Bell
Erynnis martialis (Scudder)
Hesperia metea (Scudder)
Wallengrenia otho (J. E. Smith)
Atrytonopsis hianna (Scudder)
Satyrium edwardsii (G. & R.)

TABLE 2. Butterfly species occurring in SW Virginia (VA) and N Georgia (GA) but not recorded from NE Tennessee.

Species	State
Thorybes confusis	VA, GA
Erynnis martialis	VA, GA
E. zarucco	VA, GA
E. lucilius	VA
E. persius	VA
Pyrgus centaurae	VA
Lerema accius	VA, GA
Hesperia metea	VA, GA
H. leonardus	VA
H. sassacus	VA
Polites mystic	VA
P. vibex	VA
Wallengrenia otho	VA, GA
Atrytone arogos	VA
Euphyes conspicua	VA
E. bimacula	VA
Atrytonopsis hianna	VA, GA
Panoquina ocola	VA, GA
Amblyscirtes carolina	GA
A. alternata	GA
Megathymus yuccae	GA
M. harrisi	GA
Zerene caesonia	GA
Eurema daira	VA, GA
Atlides halesus	VA
Satyrium edwardsii	VA, GA
S. kingi	GA
Incisalia irus	VA, GA
Fixenia ontario	VA
Calephelis borealis	VA
Agraulis vanillae	GA
Charidryas gorgone	GA
Speyeria idalia	VA
Clossiana selene	VA
Phyciodes batesii	VA, GA
Polygonia progne	VA
P. faunus	VA, GA
Enodia portlandia	GA
Satyrodes appalachia	VA, GA

Incisalia irus (Godt.)
Phyciodes batesii (Reak.)
Polygonia faunus (F.)
Satyrodes appalachia (R. Chermock)

Hesperia leonardus (Harr.), *H. sassacus* (Harr.), *Speyeria idalia* (Drury), and *Polygonia progne* (Cram.) have been recorded from bordering counties in Virginia and North Carolina (Opler 1983) and also seem likely to be found in NE Tennessee eventually.

It is possible that *Amblyscirtes celia belli* H. A. Freeman occurs in NE Tennessee. We have taken it flying with *Wallengrenia otho* in moist woods beside an arm of Loudon Reservoir near Knoxville, Tennessee, about 65 air km SW of our study area boundary. Similar habitats should occur around reservoirs in NE Tennessee.

Additional migratory species such as *Erynnis zarucco* (Luc.) and *Panoquina ocola* (Edw.) may eventually turn up also, but lack of direct access from the Piedmont is a hindrance to the movement of such species; to enter NE Tennessee, they must first pass through the rugged North Carolina portion of the Blue Ridge, or travel a considerable distance up valleys from Georgia.

Concentration of collecting efforts on species listed above should increase the number of butterfly species known from NE Tennessee to between 100 and 110.

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GENERAL NOTE

GLASSBERG, LEHMAN, AND PELLMYR COLLECTIONS TO THE SMITHSONIAN INSTITUTION

Dr. Jeffrey S. Glassberg has donated his collection of New World butterflies to the National Museum of Natural History (Smithsonian Institution). It consists of more than 2000 specimens, primarily Neotropical Theclinae (approximately 350 species). Dr. Glassberg is a molecular geneticist who lives in Chappaqua, New York, and is Vice President for Research of Lifecodes Corp. He has a strong interest in conservation and butterfly watching, and is currently President of the Xerces Society.

The Smithsonian Institution has received Mr. Robert Lehman's collection of Honduran Lepidoptera. There are 4222 meticulously spread specimens representing 1852 species, plus about 5000 papered specimens. The Macrolepidoptera are well represented, and there are many Pyralidae, Tortricidae, and Oecophoridae. Most of the specimens were collected along the wet Atlantic coast of Honduras, an area that is poorly represented in collections, and which augments the Smithsonian's strong holdings from Mexico, Guatemala, Costa Rica, and Panama. Mr. Lehman has been teaching elementary school science and, more recently, computer science, at the Mazapan School in La Ceiba, Honduras, for 9 years, and has been collecting in Honduras since 1968.

Dr. Olle Pellmyr has donated his collection of Fennoscandian (primarily Swedish) Lepidoptera to the Smithsonian Institution. It includes 6907 specimens of approximately 1200 species, and is rich in both Macro- and Microlepidoptera. Because so many Swedish species are close relatives of North American ones, this collection provides important comparative material. Dr. Pellmyr is an evolutionary biologist who works on chemical and ecological aspects of plant-pollinator mutualism and lepidopteran courtship behavior. He is a Swedish national, and currently a research scientist at the State University of New York at Stony Brook.

None of the collections contains primary type specimens.

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BODY WEIGHT AND WING LENGTH CHANGES IN MINNESOTA POPULATIONS OF THE MONARCH BUTTERFLY

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ABSTRACT. Body weights and rear wing lengths were obtained from about 1900 monarch butterflies captured near Minneapolis, Minnesota, during the past decade. Mean values for both were lowest in immigrants and highest in subsequent generations. Mean wing length was highest in males. Mean body weights of immigrant females were higher than those of males, but mean male body weights were higher than those of females in subsequent generations. The data argue against the return to Minnesota of emigrants from the previous year, and suggest that attainment of large adult size could be one reason for monarch migration to northern regions.

Additional key words: Nymphalidae, *Danaus plexippus*, migration, sexual differences.

During the past several years workers in my laboratory have examined various aspects of the biology of the monarch butterfly, *Danaus plexippus* L. Our studies have impressed us with the great variation exhibited by monarch populations in our locality with respect to reproductive status, hormone titers, behavior, and other variables (Herman 1985). Monarch butterflies of both sexes also exhibit predictable changes in body weights and wing lengths during their residence in our area, and such changes are the topic of this report.

MATERIALS AND METHODS

Animals used for this study were captured near Minneapolis, Minnesota, between 1976 and 1986. They were taken to the laboratory for measurement soon after capture, usually within a few h. Whole-body wet weights were determined to the nearest 1 mg using an analytical balance, and rear wing maximal lengths were measured to the nearest 0.5 mm with a ruler. Immigrant butterflies rarely arrive in our locality before 15 May, and most local monarchs emigrate by late September. The results are therefore for animals captured 16 May to 15 September, and data in Fig. 1 are summarized for 2-wk and 2-mo intervals during that period. All data are presented as mean ± standard error; statistical analysis was done using Student's t-test.

RESULTS

Mean wing lengths for both sexes were smallest during the 2-mo period 16 May–15 July (Fig. 1). Most of these animals were presumably immigrants from southern regions, since large numbers of monarchs

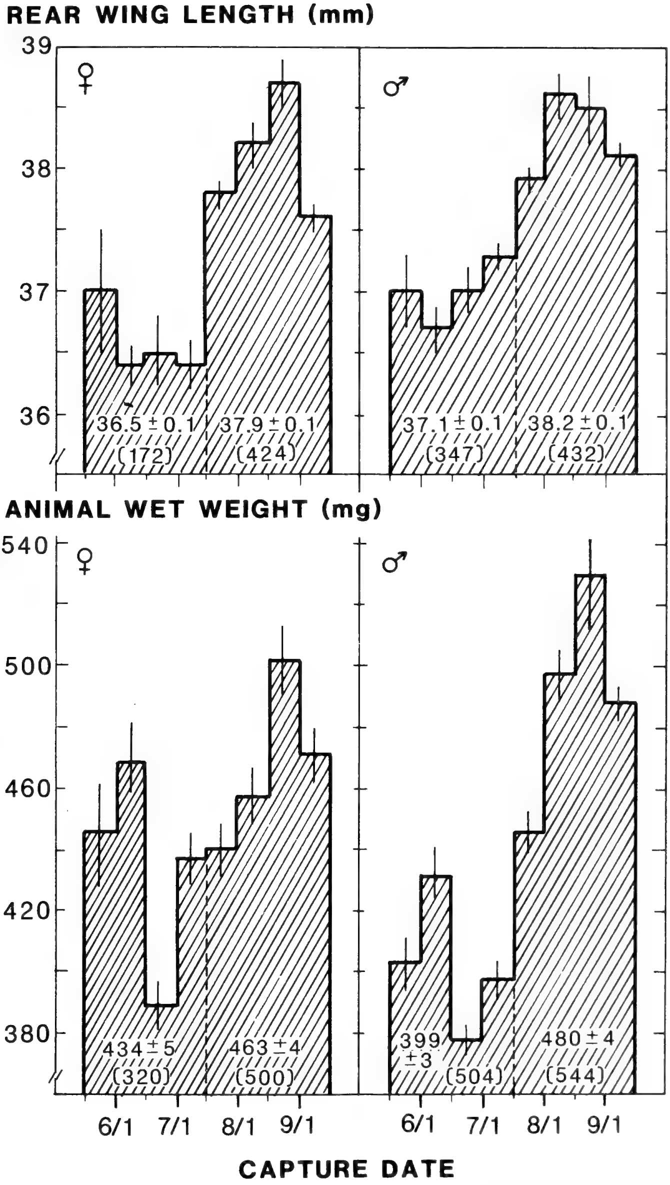

FIG. 1. Wing lengths and body weights of monarch butterflies captured near Minneapolis, Minnesota, 16 May–15 September. Data are summarized for 2-wk and 2-mo periods. Means for 2-mo periods are shown numerically, and number of individuals given in parentheses. Vertical lines indicate SE.

do not typically emerge in our area until early July. Mean wing length in both sexes increased significantly (P = 0.001 for both sexes) in the 2nd 2-mo period 16 July–15 September. Presumably, most of the latter animals emerged in our locality. Mean female wing length increased 3.8% in the second 2-mo period, that of males, 3.0%. Mean male wing lengths were significantly larger than those of females in both the 1st (P = 0.001) and 2nd (P = 0.05) 2-mo periods. Mean wing lengths recorded 16 July–15 September were indistinguishable from those observed at emergence in monarchs reared on milkweed, *Asclepias syriaca* L., in our area in July and August: 37.8 ± 0.1 mm (n = 100) and 38.0 ± 0.1 mm (n = 83) for females and males, respectively, on the day of eclosion. Rear wing length varied from 29.5 to 42.0 mm in this study, and both extremes were observed in males.

Body weights of both sexes changed in a manner similar to that of wing lengths, with low mean values characterizing the mainly immigrant populations of 16 May–15 July, and significantly higher mean values observed in monarchs that had presumably emerged in our area 16 July–15 September (Fig. 1). Mean body weights for females were elevated 6.7% in the 2nd 2-mo period, those of males, 20.3%. Mean female body weights were significantly larger (P = 0.001) than those of males 16 May–15 July, principally due to higher female weights of 16 May through 15 June. Male values were significantly higher (P = 0.005) than those of females during the final 2-mo period. The lowest mean values for both sexes were recorded in late June, when senescence and death of immigrants is most pronounced, and the highest were recorded in late August, when reproduction generally ceases in our area. The increasing mean weights for both sexes from 1 July to 15 August were recorded for populations consisting principally of actively reproducing monarchs of various ages. Mean body weights of wild-caught butterflies never reached the mean values (680 ± 32 mg [n = 26] and 652 ± 11 mg [n = 109], respectively) measured on day of eclosion for females and males reared in our area. Body weights ranged from 195 to 836 mg during this study, and both extremes were again found in males.

DISCUSSION

The data show that predictable variations occur in rear wing lengths and body weights during the period that monarch butterflies reside near Minneapolis. Small wings and low weights characterize the immigrant population, and both parameters increase significantly in both sexes when monarchs that have apparently emerged in our area predominate in the local population, as they normally do after 1 July. Causes of these variations, and their possible adaptive value, are undetermined. However, the data suggest that local environmental factors (nutrient value of foodplant, temperature, or photoperiod) during June, July and August may provide optimal conditions for larval growth, and thereby result in larger adults with longer wings. If so, suboptimal conditions for larval development of the presumed immigrant generation in southern areas could account for reduced size in immigrant butterflies. This line of reasoning implies that northward migration in spring could be, to at least some extent, an adaptation for locating regions that optimize adult size. Larger adults may have a greater probability of successful southward migration, survival in the overwintering colonies, or remigration.

The smaller wings of immigrants might somehow facilitate northward migration, while the larger wings of animals emerging in late August and September may be more advantageous for southward migratory flights. Perhaps larger wings are more efficient for soaring and gliding, phenomena reported only for monarchs migrating south (Gibo 1981). Immigrant males with smaller wings might also be more successful at mating, as reported for males in Mexican overwintering colonies (Van Hook 1986). James (1984) noted no significant differences in wing lengths of Australian monarchs observed during a full year.

The data on monarch body weight generally agree with those in other reports (Cenedella 1971, Brown & Chippendale 1974, Brower & Glazier 1975). Other studies have reported significantly higher body weights of males in southward migrating and overwintering monarch populations (Tuskes & Brower 1978, Chaplin & Wells 1982). However, others have apparently not observed periods in the monarch annual cycle when females are significantly heavier than males, as Fig. 1 records for immigrants to our area.

Data in Fig. 1 argue against the return to our locality of monarchs that emigrated the previous year. Our immigrants, especially females, have intermediate weights, and, based on body weight and external appearance, most appear to be young or middle-aged, certainly not old. Immigrants to our area also exhibit both senescence and precipitous weight loss (Fig. 1) within 2–4 wk after arrival, and it seems reasonable to assume that comparable rates of aging and weight loss occur after monarchs leave Mexican overwintering colonies. In view of these observations, it is unlikely that overwintering monarchs could leave Mexican colonies in mid-March (Norman 1986), fly northward for 8–10 wk while actively breeding, and arrive in our area with body weight and external appearance comparable to young populations of July. Similarly, smaller wings of our immigrants suggest they are not members of the emigrant generation of the previous year, since emigrants have significantly larger wings. In addition, monarchs captured in Mexican colonies in February and March 1984 had wings comparable in length to our emigrants, and significantly larger than those of our immigrants (Herman unpubl.). For these reasons, the data support an earlier conclusion (Herman 1985), and that of Malcolm et al. (1986), that most immigrants to the northern United States are probably one generation removed from individuals forming Mexican overwintering colonies.

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HABITAT AND RANGE OF *EUPHYDRYAS GILLETTII* (NYMPHALIDAE)

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ABSTRACT. Fifteen sites occupied by *Euphydryas gillettii* are compared according to 10 characteristics. All sites are moist, open, mostly montane meadows, many with a history of disturbance, commonly fire. Population size correlates with relative availability of nectar but not with overall abundance of the usual hostplant, *Lonicera involucrata*. Habitats at higher latitudes often have a southerly exposure. Reduction in hostplant size at higher latitudes contributes to the northern range limit. Three populations likely have become extinct since 1960, but the species range does not appear to be changing.

Additional key words: nectar, *Lonicera involucrata*, biogeography, extinction.

Euphydryas gillettii (Barnes), a checkerspot butterfly, occurs in discrete, isolated populations (Williams et al. 1984) in the central and northern Rocky Mountains (Ferris & Brown 1981). It is attractive and easily caught but uncommon and not often collected. Though usually considered a montane species (Williams et al. 1984), variation in sites occupied by *E. gillettii* has not been studied, and lack of knowledge about its habitats has led to uncertainty about its range.

Here I report characteristics of sites occupied by *E. gillettii*, present range of the species, and factors influencing its distributional pattern. This study is based on direct observation of the habitats of 15 populations throughout the range, thus affording an uncommon view of habitat variability in a single insect species.

METHODS

Populations of *E. gillettii* were located through correspondence with collectors and researchers listed in Acknowledgments, examination of specimen labels in collections listed in Acknowledgments, and a survey of published reports (*News Lepid. Soc.*, Seasonal Summaries 1960–1986). When directions were sufficient to pinpoint locations on a topographic map, I visited the sites, and assessed relative population size and habitat characteristics.

Population size was determined by a one-day count of adults, egg masses, and larval webs. Egg masses of *E. gillettii* are distinctive, easily found, and readily counted, thus permitting quantitative comparisons of colony size even after the flight season; in fact, egg mass counts are better indicators of population size than adult counts because the former are independent of weather. Eggs do not begin hatching until late in the flight season (Williams et al. 1984), so developmental state of egg masses at each site indicated timing of the count relative to flight season.

Females average one to two egg masses per individual (unpubl.); thus, relative population size can be estimated from sum of egg masses and adults.

In addition to population size, I recorded nine site characteristics, and searched for evidence of disturbance. Observations were quantified as much as possible for later analysis. Each site is marked on U.S. Geological Survey and Canada Department of Energy, Mines & Resources topographic maps in my possession, and latitude and elevation were measured directly from these maps. I used a compass as well as contour lines on the maps to determine exposure. I recorded number of distinct shrubs or clumps of the usual hostplant, *Lonicera involucrata* (Rich.) Banks (Caprifoliaceae) (Comstock 1940, Williams et al. 1984), in open areas where egg masses and adults were found. Nectar sources were identified (Hitchcock & Cronquist 1973), and relative nectar availability was determined by site comparison. Nearby trees were identified and cored with a 5 mm diam increment borer for age determination. Presence and distance to standing water and streams were recorded. I inferred source and history of disturbance from characteristics such as tree species and age, charring, stems gnawed by beavers, and location in a flood plain.

RESULTS

Populations

I visited 29 localities reported as sites for *Euphydryas gillettii* and found populations at 13. With my 2 previous study sites (Williams et al. 1984), I had a total of 15 colonies throughout the geographic distribution of the species for comparison. More than 15 egg masses and adults were found at 7 sites ("large" populations), while fewer than 15 were found at 8 sites ("small" populations) (Table 1).

Habitat Characteristics

All occupied sites are wet (Table 1). Most have a small stream passing through, though several are marshy without obvious flowing water; *E. gillettii* occurs infrequently near rivers, perhaps because of flood disturbance to hostplants, nectar sources, larvae, and adults. In habitat characteristics, *E. gillettii* is similar to its congener *E. phaeton* (Drury) (Scudder 1889). There is no observable relation between population size and type of water present.

There appears to be a correlation between colony size and nectar abundance ($\chi^2 = 3.2$, df = 1, P = 0.07). Only two sites have large populations with low nectar availability, but these populations are marginally "large" (sites 7 & 9, Table 1). Total amount of nectar is also important in *Euphydryas editha* (Boisduval), influencing its population

TABLE 1. Characteristics of 15 sites occupied by *Euphydryas gillettii.*

Site no.	Colony size[1]	*Lonicera invol.* abundance[2]	Nectar availability	Nearby trees (age of largest to nearest 5 yr)	Water (stream width)	Disturbance
1	>30	>30	High	Lodgepole pine (75) Engelmann spruce (65)	Stream (<1 m)	Fire[3]
2	>30	>30	High	Quaking aspen (60) Subalpine fir (75)	Streams (<1 m)	None; meadow edge
3	7	10	Low	Engelmann spruce (150)	Stream (1–3 m)	None; meadow edge
4	2	10	Low	Lodgepole pine (55)	Marshy	Fire; wet soil
5	4	20	Low	Lodgepole pine (90) Quaking aspen (65)	Stream (<1 m)	Fire; logging
6	>30	20	High	Subalpine fir (155) Lodgepole pine (15)	Streams (<1 m)	Fire[3]; logging
7	18	10	Low	Cottonwood (40) Lodgepole pine	Stream (1–3 m)	Beaver activity
8	21	10	High	Lodgepole pine (65)	Stream (>5 m)	Flooding
9	22	20	Low	Lodgepole pine (95) Engelmann spruce (70)	Marshy, stream (<1 m)	Wet soil
10	8	>30	High	Lodgepole pine (55) Engelmann spruce (50) Subalpine fir (40)	Stream (<1 m)	Fire?; meadow edge
11	7	5	Low	Subalpine fir (95) Engelmann spruce	Marshy	Fire[3]
12	3	>30	Low	Lodgepole pine	Stream (1–3 m)	Flooding; fire?
13	1	20	Low	Engelmann spruce (195) Lodgepole pine (40)	Stream (1–3 m)	Fire[3]
14	2	20	Low	Willow (no trees)	Marshy, stream (<1 m)	Wet soil; grazing
15	>30	5	High	Lodgepole pine (75)	Marshy	None; meadow edge

[1] Total number eggs and adults.
[2] Approximate number *Lonicera* clumps in 30 × 30 m quadrat.
[3] Charred tree trunks.

dynamics (Murphy et al. 1983). Nectar is supplied by a number of genera (Table 2), mostly commonly *Aster, Senecio,* and *Agoseris,* but each occurs conspicuously at no more than 9 of the 15 sites. Williams et al. (1984) found the butterflies to switch nectar sources readily when an early source senesces. Total amount of nectar thus appears more important than particular sources.

Hostplants were considered highly abundant when there were more than 15 distinct shrubs or clumps. In contrast to nectar availability, hostplant abundance does not correlate directly with population size ($\chi^2 = 0.1$, df = 1, $P > 0.5$). Reasons are considered later.

Most sites have been disturbed (Table 1), with fire being the commonest natural source. Lodgepole pine, *Pinus contorta* Dougl., is com-

TABLE 2. Common nectar sources for *Euphydryas gillettii* at 15 study sites.

Genus	Number of sites where present	Genus	Number of sites where present
Aster	9	*Polygonum*	2
Senecio	8	*Antennaria*	1
Agoseris	7	*Chrysanthemum*	1
Geranium	6	*Cirsium*	1
Achillea	5	*Geum*	1
Heracleum	5	*Helianthella*	1
Potentilla	4	*Saxifraga*	1
Valeriana	3	*Solidago*	1

mon near colonies (Table 1), indicating common disturbance history in these areas (Pfister et al. 1977). Whatever the cause, disturbance opens a site for growth by more hostplants and nectar sources. The few sites not clearly showing disturbance are on edges of permanent wet meadows of grasses and sedges.

At higher latitudes, occupied sites occur at lower elevations (Fig. 1, $r^2 = 0.49$, $P < 0.005$). This result likely reflects colder climates and reduced height of mountains at higher latitudes. Furthermore, importance of a minimum growing season length is shown in frequent southerly exposure of sites at higher latitudes, in contrast to the variable exposure of sites at lower latitudes (Fig. 1). All large northern populations occupy sites with southern exposure, while southern sites show no observable relation between population size and exposure. Williams (1981) demonstrated the importance of within-habitat exposure effects; current results suggest larger-scale influences as well.

Range

Available records of *E. gillettii* are mapped in Fig. 2. Sightings are concentrated in the mountainous regions of W Wyoming, central Idaho, NW Montana, and SW Alberta. Some regions for which there are only older records, such as Yellowstone National Park and SW Montana, undoubtedly support populations, but their inaccessibility makes collecting sporadic. Continued existence of *E. gillettii* in extreme SW Wyoming is questionable because extensive search has failed to uncover specimens (C. F. Gillette pers. comm.). A reported record from central Montana may be erroneous. There is also a single museum specimen from Ontario, but improbable date as well as location suggest mislabeling.

Sites in Alberta have smaller populations of butterflies than do those farther south, and all northern sites have one characteristic in common: *Lonicera involucrata* does not reach the large size and luxuriant growth characteristic of Wyoming and Montana sites. In moist areas at higher

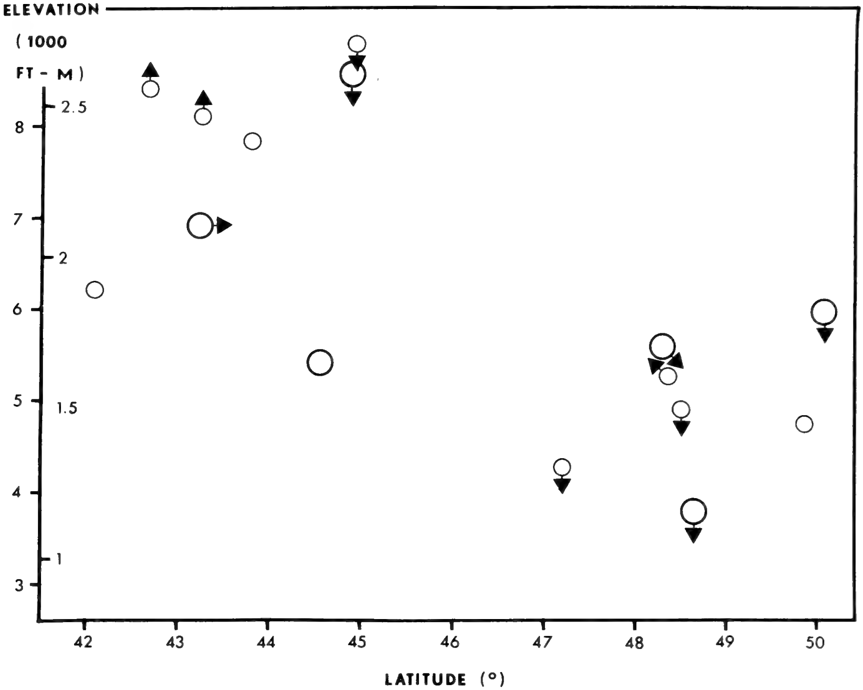

FIG. 1. Elevation and latitude of fifteen *Euphydryas gillettii* sites. Large circles represent "large" populations. Arrows pointing down indicate sites with southerly exposure; those pointing right, easterly exposure; etc. Absence of arrow indicates site has no obvious slope.

latitudes, willows (*Salix* spp.) are often taller than *L. involucrata*, shading them and making them less accessible to searching females; this rarely occurs at lower latitudes. Oviposition sites are therefore scarcer than at lower latitudes, because oviposition occurs on the highest leaves of hostplants that are fully exposed to sunlight (Williams 1981, Williams et al. 1984).

DISCUSSION

There appear to be four reasons for lack of correlation between population size and abundance of *L. involucrata*. First, and most importantly, this plant grows in moist areas regardless of amount of sunlight, while the butterfly requires sunlit hostplants (Williams 1981). In fact, the most luxuriant hostplants often grow in shade of conifers, but are not used as oviposition sites. Second, an extension of the first, much *L. involucrata* is over-shaded by willows at high latitudes, thus providing fewer potential oviposition sites in such areas. Third, some *Euphy-*

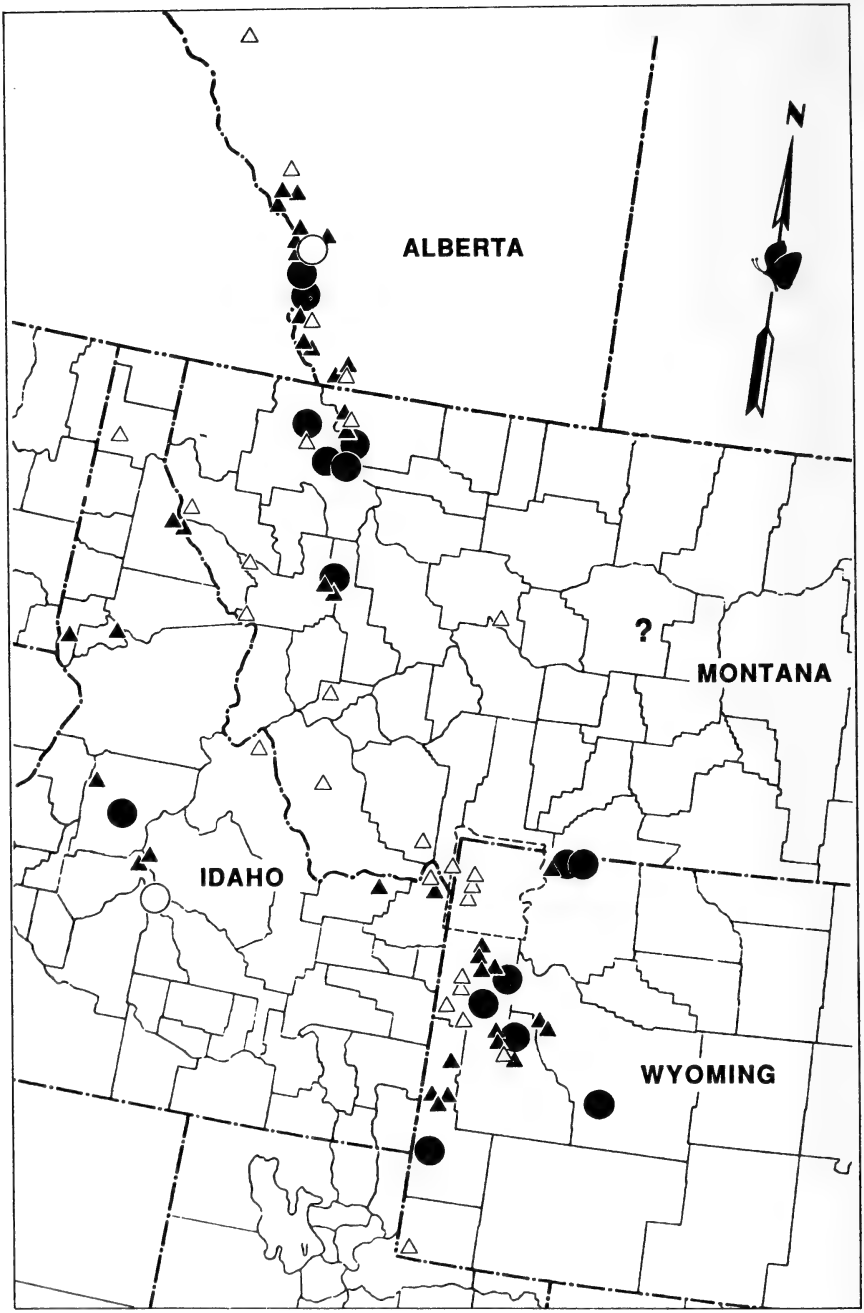

FIG. 2. Range of *Euphydryas gillettii*. Closed circles are sites described in this study; open circles are locations of populations believed extinct; closed triangles are locations

dryas gillettii populations are mostly biennial (Williams et al. 1984), and so may fluctuate greatly in abundance from year to year. While most *E. gillettii* sites are characterized by abundant *Lonicera involucrata,* these three factors limit the size of an observed butterfly population to less than might be expected given the total amount of *Lonicera.* The fourth reason is butterfly use of alternative hostplants.

Only at one site was the colony larger than would seem possible given the amount of nearby *L. involucrata.* That population (site 15, Table 1) lives where *L. involucrata* is uncommon, and the butterflies oviposit extensively on two other plants, *Pedicularis* and another *Lonicera* (in prep.). There are several possible reasons for dietary expansion in butterflies (Singer 1971, 1983); but whatever they may be for this population, other study populations have not followed suit, even though all known alternative hostplants grow throughout the *Euphydryas gillettii* range. Except for site 1, where an alternative hostplant was chosen at low frequency (less than 4% of egg masses, Williams & Bowers 1987), I did not find eggs on or see ovipositional behavior near other plants at the other 14 sites. Because of the known use of alternative hostplants, I expect other *E. gillettii* populations use alternative hostplants as well. The relation between population size and *Lonicera involucrata* abundance is thus weaker than has been widely accepted.

Because its hostplants and nectar sources require wet sites, and because adults and larvae require sunlit areas for warmth, *Euphydryas gillettii* most often occurs in open montane meadows. The one study population that is not montane occupies a permanently wet, grazed seepage area in the transition zone. Several populations were observed along forested edges of seemingly permanent montane meadows; such meadows may change little through time because of allelopathic interactions of meadow vegetation or soil instability. More commonly, open sites are created temporarily through disturbance. The most frequent disturbance is fire, and most study sites have clearly been affected by it. Other forms of disturbance, such as flooding, beaver activity, or human activities like grazing and logging, also serve to open forested areas.

Vegetational succession in disturbed areas leads to changes that make sites less suitable through time. In particular, encroachment by surrounding forest leads to greater evapotranspiration, producing a drier site and thereby limiting growth of hostplants and nectar sources. Furthermore, invasion by trees reduces the sunlight that reaches the shrub

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where *E. gillettii* has been seen since 1960; open triangles are records before 1960; question mark denotes uncertain record.

and herb layer, thus eliminating warmer microsites preferred for oviposition (Williams 1981).

Life in disturbed sites suggests that *E. gillettii* populations are subject to periodic extinction like *E. editha* (Singer & Ehrlich 1979), and such appears to be the case. I identified with precision one site where *E. gillettii* was collected in the 1960's, but by 1983 vegetational succession had taken place, most remaining *Lonicera involucrata* was shaded, and no sign of butterflies could be found. Furthermore, human development of recreational areas has led to loss of additional populations, one known and one suspected.

Habitat requirements of *E. gillettii,* including moisture for hostplants and nectar, and sunlight for larvae and ovipositing females, produce the limits of its geographic distribution. Thus, plains east of the Rockies and arid basins westward form effective biogeographic barriers to dispersal in either direction because of lack of water. Holdren and Ehrlich (1981) have shown that another arid region, the Red Desert of S Wyoming, is the southern barrier since they successfully transplanted individuals across the barrier to central Colorado where one colony has survived since 1977. Their transplant locales are similar to natural habitats farther north in being wet and having an abundance of nectar and *Lonicera involucrata.*

The northern range limit has been assumed to result from lower temperatures and shorter growing season. However, all the Alberta sites have much smaller *L. involucrata,* and willows dominate northern wet sites by growing taller than other shrubs. All populations of the butterfly at higher latitudes are smaller as well. Although no northern populations have been found to use hostplants other than *L. involucrata,* alternative hostplants used elsewhere also decline in abundance at higher latitudes. It seems likely that competition by willows reduces size and perhaps density of potential hostplants. Thus, fewer oviposition sites and poorer (more shaded) ones would be found during normal hostplant searching by females (Williams et al. 1984). I suggest that loss of oviposition sites contributes, along with shorter growing season, to the northern limit.

Euphydryas gillettii is uncommon, but there is no evidence that its range has been changing in recent decades. The greatest conservation advantage this species has compared to other uncommon species is that its habitat lies largely in mountainous areas that are not readily accessible and in which there is little immediate potential for human modification. Its greatest conservation disadvantage is its occurrence through a limited range in discrete, localized populations, which are individually susceptible to disturbance and extinction.

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BIOLOGY OF *POLYGONIA PROGNE NIGROZEPHYRUS* AND RELATED TAXA (NYMPHALIDAE)

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ABSTRACT. The life history of *Polygonia progne nigrozephyrus* is compared with that of *P. gracilis zephyrus*, *P. faunus hylas*, and *P. satyrus* in Colorado. Adult predator deterrent behaviors occur: adults resemble leaves as they rest on twigs showing leaflike undersides, roost with forewings drawn forward with antennae resting between them, and feign death when handled. Larvae also have predator-avoidance strategies: scoli presumably act as a physical deterrence, small larvae can drop using a silk thread, a ventral neck gland possibly repels predators, larvae vomit on an attacker, older larvae resemble twigs as they rest in a three-dimensional twisted-S shape, pupae resemble a dried curled leaf or short twig. Larval host plants differ between species, with some overlap. Identification features for the four species are presented for each stage. Despite adult similarity of *P. progne nigrozephyrus* and *P. gracilis zephyrus*, *P. g. zephyrus* larvae most resemble those of *P. faunus*.

Additional key words: *Polygonia gracilis*, *P. faunus*, *P. satyrus*, predator deterrence, chaetotaxy.

Scott (1984) described *P. progne nigrozephyrus* which occurs in Colorado–S Wyoming–Utah–SE Idaho–NE Nevada. It resembles *P. gracilis zephyrus* (Edw.) on the upperside, *P. p. progne* (Cram.) on the underside and in male abdominal structure, and was long confused with *zephyrus*. *Polygonia p. nigrozephyrus* is certainly the same species as *oreas* (Edw.), but some may question whether it and *oreas* belong to *P. progne*. Early stages of *nigrozephyrus* are similar to those of *oreas* and *progne*, and are distinct from *zephyrus* and other *Polygonia*; wing undersides and abdominal structures resemble those of *progne*. Therefore, *nigrozephyrus* does seem to be a subspecies of *progne*.

Since 1984, minor differences between populations of *nigrozephyrus* in Colorado have been found. Adults from the E slope of the continental divide in the Front Range usually have the dorsal hindwing darker because the submarginal spots are the same size as those of *P. g. zephyrus*, whereas adults from the W slope usually have the spots larger like those of *P. satyrus* (Edw.). However, the difference is not great enough to warrant a new name for W slope populations, and some adults from each area resemble those from the other. The Front Range populations may have slightly darker dorsal hindwings because of occasional immigration of subspecies *progne*, which has a very dark dorsal hindwing margin.

An additional difference not mentioned by Scott (1984) between some *P. p. progne* adults and other *Polygonia*, first noticed by W. H. Edwards, involves one of the dark stripes in the ventral forewing discal cell: in most *P. p. progne* the anterior stripe is unbroken, whereas in some of them and in other subspecies and species the stripe is broken into two parts.

For oviposition and larval rearing, cut host-plant sprigs were put into water-filled vials, cotton-plugged so the water would not drain when vials were on their sides. For older larvae, large host branches were cut and placed in wet sand.

Adult Stage

Adults bask with wings spread (dorsal basking). In the laboratory, some *nigrozephyrus* females closed the wings above the thorax and vibrated them rapidly (up to 2 mm apart at the tips) when lights were turned on in the morning; this is shivering behavior to raise the thorax temperature prior to flight.

Adults of *nigrozephyrus, zephyrus,* and *faunus* (Edw.), as well as *Nymphalis milberti* (God.), roost on twigs with wings closed, forewings drawn far forward (nearly out of hindwings) and covering the head and antennae which rest between the forewings. This posture perfects the resemblance to a leaf on the twig by elongating the "leaf", breaking up its margin, and hiding antennae to avoid predation during fall, winter, and spring. Adults frequently feign death when handled, which would also signal a predator that the butterfly is a dead leaf.

There is evidently a circadian rhythm of oviposition, because females laid eggs in the laboratory only during daytime, and even when lights remained lit females began roosting in late afternoon. For obtaining oviposition, fluorescent bulbs were superior to incandescent bulbs, probably because the former produce a greater and more natural amount of ultraviolet light.

Immature Stages

Host plants. *Polygonia progne nigrozephyrus* feeds on gooseberry: *Ribes inerme* Rydb., in Delta and Douglas counties, Colorado, *R. leptanthum* Gray at Williams Canyon, El Paso Co., Colorado. In the laboratory, *nigrozephyrus* larvae accepted leaves of *Ribes inerme,* but refused wax currant, *R. cereum* Dougl., and ate very little golden currant, *R. aureum* Pursh. They ate only leaves. Additional host records for *P. p. progne,* based on preserved larvae in the Smithsonian, are gooseberry (St. Albans, West Virginia, Monticello, New York) and currant (Centreville, Rhode Island).

Polygonia gracilis zephyrus usually eats *Ribes cereum* in Colorado. However, I found an egg on *R. inerme* at Tinytown, Jefferson Co., on 2 June 1984, and reared it to a mature larva; and a larva under a *R. inerme* leaf 5 km W Idledale, Jefferson Co., on 12 June 1984, which I reared to an adult. In the laboratory, *zephyrus* larvae eat *R. cereum.*

and do not move off its leaves to eat adjacent *R. inerme* leaves, although larvae will also accept *inerme*. Additional host plants of *zephyrus* are *Ribes sanguineum* (Jones 1951), and *Rhododendron occidentale* (larvae reared to adults, Big Trees Park, Calaveras Co., California, 4 June 1983, J. F. Emmel & S. O. Mattoon).

Polygonia faunus hylas (Edw.) usually eats *Salix*, but I found three first-stage larvae and five eggshells under leaves of *Ribes inerme* at Tinytown on 26 May 1984, and an adult emerged 20 June. In the laboratory, *faunus* larvae refused *Ribes aureum* leaves, but ate *R. inerme* and preferred it to *R. cereum*.

Thus all three *Polygonia* will eat *Ribes inerme* occasionally.

The only known Colorado host of *P. satyrus* is *Urtica dioica gracilis* (Ait.) Sel., though *Humulus lupulus* L. is eaten elsewhere. In the laboratory, *satyrus* larvae accepted *Humulus* and *Urtica* leaves equally well.

Life Cycle

Five larval instars have the following approximate head widths, respectively: 0.4, 0.7, 1.2, 1.7, 2.6 mm. Stage 1 is easily recognized by its black head without scoli; stage 2 has head scoli but is still black; stage 3 has head scoli but is black usually with an ochre pattern tending toward the pattern of stages 4–5. Usual laboratory durations of *nigrozephyrus* stages at 19°C were: egg, 5–6 days; larval stages, 3, 2.5, 2, 2, 4 days, respectively; and pupa, 9–10 days; totalling 27–30 days. In the cooler and more variable temperatures of nature, these periods are probably nearly doubled, so that adults should appear by late July–early August, although eggs laid in late April might produce the few fresh late-June adults known in nature. A *faunus* stage 1 larva found 26 May emerged as an adult 20 June in the laboratory, even though *faunus* emerges in nature only in late July and August. The laboratory life cycle of *P. p. progne* is 31–32 days (Edwards 1880), of *P. interrogationis* 28–40 days (Edwards 1882b), and of *P. comma* 27–33 days (Edwards 1882a). Thus all *Polygonia* have similar developmental rates indoors, and all have five larval stages. However, in Colorado *P. faunus* and *P. progne nigrozephyrus* have only one generation per year, while *P. satyrus* and *P. gracilis zephyrus* have two generations at low altitude and one at high altitude; and *P. interrogationis* has two or three generations.

Predator-Avoidance Structures and Behavior

Stinkbugs and ants were found on *R. inerme* host plants and may prey on immatures.

The scoli of stage 2–5 larvae presumably physically deter predators.

They slightly hurt the human skin when touched, evidently a physical puncturing rather than an urticating chemical.

A ventral neck gland occurs on stage 2–5 larvae of all 4 *Polygonia* species; it contains 2 internal transverse dark secretory pads which perhaps produce repellent chemicals.

When grasped, the larva often bends its head around and vomits green fluid onto the attacker.

Fourth- and fifth-stage larvae of *nigrozephyrus* grasp a twig with the prolegs, bend the front part of the body right or left, and raise the end of the abdomen. This "corkscrew" posture may make the larva resemble a dead leaf or twisted twig, perhaps lessening predation by birds. This posture also occurs in ssp. *progne* (Edwards 1880) and in *satyrus* (C. F. Gillette pers. comm.).

Young larvae of all four species rest on the underside of a leaf, and when older may also rest on a twig. Only older larvae of *P. satyrus*, also *P. comma*, live in a nest. It is made by chewing the base of the leaf on each side, thus making it droop, and silking *Urtica* leaf edges down and together below the enclosed larva, which rests on the leaf underside.

Disturbed young larvae can extrude a silk thread as they fall, then crawl up the thread to return to the plant.

Pupae are constricted in the middle where silver spots also visually break up the outline, making the pupa resemble a dead, shriveled leaf or twig.

Gooseberry hosts are armed with sharp spines which act as physical protection against vertebrates. A punctured pupa recovered completely.

Descriptions of Early Stages

Colors are based on live individuals. Immatures have been deposited in the Smithsonian Institution. Many dozen individuals of *Polygonia p. nigrozephyrus* were reared from eggs laid by females from NE of Cedaredge, Delta Co., and Nighthawk, Douglas Co. Each stage is described, and is followed by comparisons with the other three *Polygonia* species and subspecies, each of which were represented by less than 10 individuals. Segments are named T1 for prothorax, A3 for abdominal segment 3, etc. (Fig. 3). Scoli are named with the letter B followed by name of nearest primary seta. They are not preceded by S because of confusion with primary seta SD1, etc.; sp is spiracle; VNG is ventral neck gland on older larvae. Names of setae are from Hinton (1946) and Scott (1986), with slight modifications (Scott 1988) that improve homology and make head and body setal nomenclature different to avoid confusion.

Egg. Green, averaging 8.6 vertical ribs (Table 1), each rib steep-walled, increasing in height to maximum at top, then disappearing; 40–50 horizontal ribs forming ladder between adjacent vertical ribs; the day before hatching turning blackish with transparent silvery-reflecting shell as larva becomes partly visible.

Comparison. All *Polygonia* eggs green. *Polygonia p. progne* has 8–9 ribs, *P. g. zephyrus* averages 9.8, other *Polygonia* average 10.4–11.5 (Table 1).

First-stage larva (Figs. 1, 4, 5, 9, 11, 12, 16). Head black without pattern or horns. Body dark brown with long black setae, bumplike bases of which are chitin brown; with

TABLE 1. Number of vertical ribs on eggs.

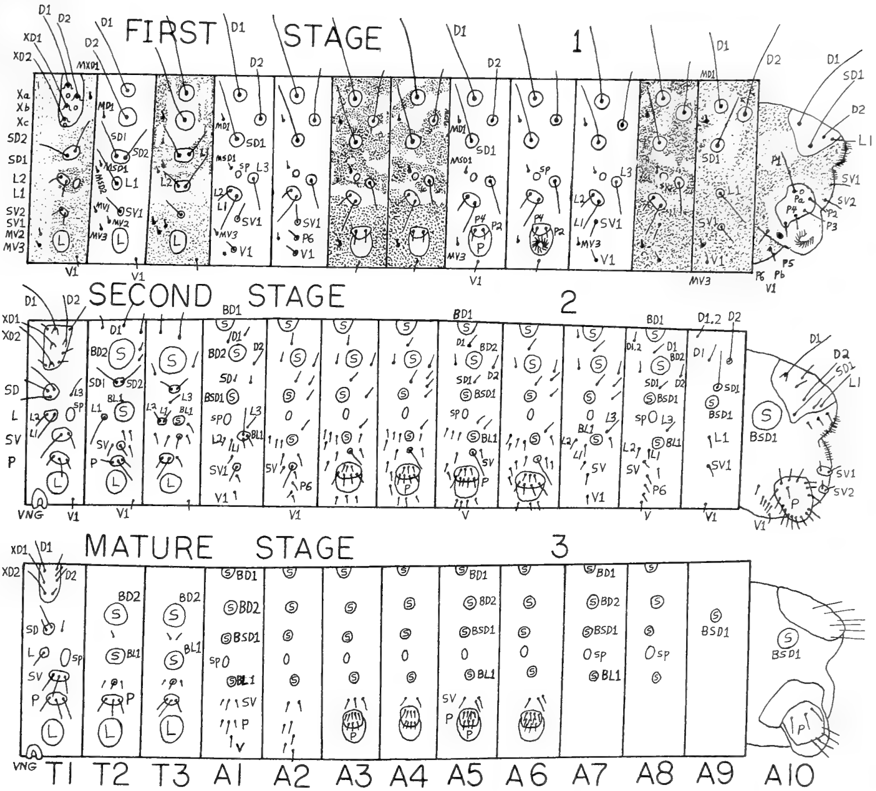
Taxon	Mean	SD	Range	N	Source
Polygonia p. nigrozephyrus	8.6	0.55	8–10	40	this paper
P. p. progne	—	—	8–9	—	Edwards (1880)
P. g. zephyrus	9.8	0.59	9–11	27	this paper
P. satyrus	10.4	0.54	10–12	43	this paper
P. faunus	10.5	0.63	10–12	31	this paper
P. interrogationis	—	—	8–10	—	Edwards (1882b), Pyle (1981)
P. comma (Colo.)	11.5	0.50	11–12	58	this paper
P. comma (Minn.)	10.6	0.54	10–12	38	this paper
Nymphalis vau-album (D. & S.)	11.0	—	9–12	—	C. F. Gillette, pers. comm.

cream spots (Fig. 1) as follows: front half of T1 cream except for small supralateral brown patch on some larvae; T1 cream in front of, behind, just beside black prothoracic shield; rest of T1 brown except for 2 cream dashes extending rearward above, below spiracle. T2–3 brown, large yellow-cream patch around D2, smaller cream patch around L1–2. A2, A4, A6 brown, with 4 pale patches: broad cream mid-dorsal V aimed posteriorly on anterior part of each segment; broad yellow-cream patch below D1; narrow supralateral light brown dash; long cream sublateral dash. A1, A3, A5, A7 brown, with 4 light brown patches on each side corresponding to pale patches on A2, A4, A6; sublateral dash cream on A3, A5, A7, A8. A8 same as A7 but 3 upper patches slightly creamier. A9 brown, subdorsal cream patch twice as long vertically as horizontally. A10 brown, suranal plate black, proleg cream, proleg plate brown, large circular cream supralateral patch.

Comparison. Other *Polygonia* larvae very similar, with black hornless head and similar body pattern. *Polygonia satyrus* same as *nigrozephyrus*, pale bumps cream-white, a few creamy sublateral dashes. *Polygonia g. zephyrus* same as *nigrozephyrus*, except pale bumps cream-white instead of yellow-white, seta D1 on T3 on whiter bump as is seta D2, no supralateral brown patch on front of T1 though it appears on some second-stage larvae so may be individual trait, supralateral dash on A2, A4, A6 cream, A1, A3, A5, A7, A8 all brown except for lateral cream dash. *Polygonia interrogationis* similar (Edwards 1882b), but *P. comma* "whitish-green" (Edwards 1882a). *Polygonia faunus* larvae differ from all other *Polygonia* in having white areas expanded away from bumps: for instance, white patch on T2, T3 includes both D1, D2 setae; on A2, A4, A6 white V lengthened anteriorly, subdorsal white patches below D1 extend posteriorly.

Second-stage larva (Figs. 2, 6–8, 17). Head black with 2 short black spiny horns (BPA2 scoli) each with 1 long seta on tip, 5 setae on crown just below, no setae on long stalks; bases of PA1, AG3, LH1, O2 pale, membranous; very narrow short pale line along middorsal groove. Body reddish brown, brownish orange toward rear, similar to 1st stage in pattern, prothorax mostly orangish yellow; orange V's on top of A2, A4, A6, yellow-cream areas of first stage now orange, scoli present with bases orangish. Scoli BD2 on A2, A4, A6 ochre on some larvae, mostly brown on most, other scoli black. BD2 scoli on T2, T3, A2, A4, A6 rest on large orange bumps making segments conspicuously paler, other scoli rest on small orangish bumps. Body has weak cream mid-dorsal, subdorsal spots which help form abdominal V's; remaining segments have thin wavy lateral cream line between BL1 scoli, thin wavy supralateral cream line between BSD1 scoli. Tiny pale subdorsal transverse dashes present. Ventral neck gland present.

Comparison. *Polygonia g. zephyrus* has slightly shorter horns, body undergoes less color change from first stage: color pattern the same, pale patches still white, though BD2 on A2, A4, A6 yellow-cream, in some larvae blackish, making segments still paler on top, other scoli black. Only BD2 on T2–3, A2, A4, A6 rest on yellow-cream bumps; other scoli rest on small whitish bumps. Tiny cream transverse dashes occur behind, before BD2 on A2, A4, A6 to help form V's as in *P. satyrus*; middorsal, subdorsal, supralateral, lateral

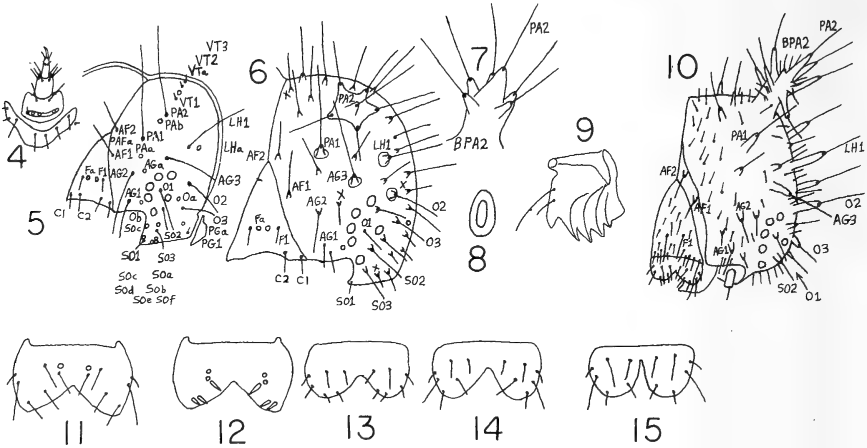


FIGS. 1–3. Setal maps of *Polygonia progne nigrozephyrus* larvae. **1,** First stage. Color pattern shown on some segments, except that plates at base of setae, including prothoracic shield and suranal plate, are dark brown; T2 and T3 patterns similar; A1, A3, A5, A7 patterns similar; A2, A4, A6, A8 patterns similar except that A8 darker; **2,** Second stage; **3,** Fifth (mature) stage. L inside circle is true leg; P inside circle is proleg; S inside circle is scolus. Hundreds of small setae not shown. See text for further explanation.

white spots present. *Polygonia satyrus* resembles 1st-stage *zephyrus*, thus head black, T1 mostly white except for black prothoracic shield. BD2 on A2, A4, A6 also yellow-cream; other scoli black, except BD1 on A6 whitish, BD1 on A4 partly whitish, BL1 on A4, A6, A7, A8 mostly white. BD2 on T2, T3, A2, A4, A6 rest on large yellow-cream bumps; other scoli rest on small tan hills, though BD1 on A2, A4, A6, BL1's rest on fairly white bumps. *Polygonia faunus* has enlarged white areas compared to other species, on at least 1 larva BD1 and BD2 on A2, A4, A6 pale. Ventral neck gland occurs in all 3 *Polygonia*.

Third-stage larva (Figs. 8, 13, 18). Head black with black scoli, following structures ochre: Mid-dorsal notch, adfrontal cleavage line (lateral to frontoclypeus), lower frontoclypeus, head just above antennae, bases of all major setae except black horns; but some individuals have head mostly black, nearly devoid of pattern. Head setae AG3, PA1, LH1, O2 on long ochre stalks. Body dark brown, with long mostly orange scoli: BL1, BSD1 mostly black; BD2 mostly orange; BD2 on T3, A2, A4, A6 strongly orange; scoli on T2, A10 mostly black. Body pattern similar to stages 4–5.

Comparison. *Polygonia g. zephyrus* larvae have BD1, BD2 more whitish cream on abdomen. *Polygonia satyrus* differs greatly: head black with cream notch on top running



FIGS. 4–15. Leg and cranial setae of *Polygonia progne nigrozephyrus*. **4,** Ventral-medial view of first-stage larval thoracic leg, showing setae typical of butterflies; **5,** Setae and olfactory pores of first-stage larval head; **6,** Head of second-stage larva. Head horn derived from, or incorporates, seta PA2. Setae PA1, AG3, LH1, O2 arise from small cones on transparent circles of exoskeleton. X's show positions of setae present on some larvae; **7,** Head horn of second-stage larva, includes PA2 seta of first stage; **8,** Ventral neck gland of larval stages 2–5 partly everted. It appears slitlike when retracted, is fully everted in some preserved larvae; **9,** Mandible of first-stage larva; **10,** Head setae of fifth-stage (mature) larva with primary setae whose origin is traceable to first-stage larval seta lettered; **11,** Labrum of first-stage larval head, anterior view showing one olfactory pore; **12,** Labrum of first-stage larval head, posterior view showing two olfactory pores, three spatulate setae; **13,** Labrum of third-stage larval head, anterior view; **14,** Labrum of fourth-stage larval head, anterior view; **15,** Labrum of fifth-stage (mature) larval head, anterior view.

forward to inverted cream V on face, head horns, setae mostly black, some setae on sides and lower face white; body has lateral cream band with cream BL1; top of body cream with cream scoli, black dashes in shape of V without point angling forward from each BD1.

Fourth-stage larva (Figs. 8, 14). Head as in mature larva. Body similar to mature larva, but scoli more orangish, BD1, BD2 on A3, A5, A7 with dark brown ring around each above base, whereas other scoli and all scoli on mature larva, lack brown ring.

Comparison. The other species also resemble mature larva.

Mature larva (Figs. 3, 8, 10, 15, 19, 20, color photo on pl. 3 of Scott 1986). Head black, horns dark brown, orangish cream notch on top, orange-red W on front consisting of streak along upper part of each adfrontal cleavage line plus streak angling down from base of each horn, lower 3rd of frontoclypeus orange-brown, orange-red patch surrounding eye cluster, orangish mottling beside neck. Some setae everywhere on head including AG3, PA1, LH1, O2 orange-red, on long orange stalks; AG2, some dorsal setae beside neck, about 3 lateral setae beside neck on smaller orange stalks. Body scoli ochre, only needle tips orange, except: BD2, BSD1 on T2 black with some orange branches; BD2 on T3 mostly black, orangish on basal 5th, BSD1 ochre; BD2 on A8 partly black, BSD1 mostly black, BD1, BL1 ochre; BD2 on A9 partly black; BD2 on A10 black. Body blackish brown in ground color, with complex pattern. T1 brown with mid-dorsal, subdorsal, supraspiracular, subspiracular orangish lines, some small mostly orange spinelike setae; mid-dorsal ochre band extending from head to T1, narrowing on T2, very narrow on T3. A few ochre transverse dorsal lines between T1, T2, between A8–10. Body joints between

T2, A8 have 5 ochre joint lines, line 2 grayish, lines 1, 3 widest, separated by 4 black joint lines, most posterior very narrow. Segments T2, T3 ochre on top, with paired short black grooves on either side of black mid-dorsal line. Segments A1, A2 similar but paired dark grooves form brown transverse streak behind BD1. A1, especially A2, begin to show dorsal black rearward-aimed V's characteristic of all *Polygonia* on A3–8. Tip of V blunt, wide, corresponding to brown transverse streak on A1–2 just behind BD1, each arm of V thickest in middle anterodorsal to BD2 where V becomes orangish black, outlined by ochre bands as thick as V itself. Three more black spots posterior to point of each V that continue point: black transverse mid-dorsal dash formed by 2 interruptions in 1st black joint line circling segment, narrower dash formed by narrower interruptions in next joint line, mid-dorsal black triangular spot on anterior edge of posterior segment. Ochre joint lines stop at 2 wavy lateral lines characteristic of all *Polygonia*. Upper wavy lateral line orange, on each segment obliquely extending from BSD1, which is ochre with orange base, up, forward then down; behind BSD1 obliquely extending down, backward then down, forward, resembling orange staple aimed down, forward, centered on BSD1. Upper line interrupted between segments by last 3 ochre joint lines which splinter into about 5 ochre wavy narrow lines that stop just above lower wavy lateral line. Lower wavy lateral line ochre, extending from each BL1 obliquely up, forward, then straight forward, then angling down toward BL1 of preceding segment. Beneath this line a vague ochre line above prolegs. Prolegs, underside blackish brown, ochre ventral bands running along abdomen on each side of mid-ventral line. Ventral neck gland present.

Of more than 50 larvae, a few slightly paler (dorsal areas yellow anteriorly, cream behind). Early 5th stage slightly more pinkish violet as orange-red scoli of 4th stage change to ochre.

Comparison. California *P. p. oreas*, based on preserved larvae, photos, same as *nigrozephyrus*, except that top front of former oranger, yellowish orange vs. orangish yellow on top of thorax, A1–2; BSD1 on orange upper wavy lateral band more orangish than *nigrozephyrus*, ochre in latter with only base orangish. Based on 50-year-old preserved larvae in Smithsonian, ssp. *progne* similar to *nigrozephyrus* in structures, all pattern elements seem present, though impossible to discern true colors; dorsal V-marks, transverse lines between segments present. Edwards (1880) described *progne* color as buff (ochre), dorsal area "reddish" (probably orangish ochre) around black V's; he described T2–3, A9–10 scoli as black, others ochre as in *nigrozephyrus*; described BSD1 as black, but contradicted on the preserved larvae, these being pale also. T1 collar described as yellow in *progne*, and is pale in the preserved larvae, whereas it is black except for mid-dorsal line in *nigrozephyrus*, other 3 species. Head seems to have larger black areas in *nigrozephyrus* than ssp. *progne*. Evidently ssp. *progne* larva does not change color from front to rear as much as western subspecies, and dark brown areas of former are smaller.

Mature larvae of other *Polygonia* species differ greatly. All 3 have black V's on top of abdomen slightly narrower than *nigrozephyrus*, point of each V less strongly connected. All 3 have wavy lower lateral lines as in *nigrozephyrus*, but these are slightly reddish cream in *zephyrus*, red-orange in *faunus*, orangish cream in *satyrus*. *Polygonia g. zephyrus* (Fig. 27, color photo on pl. 2 of Scott 1986) much more 2-toned, top of segments T2–3, A1–2 red-orange, especially T3, A2); top of A3–8 whitish, especially A4, A6 which are yellowish white. Basic pattern elements of *zephyrus* same as in *nigrozephyrus*, but wavy lateral lines weak, slightly reddish, scoli black except BL1 along lower wavy line whitish in some larvae, BD1 orange within orange areas, white within white areas. Head of *zephyrus* also mostly black, except for white mid-dorsal notch, sometimes thin orange inverted V on front, scattered small white seta bases. Some *zephyrus* larvae have T3, A2 orangest on top, A4, A6 whitest, whereas in others T2–3, A1–2 equally red-orange on top, A3–8 equally white on top. Latter characteristic of *P. faunus*, which has top of body orange in front, white behind as in photo 14 of *faunus* (=*silvius*) in Pyle (1981). *Polygonia faunus* has both wavy lateral lines red-orange, BL1 on lower line white, head black with some cream setae, cream dorsal notch, orange W on front. Thus mature larvae of *P. g. zephyrus*, *P. faunus* are similar. *Polygonia c-album* L. larvae resemble *faunus* closely (photos in Pyle 1981, Whalley 1979:19, Brooks & Knight 1985:79).

Polygonia satyrus mature larvae differ greatly from other *Polygonia* (Fig. 25, color photo on pl. 2 of Scott 1986). Top near-uniform yellow, same pattern elements present: head black, inverted cream V on front, mid-dorsal cream notch, some small cream setae; middorsal line cream on thorax, transverse rings between segments, dorsal V's present. However, entire top of body greenish yellow, T2–3, A1–2 ochre-yellow in some larvae, lower wavy line thick, pale yellow, orangish between segments in some larvae, yellow BL1's; upper wavy line nearly absent, with black BSD1's or line thin, orange, with cream BSD1's in some larvae.

Polygonia interrogationis (Fab.) mature larvae are also very different from other *Polygonia* (Pyle 1981:photo 15, Edwards 1882b). *Polygonia comma* (Harr.) mature larvae vary (Edwards 1882a).

Ventral neck gland present in stages 2–5 of *P. g. zephyrus*, *P. faunus*, *P. satyrus*.

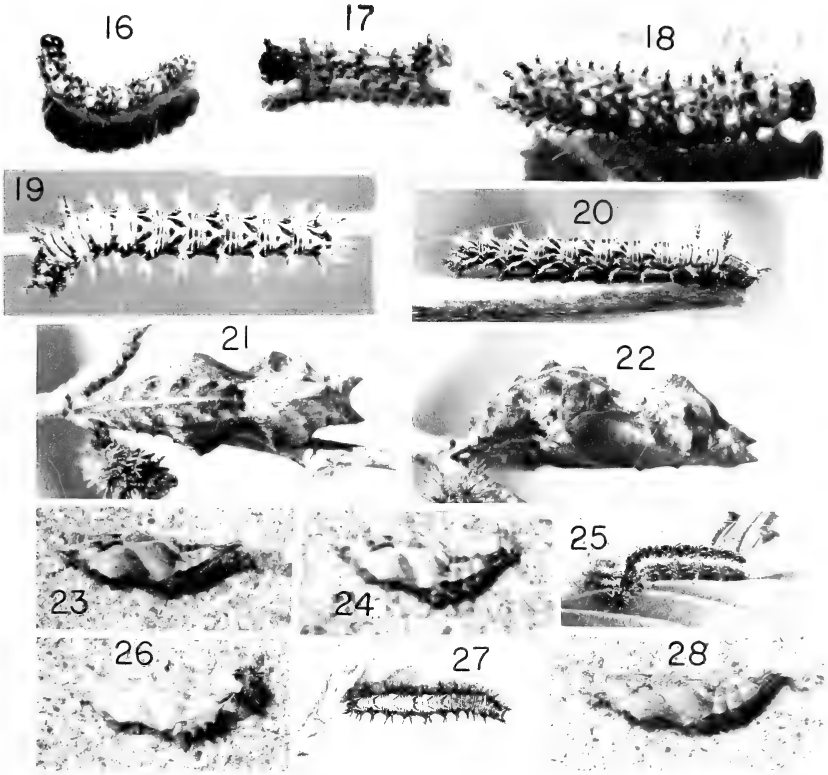
Chaetotaxy (Figs. 1–7, 9–15). Head of 1st-stage larva has only primary setae. Second-stage head has many secondary setae, scoli BPA2; each horn incorporates seta PA2 of 1st stage because scolus in same position as 1st-stage PA2, other dorsal primary setae recognizable on 2nd-stage head by large size, position. Each 2nd-stage horn has long PA2 seta on tip, 5 setae on crown below tip. Head setae, horns on stages 3–5 like those of stage 2 except for proliferation of small setae, primary setae recognizable on mature larval head by larger size, horn still including only 1 primary seta, PA2. Setae on labrum constant at 6 on each side, 3 spatulate setae on posterior oral surface, during larval stages 1–5, setae on other mouthparts also constant, except mandible setae which rise from 2 on each stage 1 mandible to about 10 on stage 5.

Proprioceptor setae, those that detect cuticular folds telescoping over, on head, body same as present in other Lepidoptera.

Body of 1st-stage larvae has mainly primary setae, also some secondary L2 setae, present on all individuals examined, on T3, A1–8; on A3–6 of some larvae 4th L seta present near L2. On 2nd-stage body, many secondary setae, scoli appear. Body scoli of 2nd-stage larva not homologous with 1st-stage larval primary setae because primary setae of 1st stage occur on 2nd stage, sometimes slightly moved in position, with scoli. Thus A10 of 1st stage has paler spot where BSD1 appears on 2nd stage, yet both stages have same dorsal primary setae on A10; on T2–3, 2nd stage retains same SD, L setae of stage 1 adds BL1; on A8, 2nd stage retains same D1–2, SD1 setae of stage 1, adds BD1, BD2. Body scoli add small setae between stages 2–5, otherwise change little. Small SD plate on T2–3 of stage 2 disappears, only 1 or 2 setae remain on stage 5. Body setae multiply between stages, hundreds of which are not shown on stage 5 setal map (Fig. 3). Crochets typical of butterflies: 14 of anterior 8 prolegs forming circle in stage 1, medial crescent in mature larvae; 12 anal crochets form anteromedial crescent in all stages. Each true leg has 5, 2, 6, 2 tactile setae plus 3, 1, 0, 2 proprioceptor setae on 1st 4 leg segments of stage 1, the usual number in 1st-stage butterflies, additional setae joining these on mature larvae, 1st segment having about 8 setae, for instance, on mature larvae. No anal comb present on any stage.

Comparison. Setae, scoli of all larval stages same in 4 *Polygonia* compared, also in mature *P. interrogationis* larvae based on preserved specimens, Petersen (1965) showing drawing of mature *interrogationis* larva: thus secondary 1st-stage L2 seta occurs in all species, L1 on A3–6 in some *zephyrus* individuals splitting into 3 instead of 2 setae, making 4 L's instead of the normal 3, head horn on stages 2–5 incorporating primary seta PA2, consisting of 1 terminal setae, crown of 5 main setae below. Secondary L2 seta on 1st-stage T3–A8 distinguishes *Polygonia* from *Nymphalis*, *Vanessa*.

Pupa (Figs. 21–24, color photo on pl. 5 of Scott 1986). Usually pinkish tan, sometimes paler, rarely blackish gray. Segments T3, A1, A2 have silver or gold subdorsal spot, usually silver on T3, A1, often gold on A2 because of reddish tan A2 top, making 6 in all, mid-dorsal silver streak sometimes on A1. Segment A2, to lesser extent A3, reddish tan on top. Four abdominal bands: lateral tan-edged brown band, mid-ventral tan-edged brown band, mid-dorsal brown-edged tan line. Basal half of each tibia brown. Sliver of hindwing just above forewing brown. Light-brown V's on A4–7, weakly on A3, on both sides of tan mid-dorsal line, 1 arm of each V ending at each subdorsal cone. Broad brown, often greenish brown, band crosses wing from tornus to mid-costa, short brown subapical band parallel to it. Many cones, bumps usually at larval scoli positions: very small mid-dorsal



FIGS. 16–28. *Polygonia* larvae and pupae. 16–24 *P. progne nigrozephyrus* from Delta Co., Colorado; 25–28 other taxa as noted from Jefferson Co., Colorado. **16,** First-stage larva, dorsal view; **17,** Second-stage larva, dorsolateral view; **18,** Third-stage larva, dorsal view; **19,** Fifth-stage larva, dorsal view; **20,** Fifth-stage larva, lateral view; **21,** Pupa, dorsal view; **22,** Pupa, lateral view; **23, 24,** Pupae, lateral views showing variation; **25,** *P. satyrus* mature larva, lateral view; **26,** *P. satyrus* pupa, lateral view; **27,** *P. gracilis zephyrus* mature larva, dorsal view; **28,** *P. faunus hylas* pupa, lateral view.

bump on A2–8; large subdorsal cone on T2–3, A1–8; supralateral bump on A3–7; lateral bump on A4–8, lateral bump on each head horn; large bump on wing base; bump on lower basal corner of wing; subventral bump on A5–6, another on head, 1 on each tibia; 2 stout cones (horns) projecting forward from each side of head; mid-dorsal keel on T2. Silk pad spun by pupating larva bright pink.

Comparison. All *Polygonia* pupae have similar silver or gold spots in saddle, similar cones, keels, horns, dark bands on abdomen, wings. Species differ in overall color, shape, size of cones, horns. *Polygonia p. oreas* resembles *nigrozephyrus*, but 2 *oreas* pupae seen were brown, not pinkish tan. *Polygonia p. progne* pupa (Edwards 1880) also pinkish brown like *nigrozephyrus*, with similar markings; head, thorax sometimes greenish brown. *Polygonia g. zephyrus* like *nigrozephyrus* in shape, but most individuals light brown, some creamy gray or tinged with green, rarely blackish gray, abdomen more mottled, subdorsal area on A4 lighter than on other segments, on A5–A7 a paler streak angling forward, down from each subdorsal cone. Few *zephyrus* pupae resemble *nigrozephyrus* in overall color, yet reddish tan top of A2 of *nigrozephyrus* identifies most. *P. faunus* pupa (Fig. 28, color photo 14 of Pyle 1981, as *silvius*) light brown (often with reddish flush on top of A2–3 as in *nigrozephyrus*) or dark gray, easily identified by elongate shape, >10% longer, long head horns, twice as long as other *Polygonia*. *P. satyrus* pupa (Fig. 26, color photo on pl. 5 of Scott 1986) paler, tan or straw, sometimes yellowish dorsally, rarely brown all over, easily identified by mid-dorsal T2 keel being twice as high as other species, subdorsal abdomen cones about twice as large. *P. interrogationis* similar in color to some *nigrozephyrus*, *faunus*, with similar sized bumps, but its T2 keel very large (color photo 15 of Pyle 1981, Edwards 1882b). *P. comma* pupa quite variable (Edwards 1882a). *Polygonia c-album* pupa brown, resembling *nigrozephyrus* in shape but T2 keel larger as in *satyrus* (Brooks & Knight 1985:79).

Oddly, silk cremaster pad spun by pupating larvae colored differently in other species: bright pink in *nigrozephyrus*, also *interrogationis* (photo in Pyle 1981); pale pink in *zephyrus*, *faunus*; yellowish white, rarely faintly pink, in *satyrus*.

ACKNOWLEDGMENTS

I thank J. R. Heitzman for larvae of *P. interrogationis*, R. K. Robbins for loans of *Polygonia* immatures from the Smithsonian Institution, P. A. Opler for photos of *P. progne oreas* immatures, and C. F. Gillette for reviewing the manuscript.

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GENERAL NOTE

DIFFERING OVIPOSITION AND LARVAL FEEDING STRATEGIES IN TWO *COLOTIS* BUTTERFLIES SHARING THE SAME FOOD PLANT

Additional key words: Pieridae, *Colotis amatus, C. vestalis*, eggs, Salvadoraceae.

There is much interest in the habit of certain butterfly species laying eggs in clusters. It is generally agreed that cluster-laying is a derived trait, the ancestral butterfly having laid single eggs. Cluster-laying has evolved independently several times in all butterfly families. Its significance has been subject to a variety of interpretations. The purpose of this paper is to present oviposition data for two closely related species of *Colotis* in New Delhi, India.

The species in question are *Colotis amatus* F., whose geographic distribution covers most of Africa, Arabia, India, and Sri Lanka; and *C. vestalis* Butler, found in NW India, Pakistan, and East Africa, but unaccountably absent from Arabia (Larsen, T. B. 1983, Fauna of Saudi Arabia 5:333–478). Together with *C. phisadia* Godart, *C. amatus* and *C. vestalis* form a small section of the genus that feed on Salvadoraceae rather than on the more usual Capparidaceae.

In New Delhi both butterflies feed on *Salvadora persica* L. and *S. oleoides* Decaisne. Usually both are phenologically synchronous, and occur on the same trees or bushes. In size and behavior they are very similar and were not the ground colours salmon and white, respectively, they would be difficult to tell apart on the wing. M. A. Wynther-Blyth (1957, Butterflies of the Indian Region, Bombay Natural History Society, Bombay, 523 pp.) even suggests they interbreed, interspecific copula having been observed.

Given the overall similarity, the difference in oviposition behavior is startling. *Colotis amatus* lays clusters averaging ca. 30 eggs on upper surfaces of fresh leaves at outer extremities of the host plant (Table 1). Eggs are evenly spaced within each clutch. *Colotis vestalis* lays single eggs deep inside the host plant, usually on a twig or a branch, rarely on an old leaf. I observed eggs being laid as far as 90 cm from the nearest leaf, a considerable distance for a small, freshly hatched larva to travel. Larvae of *C. amatus* feed gregariously on fresh foliage, but group cohesion weakens in final instars. Those of *C. vestalis* feed singly on old leaves, usually deep inside the bush or tree. I never found both species on the same leaf.

The egg of *C. vestalis* is chalk white with 20–22 keels extending from the micropyle to the base. It is covered in fine hairs, best visible when the egg is submerged in fluid. Egg volume appeared 15–20% greater than that of *C. amatus*. The latter's eggs are yellow, have only 14–16 keels, lack hairs, and unlike those of *C. vestalis* are covered with a sticky substance. Midges and mosquitoes were often found trapped on egg clutches.

S. Courtney (1984, Am. Nat. 123:276–281) mentions that *Aporia crataegi* L. in Morocco may adjust egg-clutch size to food plant quality. The data are given in more detail by S. Courtney (1986, Adv. Ecol. Res. 15:51–131). *Colotis amatus* clutch-size on the broad-leaved Salvadora *persica* averaged 28.7 eggs (n = 106), and on the narrow-leaved *S. oleoides*, 22.7 (n = 17) in my Delhi sample; the difference is not statistically significant.

Although these two common butterflies are synchronous and share foodplants, they seem to be noncompetitive. I never saw complete defoliation of food plants. There are a number of potential pathways for two such butterflies to evolve different ovipositing strategies, but data to support any specific hypothesis are not available. Probably no single causal factor underlies all egg clustering. However, available data do not support the hypothesis of R. A. Fisher (1930, The genetical theory of natural selection, Clarendon Press, Oxford, 272 pp.) that egg clustering leads to aposematism; if anything *C. vestalis*, which feeds on old leaves, should be the more aposematic of the two. I masticated a number of specimens without finding the least pungency or emetic response, although I found other aposematic butterflies emetic (Larsen, T. B. 1983, Entomol. Rec. J. Var. 95: 66–67).

The closest parallel I have seen to the two *Colotis* species is that of *Eurema hecabe* L. and *E. blanda* Boisduval in Papua New Guinea and S India. The former lays single eggs.

TABLE 1. Number of eggs in 123 clutches laid in the wild by *Colotis amatus* in New Delhi, India (autumn 1986).

No. eggs in clutch	No. clutches	No. eggs in clutch	No. clutches
1–5	0	41–45	5
6–10	2	46–50	3
11–15	10	51–55	0
16–20	24	56–60	2
21–25	25	61–65	1
26–30	19	66–70	1
31–35	17	71–75	1
36–40	13	76+	0

Average 27.9 eggs per clutch.

the latter clutches. However, in both places the two show more ecological and spatial segregation than *Colotis*; they can feed on the same plants but usually do not do so in the same locality. In Yemen I noticed that Capparidaceae-feeding *Colotis* tend towards local food plant specialisation.

The *Urtica* feeding members of the Vanessini in the Palaearctic fall into two groups. *Vanessa* lay single eggs, *Aglais* lay clutches. Members of both genera are often found on the same batch of nettles, but as in *Colotis* complete defoliation is rare.

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BOOK REVIEW

THE LIVES OF BUTTERFLIES, by Matthew M. Douglas. 1986. xv + 241 pp. 16 pp. color photographs. University of Michigan Press, Ann Arbor, Michigan, U.S.A. Hard cover. $45.00.

This attractive book is the product of a scientist and teacher whose enthusiasm is contagious. Its strengths include substantive explanations of many aspects of work on butterfly biology, its discussion of experimental and other evidence for scientific conclusions, and its emphasis on scientific literature. The book is rich in clear, often detailed, explanations of work in several major areas: anatomy, development, and evolution of morphological features of life stages; biophysical, physiological, and ecological constraints on life stages and community structure; behavioral, biochemical and ecological aspects of speciation and coevolution with plants. This exposition is accompanied by many black-and-white diagrams (often from published original drawings or photographs), a section of color photographs illustrating activities and morphological characteristics of life stages, a glossary, several appendices, and a useful index. This combination makes the book an engaging, accessible, self-contained store of information.

In addition, the author enhances the book's informational content in two ways. First, he places specific examples in a conceptual context by discussing considerations that underlie specific hypotheses. Explanations of how observations and experimental data are collected contribute to a clear sense of how scientific questions are raised and examined, and why "answers" may be open to alternative interpretations. This aspect of the book reflects the author's experience as a university professor; many of his discussions would make good lecture notes for an advanced undergraduate course. This bold focus on processes of scientific research may be the book's most important contribution to its educational goals. Second, the book's emphasis on recent research literature provides a resource for further study.

The question of readership presents problems for the book. While ostensibly written for an audience that has some background in biology, its attempt to appeal to both lay and professional audiences sometimes creates disconcerting inconsistencies. For example, the author describes "sex-limited mimicry" as a special case of Batesian mimicry in which one sex mimics unpalatable models; he includes a definition of this term in the glossary. Ten pages later, however, "sex-limited" is used colloquially to describe distribution of a trait whose pattern of inheritance is sex-linked. This colloquial use of a term that has specific meaning in genetics is confusing. Similarly, the author emphasizes his personal research experience in a way likely to engage the interest of lay readers. To a professional readership, however, such emphasis is likely to seem egotistical and annoying.

This book thus attempts the dual challenges of engaging and educating a lay readership as well as concisely reviewing recent literature for a professional audience. This is a rarely attempted goal, and the author presents us with a unique solution. The book's value to its potential professional audience lies in its conciseness and timely review of much recent literature. Its appeal to this audience is uncertain, because professors whose students study these research topics in class may assign the original literature rather than this book. However, the author's contribution to explicating butterfly biology and scientific research for a lay audience is a noteworthy success.

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Journal of the Lepidopterists' Society
42(1), 1988, 60–61

OBITUARY

ABNER ALEXANDER TOWERS (1916–1987): A Tribute

The Lepidopterists' Society lost one of its charter members with the passing of Abner A. Towers, who was well-known to collectors in the Southeast and to participants in the first of the collecting expeditions to Ecuador organized by Thomas C. Emmel and Giovanna Holbrook.

Abner Alexander Towers

Born in Gadsden, Alabama, 28 January 1916, Abner Towers developed an interest in wildlife as a boy, particularly his lifelong fascination with butterflies and moths, birds, and other flying creatures. He grew up in Gadsden, completing his primary schooling there, then attended the Kent School, in Kent, Connecticut, during which time he began to collect and study Lepidoptera seriously. At the age of eighteen, in 1934, he took his first trip to the Florida Keys expressly to observe and collect butterflies and moths. He attended the Massachusetts Institute of Technology as a general science major, and, after earning the Bachelor of Science in 1939, served as an officer in the U.S. Army Corps of Engineers. He spent most of World War II in the Aleutian and Philippine Islands. Following the war he settled in Georgia, the state he would call home for the rest of his life. Abner Towers married, raised a family, and built a career as an engineer and chemist, and was often described in both capacities by co-workers and peers as "brilliant." In August 1972, he cofounded A-Jay Chemical Company, in Powder Springs, Georgia, an industrial chemical firm he continued to administer until his terminal illness.

In the 1950's Abner resumed his study of the Lepidoptera of the region, focusing his attention almost entirely on the butterflies of Georgia and Florida, and he steadily built an impressive collection containing substantial series of virtually all the species recorded from the two states. He established a strong friendship with Lucien Harris Jr., and his contributions to Harris's *The Butterflies of Georgia* (University of Oklahoma Press, 1972) were significant, and included numerous state records and field observations. Abner's persistent and dedicated collecting subsequently added several species to the Georgia butterfly fauna, including *Mitoura hesseli* Rawson & Ziegler, and, in 1981, he participated in the discovery of a new geometrid, described as *Narraga georgiana* Covell, Finkelstein & Towers (J. Res. Lepid. 23:161–168, 1984). Occasionally, when his other responsibilities allowed, Abner traveled and collected outside the country; most notable were his collecting trips to Ecuador in 1980 and Jamaica in 1982.

Abner Towers died 18 March 1987, after a bravely fought three-year battle with leukemia. He is survived by his wife, Margaret Le Craw Towers, his children John A. Towers, Marsha Towers Endictor, and Andrea Towers Rohaly, and his sister Harriet Towers Bjelouvucic. His friends and co-workers remember him as "a man of warmth . . . who always took time to inquire of people's families, discuss their hobbies, jobs or personal interests and give advice, if asked, with a sincerity derived from a love of people. He was totally unselfish with his time, his knowledge and his abilities." (From a eulogy by Alan Shipp and Polly Buford.)

His collection was donated to the University of Florida in 1985 and deposited in the Florida State Collection of Arthropods, Gainesville. In addition to the Lepidopterists' Society, Abner was a charter member of the Southern Lepidopterists, a group he served since its founding in 1978 as Georgia zone coordinator.

"Abner Towers was a gentle man, and a gentleman. He will be missed." (Shipp and Buford.)

IRVING L. FINKELSTEIN, *425 Springdale Drive N.E., Atlanta, Georgia 30305.*

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Contributions to the *Journal* may deal with any aspect of Lepidoptera study. Categories are Articles, General Notes, Technical Comments, Book Reviews, Obituaries, and Cover Illustrations. *Journal* submissions should be sent to the editor at the above address. Short manuscripts concerning new state records, current events, and notices should be sent to the *News*, June Preston, Editor, 832 Sunset Drive, Lawrence, Kansas 66044 U.S.A. *Journal* contributors should prepare manuscripts according to the following instructions, and submit them flat, not folded.

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Cover illustration: Mature larva of *Papilio polyxenes asterius* Stoll on wild carrot, *Daucus carota* L. Submitted by John V. Calhoun.

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IMPACT OF OUTDOOR LIGHTING ON MOTHS: AN ASSESSMENT

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ABSTRACT. Outdoor lighting has sharply increased over the last four decades. Lepidopterists have blamed it for causing declines in populations of moths. How outdoor lighting affects moths, however, has never been comprehensively assessed. The current study makes such an assessment on the basis of published literature. Outdoor lighting disturbs flight, navigation, vision, migration, dispersal, oviposition, mating, feeding and crypsis in some moths. In addition it may disturb circadian rhythms and photoperiodism. It exposes moths to increased predation by birds, bats, spiders, and other predators. However, destruction of vast numbers of moths in light traps has not eradicated moth populations. Diverse species of moths have been found in illuminated urban environments, and extinctions due to electric lighting have not been documented. Outdoor lighting does not appear to affect flight or other activities of many moths, and counterbalancing ecological forces may reduce or negate those disturbances which do occur. Despite these observations outdoor lighting may influence some populations of moths. The result may be evolutionary modification of moth behavior, or disruption or elimination of moth populations. The impact of lighting may increase in the future as outdoor lighting expands into new areas and illuminates moth populations threatened by other disturbances. Reducing exposure to lighting may help protect moths in small, endangered habitats. Low-pressure sodium lamps are less likely than are other lamps to elicit flight-to-light behavior, and to shift circadian rhythms. They may be used to reduce adverse effects of lighting.

Additional key words: conservation, evolution, flight, urban ecology, light pollution.

Since the invention of the incandescent lamp over a hundred years ago, outdoor lighting has progressively increased. The growth has been characterized by expansion into new geographic areas, development of new lamps with new spectral characteristics, and increases in total amount of light and radiant energy (Riegel 1973, Hendry 1984, Sullivan 1984). Outdoor lighting has transformed the nocturnal face of the earth (Croft 1978). However, despite universal awareness that electric light disturbs behavior of nocturnal insects, the ecological impact of outdoor lighting has never been comprehensively assessed.

The possibility that outdoor lighting may adversely affect our fauna is well recognized. Lepidopterists have blamed outdoor lighting for declines in populations of North American moths, especially saturniids in the northeastern United States (Holland 1903, Ferguson 1971, Hessel 1976, Muller 1979, Worth & Muller 1979, Krivda 1980, Pyle et al. 1981). This view assumes a direct causal link between lamps and faunal change. Fundamental questions about such a link, however, have never been closely examined: What mechanisms might link lamps with changes in populations of moths? If lamps cause populations of moths to change, specifically what might the changes be? How important are effects of lighting compared to effects of other environmental disturbances? This study examines each of these questions. It investigates the hypothesis that outdoor lighting influences populations of moths.

The investigation is based on a review of literature. The presentation is organized into three sections. The first section describes distribution, growth, energy, and spectral composition of outdoor lighting. The second describes how lamps affect behavior, life functions and survival of individual moths. The third explores how such effects may disturb moth populations; it also discusses measures to reduce disturbances caused by lighting. Citations are deliberately extensive to facilitate retrieval of source material which is widely scattered among different disciplines.

LIGHTING

Nocturnal images of earth viewed from orbiting satellites show the distribution of outdoor lighting (Fig. 1). In the United States this distribution coincides with that of the country's population (Croft 1978). Nocturnal illumination is clustered around all large metropolitan areas, with greatest concentration in the Northeast corridor. Viewed from an airplane, nocturnal lighting delineates a web of interconnecting roadways lined with illumination from houses, parking lots, billboards, and other landmarks. Such aerial observation suggests that lighting forms an illuminated web that envelops the nocturnal environment of Lepidoptera. The web's density varies with human population density, and its distribution is continental.

The magnitude of lighting in a major metropolitan area is illustrated by Philadelphia's streetlighting (Table 1). Philadelphia has 100,000 high-pressure sodium streetlamps at a density of almost 300 lamps/km^2. The energy they radiate equals more than 10 kilowatts/km^2, an order of magnitude greater than the energy density of moonlight at full moon (Agee 1969). During the last 4 decades, lamp size (lumens) increased 7-fold, number of lamps tripled, and type of lamp changed from tungsten filament and mercury to high-pressure sodium (Figs. 2 & 3) (Wainwright 1961, C. A. Oerkvitz pers. comm.). Nationwide per capita consumption of electrical power for streetlighting is similar to that of

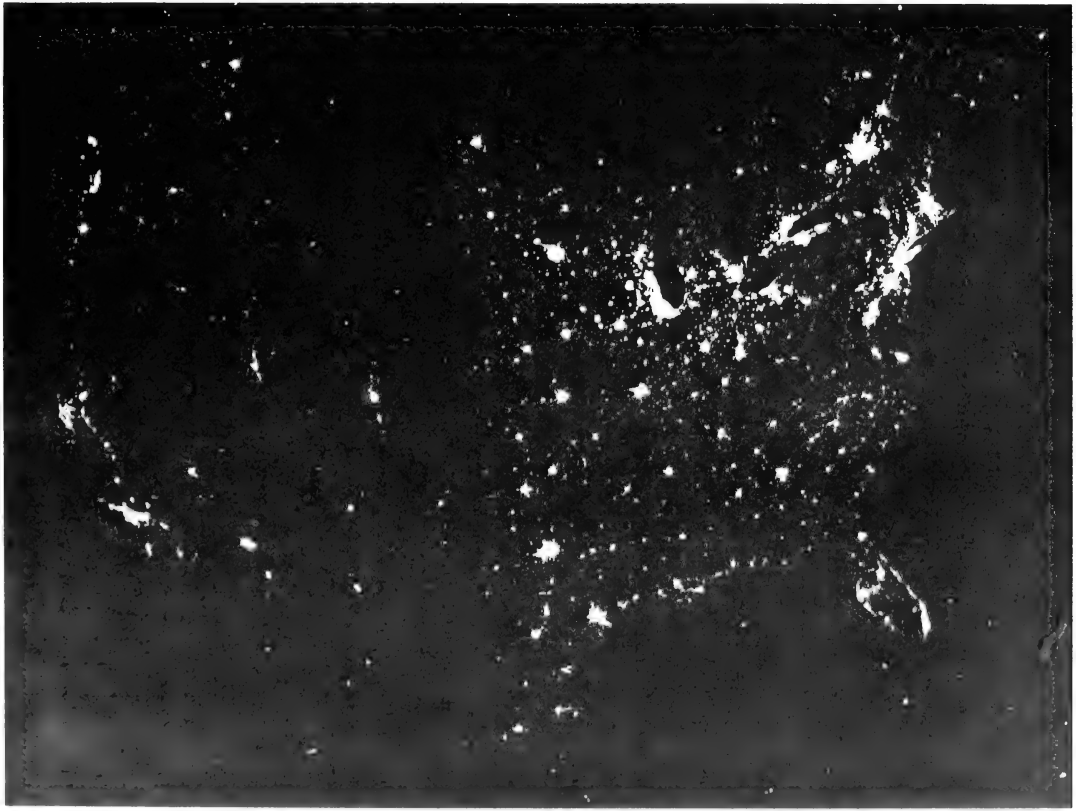


FIG. 1. Composite image of nocturnal United States, as viewed from orbiting satellite in fall 1985 (Defense Meteorologic Satellite Program). Photograph from National Snow and Ice Data Center, Campus Box 449, University of Colorado at Boulder, Boulder, Colorado 80309.

TABLE 1. Streetlamps in Philadelphia, 1983. Total lamps, lumens, and demand (watts) from C. A. Oerkvitz (pers. comm.). Radiant energy calculated from GTE Products Corp. (Sylvania) (1977b). Demographic data from *World Almanac* (1986).

Streetlamp parameter	Number		
	Total	Per capita	Per km^2
Lamps	1.0×10^5	5.8×10^{-2}	2.8×10^2
Lumens	1.8×10^9	1.1×10^3	5.0×10^6
Radiant energy (watts) emitted for wavelengths 350–700 nm	5.6×10^6	3.3	1.6×10^4
Electric power demand (watts)	2.2×10^7	1.3×10	6.1×10^4

Philadelphia, and growth in lumens has been comparable or higher (Riegel 1973, Edison Electric Institute 1971, 1985, Sullivan 1984).

Conversion from mercury to high-pressure sodium lamps reduces radiant energy at the short-wavelength end of the spectrum. However, high-pressure sodium light is spectrally broad and does include radiant energy in the blue spectral region (Fig. 2B).

In contrast to high-pressure sodium light, low-pressure sodium light is spectrally narrow. It excludes practically all energy in the ultraviolet, blue, and green regions of the spectrum (Fig. 2A). Viewed through a spectroscope, its spectrum contains a bright yellow-orange line (actually 2 spectral lines very close together) near 589 nm. Because the human eye is particularly sensitive to light in the 589 nm region, low-pressure sodium lamps can provide bright illumination with comparatively little radiant energy (Finch 1978). Compared to other lamps used for outdoor lighting, low-pressure sodium lamps minimize environmental exposure to radiant energy both in number of wavelengths and number of watts. These lamps are used for streetlighting and other outdoor lighting, but much less frequently than are high-pressure sodium lamps.

Conversion of streetlamps from mercury to high-pressure sodium has changed the spectral distribution of outdoor lighting, but it has not changed it as much or as clearly as one might suppose. Mercury lamps, for example, are still used for residential and commercial lighting in Philadelphia, and for streetlighting in neighboring areas. Tungsten filament (Fig. 3), low-pressure sodium, metal halide (Fig. 2C) and fluorescent lamps (Sorcar 1982) all contribute to spectral diversity of outdoor lighting in the city. While density and distribution of outdoor lighting have increased, spectral composition has diversified.

EFFECTS ON INDIVIDUAL MOTHS

Vision

Bright light can lower sensitivity of moth eyes 1000-fold (Bernhard & Ottoson 1960a, Höglund & Struwe 1970, Agee 1972, 1973, Eguchi

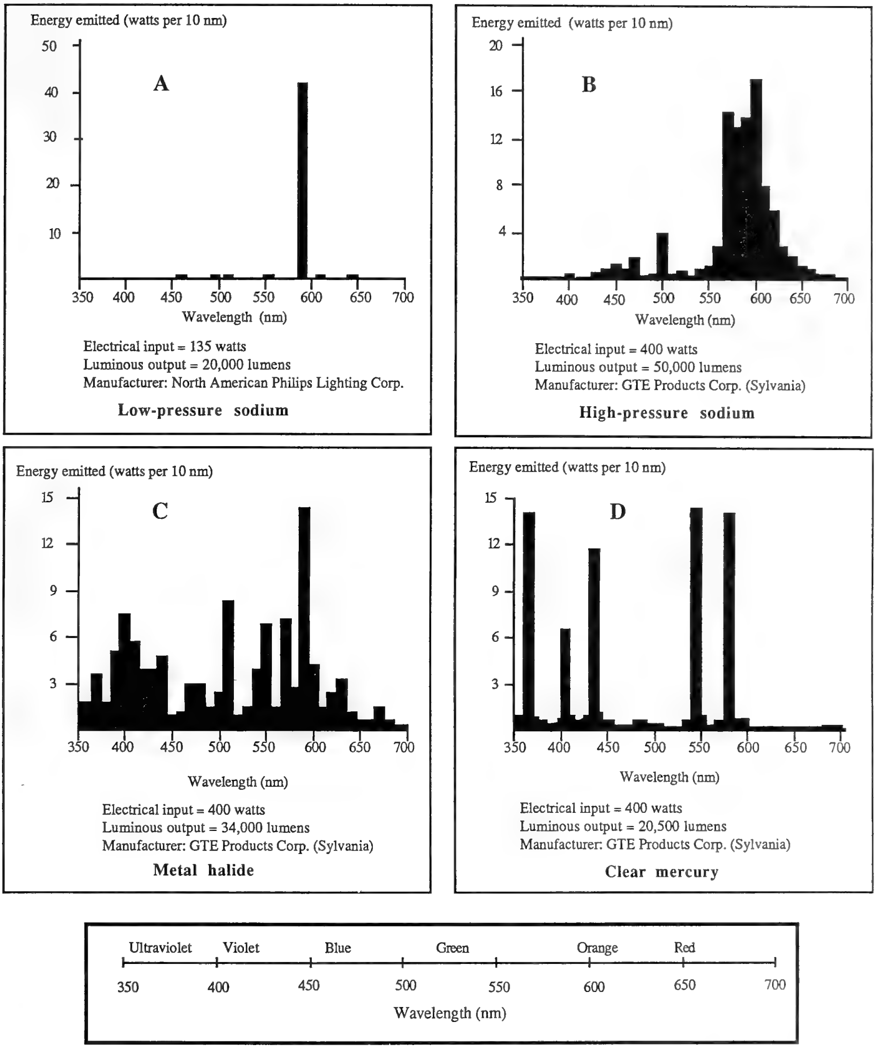
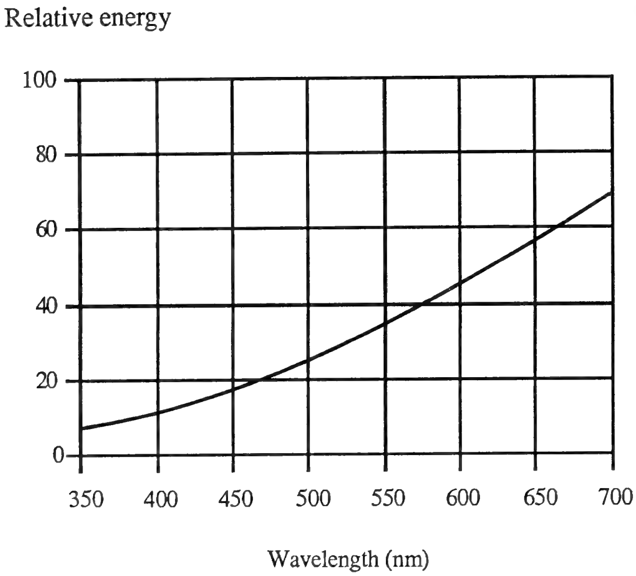


FIG. 2. Spectral energy distribution of vapor discharge lamps. Sources for A: Judd 1951, Finch 1978, Illuminating Engineering Society 1981, North American Philips Lighting Corp. 1982. Sources for B, C, and D: GTE Products Corporation (Sylvania) 1977a, 1977b, 1979.

& Horikoshi 1984). Electroretinographic studies suggest what happens to the visual sensitivity of a moth that flies to a lamp. If the moth remains at the lamp and then flies away, full visual sensitivity may not return for 30 min or longer (Bernhard & Ottoson 1960a, 1960b, Agee 1972). This effect requires exposure to the lamp over a period of time, probably 10 min or longer (Day 1941, Höglund 1963, Yagi & Koyama



Electrical input: 1000 watts
Luminous output: 23,100 lumens
Color temperature: 3030° Kelvin

FIG. 3. Spectral energy distribution of tungsten filament ("incandescent") lamp. Sources: GTE Products Corporation 1972, 1974.

1963). A moth flying away from a lamp into relative darkness on a cloudy, moonless night may be functionally blind until enough time has elapsed for it to become fully dark-adapted.

Continuous exposure to bright electric lamps could in theory "dazzle" moths. This means it could stimulate the moth retina so intensely that the retina could not respond to additional increases in light. The result would be functional blindness so long as the moth remained exposed close to the lamp. Electroretinographic evidence, however, suggests that lamps do not dazzle moths (Eguchi & Horikoshi 1984).

Net effects of electric lighting on moth vision may vary according to local conditions as well as moth behavior. Urban lighting increases background illumination which in turn may help moths see. Electric lighting in some areas has increased nocturnal sky brightness as much as 20-fold (Hendry 1984). However, the spectral composition, polarization and spatial distribution of outdoor lighting varies widely in different settings. In some locations they may differ so much from that of natural nocturnal light that they create visual artifacts and distortions. One outcome of disturbed vision is flight to outdoor lamps, but many disturbances in visual function and behavior are possible.

The suggestion that urban lighting influences nocturnal vision of moths may appear paradoxical. Municipal light sources have shifted away from mercury lamps and toward high-pressure sodium lamps. One might suppose that moth retinas are insensitive to the relatively long wavelengths which characterize most of the energy contained in high-pressure sodium light (Fig. 2B). Moths, for example, do not fly to the 589 nm light of low-pressure sodium lamps (Fig. 2A), or do so rarely (Robinson 1952). Such a supposition, however, is incorrect: electroretinograms of moths consistently demonstrate sensitivity to light in the 589 nm region, and most studies have found maximum sensitivity in the green rather than ultraviolet part of the spectrum (Jahn & Crescitelli 1939, Höglund & Struwe 1970, Hsiao 1972, Mikkola 1972, Agee 1973, MacFarlane & Eaton 1973, Langer et al. 1979, Mitchell & Agee 1981, Eguchi et al. 1982). Retinal sensitivity extends farther into the long-wavelength end of the spectrum than flight-to-light behavior typically would suggest (Mikkola 1972, MacFarlane & Eaton 1973, Mitchell & Agee 1981).

Navigation

Diversion to lamps. Three hundred fifty-six species of Macrolepidoptera, or about a third of those species found in all of Great Britain, were collected at a single light trap in England (Williams 1939). Comparable findings have been reported in Britain and North America (Dirks 1937, Robinson & Robinson 1950a, Beebe 1953, Bretherton 1954, Moore 1955, Langmaid 1959, Hosny 1959, Holzman 1961, Moulding & Madenjian 1979). Tens of thousands of moths have flown to a single lamp in a single evening (Robinson & Robinson 1950a), and huge swarms of moths have aggregated around urban light sources (Howe 1959). On the other hand, some species of nocturnal moths rarely fly to lamps even though large populations of them may be flying nearby (Bretherton 1954, Taylor & Carter 1961, Janzen 1983). A variety of physiologic, behavioral and environmental factors may determine which species of moths fly to light and when (Geier 1960, Gehring & Madsen 1963, Milyanovskii 1975, Mazokhin-Porshnyakov 1975, Janzen 1983, 1984).

Large numbers of moths flying to lamps may give a false impression that lamps divert moths from great distances. Effective radius of a 125-watt mercury vapor light trap was initially reported to be 91 m, but later estimates reduced the figure to 17 m, and the most recent analysis cut the distance to 3 m (Robinson & Robinson 1950a, Robinson 1960, Baker & Sadovy 1978). Other studies have shown flight-to-light distances of 10 m or less (Stanley 1932, Hamilton & Steiner 1939, Hartstack et al. 1971, Plaut 1971). Long-distance estimates ranging up to half a kilometer represent either extrapolation, artificial conditions or both (Graham et al. 1961, Hsiao 1972, Agee 1972, Stewart et al. 1969, Plaut 1971, Bowden & Morris 1975).

If the mechanism by which a lamp disturbs moths depends on diversion of flight paths to the lamp, then the moths disturbed must be limited to those flying in the geographic area immediately adjacent to the lamp. In this sense any direct effects of a particular lamp would tend to be local, except when topography (Beebe 1949, Beebe & Fleming 1951), foodplants, pheromones, or other factors concentrate moths near the lamp. Only in urban regions would density and distribution of lamps be great enough to influence large populations of moths over broad geographical areas.

Effects of electric lamps in urban areas, however, may be much smaller than one might expect. Robinson & Robinson (1950a) noted that lamps in isolated phone booths appear to be much more effective in eliciting flight-to-light behavior than are clusters of bright urban lamps located immediately adjacent to areas with large populations of moths. They demonstrated that lamps interfere with each other's capacity to elicit flight-to-light behavior, and the closer together the lamps, the greater the interference. The high density which characterizes distribution of urban lamps suppresses flight-to-light behavior.

Urban lighting may suppress flight to light for a number of reasons. Light trap collections vary with the lunar cycle and are lowest at full moon (Williams et al. 1956, Agee et al. 1972, Nemec 1971, Dufay 1964, Bowden & Church 1973, Janzen 1983, Stradling et al. 1983). A similar correlation with moonlight cannot be demonstrated when nocturnal flight is measured by suction traps (Williams et al. 1956, Danthanarayana 1986), pheromone-baited traps (Saario et al. 1970, Janzen 1984) or radar (Schaefer 1976). Moths active at dusk typically appear in suction traps before they appear in light traps (Taylor & Carter 1961). Eye pigment must be in a position of dark adaptation before moths will fly to light (Collins 1934), and even relatively dim background light can cause the pigment to move away from this position (Bernhard & Ottoson 1964). Diffuse urban light, like moonlight and twilight, reduces the darkness essential for flight-to-light behavior.

The moon not only increases background lighting but also constitutes a concentrated source of light by which insects may be able to orient (Sotthibandhu & Baker 1979). Moths flying by lunar navigation may bypass lamps (Baker & Sadovy 1978). Lamps may provide navigational cues which suppress flight to other lamps.

Light sources that emit large amounts of ultraviolet energy are generally most effective in eliciting flight-to-light behavior (Williams et al. 1955, Glick & Hollingsworth 1955, Klyuchko 1957, Deay et al. 1965, Mazokhin-Porshnyakov 1969, 1975, Mikkola 1972, Sargent 1976, Mitchell & Agee 1981). Conversion of mercury streetlamps to high-pressure sodium and metal halide streetlamps has undoubtedly tended to reduce flight to streetlamps. On the other hand, moths do fly to high-pressure sodium and metal halide lamps, and a small minority of species may fly preferentially to lamps with little or no ultraviolet emission (Klyuchko 1957, Mikkola 1972). Unlike high-pressure sodium lamps, however, low-pressure sodium lamps rarely elicit flight-to-light behavior (Robinson 1952).

In summary, increases in electric lighting do not necessarily impair nocturnal vision and navigation. Under some conditions they may improve moths' nocturnal vision and suppress flight-to-light behavior.

Diversion away from lamps. Electric lamps may also divert moths away from them (Robinson & Robinson 1950a, Robinson 1952, Herms 1929, 1932, Nomura 1969, Nemec 1969, Hsiao 1972). These effects may depend in part on spectral output of the lamp (Mazokhin-Porshnyakov 1969, 1975, Nomura 1969). Several theories attempt to explain this behavior (Hsiao 1972), but none accounts for diversity of flight paths at lamps (Janzen 1984): while some moths make spiral or circular flights around lamps and land several meters away, others make a beeline straight to lamps and crash into them. Flight paths approaching lamps may zig-zag or be totally chaotic (Holzman 1961, Mazokhin-Porshnyakov 1969, Janzen 1984). Diversion away from lamps has been debated (Bretherton 1950, Robinson & Robinson 1950b). Evidence that moths avoid large illuminated areas (Herms 1929, 1932, Nomura 1969, Nemec 1969) is inconclusive, but this behavior is more difficult to demonstrate than flight to lamps.

Lamps suppress flight of moths that fly to them. Moths approaching lamps may land near them and remain quiescent for a moment or for the entire night. Lamps suppress flight of some species more than others (Blest 1963, Graham et al. 1964). In some cases lamps do not appear to suppress flight; in other cases they excite quiescent moths into flight (Collins 1934, Hsiao 1972). Diurnal moths occasionally fly at night to lamps (Engelhardt 1946, Janzen 1983), but here it is unclear whether the lamps help to initiate nocturnal flight.

Diversion and suppression of flight may impair orientation and navigation based on lunar, stellar or other visual celestial cues (Mazokhin-Porshnyakov 1969, Sotthibandhu & Baker 1979, Wehner 1984) including polarization of celestial light (Danthanarayana & Dashper 1986). It also may impair navigation and orientation based on geomagnetic, gravitational, barometric, aerodynamic, inertial, olfactory, acoustic or visual terrestrial cues (Baker & Kuenen 1982, Baker & Mather 1982, Janzen 1984, Schöne 1984, Riley & Reynolds 1986). How much electric lighting disturbs use of particular cues may be expected to vary in part according to which cues the moth happens to be using at the moment it encounters the lamp.

Migration and Dispersal

Light sources divert moths engaged in migratory or dispersal flights (Cockerell 1914, Williams 1937, Beebe & Fleming 1951, Wolf et al. 1986). Urban lighting surrounds habitats isolated by urban sprawl, so that moths may have to traverse dozens of kilometers of densely illuminated territory to arrive at potential breeding sites. Moths flying high (Glick 1965) may fly to urban light sources on tall buildings (Stanley 1932, Glick 1961). Because location of natural flyways is poorly documented for North American moths, one cannot determine the extent urban lighting may intersect long-range natural migration routes here. In Venezuela, vast numbers of migrating moths aggregated around lamps near a narrow mountain pass which functions as a natural flyway (Beebe 1949, Beebe & Fleming 1951). Lighting along roads following topographical features such as valleys, rivers, and coastlines might selectively interfere with North American moth migrations (Fig. 1).

Oviposition

Electric lighting can disturb oviposition. Light-trap surveys have shown that the vast majority of females collected at lamps are gravid (Dirks 1937, Ficht et al. 1940, Glick & Hollingsworth 1954, Geier 1960, Gehring & Madsen 1963) although males usually outnumber them (Dirks 1937, Williams 1939, Sargent 1976, Worth & Muller 1979, Janzen 1984). Flight to light can shift oviposition to sites located near the lamp (Ficht et al. 1940, Martin & Houser 1941, Pfrimmer & Lukefahr 1955, Beaty et al. 1951, Nemec 1969, Brown 1984). Eggs may be deposited on lampposts, window screens, buildings, and other unsuitable sites near lamps. Egg densities may be several-fold higher on plants near lamps (Martin & Houser 1941). The result may be larval overcrowding and increased susceptibility to starvation, microbial infection, and predation.

Lamps shift the distribution of oviposition sites toward them probably by diverting ovipositing females and not by stimulating oviposition. In cornfields, *Ostrinia nubilalis* (Hbn.) (Pyralidae) tends to oviposit near lamps (Ficht et al. 1940, Beaty et al. 1951), but in the laboratory nocturnal illumination suppresses *O. nubilalis* oviposition (Skopik & Takeda 1980). Similar observations have been reported in *Pectinophora gossypiella* (Saund.) (Gelechiidae) (Pfrimmer & Lukefahr 1955, Lukefahr & Griffin 1957, Henneberry and Leal 1979). Outdoor lighting may decrease oviposition by *Cydia pomonella* (L.) (Tortricidae) and *Heliothis* spp. (Noctuidae), although the mechanism is unclear (Herms 1929, 1932, Nemec 1969).

Mating

Outdoor lighting does not prevent mating in certain Saturniidae: male *Hyalophora cecropia* (L.) and *Samia cynthia* (Drury) complete long-distance mating flights to virgin females at night across illuminated urban territory, and breed in urban habitats (Rau & Rau 1929, Pyle 1975, Sternburg et al. 1981, Waldbauer & Sternburg 1982). Most freshly emerged female saturniids do not fly at all until they have emitted pheromone and mated (Blest 1963, Nässig & Peigler 1984, Waldbauer & Sternburg 1979). Male sphingids and saturniids fly to virgin females before they fly to nearby electric lamps (Allen & Hodge 1955, Worth & Muller 1979, Janzen 1984). Almost all female *Cydia pomonella* collected at black lights have already mated (Gehring & Madsen 1963). Although more males than females typically fly to lamps, the capacity of males to mate with more than one female (Rau & Rau 1929, Allen & Hodge 1955, Lukefahr & Griffin 1957, Vail et al. 1968) may moderate the reproductive impact of disproportionate harm to males.

In contrast, electric lighting may have a major effect on mating in certain Noctuidae. *Heliothis zea* (Boddie) is an example. The peak time of night during which *H. zea* flies to light traps coincides with the period of copulation (Graham et al. 1964, Stewart et al. 1967). Only a third to a half of female *H. zea* collected at light sources have mated (Gentry et al. 1971, Vail et al. 1968). In the laboratory, *H. zea* will not mate unless its eyes are in a state of dark adaptation, as indicated by the presence of eye glow. Light intensity must be below 0.015 $\mu W/cm^2$, the intensity of light of a quarter-moon (Agee 1969). The suggestion is that *H. zea* females fly to light sources whose radiant energy suppresses mating.

A criticism of this scenario is that unmated *H. zea* females that fly to light may be migrating (Raulston et al. 1986) and therefore sexually immature (Johnson 1969). Female *H. zea* in the laboratory do not mate for 30–60 h after eclosion (Agee 1969). However, even if unmated females at lamps were sexually immature migrants, the lamps could disrupt reproductively important behavior, such as flight to locations where courtship and mating would be likely to occur. Furthermore, outdoor lighting may interfere with *H. zea* mating regardless of flight to light. Levels of light that suppress mating in the laboratory (Agee 1969) are well below ambient levels of light in electrically illuminated environments outdoors. Low levels of incandescent light (Nemec 1969) and moonlight (Nemec 1971) have influenced activities of *Heliothis* spp. in the field.

Other evidence suggests that lighting may interfere with mating. Unmated females of four other noctuid species fly to lamps (Vail et al. 1968). Male sphingids caught in light traps baited with virgin females do not seek out the females (Hoffman et al. 1966). In the laboratory, even dim electric light (0.3 lux) suppresses female *Trichoplusia ni* (Hbn.) (Noctuidae) pheromone release and male response to pheromone (Shorey & Gaston 1964, 1965, Sower et al. 1970). Electric light also suppresses female pheromone release and male response to pheromone in *Dioryctria abietivorella* (Grt.) (Pyralidae) (Fatzinger 1979). Mating by *Pectinophora gossypiella* requires a period of relative darkness lasting at least 7 h (Lukefahr & Griffin 1957).

Feeding

Moths may feed in illuminated environments. Sphingids and noctuids visit food sources in full view of electric lamps located sometimes less than a few meters away, or they fly to electric light sources after they have completed feeding (Bretherton 1954, Milyanovskii 1975, Mazokhin-Porshnyakov 1975, Janzen 1983, 1984). I have observed *Buddleja* (Gentianaceae) blossoms covered with noctuids at night (2300 h) virtually directly under a tungsten filament street lamp illuminating a heavily traveled road in Quisset, Massachusetts. Light from automobile headlamps and from a flashlight did not alter the moths' activities.

Electric lamps, however, may interfere with feeding. Orchard illumination has reduced the number of *Cydia pomonella* feeding at bait (Herms 1932). In Japan, orchard illumination has been used to protect fruit from damage by fruit-piercing noctuids (Nomura 1969). Light has disturbed nectaring sphingids (Brown 1976). Diversion of moths away from light may explain why lamps interfere with feeding. Suppression in feeding is moot for the large number of moth adults that never feed (Norris 1936).

Electric lighting theoretically could injure larval foodplants. Sodium vapor lighting may harm plants by disrupting photoperiodic regulation of growth and development (Sinnadurai 1981, Cathey & Campbell 1975, Shropshire 1977), but such effects are apparently greater indoors in greenhouses than outdoors on the street (Andresen 1978).

Time Keeping

Electric lighting can delay or advance vital activities of moths and their larvae, and these shifts could affect the insects as much as changes in the activities themselves (Beck 1980, Saunders 1982). This possibility has been the basis for proposals to exploit biological clocks for purposes of pest control (Barker et al. 1964, Nelson 1967). In a field trial, however, light exposure failed to prevent diapause in larvae of *Adoxophyes orana* (F.R.) (Tortricidae) (Berlinger & Ankersmit 1976). The trial suggests that it is easier to manipulate biological clocks indoors than outdoors where temperature and other factors cannot be controlled.

Biological clocks of flying insects, however, may be much more susceptible to outdoor electric lighting than those of larvae. This is because flight to light increases exposure to radiant energy. Exposure to a pulse of light lasting only 15 min is sufficient to attenuate a circadian rhythm in *Drosophila*; light 10^3 times more intense produces the same effect after only 10 sec; light 10^5 times more intense does it after an exposure of less than 0.1 sec (Chandrashekaran & Engelmann 1976). Energy for even a minute fraction of a second (photoflash) can disturb photoperiodic clocks in larvae of Lepidoptera (Barker et al. 1964). The anthropomorphic observation that quiescent moths adjacent to a lamp are "asleep because they think it is daytime" may be close to the truth.

Shifts in timing of nocturnal behavior of moths at lamps do not necessarily imply shifts in phase of endogenous rhythms. Changes in timing of behavior could represent other responses to light, or they could represent complex mixtures of responses. Regardless of these possibilities, magnitude and character of responses may vary according to when in the circadian cycle exposure to light occurs (Pittendrigh & Minis 1971, Skopik & Takeda 1980). Responses may also vary depending on spectral output of the lamp. For example, *Pectinophora gossypiella* has two light-sensitive clocks, only one of which responds to the 589 nm light emitted by low-pressure sodium lamps (Bruce & Minis 1969, Pittendrigh et al. 1970).

Theoretical Effects

To what extent nocturnal flight to light affects timing of nocturnal behavior has never been formally investigated. For example, if a moth flies to a light source, receives intense irradiation for 15 min, and flies away, how will its activities during the rest of the night be affected? If a male, will its mating period still coincide with that of females not exposed to light? If a female, will pheromone release still occur during the flight period of males? Shifts in mating times could cause sympatric, closely related species to attempt to mate with each other; such species normally do not mate with each other in part because their different mating periods keep them temporally segregated (Tuttle 1985).

Synchronization of activities with lunar rhythms may help moths navigate, mate, and avoid predators (Danthanarayana 1986). Lamps may disturb oviposition synchronized to lunar rhythms (Nemec 1969, 1971). To what extent moth activity synchronizes with lunar rhythms, and to what extent electric lighting may disturb such synchrony warrants investigation.

Predation

Bats, birds, skunks, toads, and spiders hunt moths flying to lamps (Stanley 1932, Thaxter 1957, Holzman 1961, Krivda 1980, Covell 1985, Brower 1986). Lamps increase predation by clumping prey, and directly exposing them to attack (Turnbull 1964). Concentrated experience with particular species may help birds learn to defeat defenses based on surprise, novelty, or deceit (Blest 1957, Wickler 1968, Coppinger 1970, Sargent 1973b, Pietrewicz & Kamil 1979). Lamps also can destroy defensive behavior, such as that required for crypsis (Sargent & Keiper 1969, Sargent 1973a, 1976). The outcome is exemplified by a dark, bark-colored moth conspicuously resting on a white wall near a lamp at dawn. Lamps may help birds learn to recognize unpalatable species, but moths unpalatable to some birds may be acceptable to others (Löhrl 1979). Lamps may enable different birds to pick and choose among different possible prey. Because moths often land before they arrive at lamps, lamps may provide predators with far more prey than one might expect from the moths immediately adjacent to the lamp (Hartstack et al. 1968).

Parasitoids of Lepidoptera fly to electric light sources (Collins & Nixon 1930, Cline et al. 1983). Electric lighting could reduce predation on Lepidoptera by suppressing populations of parasitoids (Worth & Muller 1979). It may divert parasitoids used for biological control of pest Lepidoptera in warehouses (Cline et al. 1983). Even brief exposure to intense sources of radiant energy (photoflash) may sterilize minute hymenopterous parasites which survive the radiation (Riordan 1964). Theoretically, lighting could affect secondary parasites, thus potentially disturbing the food chain at three levels, and producing changes in populations which would be difficult to predict (Frank 1986).

EFFECTS ON MOTH POPULATIONS

Evidence Against Effects

Migration and dispersal. Even though lamps may contribute to the destruction of vast numbers of moths, the impact on moth populations may be negligible. For example, more than 10000 *Autographa* (*Plusia*) *gamma* (L.) (Noctuidae) were collected in a light trap in one season in England (Robinson & Robinson 1950a). In England the population of *A. gamma* is maintained almost entirely by immigration in spring from southern Europe (Ford 1972). A particular light source in England should have a negligible influence on the breeding stock which annually replenishes the population of *A. gamma* around it. Seasonal movement of moths over long distances is not rare (Williams et al. 1942, Williams 1958, Johnson 1969, Ford 1972) and may be sustained by wind transporting moths at altitudes sometimes hundreds of meters above most electric light sources (Glick 1965, Mikkola 1986, Raulston et al. 1986, Wolf et al. 1986).

Failure to suppress agricultural pests and other species. One might expect that light traps could substantially reduce or eliminate some moth populations. However, elaborate efforts to exploit such traps for pest control have failed, and successes could not be consistently replicated (Cantelo 1974, Hienton 1974). The failure has been attributed to influx of moths from outlying areas, but light trapping may fail to control insect populations even on small islands. On St. Croix, United States Virgin Islands, 250 black-light traps were deployed during a period of 43 months. The island is 208 km^2 in area. Although decreases in light-trap collections suggested that traps were depleting the island's sphingids (Cantelo et al. 1972a, 1972b), other studies using the same traps at the same time found similar decreases in collections of *Heliothis zea* even though traps collected only a minute fraction of the island's *H. zea* population (Cantelo et al. 1973, 1974, Snow et al. 1969). Furthermore, light-trap collections of sphingids were beginning to increase at the time the study was terminated. Meteorologic and density-dependent ecological forces may determine the size of moth populations exposed to lighting, even on isolated islands.

Failure of light traps to reduce insect populations extends beyond species of agricultural interest. Williams (1939) examined 150 species of Noctuidae and Geometridae collected in his stationary light trap during a 4-year period in Rothamsted. Comparison of numbers of individuals of each species collected from year to year provided no evidence of any consistent declines in populations, except possibly in the case of one geometrid. More recent observations at Rothamsted extended Williams' studies. Taylor et al. (1978) tabulated annual number of species and number of specimens of each trapped at Rothamsted from 1966 to 1975, and also calculated an index of diversity for each year. No downward trends are apparent, despite wide fluctuations from year to year.

Prevalence of urban moths. The above studies did not simulate urban conditions where lighting is dense and widespread. However, large numbers of species have been collected in urban areas in Britain and the United States (Langmaid 1959, Lutz 1941). Collections based on a nationwide network of 172 light traps in Britain suggest that moth populations in areas undergoing urban changes can substantially recover despite electric lighting (Taylor et al. 1978). In North America, some saturniid species not only tolerate urban lighting but may actually thrive better in urban than in rural habitats. *Hyalophora cecropia* and *Samia cynthia* are two examples. The ecology of both species is complex, and numerous factors other than lighting can account for changes in their abundance in illuminated environments (Sternburg et al. 1981, Frank 1986). In New England, eight species of *Catocala* (Noctuidae) thrive in illuminated urban or suburban areas. Seven of these species can be found within a mile of downtown New Haven, and one occurs in downtown Boston. Several depend almost entirely on urban-suburban shade trees (D. F. Schweitzer pers. comm.).

Extinctions unrelated to lighting. Most declines and extinctions in moth populations can be linked to specific circumstances unrelated to lighting (Bretherton 1951, Ford 1972, Heath 1974). These include deforestation, agriculture, and draining of fens. Destruction of habitats as a cause of widespread declines in Lepidoptera populations has been described in detail for European butterflies (Kudrna 1986). In Britain, many species of moths became scarce around the middle of the last century, but after World War I the situation reversed, probably because of favorable climatic changes (Heath 1974). Declines in numbers of *Malacosoma americanum* (F.) (Lasiocampidae) in Winnipeg, Manitoba, have been attributed to English sparrows (*Passer domesticus* L., Passeridae) eating the moths at lamps (Krivda 1980), but *M. americanum* populations fluctuate at intervals independent of changes in lighting. Interval duration is about 10 years (Johnson & Lyon 1976). Attacks by microbial and parasitic agents probably account for periodic reductions in populations of this species (Lutz 1941).

Saturniid populations in the northeastern United States declined in the 1950's. This observation is supported by dates of last capture for species represented in regional collections, and by surveys of collectors (Ferguson 1971, Hessel 1976, D. F. Schweitzer pers. comm.). Populations of some saturniid species have since shown signs of recovery, whereas other saturniids, especially the two *Citheronia* species native to the area, have failed to recover in several states (D. F. Schweitzer pers. comm.). Declines that occurred in the 1950's coincided with widespread aerial spraying against gypsy moth, and recoveries coincided with drastic curtailment of this spraying (D. F. Schweitzer pers. comm., Gerardi & Grimm 1979). Whether pesticides can account for changes in saturniid populations is unclear. However, changes in populations of saturniids as a group correlate poorly with changes in outdoor lighting.

Evidence for Effects

Small colonies exposed to lighting. Evidence that outdoor electric lighting has the capacity to affect populations of moths is illustrated by

Hydraecia petasitis Doubleday (Noctuidae) in Finland. Only three or four isolated colonies are known to exist in the country. The isolation is not due to urbanization but rather to the fact that the species in Finland is at the extreme tip of its range. Two small colonies were studied, one covering 700 m^2, the other 800 m^2. A mark-recapture experiment conducted during 48 days in one colony demonstrated that a trap equipped with an 80-watt mercury lamp captured 53% of males in the colony and 30% of females at least once. The colony was estimated to consist of 218 individuals. These and other observations suggest that continuous light trapping could destroy this population. The authors point out that this species is only mildly attracted to light, and that the effect of light trapping might be more severe for other Lepidoptera (Väisänen & Hublin 1983). The number of moths the authors trapped probably underestimated the number that flew to the lamps (Hartstack et al. 1968).

The Finnish light-trap study demonstrates that a substantial proportion of individual moths within a geographically small colony may fly to an electric lamp. It is conceivable that disturbances in oviposition, mating, feeding, vision, navigation, dispersal, crypsis, circadian rhythms or photoperiodism would be sufficient to disrupt an already shaky population or to impede establishment of a new one. Disruptive effects would be even greater when caused by lamps in special conditions. These include lamps in traps equipped with electrocuting grids ("bug zappers") and lamps near bird feeders and bird houses. Lamps may incinerate or desiccate moths trapped inside poorly constructed or broken luminaires. Lamps near hostplants may disturb females attracted to the plants, or they may disturb males attracted to the females. Lamps in open garages and pavilions may direct moths into areas from which they cannot escape. Automobile headlamps and streetlamps divert moths into the paths of moving vehicles.

Urbanization and fragmentation of habitats. The same urban changes that increase outdoor electric lighting also tend to fragment habitats (MacArthur & Wilson 1967). The result is creation of small colonies exposed to electric illumination. Man has made many species of British moths in effect relict faunas, remnants of a bygone era when their habitats were much more widespread (Bretherton 1951, Ford 1972). Three species of noctuids once plentiful in southern California have been reduced to small, isolated colonies, in one instance in the vicinity of the Los Angeles International Airport (Hessel 1976). Urban gardens and parks now function as important faunal reservoirs (Frankie & Ehler 1978, Davis 1978, 1982, Owen 1978, Schaefer 1982). Urbanization increases both vulnerability and exposure of moth populations to lamps.

Lighting as a selective force. Outdoor lighting may act as a selective force against particular individuals within a population. For example, it may select against individuals that tend most strongly to exhibit flight-to-light behavior. In the Finnish light-trap study, such individuals would include those that flew into traps most frequently. Industrial melanism demonstrates that urban change may cause evolutionary change in populations of moths, and that disturbances in crypsis can generate the selective forces needed to produce such evolution (Kettlewell 1973, Cook et al. 1986). Electric lighting disturbs crypsis, but also a multitude of other functions. That some species of noctuids and other nocturnal moths do not fly to nearby light sources, or do so only rarely (Bretherton 1954, Taylor & Carter 1961, Janzen 1983), suggests that evolutionary modification of flight-to-light behavior has already occurred, although the causes are unknown.

Responses to selective pressures produced by lighting may be diverse. For species active at dusk, natural selection could favor individuals that fly at the beginning of the population's flight period, rather than at the end when flight to light occurs. The evolutionary response would be a shift in flight period rather than a specific change in flight-to-light behavior. Biological clocks are in part genetically controlled, and clock mutants affecting time of eclosion and locomotor activity have been identified in *Drosophila* (Konopka & Benzer 1971, Yu et al. 1987). In moths, different races or strains of a single species exhibit different photoperiodic behavior (Gardiner 1982, Ankersmit & Adkisson 1967), and selective pressures can account for such differences (Tauber & Tauber 1978, Hoy 1978, Waldbauer 1978). On the other hand, advancing or delaying flight times could disturb species segregation mediated through allochronic flight periods (Tuttle 1985), or it could expose moths to increased predation by birds or bats that fly only at certain times. Any evolutionary response to selective pressures generated by electric lighting would have to represent a net response to opposing selective pressures.

The diversity of moth behavior around lamps suggests a multitude of possible mechanisms for reducing adverse effects of electric light. The degree to which moths of different species fly to lamps may depend on the degree to which they respond to alternative navigational cues that compete with the lamps (Janzen 1984). Suppression of flight-to-light behavior could take the form of increasing responsiveness to competing stimuli such as olfactory, geomagnetic, aerodynamic, gravitational and inertial cues, plus alternative visual cues (Baker & Kuenen 1982, Baker & Mather 1982, Schöne 1984, Janzen 1984, Riley & Reynolds 1986). Within a population of moths, variation exists not only in tendency of different individuals to fly to light, but also in tendency to linger at the light or fly past it. Variation may also exist in tendencies to avoid lamps or oviposit near them. Evolutionary changes in response to electric lighting may be complex.

Forces opposing evolutionary reduction of flight-to-light behavior, however, are difficult to understand and assess in individual cases. Studies have employed suction traps to measure aerial densities of moth populations and at the same time light traps to measure flight to light. These studies suggest that *Xestia* (*Amathes*) *c-nigrum* (L.) (Noctuidae) is 5000 times as likely to fly to light as *Amphipyra tragopoginis* (Cl.) (Noctuidae) (Taylor & Carter 1961). Why these two noctuids behave so differently around lamps is a mystery. Failure to evolve seemingly advantageous adaptations has been well described in Lepidoptera (Ehrlich 1984). Populations of moths may resist strong selective pressures to evolve defenses against adverse effects of electric light.

Fewer moths at urban lamps. Evolutionary changes in wing coloration can be documented by inspection of collections of moths obtained over a period of time (Kettlewell 1973). Evolutionary changes in flight-to-light behavior cannot be documented in this way. Observations a century ago, however, are worth noting. Riley (1892: 51) advises collectors where to look for moths: ". . . nowadays the electric lights in all large cities furnish the best collecting places, and hundreds of species may be taken in almost any desired quantity." Denton (1900:35) was more explicit:

> While employed in Washington, D.C., I made a splendid collection of the moths of that region simply by going the rounds of a number of electric lights every evening. The lamps about the Treasury Building were sometimes very productive of fine specimens and the broad stone steps and pillars were frequently littered with moths, May flies beetles, etc., where one could stand and pick out his desiderata with little difficulty. I captured several of the Regal Walnut moths (*Citheronia regalis*) and a number of our largest and handsomest sphinxes. Besides making the acquaintance of a number of insects new to me, I met several entomologists who, like myself, had been attracted to the lights by the abundance of specimens.

Today lamps in big cities such as Washington, D.C., Philadelphia, and Boston rank among the worst places to collect moths or meet entomologists. Reductions in numbers of moths flying to lamps have been noted in other locations (Hessel 1976, Muller 1979, Janzen 1983). Decreases in moths at urban lamps can be explained by many factors, including declines in moth populations, dilution of moths among thousands of city light sources, and suppression of flight-to-light behavior as a result of diffuse background light. However, reductions in numbers of moths flying to urban lamps are what one would expect if urban moths today were genetically less inclined to fly to lamps than were those a century ago.

In densely illuminated urban environments, lighting may have favored species that either fly during the day, do not fly to lamps, or do not fly at all. Urban pests exemplify such species. These include sesiids (Engelhardt 1946) and domestic tineids (Ebeling 1978). Species with flightless females include the bagworm moth, *Thyridopteryx ephemeraeformis* (Haw.) (Psychidae), gypsy moth, *Lymantria dispar* (L.), (Lymantriidae), white-marked tussock moth, *Orgyia leucostigma* (J. E. Smith) (Lymantriidae), and fall cankerworm, *Alsophila pometaria* (Harris) (Geometridae) (Lutz 1941, Drooz 1985). The two urban saturniids, *Hyalophora cecropia* and *Samia cynthia,* do not commonly fly to urban light sources (G. P. Waldbauer pers. comm., Covell 1984). The extent to which lighting may have influenced the kinds of moths inhabiting densely illuminated urban environments is unclear.

METHODS TO REDUCE DISTURBANCES

Low-pressure sodium lamps may be used to reduce disturbances caused by lighting. Low-pressure sodium lamps elicit flight-to-light behavior less frequently than do other lamps (Robinson 1952). They do not disturb certain circadian rhythms of Lepidoptera and other insects (Frank & Zimmerman 1969, Bruce & Minis 1969, Pittendrigh et al. 1970, Truman 1976). The low-pressure sodium lamp radiates less energy than does any other kind of lamp of equal illuminance (Finch 1978).

A variety of measures may protect moths from adverse effects of outdoor lighting. Lamp-free reserves such as sheltered hollows shielded from lighting have been suggested to save the glow worm, *Lampyris noctiluca* L. (Coleoptera: Lampyridae), a species whose survival in Britain may be threatened by outdoor lighting (Crowson 1981). To reduce lighting impact in habitats already exposed to lamps, the most effective action is to turn off the lamps. Low-pressure sodium lamps may replace other lamps when illumination is essential. Filters to block ultraviolet light may be installed over mercury vapor lamps, and shields may be placed around lamps to block stray light. Low-watt orange-colored incandescent lamps ("bug lights") may replace ordinary incandescent lamps, but some moths fly to these lamps. Bird feeders may be removed from windowsills, lampposts, and other sites close to light sources. "Bug zappers" should be turned off. Natural light-traps such as open garages may be closed to prevent entry of insects. Operators of nearby commercial light sources such as illuminated billboards may be contacted and invited to save money and moths by turning lamps off during those hours of night and early morning when billboards are rarely seen.

Although the feasibility of such changes may be questioned, several North American cities have taken similar steps to reduce light pollution. Light pollution interferes with astronomical work at observatories (Hendry 1984). These cities have converted streetlamps to low-pressure sodium, required ultraviolet-blocking filters over mercury lamps, imposed curfews on the use of commercial lighting, and mandated shielding of luminaires (Hendry 1984). Low-pressure sodium lighting, however, has provoked political controversy on aesthetic and other grounds (San Jose Committee of the Whole 1980).

CONCLUSION

Effects of outdoor lighting may be divergent. They vary according to species, lamps, and habitats. Improved levels of illumination may increase nocturnal vision, but creation of visual artifacts may disturb vision. Increased numbers of lamps may promote flight-to-light behavior, but high levels of background light may suppress this behavior. Expansion of streetlighting may increase flight to streetlamps, but shifts from mercury to sodium lamps may decrease it. Diversion of moths to lamps may increase numbers of moths in illuminated areas, but diversion of moths away from lamps may decrease numbers. Lamps may suppress oviposition in the laboratory, but oviposition may increase or decrease near lamps in the field. Clumping of moths near lamps may increase predation by birds and bats, but destruction of parasitic wasps and flies at lamps may decrease predation. Disturbances such as habitat destruction and urbanization may further confound effects of outdoor lighting.

Several conclusions emerge from the observations on lighting. Outdoor lighting may destroy vast numbers of individual moths without apparently suppressing populations of moths. However, it disturbs some populations more than others, and it disturbs some individuals more than others in the same population. It generates selective pressures favoring adaptations for protection against adverse effects of lamps. The result may be evolutionary changes in behavior, or changes in the kinds of moths inhabiting illuminated environments. These changes may increase through time as urban expansion fragments habitats and exposes smaller moth populations to electric illumination.

Conservation efforts need to consider adverse effects of outdoor lighting. If one wishes to protect Lepidoptera in small, endangered habitats exposed to outdoor lighting, reducing or changing exposure may be helpful. In such habitats light traps including "bug zappers" may deplete populations of moths. Some cities have attempted to reduce light pollution to protect astronomical observatories. Whether similar large-scale restrictions on lighting might help to conserve Lepidoptera has yet to be demonstrated.

Future research could help clarify lighting impact. Despite abundant evidence that outdoor lighting affects individual moths, few studies have attempted to quantify lighting effects on moth populations. Evidence that lighting has suppressed populations of particular moths such as saturniids is weak. Studies similar to those on the effects of illumination of orchards and cotton fields (Herms 1929, 1932, Nomura 1969, Nemec 1969) could be extended to other settings and species. Faunal surveys, life history studies, and ecological studies could examine Lepidoptera in differently illuminated environments. Behavioral and physiological studies could investigate the possible evolution of tolerance to adverse effects of lighting. The method might include comparison of Lepidoptera sampled from large geographic regions that possess different levels or kinds of outdoor illumination.

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HYBRIDIZATION BETWEEN TWO SPECIES OF SWALLOWTAILS, MEIOSIS MECHANISM, AND THE GENESIS OF GYNANDROMORPHS

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ABSTRACT. Hybridization between *Papilio machaon* L. and *P. polyxenes asterius* Stoll was carried out over four generations by backcrossing black female F_1 and further hybrids with wild *machaon* males. A bilateral gynandromorph (symmetrical mosaic for the black-yellow phenotype) was obtained. In the fourth generation, one brood from a single female had negligible mortality but yielded an abnormal sex ratio opposite that predicted by Haldane's Rule (45 males/86 females, ca. 1:2). The black-yellow character followed a perfect 1:1 segregation. Reexamination of previous data suggests that meiosis in Lepidoptera follows an unusual pattern: the sister chromatids segregate during the first division, and crossing over is frequently absent in females. Bilateral gynandromorphs are generally due to fertilization of binucleate oocytes. Segregation during the first meiotic division also can explain the patterns of gynandromorphs arising as autosomal mosaics, such as those described here.

Additional key words: *Papilio machaon*, *P. polyxenes asterius*, Papilionidae, sex ratio.

Hybridization between *Papilio machaon* L. from Europe and Japan and *P. polyxenes asterius* Stoll from the United States was first undertaken more than 20 years ago (Clarke & Sheppard 1953, 1955, Ae 1966). Commercial availability of pupae of both species has allowed many breeders to easily carry out this cross since then. We recently performed such crosses, and our results are peculiar. Moreover, a spectacular gynandromorph emerged from one of our broods, and we compare this specimen with other examples recently described by Clarke and Clarke (1983).

MATERIALS AND METHODS

Papilio polyxenes asterius stocks were established from diapausing pupae obtained from Chicago, Cook Co., Illinois, and we obtained *P. machaon* from Cahors, Lot, France. The insects were hand-paired using the technique of Clarke (1952). Mated females were fed with a honey-water mixture (1:10), and allowed to oviposit in a gauze cage on carrot (*Daucus*) leaves. Either sunshine or light of a 60 W bulb at a distance of 20 cm was used to activate the insect. Number of ova laid per female

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was between 50 and 100, sometimes more. Larvae were reared on carrot leaves, or occasionally on other Umbelliferae. While no pathology was noticed in former broods, it has inhibited breeding in recent years. This fact may be related to extensive use in our neighborhood of the insecticide "Bactospéine", which contains strains of *Bacillus thuringiensis* Berl. Many diseased pupae and adults showed teratological atrophies comparable to those induced by toxin of this bacterium (Burgerjon & Biache 1967). Similar abnormalities also have been observed in pure strains of *Papilio polyxenes asterius* bred in the United States (Carter & Feeny 1985).

We encountered difficulties obtaining functional males in our breeding stocks, even among non-hybrids. Thus, hybrid females were always used, while the males were pure *machaon* from wild stocks. Crosses were performed over four generations.

RESULTS

Several broods comprised the F_1 generation (♀ *asterius* × ♂ *machaon*), and gave the same results as those of Clarke and Sheppard's (1953, 1956) experiments: each offspring was as melanic as *asterius* and the anal eye-spot was intermediate. F_2 backcrosses (♀ F_1 × ♂ *machaon*) gave the expected 1:1 segregation between "black" and "yellow". In one brood, a remarkable gynandromorph was obtained (Figs. 1, 2). It is bilateral, with all of the left side being female with a "black" phenotype, and the eye-spot very close to *machaon*. The underside, although melanic, shows a strong *machaon* influence in distal parts of the wing. These features are characteristic of this kind of backcross. Markedly smaller, the right side is mainly male, and extremely *machaon*-like. However, on the hindwing, a melanic patch is present in the anal part. Its shape is complex, and its anterior border coincides with a compartment limit (Sibatani 1983) in the middle of the cell. The body is conspicuously halved in "black" and "yellow".

The third and fourth generations were obtained by pairing melanic females from the previous backcross with wild male *machaon*. As noted by Clarke and Sheppard (1956), fertility gradually increased. In the fourth generation, we were fortunate to obtain a large, healthy brood from a single female: 131 adults from 135 ova. Among them, 65 were of the "yellow" phenotype (18 males, 48 females) and 66 of the "black" (27 males, 38 females). Therefore, if the "yellow"/"black" ratio of 65/66 is truly 1:1, the sex ratio is strongly distorted (45/86, $\chi^2 = 12.83$, $P < 0.001$). The latter proportion is close to a 1:2 ratio. The cross presents another intriguing feature: the excess of females is more marked in the "yellow" phenotype than in the "black", where it does not even reach a significant level (27/38, $\chi^2 = 1.86$, $P < 0.2$). Analysis of these data

FIGS. 1, 2. *P. machaon* × *P. polyxenes asterias* F_2 hybrid, bipartite mosaic and gynandromorph. **1,** Dorsal surface; **2,** Ventral surface. Shown at ⅔ natural size.

through a contingency table indicates that this abnormality of distribution is on the borderline of significance ($\chi^2 = 2.955$, $0.10 > P > 0.05$).

A second gynandromorph arose in another brood of the fourth generation; it is a "mosaic", with the same "black" phenotype throughout. Gynandromorphism is apparent only in the parts where the male differs from the female. This specimen resembles closely those described by Clarke et al. (1977). No element of symmetry could be observed in this individual.

DISCUSSION

Some gynandromorphs of *Papilio* have already been described. A discussion once arose in the *News of the Lepidopterists' Society* about interpretation of gynandromorphs of *Papilio glaucus* L. (Walsten 1977, Silberglied 1977); a reanalysis of these examples was provided by Clarke and Clarke (1983). We next review some problems raised by sex genetics and the origin of gynandromorphs in Lepidoptera.

Morgan and Bridges (1919) showed that, in *Drosophila,* gynandromorphism is due to an irregular disjunction of sex chromosomes, leading to the loss of an "X" in one of the daughter cells. So, one-half of the organism would bear an "XX" set and would be female, and the other an "XO" and would be male (the Y chromosome is considered to bear very little information in this insect). In only one case in Lepidoptera has this mechanism been conclusively demonstrated, in the moth *Abraxas grossulariata* (Morgan & Bridges 1919), but Clarke and Clarke (1983) consider it a very likely explanation in some other cases. In most other examples, another mechanism seems to be involved: fertilization of a binucleate oocyte, as explained by Goldschmidt (1931). During meiosis,

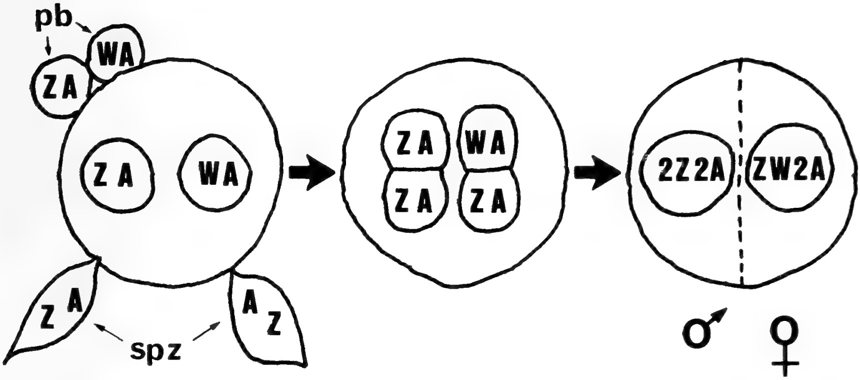

FIG. 3. Schematic presentation of the mechanism producing gynandromorphs from a binucleate oocyte. Z, W: sex chromosomes; A: autosomal stock. pb: polar bodies from the former division; spz: the two spermatozoa which will fertilize both female pronuclei.

the two successive divisions lead to four haploid nuclei. Normally, three of them are eliminated. In some cases, which appear to be scarce, but whose frequency may be increased by certain mutations, two nuclei remain in the central zone of the oocyte, and both become fertilized. There follows a juxtaposition of the two eggs, which may have a genetic composition as different as any combination of two brothers and sisters. Figure 3 illustrates this phenomenon; we use "Z" and "W" for heterochromosomes, ZZ being male and ZW female. This phenomenon has been observed and photographed by Goldschmidt and Katsuki (1927).

As Robinson (1971) pointed out, this mechanism raises problems related to chromosome segregation in meiosis. Meiosis may proceed in two ways:

1) Sister chromatids issuing from the same single parental one may separate in the first mitosis of meiosis; the second mitosis therefore dissociates mother- and father-issuing homologous chromosomes.

2) The first mitosis separates mother- and father-issuing sets of chromosomes, and the second one, the sister chromatids.

The second way is considered normal in animals and plants. Of course, division of the centromere is expected to play a key role in this phenomenon. Actually, it is very difficult to observe the process cytologically and to demonstrate it genetically. It is only in oocytes that daughter cells undergo such a dissimilar fate.

The study of gynandromorphs and mosaics originating from binucleate oocytes may provide a clue to the precise order of chromatid segregation. When such abnormalities arise, they are most likely due to the two pronuclei issuing from the second mitosis remaining in the middle of the oocyte. Gynandromorphs and bipartite mosaics can arise only if chromosome sets present in each symmetrical fertile pronuclei are genetically different. This implies that meiosis follows the first way above.

Cockayne (1935) clearly showed that there are two types of respective segregation in autosomes and sex chromosomes. 1) In *Bombyx mori*, gynandromorphs and uni- or bisexual mosaics are observed with the same frequency (Goldschmidt & Katsuki 1927). This shows that the two fertile pronuclei may either be both "Z" or both "W", or one "Z" and one "W", and it means that the chromosomes are segregating at random, likely due to an achiasmatic meiosis. 2) In *Argynnis paphia*, Goldschmidt and Fischer (1927) studied a strain where gynandromorphism occurred regularly, probably because of a mutation producing abnormal meiosis. In some cases, the autosomal and sex-conditioned mutant "*valesina*" was involved in the crosses. In contrast with *Bombyx*, "*valesina*"-normal mosaics are only observed when there is also gynandromorphism, and no unisexual mosaic occurs in this strain. The unambiguous conclusion (not stated by Goldschmidt and Fischer or Cockayne) is that always, when a binucleate oocyte is formed, one pronucleus bears a "Z" and the other a "W"—a strong argument in favor of meiosis with preliminary separation of sister chromatids. In the sphingid *Laothoe populi*, and in many other instances, things appear identical. An illustrative example was recently provided by Platt (1983), in artificial hybrids of *Limenitis arthemis* and *L. lorquini*; he also interpreted the bipartite mosaic-gynandromorph he obtained by the "double egg" theory. However, we are reminded of a halved "*alba*"-orange female of *Colias croceus* figured by Frohawk (1938); since various kinds of gynandromorphs have been described in this species (including "*alba*" female-orange male), this case might rather correspond to the silkworm type; however, mosaics may arise from various causes and, isolated, this record remains inconclusive.

Previous paragraphs deal only with bipartite gynandromorphs and mosaics; however, most sexual mosaics are asymmetrical, which can be explained in two ways: either, in the case of binucleate oocytes, one pronucleus becomes shifted from the central region of the oocyte, or sex chromosomes segregate abnormally during further division of embryonic cells. This latter event most likely explains the minute patches which characterize the bulk of so-called gynandromorphs.

The first gynandromorph described in this study fits perfectly with the double-oocyte theory, and supports the assumption that meiosis obeys the first-named way in *Papilio*. In the double oocyte that gave rise to this individual, the left pronucleus was "W" and "black" and the right one "Z" and "yellow" (Fig. 4). The only puzzling point comes

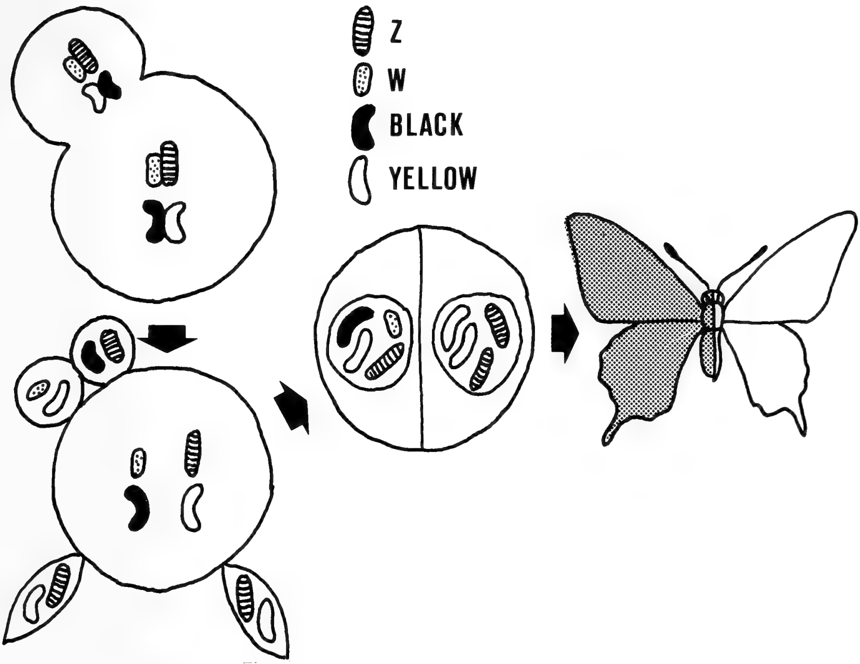

FIG. 4. Scheme of the mechanism leading to the gynandromorph of Figs. 1, 2. Only the color character-bearing autosome pair is figured.

from the small melanic patch on the right hindwing. It is inadmissible that it arose from a chromosome loss, since "black" is dominant and could not be present in the genetic stock of the right half. Thus it should be due either to presence of an uneliminated third pronucleus, remnant from the first division of meiosis, or to an erratic cell coming from the left half. The second gynandromorph may be best explained by an atypical segregation of sex chromosomes during embryogenesis. If it arose from a binucleate oocyte, this would imply that achiasmatic meiosis could occur in *Papilio* as in *Bombyx*.

According to Suomalainen (1965), the first-named type of meiosis is determined by the holocentric nature of centromeres, which he has indeed observed in Lepidoptera; he states also that, in this order, no crossing over occurs in the female sex. These assumptions have suffered controversy from Robinson (1971) and White (1973) as remaining undemonstrated in the whole of Lepidoptera, but they have been firmly ascertained for some species, such as *Bombyx mori* (Tazima 1964), *Heliconius* (Turner & Sheppard 1975), *Anagasta kuehniella* (Traut 1977).

The abnormal sex ratio observed in one brood of the fourth generation (which is corroborated by other less quantitative observations made at the same time) is most difficult to interpret. We have no definitive explanation to propose; we only offer remarks that may help future investigations. The distortion goes against Haldane's (1922) Rule. Here, it is the heterogametic sex that is favored; the ♂/♀ ratio is close to 1:2. It is not possible to explain this discrepancy by the death of one-half of the males, since the mortality from egg to adult was very low. We must invoke a possible abnormality during meiosis.

A non-disjunction of "Z" chromosomes during oogenesis could produce a sex ratio distortion in the direction observed. It should give rise to a proportion of 2 (W, A) oocytes, 1 (ZZ, A) and 1 (O, A). Hence, following fertilization, we should have 1/2 ZW, 2A normal females, 1/4 ZO, 2A females (such a formula is usually considered to correspond to females) and 1/4 ZZZ, 2A males. But should the two latter types of individuals display a viable phenotype? We could not detect any abnormality in offspring of the concerned brood. Moreover, if generalized, this mechanism should give rise to 3/4 females, while we observed 45/86 ($\chi^2 = 6.5$, $P < 0.01$); therefore, non-segregation acted only partially.

Meiotic drive is another phenomenon which could lead to sex ratio distortion. This is a preferential segregation of certain chromosomes in functional gametes (detailed review in Zimmering et al. 1970). Recent data indicate that this phenomenon is rather widespread, and involves a higher frequency sex and "B" (heterochromatine) chromosomes. Sex chromosomes differ in both of our species by a heterochromatic segment present only in *machaon*. Moreover, the "W" from *asterius* does not pair perfectly with the "Z" from either species (Clarke et al. 1977). Do these peculiarities trigger meiotic drive preferentially directing the "Z" towards a polar body? Such a phenomenon would produce normal karyotypes; being unaware of the problem, we did not check karyotypes.

Moreover, we should consider that sex ratio distortion perhaps affects the "yellow" phenotype somewhat more; this could mean that there is "attraction" between the *asterius*-originated "W" and the color-controlling autosome which comes from *machaon*. One possible explanation is that these two chromosomes possess certain sequences in common, and that they could pair, at least partly, during meiotic prophase. This should obviously affect further segregation, the color-bearing autosomes being the "drivers", as is indicated by their overall 1:1 proportion. Both species should therefore differ by a translocation between sex chromosomes and color-bearing autosomes. This hypothesis is not as fancy as it may appear at first sight, since in related American species such as *Papilio glaucus*, the color-controlling segment itself is carried on the "W" chromosome (Clarke & Clarke 1983).

CONCLUSION

Reexamination of previous data and analysis of the experiments presented here allow us to conclude that:

1) In butterflies, at least in the vast majority, meiosis obeys a rather unusual pattern where chromatid segregation follows an order opposite the normal one. This is also probably true for moths (the Silkworm case being the most extreme, since in its meiosis it is achiasmatic).

2) Bilateral gynandromorphs arise most often from fertilization of a double oocyte. The determinism of mosaic gynandromorphs is more complex and may result from completely different causes.

3) In *Papilio,* one can carry interspecific crosses over a large number of generations by using backcrosses, in a kind of "monitored introgression".

4) Even in *Papilio,* however, a residual amount of genetic incompatibility occurs. Sex chromosomes are the most sensitive to disturbances resulting from this incompatibility.

We surmise that some kind of abnormal chromosome segregation takes place in interspecific crosses, and we hope our findings will stimulate further research on these questions.

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EXTERNAL GENITALIC MORPHOLOGY AND COPULATORY MECHANISM OF *CYANOTRICHA NECYRIA* (FELDER) (DIOPTIDAE)

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ABSTRACT. External genitalia of *Cyanotricha necyria* (Felder) exhibit characters that occur in the Notodontidae and Dioptidae. These provide further evidence that the two groups are closely related. Dissection of two *C. necyria* pairs *in copulo* revealed two features unique among copulatory mechanisms described in Lepidoptera. First, only the male vesica, rather than the aedoeagus and vesica, are inserted into the female. Secondly, during copulation the female is pulled into the male abdomen, and his eighth segment applies dorsoventral pressure on the female's seventh abdominal segment. This mechanism is facilitated by a long membrane between the male eighth and ninth abdominal segments. The first trait is probably restricted to only some dioptid species, while the second may represent a synapomorphy for a larger group that would include all dioptids, and all or some notodontids.

Additional key words: Noctuoidea, Notodontidae, Josiinae, functional morphology.

Genitalic structure has been one of the most important sources of character information in Lepidoptera systematics. Taxonomists often use differences in genitalic morphology to separate species, and homologous similarities have provided characters for defining higher categories in Lepidoptera classification (Mehta 1933, Mutuura 1972, Dugdale 1974, Common 1975). Unfortunately, we know little concerning functional morphology of genitalia. A knowledge of function may aid in determining homology of genitalic structures, something that has proved to be extremely difficult and controversial. In addition, a functional approach can provide important new characters for understanding phylogenetic relations. For example, Stekolnikov and Kuznetsov (1982) used functional morphology of male genitalia to provide characters for higher classification of ennomine geometrids, and Stekolnikov (1967a) contributed new data concerning familial relations among butterflies. In this paper I describe the external genitalia and mechanism of copulation in a dioptid moth, *Cyanotricha necyria* (Felder).

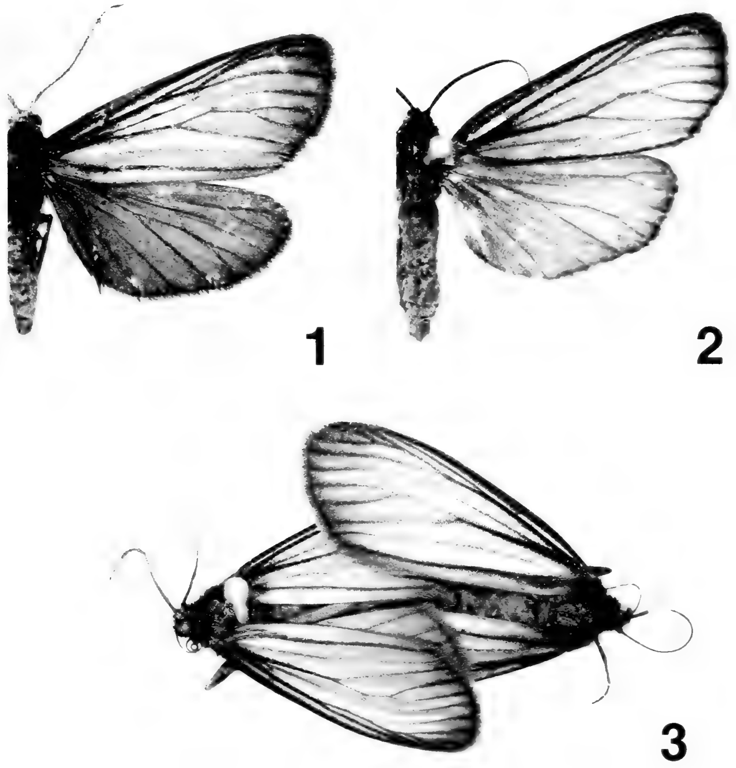
Forbes (1939) was among the first to examine musculature of male genitalia in Lepidoptera, and his study provided the basis for subsequent research (Birket-Smith 1974). Several workers have described musculature of male and female butterfly genitalia (Shirozu & Yamamoto 1953, Hannemann 1954a, 1954b; Ehrlich & Davidson 1961, Stekolnikov 1967a), while there have been fewer such studies on moths (Hannemann 1957, Stekolnikov 1967b).

Studies of copulatory mechanisms in Lepidoptera are rare. Perhaps the first was that of Chapman (1916a, 1916b), who attempted to determine the mechanism of copulation in lycaenids. However, he was unable to adequately preserve specimens *in copulo*. Arnold and Fischer (1977) analyzed genitalic muscle attachments and the method of copulation in three *Speyeria* species (Nymphalidae), and De Jong (1978) described the copulatory mechanism in *Carcharodus boeticus* Reverdin (Hesperiidae). Stekolnikov (1965) compared copulatory mechanisms of four moth species, *Spilosoma menthastri* Esper (Arctiidae), *Acronicta rumicis* L. (Noctuidae), *Antheraea pernyi* Guérin (Saturniidae), and *Dendrolimus pini* L. (Lasiocampidae). In a remarkable series of papers, Callahan (1958, 1960), Callahan and Chapin (1960), and Callahan and Cascio (1963) presented a detailed analysis of copulation, spermatophore production, and egg formation in Noctuidae. They examined 11 noctuid species, including *Helicoverpa zea* (Boddie), *Pseudaletia unipuncta* (Haworth), *Peridroma saucia* (Hübner), and 8 members of Plusiinae. Their methods included serial dissection of moth pairs at various stages during copulation.

The study described here is the first on moths related to notodontids, and illustrates some unique features concerning their genitalia and mechanism of copulation. *Cyanotricha necyria* is a member of Dioptidae, a group comprising approximately 400 species of diurnal, Neotropical moths (Bryk 1930, Hering 1925). Although it is acknowledged that they are closely related to Notodontidae (Franclemont 1970), their precise phylogenetic position remains unresolved; the group may ultimately be reclassified as a notodontid tribe (Minet 1983, Miller 1987, S. Weller unpubl.). The genus *Cyanotricha* Prout, which contains only two species, *C. necyria* and *C. bellona* (Druce), was placed by Kiriakoff (1950) in the dioptid subfamily Josiinae, a well-defined monophyletic group of approximately 100 species (J. Miller unpubl.). *Cyanotricha necyria* (Figs. 1 & 2) is an iridescent blue-green moth with an orange-brown dash at the forewing base between veins Sc and Rs, and a forewing length between 15 and 18 mm. It is found from central Peru N to southern Colombia, whereas the other *Cyanotricha* species, *C. bellona*, which is less common in museum collections, has been recorded only in central Peru at elevations up to 4200 m. Like many other members of Josiinae, *C. necyria* larvae feed on *Passiflora* (Passifloraceae), and the moth is currently being tested as an agent to control the spread of *P. mollissima* (HBK) Bailey, a forest weed in Hawaii (Markin et al. in press).

METHODS

Two pairs of pinned *Cyanotricha necyria*, preserved *in copulo*, were found in the collection at the United States National Museum. Each



FIGS. 1–3. *Cyanotricha necyria* (Felder) in dorsal view. **1,** Male; **2,** Female; **3,** *In copulo,* male at left.

had been prepared by putting a pin through the male thorax, and the wings of the male and female had been left folded (Fig. 3). According to label data, both pairs were from the Dognin collection and had been collected in the "Environs de Loja", Ecuador, by Abbé Gaujon, one pair in 1885 and the other in 1886.

For both pairs I used the same dissecting technique. The abdomens were broken from the male and female thoraces and placed, still joined, in 10% KOH for 12 h. They were then moved to 70% ethanol, cleaned of scales and soft tissues, and drawn using a camera lucida attached to a dissecting microscope. Drawings were made at two points during dissection: (1) with abdominal segments 1–6 of the male and female removed; and (2) with abdominal segments 7 and 8 and the left valve

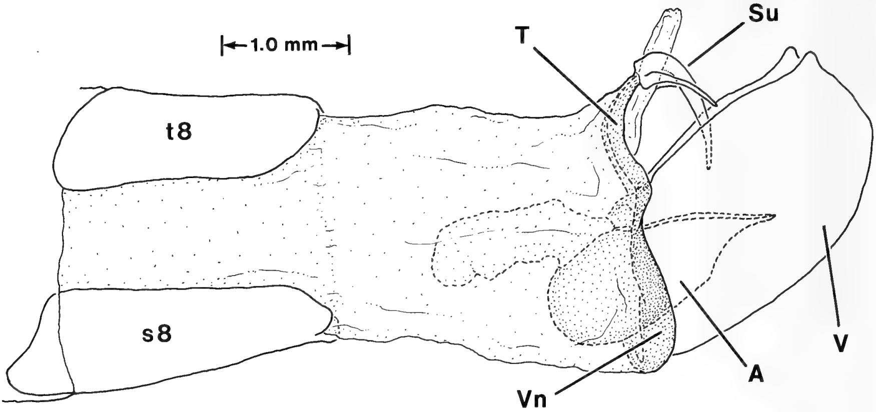


FIG. 4. Male terminalia of *C. necyria* in lateral view, anterior at left. A, aedoeagus; s8, sternite 8; Su, uncus; T, tegumen; t8, tergite 8; V, valve; Vn, vinculum.

of the male removed, and abdominal segment 7 of the female removed. These drawings were overlaid to produce Fig. 11.

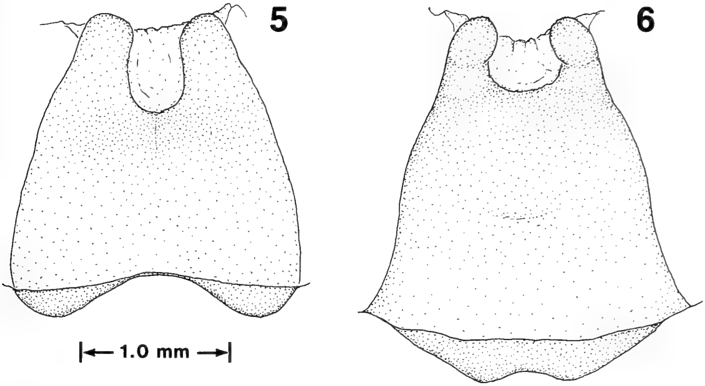
To better understand genitalic morphology in *C. necyria,* I dissected three additional males and three additional females, all from the same locality and collector as the pairs taken *in copulo.* The unpaired specimens were prepared and stained using techniques previously described (Miller 1987). All preparations are in the U.S. National Museum, Washington, D.C.

Morphological terminology follows Klots (1970), Sibatani (1972), and Ogata et al. (1957). Rather than follow the recommendation of Ogata et al. and Sibatani, who proposed the term sociuncus, I use two terms, socii and uncus, following Klots.

RESULTS AND DISCUSSION

General Features of *Cyanotricha necyria* Genitalia

External genitalia of *C. necyria* exhibit features unique to notodontids and dioptids. These strengthen the argument that the two groups are closely related. In *C. necyria* there is a long membrane between segment 8 and the tegumen + vinculum (Fig. 4). The latter are collectively termed the ring, which is thought to be homologous with abdominal segment 9 (Snodgrass 1935, Klots 1970). Genitalia in this species are normally enveloped within the abdomen. In *Speyeria,* where there is also extrusion of male genitalia during mating, movement is effected by protractor and retractor muscles, aided by hemolymph pressure (Arnold & Fischer 1977). An extremely long membrane between segments 8 and 9, combined with ability to withdraw genitalia inside the



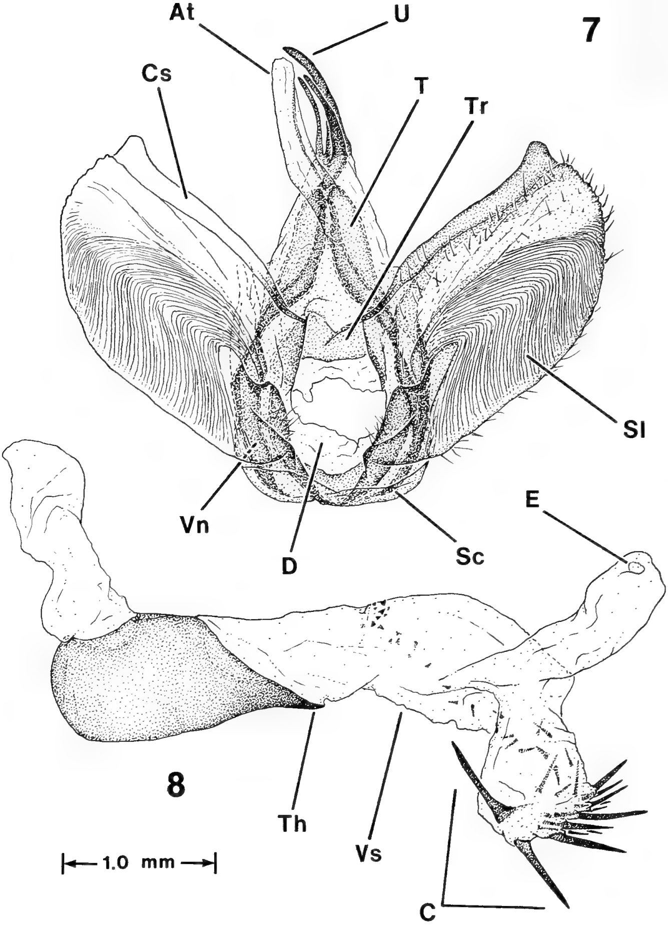
FIGS. 5, 6. Male eighth abdominal segment of *C. necyria*. **5,** Tergite (dorsal view); **6,** Sternite (ventral view).

abdomen, is typical of dioptids, but is also found throughout Notodontidae (Mehta 1933). This trait may represent a synapomorphy for the notodontid-related groups.

The male eighth abdominal segment in dioptids and notodontids is usually modified. In *C. necyria* there are excavations along the posterior margins of the tergite and sternite, and apodemes on their anterior margins (Figs. 5 & 6). In many dioptids and notodontids the posterior margin of the sternite and tergite is heavily sclerotized, sometimes bearing spines (J. Miller unpubl.). There is also much variation in shape of the apodemes on the anterior margin of sternite 8; they are frequently much longer than in *C. necyria*.

The sacculus of the valve in *C. necyria* is large with numerous pleats (Fig. 7), and the rest of the valve, except for the costa, is membranous. The pleated sacculus was described by Barth (1955) for *Hemiceras* (Notodontidae), but is another feature found frequently in dioptids and notodontids (Forbes 1942, Holloway 1983, Miller 1987). The pleats enclose androconia, and probably unfold during courtship, extruding the scales, which then presumably disseminate male scent. Mehta (1933) characterized notodontids as lacking the saccus, an internal extension of the vinculum. Male genitalia of *C. necyria* illustrate that the saccus is absent in some dioptids as well. The slender uncus and socii are hinged on the tegumen.

The aedoeagus of *C. necyria* (Fig. 8) is typical in shape for members of Josiinae, being short, deep dorsoventrally, and large relative to the rest of the genitalia. A row of cornuti on the vesica, terminating in a set of robust, spinelike cornuti, is also common in the group (J. Miller unpubl.).



FIGS. 7, 8. Male genitalia of *C. necyria*. **7,** Genitalia in posterior view with aedoeagus removed; **8,** Aedoeagus in lateral view (anterior at left). At, anal tube; C, cornuti; Cs, costa of valve; D, diaphragma; E, opening of vesica; Sc, saccus; Sl, sacculus; U, uncus; T, tegumen; Th, ventral tooth of aedoeagus; Tr, transtilla; Vn, vinculum; Vs, vesica.

In female genitalia of *C. necyria* (Fig. 9), tergite 8 is membranous dorsally. The ostium is surrounded by postvaginal and antevaginal plates, which hinge on a point dorsal to the opening. There are small spines inside the proximal portion of the corpus bursae. A feature found in *C. necyria* and only a few other dioptids is the large, convoluted, sclerotized band which wraps around the corpus bursae. In noctuids, large muscles attach to the corpus (Callahan & Cascio 1963). Once the male has deposited the spermatophore in the corpus bursae, these mus-

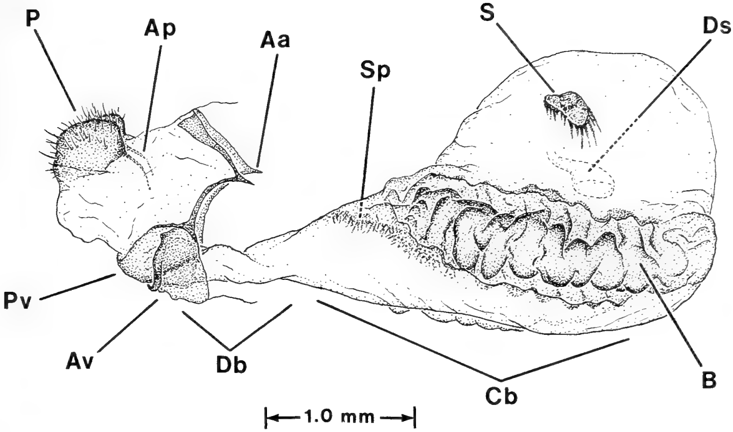


FIG. 9. Female genitalia of *C. necyria* in lateral view, anterior at right. Aa, anterior apophyses; Ap, posterior apophyses; Av, antevaginal plate; B, sclerotized band; Cb, corpus bursae; Db, ductus bursae; Ds, ductus seminalis; P, papillae anales; Pv, postvaginal plate; S, signum; Sp, basal spines of corpus bursae.

cles are thought to squeeze seminal fluid and sperm into the ductus seminalis. The sclerotized band of *C. necyria*, in conjunction with these muscles, may serve to break up the spermatophore. In *C. necyria* the ductus seminalis is located laterally on the corpus bursae, whereas in most dioptids it is located on the ductus bursae (J. Miller unpubl.). The signum is composed of a group of long spines protruding into the corpus bursae from a concave sclerotized region. Petersen (1907) and Callahan (1958) suggested that the signum functions to hold the spermatophore in place. It is a site of muscle attachment in *Helicoverpa zea* (Callahan & Cascio 1963).

Copulatory Mechanism of *Cyanotricha necyria*

The interrelations of male and female genitalia during copulation are shown in Figs. 10 and 11. Between the papillae anales of the female, a membranous invagination allows for insertion of the male uncus, which is reflexed downward. In these preparations the uncus almost engages the postvaginal plate of the female. In freshly preserved material with the musculature intact, it most likely would do so. Stekolnikov (1965) found that the uncus engages the postvaginal plate in *Spilosoma menthastri*; the configuration he described is almost identical with that of *C. necyria*. Stekolnikov stated that the uncus in *Acronicta rumicis* engages the female's eighth sternite, but his illustration suggests that the 'eighth sternite' in *A. rumicis* is the same structure as the postvaginal plate in *Spilosoma* and *Cyanotricha*.

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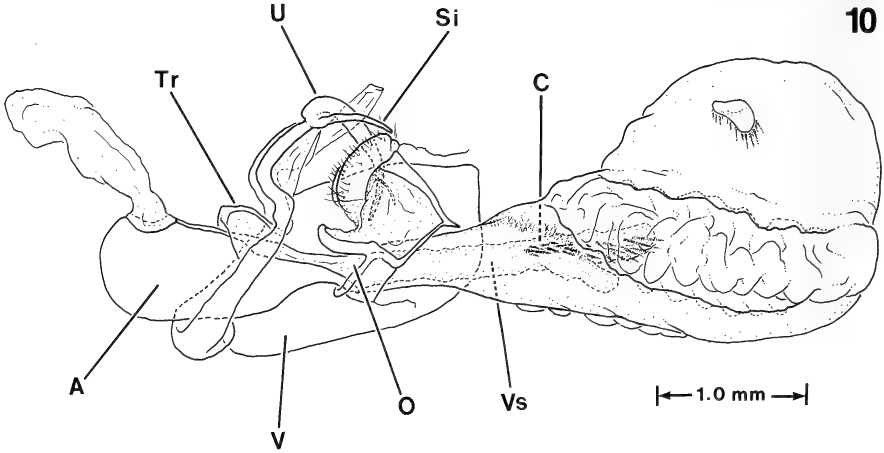

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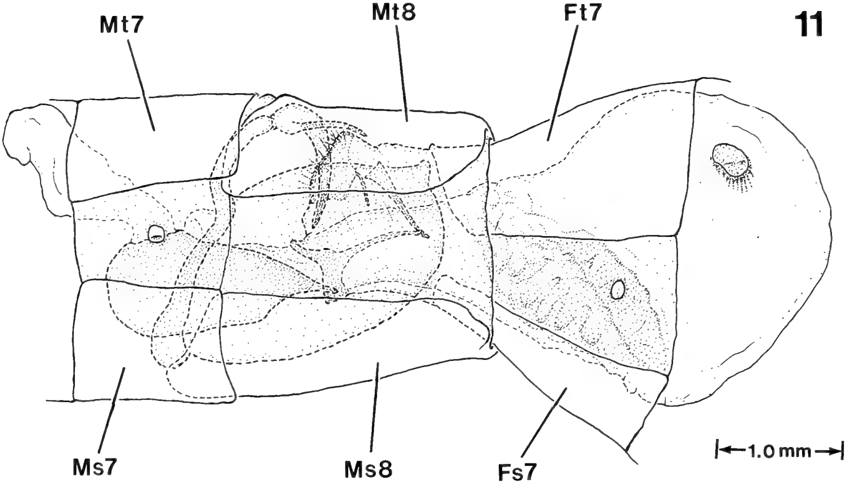

FIGS. 10, 11. Lateral view of male and female *C. necyria in copulo,* anterior of male at left, anterior of female at right. **10,** Pair #1 with abdominal segments 1–8 and left valve of male removed, and abdominal segments 1–7 of female removed; **11,** Pair #2 with abdominal segments 1–6 and left valve of male removed, and abdominal segments 1–6 of female removed. A, aedoeagus; C, cornuti; Fs7, female sternite 7; Ft7, female tergite 7; Ms7, male sternite 7; Ms8, male sternite 8; Mt7, male tergite 7; Mt8, male tergite 8; O, ostium bursae of female; Si, socii; Tr, transtilla; U, uncus; V, valve; Vs, vesica.

In *C. necyria* the socii rest on top of the papillae anales during copulation and would seem to apply downward pressure on them (Figs. 10 & 11). A large muscle ("#1" in Forbes 1939) has its origin on the tegumen and its insertion at the base of the socii. This muscle has been observed in all Lepidoptera studied, and acts to flex the socii and uncus (Stekolnikov 1965, Arnold & Fischer 1977).

Judging from their position, the valvae of *C. necyria* apply lateral pressure on the female terminal segments. The sacculus is elongate and fairly rigid in most Lepidoptera. Muscles originate on the sacculus and insert on the clasper of the valve. When these are flexed, the claspers squeeze the female laterally (Forbes 1939, Arnold & Fischer 1977). The valve of *C. necyria* has a membranous sacculus and lacks a clasper (Fig. 7). It may be that only the valval costa provides traction during copulation.

Eversion of the vesica is effected by the combined forces of aerostatic pressure and muscle action (Callahan 1958). In Noctuidae the cornuti appear to serve two functions (Callahan 1958, Callahan & Chapin 1960): First, while the vesica is being everted, the cornuti, which at this time point inward, help drag the formed collum of the spermatophore into the ductus bursae. Secondly, when the vesica is fully everted and the cornuti point outward, they help manipulate the spermatophore so that it properly orients in the corpus bursae. Shape and orientation of the spermatophore is extremely specific in lepidopteran species (Williams 1940, 1941, Callahan 1960). Usually its aperture is placed in close proximity to the opening of the female's ductus seminalis. In addition, the movements of the vesica within the corpus bursae can be extremely complex. Callahan and Chapin (1960) argued that there is a "lock and key" mechanism at work during copulation that serves to inhibit mating between species. However, their research convinced them that it is not the relative shapes of the male valvae and female genitalia that is critical, as most previous authors had proposed, but is instead the configuration of the everted vesica and its ability to correctly place the spermatophore.

Unlike Noctuidae (Callahan & Chapin 1960, Takeuchi & Miyashita 1975) and Arctiidae (Stekolnikov 1965), the aedoeagus of *C. necyria* does not actually enter the female, but a small ventral tooth on the aedoeagus (Fig. 8) appears to insert into the antevaginal plate (Figs. 10 & 11). The diaphragma of *C. necyria* holds the aedoeagus tightly in place, whereas in many other Lepidoptera it is loose and allows the phallus to penetrate the female when the aedoeagus protractor muscles are activated (Forbes 1939, Stekolnikov 1965, Arnold & Fischer 1977). Opposing muscles insert on the saccus, and lack of movement of the aedoeagus in *C. necyria* may account for absence of the saccus. Judging from the morphology of the diaphragma and aedoeagus in other dioptids, the characteristic of having only the vesica enter the female may define a restricted group of species. In copulating *C. necyria*, cornuti of the everted vesica were in apposition with basal spines of the corpus bursae (Figs. 10 & 11). This seemed to hold male and female genitalia together even after the left valve of the male had been removed. The two sets of spines may become entangled.

During copulation, the male genitalia of *C. necyria* are withdrawn into the abdomen to a point approximately even with segment 7 (Fig. 11). This is facilitated by the long intersegmental membrane between segment 8 and the ring (Fig. 4). It would be useful to know which muscles pull the genitalia in. Their morphology may prove to be another unique feature of dioptids and notodontids. In *C. necyria* the tergite and sternite of male segment 8 have an important holding function; when the female is pulled into the male abdomen, they appear to apply dorsoventral pressure on her seventh segment. Highly modified male eighth tergites and sternites are found in many notodontid and dioptid species (Franclemont 1970, Holloway 1983), which suggests that a holding function is typical for the group, and possibly represents a synapomorphy for the entire lineage.

CONCLUSIONS

One feature of copulation seems common to all lepidopterans studied: the male uncus is inserted between the papillae anales and applies pressure on the dorsal surface of the female's postvaginal plate. Other aspects are unique to each species. The female of *Speyeria* is held at three points: the uncus secures the tergum of segment 8, valvae apply lateral pressure on the papillae anales, and the base of the valve secures sternite 7 of the female (Arnold & Fischer 1977). In *Carcharodus* the intersegmental membrane between segments 7 and 8 of the female is expanded. The uncus engages the postvaginal plate, and valvae grip the female's intersegmental membrane (De Jong 1978). There are two points of contact in *Spilosoma* and *Acronicta*: the uncus secures the female postvaginal plate, and valvae apply lateral pressure at the base of the ductus bursae (Stekolnikov 1965). My study has shown that the female of *Cyanotricha necyria* is held in three places: the uncus engages the female postvaginal plate, valvae grasp her terminal segments laterally, and the male eighth abdominal segment applies dorsoventral pressure on female segment 7. A fourth possible point is the cornuti of the vesica, which seem to become entangled with spines located at the base of the corpus bursae, but dissection of freshly preserved material is required to confirm this.

Copulation in *C. necyria* is unique among Lepidoptera so far described in that an exceptionally long membrane between abdominal segments 8 and 9 of the male allows the female to be pulled into the abdomen during copulation. The male eighth segment then aids in grasping the female, and may provide the majority of force for holding the pair together. This trait could prove to be another synapomorphy for the dioptid-notodontid lineage, but its distribution among species has not been adequately documented. Such information may be crucial in clarifying phylogenetic relations among these taxa.

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A NEW SPECIES OF *CATOCALA* FROM THE SOUTHEAST UNITED STATES

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ABSTRACT. *Catocala charlottae* is described from Louisiana and Florida, the type series consisting of 100 males and 64 females. The new species is differentiated from its most similar ally, *C. alabamae* Grote, mainly by genitalic characters. Adults and genitalia of both sexes of both species are illustrated.

Additional key words: Noctuidae, *Catocala charlottae, C. alabamae,* taxonomy, underwings.

The small-bodied underwing described here, *Catocala charlottae,* closely resembles *C. alabamae* Grote both superficially and in male genitalia. *Catocala charlottae* has been taken at the type locality in Louisiana, and at several Florida localities.

Louisiana *C. alabamae* are similar to those occurring through most of its known range. A lifesize color photo of the *C. alabamae* holotype in the British Museum (Natural History) was examined and it precisely matched Louisiana *C. alabamae.*

Catocala charlottae Brou, new species
(Figs. 1, 2, 5, 6)

Forewing length of males averaging 19.5 mm (18.5–21.2 mm, N = 54); of females, 20.9 mm (19.7–21.8 mm, N = 32). Forewing slate gray with distinct bold black antemedial line and anal dash. Most specimens have a bold medium brown broad line paralleling basal side of antemedial line, absent above R_1. Same brown coloring evident between postmedial and subterminal line and especially noticeable as a distinct brown patch below anal dash. Brown spot at middle of costal margin above vein R_1. Reniform and subreniform present, sometimes diffuse and indistinct. Forewing underside exhibiting a pale yellow postmedial band bordered on both sides with dark brown bands. Fringe dark with darker brown bars. Basal half of forewing stronger orange-yellow than outer half with fine black line on Cu_2.

Hindwing above with black inner band and outer marginal band with connecting black-barred off-white fringe. Underside with yellow postmedial band bordered on both sides with dark brown bands. Yellow on costal half of hindwing pale, while that half along inner margin is bolder orange-yellow.

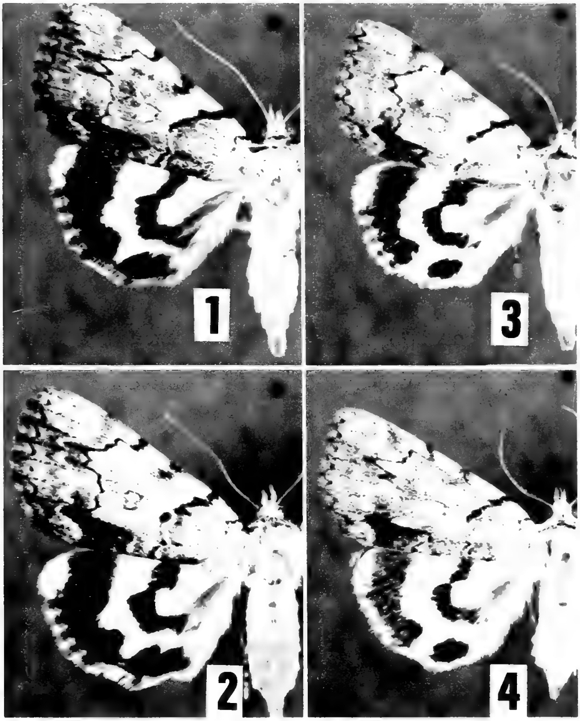
Male genitalia (Fig. 5) (N = 12). Cucular areas along costal margin of valva sickle shaped; mid-costal edge minimally squared, terminal edge finely serrated. Uncus semicircular and acuminate.

Female genitalia (Fig. 6) (N = 10). Papillae anales elongated, strongly sclerotized. Posterior edge of lamella antevaginalis straight, abruptly angled inwardly to ostium bursae in a long narrow V-shape.

Flight period. At the type locality, specimens were taken at light and fermented bait from 30 April to 23 June, with peak occurrence on 22 May (N = 177). Specimens taken after the fourth week usually were worn and tattered.

Discussion. In Louisiana, *C. charlottae* appears on the wing about two weeks earlier than *C. alabamae.* In Louisiana, adult *C. alabamae* were taken from 13 May to 16 June (N = 38), with peak occurrence on 2 June.

Both Louisiana and Florida populations of *C. charlottae* are consistent in maculation



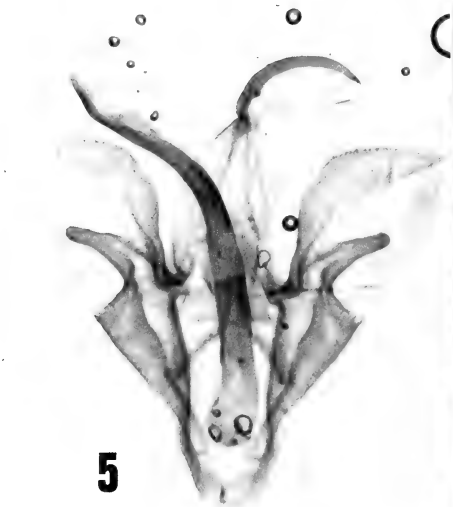
FIGS. 1–4. *Catocala* adults from the *C. charlottae* type locality. **1,** *C. charlottae,* ♂ holotype; **2,** *C. charlottae,* ♀ allotype; **3,** *C. alabamae,* ♂ coll. 13 May 1985; **4,** *C. alabamae,* ♀ coll. 10 June 1985.

and size; the only noticeable exterior difference is the slightly darker appearance of Florida specimens. Forewing lengths of male Louisiana *C. charlottae* (N = 108) average 7% larger than those of male Louisiana *alabamae* which average 18.2 mm (16.6–19.5 mm, N = 20). Forewing lengths of female Louisiana *C. charlottae* (N = 32) average 9% larger than those of female Louisiana *C. alabamae* which average 19.1 mm (17.9–20.1 mm, N = 14). The upper forewings of *C. charlottae* lack the overall blue-green suffusion present on *C. alabamae*. Occasionally, fresh *C. charlottae* exhibit a few diffuse greenish scales around the reniform, but these are sometimes evident only with magnification.

Male genitalia of *C. charlottae* are similar to *C. alabamae* (N = 8) except that the mid-costal margin is squared to a lesser degree in the former (Figs. 5, 7). Female genitalia of *C. charlottae* differ more noticeably from those of *C. alabamae* (N = 6). In the latter, the posterior edge of the lamella antevaginalis is angled caudally approaching the midline and abruptly angled inwardly to ostium bursae in a wide V-shape (Fig. 8).

Since *C. charlottae* has been collected with typical *C. alabamae* in both Louisiana and Florida localities, a distance of 660 miles (1062 km), it does not seem likely that the former is part of a phenotypic cline of the latter.

More than 30 *Catocala* species have been collected at the *C. charlottae* type locality. This habitat is a longleaf pine region, a gently rolling hilly area interspersed with flatwoods and sloughs. It is rich in diverse natural vegetation, the secondary growth being so dense that it is impenetrable except in slough areas. The *C. charlottae* larva may be a Rosaceae feeder. Four possible host species common at the type locality are *Prunus serotina* Ehrh., *Malus angustifolia* (Ait.), *Crataegus marshallii* Ellgeston, and *Aronia arbutifolia* (L.)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FIGS. 5–8. *Catocala* genitalia from the *C. charlottae* type locality. **5,** *C. charlottae,* ♂ coll. 10 May 1986; **6,** *C. charlottae,* ♀ coll. 15 May 1986; **7,** *C. alabamae,* ♂ coll. 2 June 1986; **8,** *C. alabamae,* ♀ coll. 3 June 1986.

Catocala alabamae has the broader geographic range, occurring in Missouri, Texas, the southwestern States, the Gulf States, Tennessee, South Carolina, and Florida (Barnes & McDunnough 1918, Holland 1903:269, Sargent 1976:70, Covell 1984:315).

Types. Holotype ♂ (Fig. 1) 4.2 miles (6.7 km) NE Abita Springs, sec. 24,T6SR12E, St. Tammany Parish, Lousiana, 7 May 1985, V. A. Brou Jr.; allotype ♀ (Fig. 2) same data, 30 April 1985; Both in United States National Museum, Washington, D.C. Paratypes: same locality, 96 ♂, 56 ♀, 30 April to 23 June 1983–87; Jacksonville, Duval Co., Florida, 3 ♂, 5 ♀, 15 May to 7 June 1977–85; Seminole Jr. College, Seminole Co., Florida, 1 ♀, 21 May 1974; Sanford, Seminole Co., Florida, 1 ♀, 13 May 1985. Paratypes are deposited in the Florida State Collection of Arthropods, Gainesville; Louisiana State University, Baton Rouge; and the author's collection.

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BIOLOGY OF THE BLUEBERRY LEAFTIER *CROESIA CURVALANA* (KEARFOTT) (TORTRICIDAE): A FIELD AND LABORATORY STUDY

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ABSTRACT. Biology of *Croesia curvalana* (Kearfott) is described for the first time. Laboratory-laid eggs were white, later brown, 0.6 mm in diam., and were deposited singly under blueberry branches. Seventy-five percent hatched when given a 7-day chilling at 6°C followed by a 24-week cold treatment at 0°C. Four instars occurred during the 21-day larval development period at 21°C. Male pupal stage was 9 days, 2 days less than females. Field eggs were laid on surface litter under blueberry plants in July and August, and eggs overwintered. Flower buds were invaded by emerging larvae in the last part of April and early May, and pupation occurred during the first half of June. During four years of study, the flight season began at Blackville, New Brunswick, during the first week of July, and later at Pouch Cove, Newfoundland. Larvae from Pouch Cove were parasitized by *Chorinaeus excessorius* (Davies). In trapping experiments, virgin female *Croesia curvalana* attracted the largest proportion of males between 2200 h and 2400 h. Male *Croesia curvalana* were attracted to sex attractant lures and virgin *Choristoneura fumiferana* (Clem.) females between 2000 h and 0400 h.

Additional key words: Tortricidae, eggs, diel periodicity, trapping, *Vaccinium angustifolium*.

Croesia curvalana (Kearfott), commonly called blueberry leaftier (BBLT), are responsible for serious crop losses in Newfoundland, where lowbush blueberries, *Vaccinium angustifolium* (Ait.), are a two-million-pound export crop (Morris 1981). The insect was first recorded in Newfoundland in 1979, and subsequently reported to infest up to 30 percent of blueberry buds in 12 fields sampled in New Brunswick (G. Wood pers. comm.). Incidence of infestation is increasing due to change in blueberry cultivation practices: field burning every two years has been replaced by mowing because of rising oil prices and soil damage.

Kearfott (1907) described *Croesia curvalana,* as one of four "varieties" of *Tortrix albicomana* (Clemens) feeding an oak, rose, and huckleberry. MacKay (1962) described larval morphology based on a probable last instar. She placed it in the tribe Tortricini, genus *Argyrotoza.* Larval host plants were said to be Vacciniaceae, with distribution from Nova Scotia to British Columbia. Subsequently Powell (1964) and Hodges et al. (1983) listed the insect as *Croesia curvalana.*

In 1979 we discovered that adult male *C. curvalana* were attracted to virgin spruce budworm, *Choristoneura fumiferana* (Clemens), (SBW) adult females. Trapped moths were identified by the Forest Insect and Disease Survey (FIDS) of Environment Canada, and the Biosystematic Research Centre, Agriculture Canada. Initial trap capture of *C. curvalana* occurred in traps hung at 1.5 m above ground in balsam fir stands. This finding suggested that some components of spruce budworm sex pheromone were also BBLT sex attractants. Sanders and Weatherston (1976) identified the primary components of SBW sex pheromone as (E) and (Z)-11-tetradecenal (96:4), and Silk et al. (1980) found traces of tetradecanal and E-11-tetradecenyl-acetate in the effluvia.

Little is known of BBLT biology. This paper describes laboratory studies from 1980 to 1983 concerning duration of egg diapause, larval, and pupal development; suitability of oviposition substrates, and fecundity. Field studies are also presented which explore the BBLT life cycle and examine diel periodicity of male attraction to calling females.

MATERIALS AND METHODS

Laboratory

Egg treatment during diapause. Eggs collected in August 1981 failed to hatch when held in the laboratory for 4 months at 21°C with temperature variations of ±2°C. A cold treatment was therefore provided for egg collections made the next year. Sequencing of temperature and photoperiod throughout diapause in the laboratory was similar to that used for SBW (Stehr 1954). Field-collected eggs laid on dead leaves under blueberry plants were stored in Petri dishes lined with dampened filter paper, sealed with parafilm, and held at 21 ± 2°C for 18 to 37 days. One batch of 1144 eggs was chilled at 6 ± 1°C for 7 days in a dark refrigerator. A 2nd batch of eggs was exposed to cold treatment of 0 ± 1°C in a freezer with no chilling. Samples from both batches were removed from the freezer after 18, 21 and 24 weeks. All eggs were placed in a refrigerator at 6 ± 1°C for 2 days before being exposed to a constant temperature of 21 ± 2°C in a 17L:7D photoperiod. Time required for eggs to hatch after removal from the freezer and percentage hatch were measured.

Larval and pupal rearing. After hatch, 994 larvae were transferred using a mohair brush to artificial-leaf-meal diet in plastic creamer cups (4 per cup) or to young foliage, and reared at 21 ± 2°C in a 17L:7D cycle at 70% RH. Diet was that developed for SBW (McMorran 1965) as modified by Grisdale (1973), to which was added dried blueberry leaf meal (50% v/v). The meal was produced by drying and grinding previously frozen leaves from June collections. The diet was allowed to dry for a day at room temperature, which made it draw away from cup sides and provide niches for larvae. Twenty larvae were reared singly from hatch to adult emergence to determine number of larval instars and time required for maturation. Exuvial head capsules were collected and widths measured.

Oviposition substrates. When neonate larvae were transferred from leaves to diet, mold spores also transferred immediately contaminated the diet. Therefore, a study was undertaken to examine suitability of other oviposition substrates. In 1983, 10 newly emerged virgin females were placed with males at a ratio of 1:1.5 in each of 8 screened cages measuring 30 cm^3. Moths were provided with a live blueberry branch, a 10% sucrose source, and a selection of oviposition substrates: parafilm, waxed paper, aluminum foil, filter paper strips, all 3 cm × 15 cm, and glass (2 bottles each of 21 cm surface area) which were placed on cage bottoms. In two cages, dried leaves were also offered as an oviposition substrate. Numbers and viability of eggs deposited on each substrate were determined. Cages were maintained in a 17L:7D light cycle at corresponding temperatures of 21 and 17°C with 70% RH for 3 weeks, after which eggs were counted. Eggs on the various substrates were given the cold treatment found effective in the initial diapause study, and emerging larvae counted.

Fecundity. Numbers of eggs produced by virgin and mated female moths under laboratory conditions were investigated. Single virgin females and male-female pairs were reared in 12-ml vials containing a 10% sucrose source. Seventy-one virgins 0 to 11 days old were dissected and their eggs counted. Females were dissected in a 5.5-cm Petri dish to expose the reproductive system. One or more drops of Shaeffer Script permanent blue-black ink diluted 50% with water was added to the preparation. Ovarioles were separated and eggs counted using a base-lit dissecting microscope at 160–400 magnification. Eggs were regarded as mature when they reached ca. 0.3 mm diam., the size at oviposition. Eggs, unfertilized and fertilized, were also counted from 31 mated 5- to 10-day-old females.

Field

Areas studied. Two geographically distinct regions were selected for study. The Pouch Cove, Newfoundland, blueberry barrens, which were used in 1984 and 1985, were rocky and windswept. An area near Blackville, New Brunswick, which was used from 1980 to 1984, had less open terrain, and blueberry plants were often interspersed with ferns, small trees, and bushes.

Life history. In late August 1981, two weeks after the flight season, whole live blueberry plants, surrounding vegetation, and surface litter were collected at Blackville. All materials were examined in the laboratory for BBLT eggs. Samples of leaf litter were again collected from the same area in October to check for egg hatch.

Timing of insect development at Blackville was investigated in 1981. First invasion of flower buds by larvae was monitored by microscopic

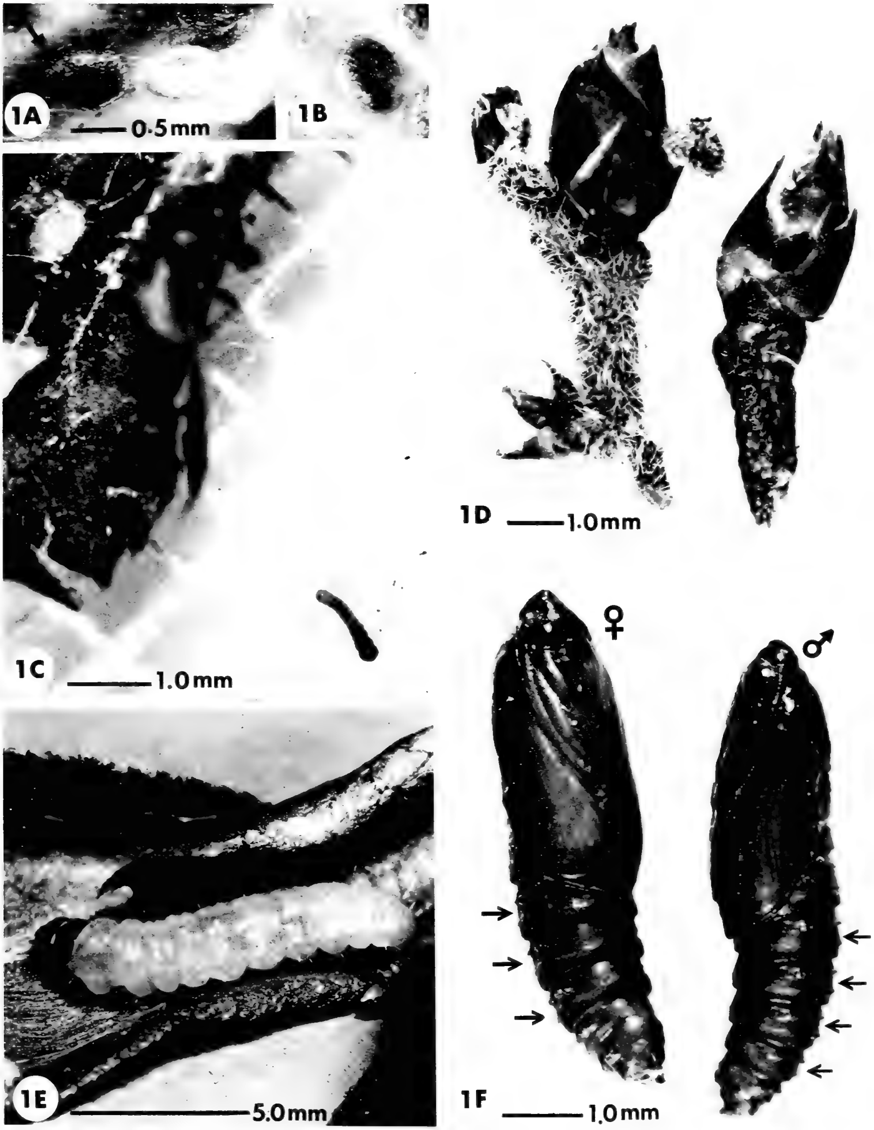

FIG. 1. *Croesia curvalana* life stages and injury to host. **A,** Fertile (arrow) and infertile eggs; **B,** Fully mature egg two days before eclosion; **C,** Newly emerged larva with empty egg; **D,** First-instar entry holes in blueberry buds; **E,** Fourth instar; **F,** Male and female pupae (arrows indicate moveable abdominal segments).

TABLE 1. Effect of chilling at 6 ± 1°C and duration in freezer at 0 ± 1°C on timing and success of *Croesia curvalana* egg hatch. All eggs received a post-freezer period of 2 days in refrigerator at 6 ± 1°C before being incubated at 21 ± 2°C. N = 2100.

No. chilling days in refrigerator	No. weeks in freezer	Percent of hatching eggs after removal from freezer				Percent hatch of eggs subjected to treatment
		5–11 days	12–18 days	19–25 days	26–32 days	
7	24	45	44	9	2	75
7	21	4	66	28	2	57
7	18	0	64	35	1	55
0	24	8	55	31	6	49
0	21	0	55	45	0	20
0	18	0	36	47	17	31

examination of blueberry plant clippings beginning in early April. Foliage was subsequently clipped for examination at two-week intervals for observations of larval and pupal development.

Parasites. In 1984, 528 late instars collected at Blackville and 102 from Pouch Cove were reared singly in the laboratory on foliage to determine incidence of parasitization.

Trap height. Height of male flight and trap height for optimal male capture were investigated at Blackville in mid-August 1980. Initial capture of male BBLT in SBW-baited traps had occurred at a height of 1.5 m. Four Pherocon® 1C sticky traps were each baited with 2 spruce budworm virgin females 0 to 24 h old in small screen cages, and 4 Pherocon® traps were left empty. Two moth-baited traps, and two empty Pherocon® 1C traps were hung 1.5 m above the blueberry canopy and 2 of each at 10 cm above the canopy. Traps were 30 m apart. Captured moths were counted each day for 10 days and the SBW virgins were replaced every 2 days.

Flight season. Onset and duration of the flight season was studied during four seasons in Blackville and two seasons at Pouch Cove by sweep netting and by capturing males in sticky traps. Traps were placed at canopy level in advance of the flight season and monitored every 48 h. They were baited with polyvinyl chloride (PVC) lures (Fitzgerald et al. 1973) formulated by G. Lonergan, Department of Chemistry, University of New Brunswick, to release (E) and (Z)-11-tetradecenal (95:5) with small amounts of (E)-11-tetradecanyl-acetate (0.2) at the rate of 1 SBW equivalent (Sanders 1981). These had attracted leaftier males in previous experiments (Ponder unpubl.).

Periodicity of sexual activity. Diel periodicity of sexual activity under field conditions was observed at Blackville between 13 and 16 July 1982 in a 96-h trapping study. Pherocon® 1C traps were each baited with one of the following: two virgin SBW females, two virgin BBLT females, a PVC lure releasing a sex attractant at the rate of one SBW equivalent, or a blank PVC formulated without attractants. Each trap type was replicated three times within the array. Virgin SBW females were included in this experiment as lures because of their proven success in the capture of male leaftiers. Traps were separated by 30 m and their initial positions in the 12-placement array were selected by random numbers. Trapped moths were counted and traps were moved foward by 1 position every 2 h because the population was not uniformly distributed.

RESULTS AND DISCUSSION

Laboratory

Egg treatment during diapause. Three to 4 days after removal from 18 to 24 weeks in the freezer, and 2 to 3 days before hatch, a black head and larval outline could be observed inside eggs (Fig. 1B).

Significant decreases in egg mortality occurred with acclimation. Chilling eggs at 6°C in the refrigerator for one week before putting them in the freezer enhanced hatch (Table 1). The longer period of 24 weeks in the freezer resulted in significantly increased egg hatch (2-way ANOVA w/o replication, $P < 0.05$). Seventy-five percent of eggs hatched if given a 24-week freezer treatment after 7 days of chilling (Table 1).

Larval and pupal rearing. Larvae matured through 4 instars to pupation in 21 (SD ± 3, N = 20) days at 21 ± 2°C. Mean head capsule widths (mm ± SD) progressing through instars were 0.25 ± 0.03, 0.35 ± 0.04, 0.57 ± 0.05, and 1.22 ± 0.04. Hatchlings were 1.2 mm long, cream colored, with a dark thoracic shield and black head (Fig. 1C). Second and third instars remained cream colored, had black heads and thoracic shields, and dark anal shields. Fourth instars (Fig. 1E) became yellow, and the head changed to cinnamon brown; the thoracic shield was cinnamon brown medially, shading to dark brown laterally. Male gonads in the fifth abdominal segment were maroon, simplifying larval sexing. Exuvial head capsules appeared slightly lighter in color than the head in the last two instars.

Mortality was high in the 994 larvae fed leaf-meal diet; only 22% survived compared with 50% on fresh foliage under the same conditions, though maturation time was approximately equal. Mortality of diet-fed larvae could be attributed in part to mold transferred with hatchlings from leaves to diet. No attempt was made to surface-sterilize eggs. Larvae did not feed on previously frozen blueberry foliage unless mixed with SBW diet. An attempt had been made in 1980 to rear 230 larvae on SBW diet without addition of blueberry meal. Three larvae survived

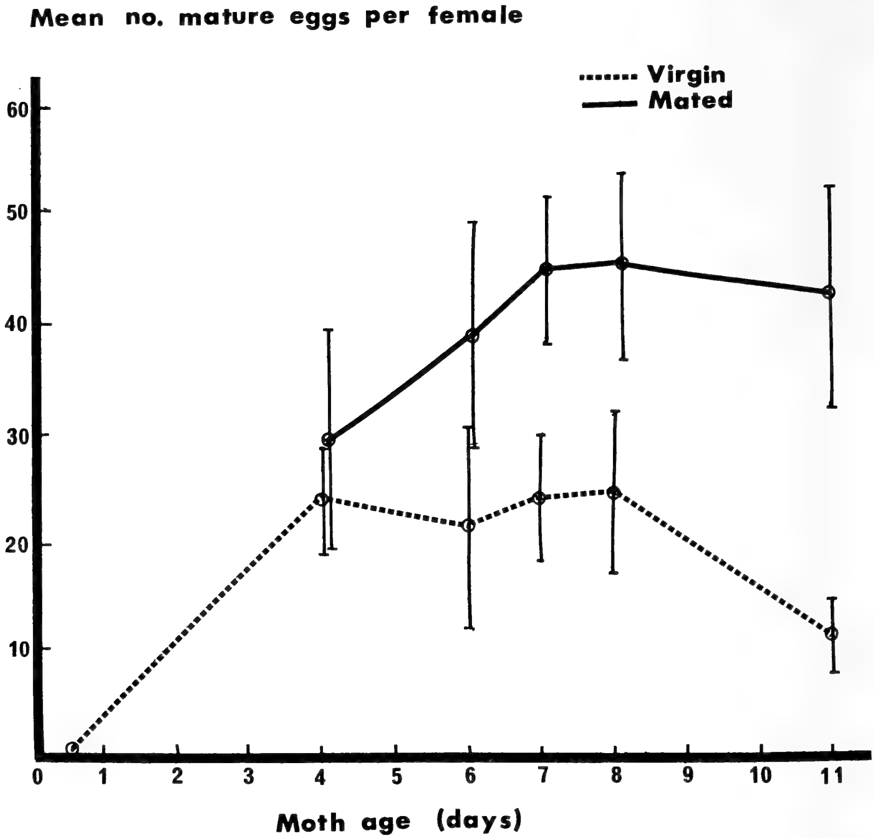

FIG. 2. Numbers of mature eggs in mated (N = 31) and virgin (N = 71) female *Croesia curvalana* in relation to age. Vertical bars indicate SD.

to pupation, and larval development time was 75 to 80 days. Newly hatched larvae seldom burrowed into flower buds (Fig. 1D) on diet, but rather spun nests between the diet and creamer cup wall.

Pupation occurred either in spun nests between diet and creamer cup wall, or under the lid. Males pupated before females, and mean male pupal duration was 9.2 (SD ± 0.8, N = 20) days which was shorter by 2 days than mean female pupal duration of 11.5 (SD ± 1.3, N = 20) days. Male pupae could be distinguished by presence of a fourth moveable abdominal segment (Fig. 1F), females having only three moveable segments.

Oviposition substrates. Few eggs were deposited by BBLT females in the laboratory. Such eggs were scattered singly on materials placed in cage bottoms. Eggs were white, flattened, convex, 0.6 mm in diam., and had a clear pebbled surface. Within a week they changed to reddish brown as the enclosed embryo matured (Fig. 1A). In total, 1061 eggs were collected in 1983 on synthetic substrates, 44% on waxed paper, 37% on parafilm, 8% on aluminum foil, 7% on filter paper, and 4% on glass. No preference was shown for dried leaves as an oviposition substrate. Egg maturation and hatch after diapause was 66% on waxed paper, and 64% on filter paper, but only 32% on parafilm. Other substrates resulted in less hatch.

Fecundity. No mature eggs were found when 5 newly emerged virgins were dissected; however, a mean of 90.8 (SD ± 11.4) immature eggs were counted. In mated females, ca. ⅓ of eggs matured by the 4th day (Fig. 2), and up to 50% matured by the 7th day after emergence. Twenty-six percent matured by the 7th day in virgins. Both mated and virgin females laid few eggs in vials. A total of 4 unfertilized eggs laid by the 71 virgins remained white. Fifty-five fertile eggs which changed from white to brown were laid by the 31 mated females.

Decrease in numbers of eggs in virgin females between days 8 and 11 (Fig. 2) suggested that their eggs were resorbed. Most moths (79%) died between 11 and 12 days after emergence; however, some lived 15 days.

Many factors contributed to the difficulty of rearing this insect on artificial-meal diet. Fecundity was low. The preferred oviposition substrate was ill-defined, and many substrates proved unsuitable for complete egg maturation. Hatchlings were small, delicate, and difficult to locate even with a microscope. Year-round rearing of BBLT using fresh vegetation would be impractical without light- and temperature-controlled greenhouse and refrigeration for continuous propagation of blueberry plants.

Field

Life history. Eggs were laid singly on dried leaf litter under blueberry plants, and were difficult to locate even with a microscope. No eggs were located on living plant leaves, stems, or branches. October collections of eggs indicated that hatch had not yet occurred. Seventy-five percent of field-collected eggs hatched successfully in the laboratory when given a treatment of 1 week at 6°C and 24 weeks at 0°C. These findings indicate that eggs overwinter. Blueberry cultivation practices that incorporate field mowing rather than burning may therefore result in increased leaftier populations.

Foliage clipped weekly from April to mid-June at Blackville indicated that infestation of flower buds by first-instars occurred during the last two weeks of April (Table 2). Larvae burrowed into closed flower buds leaving a round hole marked by an accumulation of yellow frass. Fre-

TABLE 2. Development of *Croesia curvalana* larvae, Blackville, N.B., 1981.

Date	Stage of blueberry foliage	No. larvae collected	Instar no. or stage
18 April	Closed buds	0	
24 April	Closed buds	6	1
6 May	Expanded flower buds	327	1
12 May	Expanded leaf buds	121	1
		129	2
22 May	Young leaves	62	2
		102	3
2 June	Expanded leaves and flowers	247	3
		153	4
12 July	Flowers and immature fruit	2	4
		187	pupae
		15	pupal cases

quently, two larvae were found feeding in the same bud. Larvae subsequently fed on swelling leaf buds. Numbers of buds infested with larvae increased to mid-May, indicating a three-week period of egg hatch. Visible plant damage peaked just before larvae pupated. At this time, terminal leaf growth was webbed and eaten, and larger leaves were folded or webbed together to form shelters. Increased numbers of abandoned shelters during late-instar development suggested that larvae moved frequently.

First appearance of pupae in the field at Blackville ranged from the first to third weeks in June. Males pupated before females. The dark brown pupae could be found sandwiched in shelters or occasionally hanging freely by the cremaster from blueberry twigs.

The moths were 5 to 7 mm long, and were of a yellowish hue with forewing markings of rust and yellow. Toward the end of the flight season, spent moths lost many wing scales, which made them appear cream colored. First male moth emergence at Blackville, as established by trap capture, occurred during the first week of July in all four years of study. It occurred thus regardless of differences in weather during the larval and pupal stages. Sweep-net collections indicated that, as in the laboratory, males emerged before females. Sweep-net collections were achieved two to three days after first male trap capture. First sweep-net collections had a male : female ratio per sweep of 0.116:0.044, which changed to 0.009:0.008 by the end of the flight season. At Pouch Cove where the population was higher, the ratio changed from 0.23:0.02 to 0.22:0.16 by the end of the flight season. Moth location may have had a bearing on results. At Blackville where mean day time temperatures were 5°C higher than Pouch Cove, moths preferred shad-

TABLE 3. Trap capture of male *Croesia curvalana* in Pherocon® 1C traps hung at different heights in 10 days, Blackville, N.B., 1980. Number of traps = 8.

Trap height above blueberry canopy	Mean 24-h catch per trap by virgin spruce budworm	Mean 24-h catch per unbaited trap
1.5 m	6.0	0.1
10 cm	17.6	0.7

ed areas, while at Pouch Cove where the barrens had mean wind velocities of 21.6 km/h and mean RH of 82%, moths were located in sheltered areas of deep vegetation. Female moths may have been at a lower stratum or beneath vegetation during oviposition, making sampling for females by sweep-net unreliable.

Length of flight season in the 4 years of study at Blackville ranged from 30 to 47 days; at Pouch Cove, it began in 1984 on 12 July and lasted 35 days in 1984, and in 1985 on 19 July and lasted 28 days.

Parasites. Larvae collected at Blackville were parasitized 10% by tachinid flies which emerged as larvae from their hosts. Tachinid puparia were held in the laboratory for eight months without a cold period. One fly emerged in too poor condition to identify. No tachinids were found in larvae from Pouch Cove. Two ichneumonids emerged as adults from pupae collected as larvae at Pouch Cove. These were identified by the Biosystematic Research Centre, Agricultre Canada, as *Chorinaeus excessorius* Davies. This parasite has not been reported previously from BBLT.

Trap height. Significantly more male BBLT were captured in traps hung at 10 cm than at 1.5 m above the foliage in both unbaited and virgin SBW baited traps $\chi^2_c = 109.3$, $P \ll 0.001$, $df = 1$) (Table 3) which confirmed visual observations that moths flew immediately above the foliage.

Croesia semipurpurana (Kft.), a species morphologically similar to *C. curvalana*, is attracted to traps hung at 1.5 m baited with components (Grant et al. 1981) which are also part of the spruce budworm sex pheromone bouquet.

Periodicity of sexual activity. The largest proportion of BBLT males trapped by all bait types was between 2200 and 0200 h (Table 4). Virgin BBLT females captured the largest proportion of BBLT males from 2200 to 2400 h ($P = 0.05$, Chi square for multiple proportion, Zar 1984) indicating that female sex pheromone release (calling) took place during these hours. PVCs which released attractant continuously over a 24-h period attracted BBLT males consistently between 2000 and 0400 h, suggesting that male flight period and attraction to lures may extend

TABLE 4. Proportion of 96-h trap capture of male *Croesia curvalana* by 2-h intervals at Blackville, N.B., 1982. Baits in Pherocon® 1C traps were replicated 3 times (N = 1513). No moths were captured between 1000 and 1400 h.

	Trapping interval (h) (AST)									
Bait	1400–1600	1600–1800	1800–2000	2000–2200	2200–2400	2400–0200	0200–0400	0400–0600	0600–0800	0800–1000
Two virgin BBLT	0.00	0.00	0.00	0.08	0.55	0.27	0.02	0.02	0.02	0.05
Blank PVC	0.11	0.00	0.00	0.04	0.44	0.33	0.04	0.00	0.04	0.00
PVC sex	0.01	0.01	0.01	0.26	0.30	0.30	0.11	0.01	0.01	0.00
Two virgin SBW	0.00	0.00	0.00	0.23	0.57	0.16	0.03	0.00	0.00	0.01

on either side of the virgin female BBLT calling period. This was confirmed by the finding that virgin female SBW, which would have been calling from 2000 h to 2400 h (Palaniswamy & Seabrook 1985), also attracted BBLT males before the BBLT female calling period.

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HYLESIA ACUTA (SATURNIIDAE) AND ITS AGGREGATE LARVAL AND PUPAL POUCH

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ABSTRACT. Developmental stages of *Hylesia acuta* are described and illustrated, and two examples of aggregate larval and pupal pouches are reported. Larval development from eggs gathered in Chiapas, Mexico, required ca. 80 days at 25–32°C. Late instars constructed a tough, silk pouch where they remained by day, emerging to feed at night. The first instar is pale yellowish tan with a black head; the mature larva is dark saffron mottled with green. All instars possess urticating spines, but not adults. Larvae constructed individual cocoons before pupating together in the pouch, in which they remained for eight months before emergence. A wild pupal pouch found in Veracruz, Mexico, contained 46 pupae from which 42 adults emerged. A dissected female yielded 374 ova. The species appears to be univoltine, adults emerging during the tropical wet season.

Additional key words: Mexico, silkmoths, immature stages.

The American genus *Hylesia* contains about 100 species of small silkmoths (C. Lemaire pers. comm.), the biology of most unknown. The genus has achieved notoriety in parts of South America because of urticating abdominal hairs of some females (Lamy & Lemaire 1983) used to cover egg masses (Gardner 1982). Hairs in some species cause severe dermatitis in man (Pesce & Delgado 1971, and others).

In the Central American *Hylesia lineata* Druce, ova pass the dry season in a felt nest (Janzen 1984). Though *H. nigricans* Berg, whose immature stages and behavior were illustrated by Lampe (1986), also has overwintering eggs, at least several other species do not (Gardner 1982). Pupation is solitary in most known species.

Aggregate pupation above ground in a silk pouch is unusual among Saturniidae. A "communal cocoon" of an unidentified species of *Neodiphthera* (Saturniinae) from New Guinea contains about a dozen cocoons (R. S. Peigler pers. comm.). Stoll (1791) illustrated a "gregarious cocoon" ascribed to *Phalaena Bombyx bibiana,* which Bouvier (1925) believed was a *Hylesia* (Hemileucinae) species. Beutelspacher (1985) found *Hylesia frigida* Schaus gregarious larvae and pupae in loose silk pouches in Mexico. Cockerell, in Packard (1914), quoted Dyar as having a specimen of *Hylesia tapabex* Dyar "bred from a 'gregarious podlike cocoon.'" Bouvier (1924a, 1924b, 1925) described two aggregate pupal pouches of this species from Venezuela. A nest of *H. tapabex* is preserved in the Muséum national d'Histoire naturelle, Paris (C. Lemaire pers. comm.). The present study establishes that *Hylesia acuta* Druce, closely related to *H. tapabex,* also pupates in a shared pouch.

Hylesia acuta is a small moth (forewing length 2.5–3.1 cm) with marked sexual dimorphism, the female resembling many *Hylesia* species, while the male is distinctive (Fig. 3). Described by Druce (1886) from "North Mexico," its known range extends along the eastern and western lowlands of central Mexico S into Guatemala and E into Yucatan and British Honduras (Schüssler 1934, Hoffmann 1942, C. Lemaire pers. comm.). Its biology and aggregate pupation behavior have not been previously reported.

REARED MATERIAL

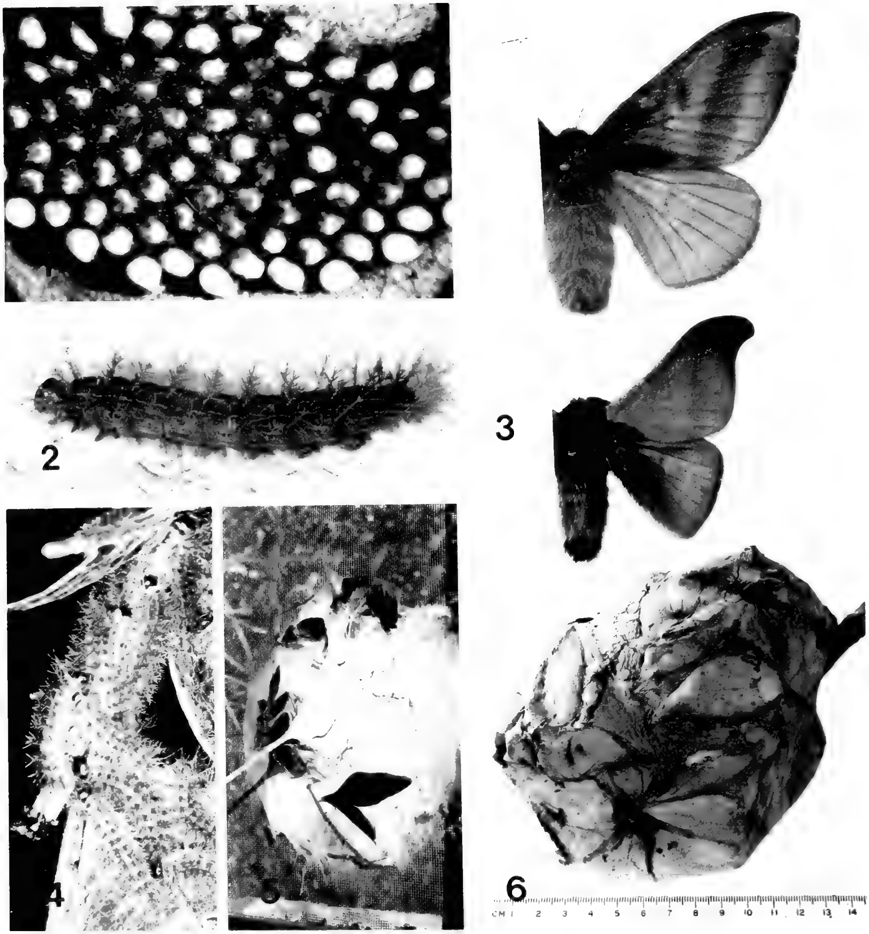
A wild female captured near Huixtla, Chiapas, Mexico, oviposited in a paper bag on 10 July 1983. The eggs were white, upright ovals placed in a single-layered dense cluster, partially hidden with brown abdominal hairs (Fig. 1). They numbered ca. 100. Refrigerated at ca. 50°C for 8 days to delay hatching, the eggs were then kept in a covered plastic petri dish under natural daylight at temperatures varying between 25 and 32°C. They hatched in 25 days, and were transferred to a tight styrene box 11 × 11 × 4 cm. During the first week they refused to feed on any plants offered, instead eating eggshells. Occasionally they wandered in single file, returning to the nest without feeding. Eventually most did accept Brazilian pepper tree, *Schinus terebinthifolius* Raddi (Anacardiaceae). Plants refused included plum, *Robinia pseudoacacia* L., *Rhus laurina* Nutt., *Quercus agrifòlia* Née, and others. Larvae were then placed on small pepper tree branches in a container of water in a screened cage in a humid greenhouse at 25–32°C, with foliage replaced daily. From the earliest stages they spun a loose silken platform to which they returned after group wanderings or feeding.

Six weeks after hatching, the half-grown larvae spun a silk tent at the end of a branch. It appeared as a small, broad cone (ca. 7 cm diam.), of dense silk tipped on its side. A hole near the vertex allowed larval access; frass fell through a slit at the bottom.

When the tent was completed, the larvae became nocturnal, not appearing until at least 1 h after dark when they emerged and traveled in single file, stopping to feed in densely packed rows on mature (darker) leaves. Such tandem movement in early instars is typical among hemileucines as noted in *Hemileuca oliviae* Cockerell (Capinera 1980), *Hylesia lineata* (Janzen 1984), and other species (Lemaire 1971).

The earliest instars were pale yellowish tan, with typical hemileucine spination retained by all subsequent instars (Figs. 2, 4). This color deepened, and after the fourth instar was dark saffron indistinctly mottled with green. One dorsal and two subdorsal longitudinal stripes were straw colored. Mature larvae were plump (Fig. 2). Instar duration and number were not determined.

Half-grown larvae became diurnally active during two days as they spun a larger tent (ca. 15 cm diam.). Incorporating material from the



FIGS. 1–6. *Hylesia acuta*. **1,** Eggs partially hidden by female abdominal hairs; **2,** Mature larva; **3,** Adult female (upper) and male (lower); **4,** Early instars feeding on *Schinus terebinthifolius*; **5,** Aggregate larval and pupal "nest" pouch of captive reared larvae; **6,** Pouch containing wild pupae.

first tent, its walls resembled thin leather, shiny on the inside, and white on the outside (Fig. 5).

Larvae molted within the tent, and the cast-off skins fell through the bottom slit. Shortly before pupation larval mortality increased. Five survivors ceased feeding at 10 weeks, reaching a length of ca. 50 mm. A flashlight beamed through the tent at night revealed their silhouettes, which became progressively less visible as they worked during three weeks to fill it with firm, woolly white silk. Four small holes or "escape" tunnels to the outside were made, two by larvae chewing through the cage's fiber glass screen where it adhered to the pouch.

By 1 December noticeable larval activity had ceased. Several weeks later, the pouch was opened, revealing a small mass of cocoons imbedded in silk. From hatching to pupation was ca. 80 days. The next year in the first week of August, five imagines emerged.

WILD MATERIAL

A cordiform pupal pouch of *H. acuta* with viable pupae was found near Papantla, Veracruz, Mexico, in a small, dead tree ca. 4 m above ground on 27 July 1986. Surrounded by a fresh growth of tall grasses, the tree appeared to have been *Bursera simaruba* (L.) Sarg. (Burseraceae). Imprints of fresh leaves were imbedded on the surface of the pouch. The pouch measured 13.0 × 9.5 × 5.0 cm, and contained 46 pupae. It had been constructed during the previous wet season, since a new wet season was just beginning.

This pouch was angular (Fig. 6), and possessed three widely spaced holes on its upper surface, providing access for feeding larvae and exits for emerging imagines.

Inside, pupae were arranged in double-walled, fusiform cocoons, tightly fit and adhering to one another. Cocoons were parallel in a band three layers thick which wrapped around the supporting branch within the pouch. Exit vents were oriented upward, and opened on several smooth-lined corridors through the dense silk wool to the outside openings of the pouch.

The pupae conform to Bouvier's (1924a, 1924b, 1925) description of *Hylesia tapabex*. He pointed out that while *H. tapabex*, known to pupate aggregately, does not possess a cremaster, solitary pupating *Hylesia* species do possess one. This is further evidenced in the solitary pupae of *H. nigricans* (Lampe 1986) and *H. lineata* (pers. obs.) which possess cremasters.

Emergence of imagines began in September. From 46 pupae, 19 males and 23 females emerged during three weeks. Average emergence was at 1715 h PDT (SD = 1554–1836 h PDT, n = 9). Notably, no parasitism was found. Numerous attempts were made to achieve matings between emerged siblings without success.

Observations of captive females suggest that *H. acuta* oviposits three or more clusters. Dissection of a newly emerged female yielded 374 ova. Females produced no stinging when their abdomens were rubbed on the author's skin.

Voucher imagines are in the San Diego Museum of Natural History, and collections of C. Lemaire, S. Stone, M. Smith, D. Herbin, and the author.

DISCUSSION

Hylesia are among the smallest American saturniids. Those that live under extreme seasonal conditions have evolved strategies to survive the harsh conditions of a dry season (Janzen 1984). In *H. acuta,* a protective nest has evolved in which pupae survive the dry season. The tough, leathery pouch filled with silk wool protects them against adverse weather and perhaps parasites. Its light silvery gray color reflects heat, and its resemblance to a wasp nest may discourage avian predation.

Published records (Beutelspacher 1978), correspondence (C. Lemaire pers. comm.), and labels of wild collected specimens indicate dates of capture predominately from June through August, with records as late as September, during the season of heaviest rains.

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EUROPEAN CORN BORER REPRODUCTION: EFFECTS OF HONEY IN IMBIBED WATER

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ABSTRACT. European corn borer adults are well known to imbibe water, without which their reproduction is greatly decreased. Whether their reproduction is enhanced by sugars in imbibed water has long been unresolved. Two groups totalling more than 50 captive fertile pairs, one group receiving 15% honey-water to imbibe, the other plain water, were compared with respect to 10 reproductive attributes. Honey in imbibed water significantly improved performance in four attributes, resulting in heavier eggs, more females maintaining or increasing egg weight during the oviposition period, fewer females with immature oocytes at death, and more unlaid eggs that were mature. Adult nutritional ecology seems a potential factor in the dynamics of populations.

Additional key words: *Ostrinia nubilalis*, Pyralidae, Pyraustinae, fecundity, egg weight.

Imbibing of water by adults of the European corn borer, *Ostrinia nubilalis* (Hübner), is well documented (Vance 1949). Imbibed water greatly increases adult lifespan and fecundity; without it, reproduction is severely depressed (Barlow & Mutchmor 1963, Kira et al. 1969). Concerning sugars in imbibed water, reported effects are contradictory, one paper claiming no further improvement in reproduction (Caffrey & Worthley 1927), and another claiming the opposite (Kozhantshikov 1938). Unfortunately, the first paper offers no supporting data, and the second enumerates data insufficiently for independent assessment. Although this contradiction has never been addressed, the prevailing view, as reflected in mass rearing practice (Reed et al. 1972), is that sugars in imbibed water do not enhance reproduction. Clarification seems desirable for at least two reasons. First, European corn borer adults aggregate in grass and weedy vegetation bordering host fields (Showers et al. 1976), where potential adult food sources such as nectaries and honeydew-producing insects may occur. Second, if sugars do enhance reproduction, mass rearing programs might thereby increase production with little extra effort.

Here I report how European corn borer adults receiving honey-water and plain water performed in the 10 reproductive attributes listed in Table 1.

MATERIALS AND METHODS

One experiment was done. In it, 78 single female-male pairs of pupae were numbered, and the 39 even-numbered ones assigned to the treatment group, and the 39 odd-numbered ones to the control group. After adults eclosed, treatment pairs received honey-water to imbibe, control pairs plain water. After all moths had expired, reproduction data gathered from both groups were compared.

Pupae were obtained from a culture at the University of Minnesota originating in Iowa and maintained according to standard European corn borer production methods (Reed et al. 1972). The pupae were sexed, and pairs placed in 1-pint (0.47 liter) cardboard ice cream containers capped with Petri dish lids. Lids were lined with waxed paper to ensure a surface suitable for oviposition. Containers were kept in a walk-in environmental chamber programmed for 16 h light at 27°C and 8 h dark at 17°C, both at 60% RH.

Each container had a 35 cm^3 foam-latex sponge that dispensed distilled water in the control group and 15% (by volume) honey-water in the treatment group. Sponges and liquids were renewed every second day. Honey was used as the sugar source because in composition (White 1975) it conveniently simulates hexose-rich shallow-flower nectar (Baker & Baker 1983) and insect honeydew (Auclair 1963).

Reproduction data were gathered once daily near mid-day. Mating and fertilization success was ascertained by holding one or several early egg masses for a week or until the dark larval heads showed through chorions. Preoviposition period was measured from female eclosion to first oviposition; such data were used only when the male of the pair eclosed no later than one day after the female because late male eclosion prolonged the period.

"Early eggs" refers to eggs laid on the first or second day of oviposition, "late eggs" to eggs laid on the fourth to eighth day of oviposition. Mean egg weight was determined from one or more masses totalling 17 to 184 eggs removed intact from the waxed paper and weighed to the nearest 0.5 mg. Mature unlaid eggs were counted in excised ovaries at stereomicroscope magnifications up to 65×. Maturity of unlaid eggs was judged by size and chorionation. Eggs were deemed chorionated if they did not readily absorb 0.3% aqueous methylene blue after 3 min exposure (Jennings 1974). Immature oocytes in expired females could not be counted accurately, so only their presence or absence was recorded. Only data from fertile pairs were analyzed because some reproductive attributes are atypical in the absence of insemination.

Referral of species mentioned in this paper to Pyraustinae is based on the classification of Fletcher and Nye (1984).

RESULTS AND DISCUSSION

Of the 78 pupal pairings, 79% resulted in fertile eggs, a level believed high enough to provide representative adult performance. Data were analyzed from fertile pairs numbering 25 and 27 in the plain-water and honey-water groups, respectively, these numbers also reflecting losses from mishaps like moth escapes. The fewest number of observations on any attribute in either group was 19 for preoviposition period in the water-imbibing control, reflecting a further loss of data on this attribute resulting from late male eclosions.

Four differences between the two imbibing groups were significant (Table 1). Thus, in the honey-water group, a greater proportion of unlaid eggs was mature, fewer expired females contained immature oocytes, late eggs were heavier, and more females maintained or increased egg weight during the oviposition period. The first and second differences suggest that honey-water imbibers approached full reproductive potential more closely than plain-water imbibers. The third and fourth differences presumably reflect conversion of glucose and fructose in honey to lipid that became incorporated into oocytes during egg maturation (Kozhantshikov 1938, Downer & Matthews 1976). Consequences of differing egg weights have not been investigated in the European corn borer, but in other moth species, heavier eggs produce larvae more likely to survive (Barbosa & Capinera 1978, Harvey 1985). Hence, sugars in imbibed water might enhance European corn borer fitness if females live long enough to lay the heavier eggs. Some do live long enough (Elliott et al. 1982): in 9 of 14 samples taken from June to September, $\frac{1}{6}$ of wild mated females were 4 or more days old, the onset age for heavier eggs in the present study.

Although 6 of the 10 reproductive attributes did not differ significantly between imbibing groups ($P \geq 0.06$, one-tailed Student *t*-tests), all attributes except female lifespan show differences of 1 to 150% in favor of the honey-water group (Table 1). Shorter female lifespan in the honey-water group seems anomalous, but no cause was evident. Despite this attribute, the honey-water group outperformed the plain-water group in an overall comparison of reproduction as follows. Of eight independent attributes (omitting number of unlaid mature eggs and percentage females maintaining or increasing egg weight, which are facets of other attributes), seven show gains resulting from honey imbibing whether individually significant or not, and such an outcome is not likely due to chance ($P < 0.05$, one-tailed sign test).

Because European corn borer fecundity varies directly with body size (Vance 1949), the possibility that body-size differences between imbibing groups caused attribute differences was examined. Vance (1949) did not express the relation mathematically; he tabulated six class means for number of eggs laid (y) and corresponding initial adult female weight (mg) (x). Based on retrospective frequency-weighted analysis of class means, the relation can be quantified as $y = 8.5x + 153$ ($66n$, $r^2 = 0.88$, $P < 0.001$). The correlation coefficient is overestimated because it is derived from means rather than individual values,

TABLE 1. Reproductive performance of European corn borer adults receiving plain water and 15% honey-water. Means and percentages are based on 19 to 27 observations per treatment group.

Attribute	Mean (±SD) or percentage		% change due to honey
	Plain water	Honey-water	
Lifespan, days			
Female	17.5 ± 5.4	16.5 ± 5.4	−6
Male	16.8 ± 4.0	18.2 ± 4.5	8
Preoviposition period, days	2.8 ± 1.3	2.3 ± 1.2	−18
No. mature oocytes			
Laid	601 ± 191	623 ± 237	4
Unlaid	28 ± 38	50 ± 53*	78
Total	630 ± 170	673 ± 209	7
% females containing immature oocytes at death	86	53*	−38
Egg weight, mg			
Early eggs	0.0638 ± 0.0048	0.0643 ± 0.0060	1
Late eggs	0.0618 ± 0.0066	0.0652 ± 0.0070*	6
% females maintaining or increasing egg weight	24	60*	150

* Significantly different ($P < 0.05$, based on one-tailed Student *t*-tests for means; 2 × 2 contingency tables and adjusted-G tests for numbers underlying percentages).

but the relation is nevertheless striking. Such a relation could not have affected attribute differences in the present study for two reasons. First, length of one forewing, a surrogate for body weight (Miller 1977), averaged 13.5 (SD ± 0.6) mm and 13.4 (SD ± 0.8) mm in females of the plain-water and honey-water groups, respectively. These means are identical statistically, the difference, 0.1 mm, being less than 1% of either. Second, in neither imbibing group did any egg attribute correlate significantly with female forewing length ($r^2 < 0.08$, $P > 0.20$).

In virgin European corn borer females, 80 egg follicles have been seen in one ovariole (Drecktrah & Brindley 1967). This number translates to 640 per female, near the average total number of mature eggs per female in the present study (Table 1). Number of oocytes already mature at female eclosion averaged 92 (SD ± 16, 4n) in the present study, as determined for females 0–4 h old averaging 14.0 mm in forewing length. Subtracting 92 from total mature eggs in the plain-water and honey-water groups leaves 538 and 581 eggs, respectively. The latter numbers suggest that more than 80% of oocytes mature after females eclose (538/630 = 0.85; 581/673 = 0.86), and that ample opportunity exists for adult nutrition to enhance oogenesis.

Although European corn borer adults have not been reported to imbibe sugary liquids in the wild, it is possible they do so opportunistically because adults of other Pyraustinae use such liquids. Both sexes of *Pyrausta orphisalis* Walker have been seen taking nectar from flowers (Campbell & Pike 1985). In *Cnaphalocrocis medinalis* (Guenée), imbibed sugars and planthopper honeydew greatly increased adult lifespan and fecundity (Waldbauer et al. 1980). Moreover, both sexes of European corn borer have well developed proboscides: females with forewing length (w) averaging 14.0 mm had proboscides with uncoiled length (p) averaging 7.3 mm (4n), forming a p/w ratio of 0.52. This length of proboscis could provide access to floral nectar of many kinds of plants, and the ratio is well within the range signifying flower visitation in other lepidopterans (Opler & Krizek 1984:31).

In conclusion, some differences in reproductive attributes between treatment groups are subtle. They nevertheless bring one step nearer resolution the old uncertainty whether sugars in imbibed water affect European corn borer reproduction. The adult's use of sugary liquids in nature remains to be shown. If it is shown, adult nutritional ecology could be a factor in the dynamics of populations, with sugar consumption perhaps elevating population quality and crop damage. Such an outcome could lead to removal of natural sources of sugar as a supplemental management technique for the insect.

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GENERAL NOTE

PARASITOID AND HOSTPLANT RECORDS FOR GENUS *SCHINIA* (NOCTUIDAE) IN TEXAS

Additional key words: *Schinia bina, S. arcigera, S. chrysella,* Tachinidae, Hymenoptera.

In an earlier report, R. S. Peigler and S. B. Vinson (1984, Southw. Entomol. 9:48–51) listed 24 species of *Schinia* Hübner collected in Brazos Co., Texas, and commented on abundance of the adults. The present paper deals with some observations on the immature stages. The life-cycle for most species is as follows: eggs are deposited in autumn into flowers of composites (Asteraceae), most species specializing on one or a few host genera. Larvae mature in less than one month, pupation is below ground, and adults emerge the following autumn. Peak abundance of larvae as well as adults is in fall.

We experienced difficulty in associating field-collected larvae with adults because diapause was not terminated by various treatments, and pupae often died before adults emerged. Reared material emerged at the next normal flight time for some species, but this was the exception. A few pupae produced adults only after being held for two or more years. Some parasitoids were equally delayed in emerging as adults. Consequently, some records below are cited as "*Schinia* sp." where we were unable to associate larvae with adults. Interspecifically, *Schinia* larvae are as variable as adults in color and pattern (Covell, C. V. 1984, A field guide to the moths of eastern North America, Houghton Mifflin, Boston, Pl. 29), but larvae can confidently be assigned to this genus based on general appearance.

Previously published records of parasitism in *Schinia* are few. P. H. Arnaud (1978, A host-parasite catalog of North American Tachinidae (Diptera), U.S. Dept. Agr. Misc. Publ. 1319, 860 pp.) listed only one record for a tachinid attacking *Schinia*: *Winthemia quadripustalata* (Fabricius) parasitizing *Schinia septentrionalis* Walker (=*S. brevis* Grote). Only one record for a hymenopterous parasitoid attacking *Schinia* was cited by P. M. Marsh (*in* Krombein, K. V., P. D. Hurd, D. R. Smith, B. D. Burks (eds.), 1979, Catalog of Hymenoptera in America north of Mexico, vol. 1:263, Smithsonian Press, Washington, D.C.): the braconid *Cardiochiles magnus* Mao in *Schinia* sp. Another braconid, *Microplitis croceipes* (Cresson) (det. by P. M. Marsh) was reared from *Schinia olivacea* J. B. Smith collected in Live Oak Co., Texas, and another tachinid, *Gymnoclytia unicolor* Brooks (det. C. W. Sabrosky) from *Schinia olivacea* in Bexar Co., Texas (R. O. Kendall pers. comm.).

Our larvae were collected in or on composite inflorescences. They were kept individually in the laboratory on artificial diet (Vanderzant, E. S., C. D. Richardson & S. W. Fort 1962, J. Econ. Entomol. 55:140) in plastic shell vials plugged with cotton. It was necessary to isolate larvae to prevent cannibalism, a problem also noted by D. F. Hardwick (1958, Can. Entomol. Suppl. 6:1–116). For hostplants, we follow nomenclature of D. S. Correll and M. C. Johnston (1970, Manual of the vascular plants of Texas, Texas Research Foundation, Renner, Texas, 1881 pp.). All records below are from Brazos Co., in E-central Texas. Species of *Schinia* most commonly collected by us in the larval stage were *S. bina* (Guenée), *S. arcigera* (Guenée), *S. chrysella* Grote, and *S. bifascia* Hübner. Also, many larvae of *S. nundina* (Drury) were collected from flowers of goldenrod (*Solidago* spp.) in October, but few adults were because they are rarely phototactic.

The following parasitoids were reared:

Diptera
  Tachinidae

Plagiomima similis (Townsend). One specimen reared from larva of *Schinia bina* collected in fall. Puparium formed outside host and overwintered before emerging.

Eucelatoria sp. (*armigera* Coquillet of authors). One specimen reared from *Schinia* sp. Puparium formed outside host, adult emerged in fall without diapausing.

Winthemia rufopicta (Bigot). One specimen reared from *Schinia* sp.

Hymenoptera

Ichneumonidae

Ophion sp. (det. R. S. Peigler using I. D. Gauld & P. A. Mitchell, 1981, The taxonomy, distribution and host preferences of Indo-Papuan parasitic wasps of the subfamily Ophioninae (Hymenoptera: Ichneumonidae), Commonwealth Agric. Bur., Slough, 611 pp.). One reared from *Schinia* sp.

Campoletis sonorensis (Cameron). A few reared from 3rd instar *Schinia bina* and *S. chrysella*. White cocoons formed alongside dried host remains.

Pristomerus spinator (Fabricius). One reared from 2nd instar *Schinia bina*.

Braconidae

Cardiochiles abdominalis (Cresson). Thirty parasitoids reared from *Schinia bina* and *S. arcigera*. Larvae of both host species were collected on *Aster spinosus* Benth.

Microplitis croceipes (Cresson). Two reared from larvae of *Schinia chrysella* collected on *Xanthocephalum dracunuloides* (DC) Shinners.

Cotesia marginiventris (Cresson). From larvae of *Schinia chrysella* collected on *Xanthocephalum dracunuloides* we reared 58 parasitoids. From larvae of *Schinia bifascia* collected on *Ambrosia trifida* L. we reared 13 parasitoids.

Meteoris sp., probably *laphygmae* Viereck. One specimen reared from *Schinia* sp.

Schinia belongs to the same subfamily as *Heliothis virescens* (Fabricius) and *H. zea* (Boddie), two important agricultural pests. Entomologists working on *Heliothis* would be well advised to determine which species of *Schinia* occur in their region and at what population levels, since these could be significant alternate hosts for *Heliothis* parasitoids. Most of the parasitoids listed here attack *Heliothis* (Krombein et al., above).

We thank P. M. Marsh, C. W. Sabrosky, and R. W. Carlson (Systematic Entomology Laboratory, U.S. Department of Agriculture, Beltsville, Maryland) for identifying parasitoids. Robert Wyatt (University of Georgia, formerly Texas A&M University) identified hostplants. Roy O. Kendall kindly offered his previously unpublished records. Adult *Schinia* were determined by D. F. Hardwick (Biosystematics Research Institute, Agriculture Canada, Ottawa). Voucher specimens of parasitoids are in the National Museum of Natural History (Washington, D.C.) and Texas A&M University Entomology Department collections. Paper approved as TA-23149 by Director, Texas Agricultural Experiment Station.

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BOOK REVIEWS

ANIMAL EVOLUTION IN CHANGING ENVIRONMENTS WITH SPECIAL REFERENCE TO ABNORMAL METAMORPHOSIS, by Ryuichi Matsuda. 1987. John Wiley & Sons, New York. 355 pp. $44.95.

> Truth *happens* to an idea. It *becomes* true, is *made* true by events. Its verity *is* in fact an event, a process: the process namely of its verifying itself, its verification. Its validity is the process of its validation.—William James, *The Varieties of Religious Experience* (1902)

What is truth? Specifically, what is truth in evolutionary biology? Neo-Darwinism remains constantly under attack; Fundamentalist Christians may be its most conspicuous antagonists, but neither Darwinism nor the neo-Darwinian synthesis has ever sat well among secular philosophers and humanists of various persuasions, and their objections to them surface and resurface periodically—the proverbial old wine in new bottles. The inheritance of acquired characteristics is an idea hallowed by time if not by recent consensus; it was a familiar theme in 19th- and early 20th-century lepidopterology, which in those days was at the frontier of evolutionary science. Its revival and embrace in Stalin's Soviet Union, with the concomitant suppression of Mendelian genetics for decades, added to its discredit elsewhere. But the idea of Lamarckian inheritance survives, and not only among nostalgic old Reds. It has a certain appeal to idealistic young radicals with no ties to Stalinism but with a faith in the perfectability of mankind through struggle, shared by old Lamarckists like Paul Kammerer. It also survives apart from politics among those who cannot accept an *undirected* ("random," but this word is always misused in such literature) process which leads to *adaptive* results. This position leads to some kind of vitalism. *Animal Evolution in Changing Environments* has links to the vitalist tradition. It is an exercise in wish-fulfillment: neo-Lamarckism *must* be true, therefore it *is*. Such declarations, alas, have no bearing on truth itself, only on our perception of what constitutes persuasive evidence pro or con. For lepidopterists this book is a window on an acrimonious argument which is an important part of our tradition, and is once again prominent in the broader sphere of evolutionary biology.

The book is in two parts. Part I is a polemic in favor of the notion that radical novelty in evolution is generated by genetic assimilation acting on components of the process of development, particularly on metamorphosis as expressed in stressful environments. Essentially the entire argument was advanced by Matsuda in an article in the *Canadian Journal of Zoology* in 1982, which can be seen as a précis of the book. It is summed up even more concisely by fig. 6 of the present volume (p. 244). Part I occupies the first 53 pages, concluding with a "proposal of pan-environmentalism": "Environment consists of both morphogenetic and selective factors . . . the former induces, by response of the genotype, variation upon which the selective factor(s) works . . ." and, graciously, "Neo-Darwinism may be retained as a method of analysis of the evolutionary process where the effect of environmental change or development is minor or negligible" (pp. 52–53). Part II occupies pages 57–355 and is a comprehensive and detailed bibliographic catalogue of cases of abnormal metamorphosis, neoteny, etc. judged by the author to be evolutionarily significant, arranged by taxa. (It also contains, in the aforementioned fig. 6 and accompanying text, the clearest statement of what the author's model *is*.) This is a remarkable achievement which would be of great value to theoreticians (who in these intellectually impoverished times in the English-speaking world know little comparative zoology as a rule)—if only they would read it. It does not read like a novel. It reads more like the telephone book. Matsuda is no Darwin or Gould or Dawkins, and the book suffers from disorganization and choppiness as well as a remarkably dull style for so fervent on advocate. And it must be read critically; like most compilers (the eccentric biogeographer Leon Croizat is a very good comparison), Matsuda himself accepts too much at face value and is prone to wish-fulfilling interpretation. As a student of genetic assimilation myself, however, I confess that about half of Matsuda's bibliography was new to me.

Because I have worked on phenotypic plasticity and genetic assimilation in butterflies for some 20 years, Matsuda and I maintained a correspondence for some time which ultimately led to shared frustration. It was frustrating for Matsuda because he interpreted my results differently than I did, but was unable to convince me that he was right; it was frustrating for me because he seemed so plainly an enthusiast who was after verification of his ideas, which he equated with truth. (To be fair, clearly he saw me as unduly wedded to conventional neo-Darwinism.) More recently I had a somewhat similar interaction with Mae-Wan Ho, of Ho and Saunders, *Beyond Neo-Darwinism*; interestingly, Matsuda and Ho never did agree on the mechanism of genetic assimilation, although both professed a post-Darwinian, neo-Lamarckian viewpoint. A sociology-of-science approach to genetic assimilation as a problem has been undertaken by an American student, and his work should be forthcoming soon. It may clarify some of the issues, but its author has expressed the desire to avoid ideology as a factor. I think this is a mistake.

I am unhappy with Matsuda's handling of my own work and of butterfly polyphenism generally. This is no trivial matter. Historically, butterfly work informed and shaped the opinions not only of specialists like Standfuss and Fischer, but of generalizers and theoreticians who inspired much work and controversy—people like Kammerer, Weismann, Schmalhausen, and Goldschmidt, to name a very mixed bunch. I am especially unhappy because I think Matsuda was really on to something, and his premature declaration of victory will turn so many readers off that what is valid and important in this book will once again be relegated to oblivion. Matsuda, a morphologist by trade, had a fair grasp of both vertebrate and invertebrate endocrinology, but his model depends on his repeated invocation of "the mechanism of gene control," and this does not ring true. It is akin to the promiscuous use of similar language by paleontologists—macroevolutionists. One such, a friend of mine in fact, invoked "reverse transcriptase" in a seminar and was asked in all innocence by a paleontology grad student if he could explain what that was and how it worked; of course he could not. Neither could Matsuda, and he stopped short even of citing relevant literature, including references I gave him. Literature searching ended in 1983, but a lot of highly relevant stuff was already available by then. One searches in vain for the *real* quasi-Lamarckian literature here—exciting stuff such as Gorczynski and Steele on the immune system, John Campbell on gene automodulation, Spergel and others on heritable drug-induced metabolic defects and hormone problems, Cullis on genotrophy in flax—none of which would prove Matsuda's case, but which might at least render it more plausible. As it is, Matsuda clearly did not grasp this literature, and his death shortly before the book went to the publisher denied him the opportunity to make a case to impress any but the already-convinced.

Studies of wing-pattern modification in butterflies may or may not ultimately help to unravel the Lamarckian problem, but we may continue working with the knowledge that this book does not close the matter. Perhaps someday someone will be able to make the assertions Matsuda made in this book, and back them up with a solid case rather than a lot of arm-waving. Then and only then will truth "happen to" the neo-Lamarckian idea.

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THE BUTTERFLY GARDEN, by Mathew Tekulsky, introd. by Robert Michael Pyle, illus. by Susanah Brown. 1985. Harvard Common Press, Boston. x + 144 pp. $8.95 (paper), $16.95 (cloth).

THE BUTTERFLY GARDENER, by Miriam Rothschild and Clive Farrell, illus. by Elisabeth Luard. 1983. Michael Joseph Ltd. and Rainbird Publishing Group Ltd., London. 128 pp. UK £7.95 (hardbound).

When L. Hugh Newman and Moira Savonius published their classic book *Create a Butterfly Garden* in 1967 (John Baker, London), they crystallized and explored for the first time the theory of gardening to encourage butterflies. Native butterflies must be tempted into gardens by their favorite nectar flowers, they asserted, and some may establish breeding populations in gardens if the proper larval foodplants are grown.

Occasional articles on the subject have since been published in horticultural, lepidopterological, and environmental journals, but Rothschild and Farrell's *The Butterfly Gardener* and Tekulsky's *The Butterfly Garden* are the first book-length treatments of this special type of horticulture to appear in almost 20 years. Both are welcome, helpful additions to the limited and scattered literature on butterfly gardening.

The Butterfly Gardener is a strange marriage of what might better have been two separate volumes. The first part, "The Outdoor Butterfly Gardener," is by Miriam Rothschild of the renowned family of British naturalists (daughter of Charles, niece of Walter), an eminent, even awesome entomologist, naturalist, and conservationist in her own right. The second part, "The Indoor Butterfly Gardener," is by Clive Farrell who designed and established the famous London Butterfly House at Syon Park. Rothschild further treats the theme begun by Newman and Savonius, while Farrell explores a very different subject—the butterfly zoo, wherein breeding populations of tropical butterflies are maintained inside a special greenhouse containing their caterpillar hostplants and nectar flowers.

"Flowers and insects have travelled down the ages together, bound up in a kaleidoscopic rainbow relationship of mutual benefit and mutual exploitation," writes Rothschild. Her large garden is divided into three sections, a stone-walled kitchen garden, the grounds surrounding the house and courtyard, and an acre of flowering hayfield in which she has established more than 100 species of wild plants. Her seasonal approach is practical, emphasizing cultivation, conservation, and management of grasses, shrubs, and wildflowers that serve as larval foodplants and adult nectar sources for butterflies. The book includes directions for gathering and sowing wildflower seeds, techniques for mowing fields to minimize disturbance to butterflies in all life stages, and a butterfly garden design. Likewise, much useful information on British butterflies is enmeshed in anecdotes and in historical, cultural, and literary allusions that are a pleasure to wander through, just like a butterfly-filled garden itself. Her chapter on "Grass" is one of the most original, inspired, and delightful short essays I have read. The book deals less with butterflies and gardening than with the author's unique appreciation of them. Her wit and erudition, child-like curiosity, sensitivity, and humility, as well as her love of gardens, plants, butterflies, and people and her understanding of how they interact, shine in every line. This is a piece of great literature. Like Carl Sagan, she is able to distill the spirit of her subject in popular prose.

Farrell's chapters detail the indoor culture of exotic butterflies and their foodplants as a display for public education and enjoyment. Warmth, light, humidity, and ventilation are important considerations in a greenhouse managed for insects as well as plants. Also, an enclosure of this type must be very tight to prevent escape of butterflies and entry of parasites and predators, and no pesticides can be used. In richly informative, straightforward prose, Farrell treats each aspect of indoor butterfly culture, concentrating on easily reared tropical species. His level of detail is thoughtful, helpful, and indicates vast experience and a real talent to communicate. His directions for breeding captive butterflies are among the best available. Farrell's contribution is unique in the literature.

Mathew Tekulsky's *The Butterfly Garden* is the first comprehensive textbook on the subject, and the first butterfly gardening book slanted to the United States and Canada. The author basically reviews existing butterfly gardening lore, giving detailed abstracts of longer original treatments. He includes three chapters on garden setup and plants, plus information on feeders for butterflies like those for hummingbirds, hibernation boxes for adult anglewing butterflies, bait traps, and educational activities for the butterfly garden. Although the author lives in California, he included examples of plants and butterflies from all parts of the continent north of Mexico. Tekulsky is an excellent writer (his chapter transitions are especially well done), but I have a vague sense of disappointment at the lack of original material. Even so, I expect the book to become a classic because it is so thorough. It proved a useful text for a butterfly gardening class I taught in 1987.

Both books are well illustrated. Rothschild and Farrell's has eight exquisite color photographs by Kazuo Unno, Carl Wallace, and Tony Evans, a color dust jacket, and 21 pen-and-ink drawings and decorations by Elisabeth Luard. Tekulsky's has 43 lovely pencil drawings and a beautiful color cover by Susanah Brown. Luard's designs are often very fine (especially the frontispiece), and her drawings do successfully communicate concepts, but poor technique frequently shows in an irritating overuse of stipple-dots. Brown's pencil drawings are wonderful. Both artists have depicted plants and butterflies in lifelike poses.

Each book contains appendices on garden butterflies; wild and cultivated nectar flowers; commercial sources of seeds, plants, butterflies, and equipment; organizations and publications dealing with horticulture, Lepidoptera, wildflowers, and conservation; and references. Tekulsky's section on "Further Reading" is the most complete bibliography of the subject I have seen. The appendices are the most practical sections of the works.

For those who derive great pleasure from seeing the living, moving color of wild butterflies among their blooms, these books are a must!

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SPHINGIDAE MUNDI. Hawk Moths of the World, by Bernard D'Abrera. E. W. Classey, Faringdon, England. 226 pp. 79 plates. 250 × 340 mm, hard cover. £97.50 (ca. $145.00).

Somebody once remarked to Dr. O. Niemeyer, the architect who designed most of the government buildings in Brasilia, the modern capital of Brazil, "your architecture is beautiful, but not always functional". Niemeyer kindly replied: "beauty *is* a function". D'Abrera's book *is* a beautiful book, and, in Dr. Niemeyer's concept, this book fulfills that function perfectly. It is artistically designed, and the plates are magnificent. The colors of specimens, especially those of Neotropical species, are well-balanced. Except for species represented by old, faded, and descaled specimens, the creatures would not be ashamed of their portraits.

To help the reader understand viewpoints to follow, we provide some background information. The first author met D'Abrera in 1979 at the British Museum (Natural History). They frequently spent long hours discussing work, dreams, and difficulties. D'Abrera does not regard himself a professional entomologist. He is, above all, an artist whose main interest is to express his talents through butterflies and moths, and at the same time to produce something beautiful and useful to others. Also, he is not supported by taxpayers, so has to work under great pressures, especially economic pressures. It is difficult to write books on butterflies and moths for a livelihood and to finance publication. This includes the cost of travelling more than 12,000 miles (19,300 km) from his home to the British Museum (Natural History), where he has to do his work, and production financing which includes preparing plates, writing text, designing, type setting, color separation, printing and binding, and export!

We offer this background for several reasons. First, it is important to recognize the motivation and personal sacrifice behind D'Abrera's books. Second, previous reviews of D'Abrera's books may have been unfair. We do not deny there are mistakes, but are they solely the author's fault, or do they reflect the chaotic state of lepidopteran taxonomy? D'Abrera clearly says that the main objective of this book ". . . is to provide, in a synoptic form, a modern illustrated systematic list of the known species of the Hawk Moths

(Sphingidae) of the World. It is not a revision." Is it the responsibility of authors who produce such books to solve all the taxonomic problems before publishing something useful? The task would take many years and involve many workers. Finally, it is possible that some previous reviewers did not, or did not try to, understand the audience to which D'Abrera's books are directed. Professional entomologists might feel that D'Abrera's books only add to the confusion already accumulated. But, what about the people who do not have access to good collections, who cannot travel to museums around the world to examine material, who do not have access to an extensive library? Should they wait another century until the taxonomic chaos is sorted out? In this case, it is preferable to have his work with errors than nothing at all.

This book is divided into four sections: introduction, text and plates, bibliography, and index. The introduction consists of a Foreword explaining objectives, conditions under which the work was carried out, and the style followed throughout. It is followed by an Acknowledgements section expressing gratitude to the late Alan Hayes. The book is based on a check list prepared by Hayes, and on the collection he curated for more than 20 years at the British Museum (Natural History). The Introduction is elegantly written, and describes previous works and general sphingid biology. A useful two-page section entitled "Notes for the Guidance of the Reader" explains abbreviations and symbols used in text and plates, and includes three figures showing important features of wings, pretarsal joint, and head. A Systematic Catalogue of Genera, listing genera in the same order as the text, ends the introduction.

The body of the book—the text and plates—is organized practically. The book was designed to present text alternating with plates so that when the book is opened, text is on the left-hand side, and figures are on the opposite page. This allows the reader to consult the book without having to turn pages back and forth to compare text and figures. This format could not be followed consistently, however, because when many small specimens are on a plate, the accompanying text cannot be included on a single page. The text provides useful information such as variation in color patterns, diagnostic characters, and larval host plants. The plates show entire moths in actual size, and in several cases the underside is also shown to distinguish similar species. The Appendix consists of 4 plates which illustrate 39 type specimens of species not represented in the British Museum (Natural History). They vary in quality: some are good; others are poor, but useful, since most have never been figured. Selected References omits some important works such as M. Draudt (1931. *In* A. Seitz, *Macrolepidoptera of the World*); W. Rothschild & K. Jordan (1907. *Genera Insectorum*); and H. Wagner (1913–1919. *Lepidopterorum Catalogus*). Finally, there are two indexes, one for genera and one for species.

This book has long been needed. The last comprehensive treatment of Neotropical Sphingidae was that of Draudt (cited above). D'Abrera recognizes approximately 1050 species, and illustrates more than 1000. Draudt listed only around 480 names and figured 260 Neotropical specimens. Further, Draudt's work had many faults, specifically with regard to combinations, that are corrected in D'Abrera's book. But we disagree with the sinking of *Neococytius*, and the transfer of *N. cluentius* to *Cocytius*; several cases pointed out by D'Abrera, such as *Dolba* and *Dolbogene*, should have been synonymized following the same criteria. D'Abrera himself regards the latter differences as "trivial." It would have been better to use the same criteria throughout, or to leave genera alone.

The Neotropical species were checked, and no misidentifications found. However, the book has a few mistakes that should have been corrected by the editorial panel. The most serious is authorship and date of family Sphingidae, which is actually Latreille 1802, not Samouelle 1819; and the nominate subfamily name should bear the same authorship and date. Other mistakes include incongruences between numbers of species given by the author and numbers treated in genera. For example, under *Paonias* it is stated that there are two species, but three are actually treated. The same occurs with *Hemeroplanes*, where the numbers are four and five, respectively. In the plates, *Callionima neivai* and *Eumorpha adamsi* are identified as "*neavei*" and "*damasi*." A figure of *Protaleuron rhodogaster* is stated to be in the Appendix, but no figure was found.

By examining this book, it becomes evident that Sphingidae are in desperate need of a revision of higher classification. Several groups such as *Xylophanes*, *Theretra* and

Cechena have species that are difficult to tell apart superficially but are kept in separate genera because they occur in different faunistic regions. Because the groups were too large, or because of difficulties in communication, each fauna was studied separately. The result is that each faunistic region has an independent set of genera. It would be useful to subject the genera to a rigorous character analysis. Cladists, here is a good subject to study!

D'Abrera did a good job on this book. For those who want to start or to organize a collection, and to study the group, it is a good starting reference. We recognize that for many who live in the Poor World, £97.50 is a lot of money. However, when we consider the quality of this book, the prices of books of lesser quality, and the fact that this is a book one would buy only once in a lifetime, it is a bargain.

We thank R. W. Hodges for critically commenting on the review.

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MANUSCRIPT REVIEWERS, 1987

The merit of a scientific journal depends on the quality of its reviewers as well as of its authors, but the former are usually unknown to readers. The *Journal* acknowledges with gratitude the services of the people listed below from whom the editor received manuscript reviews in 1987.

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Sheppard, P. M. 1959. Natural selection and heredity. 2nd ed. Hutchinson, London. 209 pp.

——— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10:165–216.

In General Notes and Technical Comments, references should be shortened and given entirely in the text as P. M. Sheppard (1961, Adv. Genet. 10:165–216) or (Sheppard, P. M., 1961, Sym. R. Entomol. Soc. London 1:23–30) without underlining.

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CYRIL FRANKLIN DOS PASSOS (1887–1986)

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Cyril Franklin dos Passos, eminent student of Nearctic Rhopalocera, and a Charter and Honorary Life Member of the Lepidopterists' Society, died on 29 October 1986, only a few months before he would have celebrated his 100th birthday.

Many who are aware of Cyril's entomological contributions may not know that during an extraordinarily long and full life he had two quite distinct and successive careers. The second is of more concern to us, but as Cyril did not begin his work on butterflies until he was past the age of 40, something must be said of the first.

Cyril was always aware of the Portuguese heritage of his family, a fact that this writer recalls most vividly because of the excellent Madeiran wines served at the dos Passos table. Cyril's paternal grandfather Manoel (later Manuel) dos Passos emigrated to the United States from Ponta do Sol, Madeira, in 1830, becoming a cobbler and later a shoemaker, and finally settling in Philadelphia where he married Lucinda Cattell. There were six children, including Cyril's father Benjamin Franklin Dos Passos (the American family had capitalized the Portuguese lower case d) and an older brother, John Randolph, who would also be of considerable importance in Cyril's life.

John Randolph studied law and became an eminent and affluent New York City attorney, specializing in brokerage and corporation law. He defended trusts, opposed regulation of business by government, and wrote extensively on these and other subjects. He took Benjamin Franklin into his law firm, which became Dos Passos Brothers. Cyril, an only child, was born in New York on 7 February 1887. His mother, Isabel Kirker Strong, was of English descent. His father died in 1898 when Cyril was eleven.

By his own account of his education, Cyril attended several private schools, finally spending eight years at Cutler School in New York City, and graduating in 1905. He read law for two years at Dos Passos Brothers, and entered New York Law School in 1907. Cyril attended classes while working half days in his uncle's Broad Street offices. After receiving his LL. B. *cum laude* in 1909, he was admitted to the New York bar and began to practice in the family firm, becoming a partner.

John Randolph Dos Passos represented railroad interests, and played a large part in the reorganization of various lines. His protégé Cyril eventually entered the railroad business, becoming president and a director of the Kansas, Oklahoma & Gulf Railway Company, which ran from Joplin, Missouri, to Denison, Texas. When a competing line forced Cyril's company into receivership, he incorporated and became secretary, treasurer, and later president of a brokerage firm, the New York and Hanseatic Corporation. During these business activities Cyril maintained his place in the law firm. When John Randolph died in 1917, Cyril inherited the "good will, name and business of Dos Passos Brothers" and his uncle's extensive law library. He was, however, Cyril *dos* Passos, because his mother had encouraged him to use the Portuguese form. (Despite an interest in his own Portuguese heritage, John Randolph's son and Cyril's cousin, the well-known literary figure John Roderigo Dos Passos, chose to retain the Americanized capitalization.)

On 3 August 1927 Cyril married Viola Harriet Van Hise, who would direct his interests toward entomology. She was the youngest daughter of Anthony H. Van Hise and Harriet Louise Archer, and was born at Newark, New Jersey, on 24 November 1891. Having earned a comfortable fortune, Cyril was able in 1928 to retire from law and business, and devote his time to leisure pursuits. The couple lived in Ridgewood, New Jersey, for several years, and enjoyed their summers at the Rangeley, Maine "camp" which Cyril had built before the marriage for hunting, fishing, and other recreation. Their son Manuel, who survives him, was born on 4 February 1929.

Thus was the stage set for Cyril dos Passos' second career. In later life he enjoyed telling the story of his discussions with Viola about taking up an instructive and useful pursuit. Cyril suggested art. Viola, who had been reading copies of W. J. Holland's butterfly and moth books, voted for entomology. She won the day. They decided that she would collect and study Nearctic moths, and he would devote his attention to butterflies.

Collecting began in earnest at the Rangeley camp in 1929. The two set out a sugaring trail, a line of Rummel bait traps, and eventually had a large light trap constructed. A neighbor suggested that Cyril visit the Department of Entomology of the American Museum of Natural History (AMNH), and he did so, making the friendship of Frank E.

Cyril F. dos Passos and friend at Quimby Pond Camps, Rangeley, Maine, 1973

Watson, who helped identify his and Viola's captures. Cyril assisted Watson in disinfecting and otherwise caring for the AMNH collection, and was soon an unofficial "regular," enjoying the encouragement of the department curator, Frank E. Lutz.

Meanwhile, planning was under way for the magnificent French Provincial house which would become well known to Cyril's scientific friends. He had always been partial to things French; his mother (who spoke French fluently and had a French maid) had taken him to France a number of times. Ideas for the house and grounds were assembled from books on minor chateaux and turned over to an architect. Construction began in spring 1931 on ninety partially wooded acres in Mendham, New Jersey. Cyril and Viola wished to move in at the earliest opportunity, and were able to do so by winter.

At the Mendham "chateau" part of the second story was devoted to specimen storage and a rapidly growing entomological library. Viola placed her moths in traditional cabinets, separated by a partition from Cyril's collection. He adopted the use of Watson-Comstock store boxes, designed by his AMNH friends Watson and William P. Comstock, and constructed at Cyril's expense by the museum carpenter. Cyril described the box in his 1957 obituary of Comstock as "quite an ingenious, light and inexpensive affair with top and bottom of heavy cardboard and sides of wood. The bottom is lined with pressed cork." As the collections grew, Viola's moths were moved to another spacious room, and Cyril's specimens filled the original area.

His earliest entomological publications were undertaken with a young correspondent and collecting companion, L. Paul Grey, who has contributed a memoir of his own to this *Journal* issue. The 1934 dos Passos-Grey annotated list of Maine butterflies and its supplement were natural beginnings for the initially Maine-oriented pair who would later revise the Nearctic "argynnids." Cyril gradually became a respected taxonomist, but during his career also published investigations of life histories of imperfectly known butterflies. He was an avid field collector, and because of his financial resources was able to augment his own efforts greatly by hiring collectors to work for him in some remote areas. For example, the first of his many papers with descriptions of new subspecies was based on material sent to him from Newfoundland by Hugh McIsaac.

In 1936 Cyril was appointed Research Associate in the Department of Entomology, AMNH, through Lutz's recommendation. The appointment was regularly renewed until the year before Cyril's death, so that he served a full half-century on the scientific staff. He was instrumental in acquiring the first really large collection of North American butterflies to be added to the AMNH's then relatively modest holdings, being a substantial contributor to the purchase of Jeane D. Gunder's 27,000 specimens in 1937. Cyril later published a catalogue of the Gunder types; he also obtained Gunder's library and added it to his own. As time passed, Cyril was able to buy a number of established collections of significance and integrate them into his previous holdings. One of his purchases was the Alberta and Illinois material of Thomas E. Bean, a correspondent of William Henry Edwards who supplied considerable data used in the third volume of *The Butterflies of North America;* among others were the collections of Max Rothke, E. H. Blackmore, R. F. Sternitzky, Owen Bryant and Louis Doerfel. Types went to AMNH, although Cyril retained most paratypes. When his purchases included moths, these were placed in Viola's cabinets.

Cyril's concern about the significance of types led him to devise an improved method of photographing type specimens and their labels. An apparatus for the purpose had been described by Gunder in 1930, but it had defects, which Cyril remedied. His folding device, utilizing a Leica Model F camera and adjustable floodlights, could adequately record the insect and the many labels often found on types, and could be placed in a suitcase for travel. Cyril visited American and European museums with his camera, and although he restricted his activities chiefly to recording types of North American Rhopalocera, he hoped that through cooperation all remaining type specimens of Lepidoptera could be photographed; while many types might be lost to science over the years, Cyril argued that photographs would create a record that could last indefinitely. By 1945, when he published a description of his apparatus, he had recorded as many as 1200 types. The project was continued, and Cyril's photographs are now in AMNH. Some have been reproduced in his own papers and those of other workers. His original idea still has merit.

Cyril's early taxonomic work chiefly concerned Lycaenidae and Satyridae, although he also published on nymphalids. His first synonymic catalogue, which appeared in 1939, was of the North American Satyridae, part of a proposed but ill-fated catalogue with references to original descriptions of all Rhopalocera north of the Mexican border, edited by F. Martin Brown and R. W. L. Potts, which failed from lack of funding.

During World War II Cyril suffered a great loss. Viola, who had continued to collect moths, had a heart attack in 1939, and her activities were restricted. She died at Rangeley on 29 August 1944. Later in that year Cyril donated her collection, which included over 12,000 specimens, to AMNH.

The collaboration with L. Paul Grey on the Argynninae, discussed in the accompanying memoir, began to bear fruit during the war years. Their first three joint papers appeared in 1942 and 1945; the third was one of three independent genitalic studies (the others by B. C. S. Warren and F. A. T. Reuss) which led to a new scheme of classification of the subfamily, restricting the genera *Argynnis* and *Brenthis* to the Palearctic region, leaving *Boloria* as Holarctic, and *Speyeria* and *Euptoieta* as Nearctic genera. The dos Passos-Grey systematic catalogue of *Speyeria* was published in 1947. They concluded that although 109 published names attributable to *Speyeria* were valid, only 13 species were involved.

Reviewing the revision in *The Lepidopterists' News,* Charles L.

Remington noted that before the work of dos Passos and Grey, "different authors accepted a widely varying number of distinct species in the group, many supposed affinities were entirely wrong, and uncorrelated new 'races' continued to be described. The challenge of ordering the chaos was grasped at that time by L. Paul Grey, who disposed of his excellent collection of North American Lepidoptera to devote all his time and space to the 'Args.' He was fortunate to be joined by C. F. dos Passos, who had the means, the equipment, and the methodical mind to scour the scattered literature, visit a number of museums to examine carefully the types, and study the numerous nomenclatorial problems." The 1947 paper has recently been mentioned by Scott in *The Butterflies of North America* (1986) as helping to turn the trend of "splitting" into the more sophisticated concept of species we have today.

When the Lepidopterists' Society was formally constituted in May 1947, Cyril was a charter member. He served on the very early Board of Specialists (which identified specimens for Society members) for the family Satyridae. For the first two and a half years of its existence the Society operated under "articles of organization," published in the first issue of *The Lepidopterists' News.* In 1950 editor Remington asked Cyril to prepare a formal constitution and by-laws. He did so, and served as chairman of an international committee to study and approve the draft, which was ratified by members at the first annual meeting. Cyril's committee appointed temporary officers to serve the Society until the first election by the membership, and it was due to the dos Passos committee's good judgment that the Society's first president was a lepidopterist of the very highest reputation, Cyril's friend James H. McDunnough, whom he had met while photographing types at the Canadian National Collection in the 1930's. Cyril served on the Karl Jordan Medal Awards Committee, and was elected an Honorary Life Member in 1973.

He attended the International Congresses of Zoology at Paris (1948), Copenhagen (1953), and London (1958), participating in the prior colloquia, sections, and other activities devoted to nomenclature. He read papers on nomenclature at Copenhagen and London, and frequently during the decade (as well as occasionally afterwards) contributed to the *Bulletin of Zoological Nomenclature,* proposing and commenting on decisions of the International Commission, and discussing and suggesting amendments to the *Règles Internationales,* later the *International Code of Zoological Nomenclature.* He also traveled to a number of International Congresses of Entomology, and during these and other journeys out of the country, he made many scientific friendships and added considerable material to his entomological holdings. He especially enjoyed collecting in Europe, and did so widely.

During this active period, Cyril was appointed Research Associate by the Carnegie Museum (1952). He continued to publish on Satyridae and on topics as diverse as the eye colors of *Colias* and the ethics of scientific criticism. On 3 September 1959, Cyril married Maria Amália Pita Pestana Reis, who survives him. She is the daughter of Maria Pita de Macedo and Miguel Pestana dos Reis and was born in Ponta do Sol, the birthplace of Cyril's paternal grandfather. Maria Amália brought Cyril much happiness, and the great success of his second marriage was evident to his friends.

The result of a project of some years' length appeared in 1964 as *A Synonymic List of the Nearctic Rhopalocera,* this Society's Memoir No. 1 and, with its supplements, Cyril's most significant and useful contribution as single author. Much of his time in later years was devoted to the full catalogue of Nearctic butterflies announced as forthcoming in the introduction to his 1964 checklist. The typescript eventually grew to seven volumes, but the work was discontinued due to the impending appearance of Miller and Brown's *A Catalogue/Checklist of the Butterflies of America North of Mexico* (1981).

Work on such tasks as the checklist and catalogue was made easier because Cyril had built one of the most extensive private entomological libraries in America. When he wished to search the literature he seldom had to leave his home, for most of the works in which North American butterflies were described, from the 18th century onward, were there, not only monographs but runs of journals. For an historian and bibliographer of entomology, the most exciting part of a visit to the dos Passos chateau was the time spent in the library. One example will suffice; during research on John Abbot, I was examining varying watermarks in copies of Smith and Abbot's *The Natural History of the Rarer Lepidopterous Insects of Georgia* (1797) to determine the length of its publishing history. Cyril was able to show me not one copy but two, the second being a volume of the plates issued later with a publisher's imprint I have never seen elsewhere than in the great library which was donated to Wittenberg University, Springfield, Ohio, during Cyril's last years.

His concern with books and libraries, and his devotion to AMNH led Cyril to give considerable assistance to the Museum's library. He published a number of bibliographical papers and (with William D. Field and John H. Masters) a very useful volume, *A Bibliography of the Catalogs, Lists, Faunal and Other Papers on the Butterflies of North America North of Mexico Arranged by State and Province* (1974).

Some of Cyril's bibliographical writings dealt with the actual dates of publication of literature containing descriptions of insects, which of course are important in determining priority. Cyril's frequent work with descriptions quite naturally led to an interest in the history of entomology, to which his major contribution was his edition of William Henry Edwards' entomological reminiscences (1951); the manuscript was loaned to him for the purpose by Edwards' granddaughter.

Among Cyril's later publications were two substantial studies (and models for emulation) co-authored with Alexander B. Klots. The first (1969) concerned the pierid *Anthocharis midea* (Hübner). As explained in their introduction, for many years they had recognized the need for a detailed investigation of *midea* to clarify such problems as geographic variation and nomenclature, and had been accumulating data and specimens toward that end. The resulting paper, which also treated life history, foodplants, and parasites, was an exemplary discussion of a species and its subspecies. They had also been gathering data about the lycaenid *Erora laeta* (W. H. Edwards), and had jointly and severally conducted field studies between 1934 and 1968. Their thorough paper on the genus *Erora* (1982) examined early stages, ethology, ecology, and geographic distribution of *laeta* and *E. quaderna sanfordi* dos Passos, and provided synonymies. An extensive taxonomic study of the satyrids *Lethe portlandia* (Fabricius) and *L. anthedon* (Clark) was published by J. Richard Heitzman and Cyril (1974); incidentally, these three papers provide excellent examples of the use of Cyril's photographs of type specimens. On his own, Cyril produced his usual variety of publications nearly to the end, although his last appearance in print was as co-author with Clifford D. Ferris, James A. Ebner, and J. Donald Lafontaine of an annotated list of Yukon butterflies (1983). It was appropriate that Cyril's final paper concerned the far-northern fauna he loved.

Cyril donated his entomological collection to AMNH in 1980. At that time the butterflies were contained in over 1250 store boxes. Announcing the event in the *Journal*, curator Frederick H. Rindge stated that the collection was undoubtedly "the single largest and most complete one of North American butterflies ever made by one individual." He noted that the gift included over 65,000 specimens; of those which were mounted and identified, 57,870 were North American and 6182 were European. There were 464 paratypes (Cyril had consistently deposited holotypes and allotypes in AMNH) and 617 slides, chiefly of genitalia but also of venation. Cyril intended that his correspondence and other manuscript materials should go to AMNH, and the transfer was made by Maria Amália in 1987.

Cyril was a member of a number of scientific societies, and a Fellow of the Royal Entomological Society of London (1950–). He was also a Fellow of the Linnean Society of London (1977–), where many years previously he had photographed Linnaeus' types of North American butterflies. Wittenberg University awarded him an honorary D.Sc. in 1965, and McDunnough named the copper *Lycaena epixanthe dospassosi* after him in 1940.

Those who knew Cyril were aware that his interests were by no means limited to entomology. They ranged over the entire field of natural history, including ornithology, geology and paleontology, and extended to archaeology. He assembled extensive and valuable holdings of classic postage stamps and covers of the United States, including proofs, and also acquired the stamps of Nepal, Tibet, Heligoland, the British Commonwealth, and France. He was a contributor to philatelic journals.

Cyril was a man of many parts. He gave to entomology an unrivaled private collection of Nearctic Rhopalocera, many examples of financial generosity, and 50 years of publications of high professional quality. Much has been written by historians about the professionalization of science, a relatively recent transition from a past in which scientific foundations were laid by workers educated in other areas. In some cases the process has led to too rigid a distinction between professional and amateur. It is still possible to make important and lasting contributions to entomology without earning a graduate degree in the subject or a related discipline; witness Cyril F. dos Passos, an amateur who made our science his profession and served it very well.

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MEMORIES OF CYRIL F. DOS PASSOS (1887–1986)

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The magnitude of "d.P.'s" accomplishments, as chronicled in the preceding article by R. S. Wilkinson, will attest that he was an unusual individual. Some of my memories of him, and experiences with him as a correspondent, collaborator and friend, perhaps will add to the picture of the kind of person who could live so full a life, with outstanding success in so many varied endeavors.

Quite inevitably he had to be an energetic worker, but in addition he carried methodical procedure and time budgeting almost to the status of an art form. When he was in his prime, few if any random intrusions crept into schedules determined days or weeks in advance. Usually there was a brief nap after lunch, followed by a half-hour's walk; aside from this, very little else in the way of relaxation except at meals. Those were ceremonious, especially at dinner, and served at the precise times appointed. He had uncompromising ideas about how things should be done, including the conduct of his own life and the running of his household. When you dined with him you wore a coat and tie. I used to describe him (jokingly, and never within his hearing) as "the last of the barons". Indeed he was more the Old World aristocrat (in the best sense) than the American businessman.

My first contact with him came shortly after he had begun studies at the American Museum. He wrote to me for information on collecting Maine butterflies. I learned that he had a summer camp at Rangeley, where he came to escape his perennial troubles with hay fever. This lead to meetings, discussions, and the beginning of a lifelong friendship. Our first meeting probably left a lingering impression, to put it delicately, since I was on a manure cart at the time, spreading richness on my father's farm. Anyhow, he never forgot that I was his "very first entomological correspondent", and he came to be my closest associate among the amateur lepidopterists who, at that time, in the very early 30's, comprised a rather small fraternity.

On one of our earlier outings we collected *Oeneis katahdin* Newcomb. Cyril had reserved a cabin for us at a sporting camp on Daicey Pond, reached by a long hike from where we had to leave the car. The next day we paddled across the lake and struck out through the woods with only occasional glimpses of the distant mountain. The region then was almost as wild as in Thoreau's time, with few trails. We finally came out in a clearing where a major campground of Baxter State Park now is located; here we picked up Katahdin Stream which we followed up to the steep slopes of the spruce belt, and from thence to timberline and up over the rocks to the tableland. I still remember how amazed I was that a city lawyer could find his way through the woods as well as a country native, and could endure the long day's ordeal without apparent discomfort. Worse yet, he caught more *katahdin* than I did, using the slow stalking approach while I was dashing hither and yon making wild swoops at anything arising from the tundra. Even the day's end had a lesson for me, when, in the evening back at our cabin, he spent a few minutes writing in a diary, advising me to consider the uses of such. For him, in future years, there would be no doubt concerning what he had accomplished during this particular day of his life, nor would there be any lack of details should he ever wish to refresh his memory about his series of *katahdin* butterflies and the place where he took them.

Subsequent occasions bore out the conclusion that Cyril was a tough physical specimen, which never would have been guessed in view of his small stature and rather delicate frame. But then, this seems to have been a family heritage, judging from stories told of his cousin, John, the well-known author. Apparently the latter had lead a wild life, soaking up "local color" in some of the most dangerous places on earth, a midget holding his own among giants. As one commentator put it, "John actually did the things Hemingway bragged about doing". This was a clue and key to much of Cyril's success and also to a reputation he gained at the Museum of being difficult to get along with, namely, the trait which psychologists term "overcompensation". He always was aggressive when challenged.

In retrospect I marvel that we remained friendly, since I ventured to argue with him rather hotly on various issues. Predictably, he was laissez-faire capitalist in philosophy, often in a rage against the socialist trends of the day. In view of our present national debts and deficits I am becoming convinced that his opinions made far more sense than mine.

Certainly our entomological relations always were very cordial. A mountain of correspondence passed between us as we worked out details of a major joint project, a study of nearctic "*Argynnis*". This was for several years a shared labor, with results which at that time proved to be somewhat controversial. As Scott has pointed out, in the latest *Butterflies of North America,* we made a break in tradition toward synthesis, away from the (European-fueled) tendency to finer and finer splitting. Cyril's role in all of this sometimes has been underestimated. He was in every respect the senior author. He did a lion's share of the work and definitely was the "maker-possible" for my contributions. A bit of review may be of historical interest:

I can pinpoint the exact moment when this project was born. It was sparked by our shared exasperation that nobody seemed able to identify our western material, and ignited one day when Cyril was showing me some California specimens which he had purchased with the understanding that they were to have been identified by the collector. But they arrived minus names, aside from one specimen which bore a label stating "this looks like an oddball". So it did, and to our eyes so did all the rest.

From that time onward we each began a serious study of those enigmas, Cyril working with the literature and with the problems of nomenclature hinging on locating and identifying type materials, while I accumulated specimens and solicited all my collector friends for locality data. Apparently we each had intuitively analyzed our respective strengths and adapted to integrate them. He trusted and never questioned my developing ideas concerning the speciations, while I certainly was in no position to question his grasp of the literature or his plans for organizing our subjects. It made for a smooth-working partnership.

Wilkinson has noted some of the instances of Cyril's quiet philanthropies. I suspect Cyril derived considerable enjoyment in introducing me to the world beyond my native turf. He paid my way for trips to Boston, New York, Philadelphia and Pittsburgh, where I expanded our argynnid data and was able to see numerous types. An incidental but priceless feature of those journeys was the opportunity to meet and talk with people such as Andrei Avinoff at Pittsburgh, Vladimir Nabokov and Nathan Banks at the Museum of Comparative Zoology, and of course the entomologists then at the American Museum, including Lutz, Mitchener, Klots, and that very gracious gentleman, W. P. Comstock. Also, Cyril took me to meetings where I heard lectures by such legendary figures as "William T. Davis of Staten Island" (the two are inseparable) and Robert Cushman Murphy, the great authority on oceanic birds. All in all, quite an education for a youth from the backwoods! These debts are gratefully acknowledged.

Also, I should express my appreciation for his cautious guidance as we came nearer to our goal of revising the North American argynnids. It had become apparent fairly early that the records seldom indicated more than 6 or 8 distinct kinds of populations of those butterflies in any single general area, a fact of significance when compared against the listings then current, which ran to 100 "species" or more. Collations of local data sets also indicated numerous instances of intergrading. I felt that we were on the verge of solving the puzzle, but Cyril then urged that we had a duty to enlarge the perspective to include whatever might appear when native argynnids were compared with those on the other continents. A fairly comprehensive genitalic survey of the Nearctic species had been completed, but the task of studying the world argynnines was slowed by difficulties in procuring the needed material.

Thus, it was 1947 before our Systematic Catalogue of *Speyeria* finally was published. A few corrections have been required, both to Cyril's nomenclatorial and other data and to my concepts of the speciations, but these have been gratifyingly few considering the tangle we were dealing with. It was, indeed, as Scott has noted, a turning point in the philosophy of butterfly "species", but unfortunately we were too much captives of the times to have broken loose from the addiction to "subspecies". In fact, back at that time it would have been unwise to have reduced the number of such taxa, even though many are hardly more than unstable local color forms. As Cyril had warned me, we encountered considerable resistance to our radically altered classification, the big difficulty lying with our downgrading of many taxa traditionally hallowed as "species". To help soften those outrages to custom we thought it essential to retain numerous subspecific names and even to propose some new ones for the same purpose of indicating some of the connecting links and the widespread continuity of intergrading within the series discriminated as constituting polytypic species.

After those prolonged associations it seemed only natural that we should remain close and affectionate friends. When failing health forced him to curtail his entomological activities he presented me with the entire contents of his laboratory. I remain surrounded by reminders of his kindness.

In closing, it seems fitting to recall one of Cyril's most striking mannerisms. He never lingered when the time came to part—a wave of the hand, a "bye-bye" and he would turn abruptly and walk away. Fond recollections remain.

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ANNOTATED BIBLIOGRAPHY OF THE ENTOMOLOGICAL PUBLICATIONS OF CYRIL F. DOS PASSOS (1887–1986)

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This bibliography includes all of Cyril dos Passos' entomological publications known to me except his abstracts of current literature published in early issues of *The Lepidopterists' News.* All publications have been personally examined; in most cases separates or reprints had been furnished to me by the author during his lifetime with a bibliography in mind, and a search of the literature has revealed additional publications.

Arrangement of entries is chronological according to actual dates of publication, which were determined by examination of journal issues, and through correspondence and other methods. Items identified by asterisk (*) have not been dated precisely, but these do not affect the chronology. Titles of publications are exact, although I have uniformly italicized generic and specific names. Citations of place of publication are followed by stated date and, in parentheses, actual date if it differs or is more precise. The summaries of content are, of necessity, somewhat uneven; as might be expected, those of notes or brief papers may include details that would not have been mentioned had the work been of greater length. All new names proposed by dos Passos have been included. When new species, subspecies, or forms were named, I have provided the type locality, either the name of the collector of the holotype or the collection from which it was selected (the latter if the collector is not specifically named in the paper), and the holotype repository, all as indicated by dos Passos. All fixations of type localities and designations of lectotypes and neotypes have been documented. In the summaries, names are given the standing accorded to them by dos Passos, and are printed as they appeared in print (forms are italicized, for example).

I am grateful for the extensive assistance of Maria Amália dos Passos and F. Martin Brown, and for the kind cooperation of L. Paul Grey, who has informed me that he holds, entrusted to him by the author, an incomplete dos Passos manuscript not yet prepared for publication.

The following are some abbreviations used: AMNH: American Museum of Natural History, New York City; CM: Carnegie Museum of Natural History, Pittsburgh; USNM: U.S. National Museum, Smithsonian Institution, Washington, D.C.; j.a.: junior author; s.a.: senior author; t.l.: type locality. Postal abbreviations are used for States.

1934

1. With L. P. Grey, j.a. A list of the butterflies of Maine with notes concerning some of them. Can. Entomol. 66:188–192, Aug. 1934 (2 Sep. 1934). 110 taxa reported including subspecies, forms.
2. With L. P. Grey, j.a. Additions and corrections to "A list of the butterflies of Maine." Can. Entomol. 66:278, Dec. 1934 (31 Dec. 1934). 7 taxa added; 2 deleted.

1935

3. Some butterflies of southern Newfoundland with descriptions of new subspecies (Lepid. Rhopal.). Can. Entomol. 67:82–88, Apr. 1935 (4 May 1935). Discussion of collection made in 1934 by H. McIsaac; *Coenonympha inornata mcisaaci,* n. ssp. (t.l. Doyles Station, Newfoundland, H. McIsaac); *Oeneis jutta terrae-novae,* n. ssp. (t.l. Doyles Station, Newfoundland, H. McIsaac); *Argynnis atlantis canadensis,* n. ssp. (t.l. Doyles Station, Newfoundland, H. McIsaac); *Phyciodes tharos arctica,* n. ssp. (t.l. Table Mountain, Port au Port, Newfoundland, G. C. Hall); all holotypes in AMNH; McIsaac's collection included 21 taxa; 12 additional taxa listed as occurring in Newfoundland.

1936

4. Further notes on the butterflies of southern Newfoundland. Can. Entomol. 68:98, May 1936 (6 Jun. 1936). In 1936 H. McIsaac collected 2 species not previously reported from Newfoundland.
5. The life history of *Calephelis borealis* (Lepidoptera). Can. Entomol. 68:167–170, 1 pl. incl. 6 figs., Aug. 1936 (29 Aug. 1936). *C. borealis* appears to be single-brooded in NJ; females observed ovipositing on *Senecio obovatus* Muhlenberg; insect reared; egg, instars of larva, pupa discussed, figured.
6. Some early stages of *Brenthis montinus* Scudder (Lepidoptera—Nymphalidae). Can. Entomol. 68:239–241, 1 pl. incl. 4 figs., Nov. 1936 (5 Dec. 1936). Specimens confined over various plants; all eggs on *Solidago cutleri* Fernald except some on sides of breeding cages; perhaps eggs are dropped on ground, fall into detritus in which larvae, upon emerging, hibernate; egg, first instar larva discussed, figured.

1938

7. Some new subspecies of North American Lycaenidae (Lepid.). Can. Entomol. 70: 45–48, 1 pl. incl. 16 figs., Mar. 1938 (2 Apr. 1938). Material from various collections described as *Lycaena nivalis browni,* n. ssp. (t.l. Snowslide Canyon, 8 mi [13 km] from Montpelier, ID, W. J. Gertsch); *Plebeius saepiolus gertschi,* n. ssp. (t.l. Cedar Breaks, nr. Cedar City, UT, W. J. Gertsch); *Plebeius icarioides buchholzi,* n. ssp. (t.l. White Mts., AZ, 8500 ft [2591 m], E. Y. Dawson); *Plebeius acmon lutzi,* n. ssp. (t.l. Snowslide Canyon, 8 mi [13 km] from Montpelier, ID, W. J. Gertsch); all holotypes in AMNH; holotypes, allotypes figured.
8. Synonymic notes on *Aglais milberti* (Godart) with the description of a new subspecies (Lepidoptera—Nymphalidae). Can. Entomol. 70:72–73, 1 pl. incl. 6 figs., Apr. 1938 (14 May 1938). Type locality of *A. milberti* fixed; Godart's type figured; *A. m. rothkei* Gunder jr. synonym of *milberti*; *Vanessa furcillata* Say distinct form of *milberti*; *V. m.* var. *subpallida* Cockerell distinct form of *milberti*; Cockerell's type figured; *Aglais m. viola,* n. ssp. (t.l. Doyles Station, Newfoundland, H. McIsaac); holotype in AMNH; holotype, allotype figured.
9. The types of Lepidoptera described by J. D. Gunder. Am. Mus. Novit. No. 999, 16 pp., 26 Jul. 1938. Gunder's collection of North American Lepidoptera (chiefly western Rhopalocera), recently acquired by AMNH, contains type material for 171 of 212 taxa described by him; all types listed; references given to original descriptions, type localities, collectors' names, disposition of types when not at AMNH.
10. A new race of *Euphydryas chalcedona* Dbldy. & Hew. from Arizona (Rhopalocera—Nymphalidae). Can. Entomol. 70:199–200, 1 pl. incl. 4 figs., Oct. 1938 (5 Nov. 1938). Material received for several years as *E. hermosa* (Wright) described as *Euphydryas*

chalcedona klotsi, n. ssp. (t.l. Roosevelt Lake, AZ, D. K. Duncan); holotype in AMNH; holotype, allotype figured.

11. A new race of *Basilarchia archippus* Cramer from Louisiana (Rhopalocera—Nymphalidae). Can. Entomol. 70:243, 1 pl. incl. 4 figs., Dec. 1938 (31 Dec. 1938). A previously undescribed "race" in Gulf States, *Basilarchia archippus watsoni,* n. ssp. (t.l. Alexandria, LA, J. Woodgate); holotype in AMNH; holotype, allotype figured.

1939

12. A catalogue of the original descriptions of the Rhopalocera found north of the Mexican border. Part two: the Satyridae. Bull. Cheyenne Mountain Mus. 1, part 2, 13 pp., 20 Apr. 1939. Synonymic catalogue with type localities and full citations to descriptions.

1940

13. A new subspecies of *Erora laeta* Edwards from Arizona and New Mexico (Rhopalocera: Lycaenidae). Am. Mus. Novit. No. 1052, 2 pp., 15 Mar. 1940. *Erora laeta sanfordi,* n. ssp. (t.l. White Mts., AZ, 8000 ft [2438 m], D. K. Duncan); holotype in AMNH.
14. A new subspecies of *Erebia discoidalis* Kirby (Rhopalocera: Satyridae). Am. Mus. Novit. No. 1053, 2 pp., 22 Mar. 1940. Material from Alberta to AK described as *Erebia discoidalis mcdunnoughi,* n. ssp. (t.l. White Horse, AK, J. A. Kusche); holotype in AMNH.
15. A new species of *Incisalia* from southern California (Rhopalocera, Lycaenidae). Can. Entomol. 72:167–168, Aug. 1940 (31 Aug. 1940). *Incisalia doudoroffi,* n. sp. (t.l. Big Sur, Monterey Co., CA, M. Doudoroff); holotype in AMNH.
16. On the occurrence of *Papilio polydamas* Linnaeus within the United States. Can. Entomol. 72:188, Sep. 1940 (30 Sep. 1940). *P. p. lucayus* not only subspecies in U.S. as *P. p. polydamas* also occurs here; TX specimens in collections acquired by dos Passos.

1942

17. With C. D. Michener, s.a. Taxonomic observations on some North American *Strymon* with descriptions of new subspecies (Lepidoptera: Lycaenidae). Am. Mus. Novit. No. 1210, 7 pp., 5 figs., 13 Nov. 1942. *Strymon* of *calanus* group discussed; *S. liparops* (Boisduval & LeConte) synonym of *S. favonius* (J. E. Smith), so species usually called *liparops* becomes *strigosus* Harris; *Strymon strigosus aliparops,* n. ssp. (t.l. Glenwood Springs, CO, Oslar); holotype in AMNH; *S. liparops* (Fletcher) homonym of *liparops* (Boisduval & LeConte), renamed *Strymon strigosus fletcheri,* n. name; lectotype designated (cotype of *Thecla strigosa liparops* Fletcher, USNM); neotype designated for *S. edwardsii* (Grote & Robinson); genitalia figured.
18. With L. P. Grey, j.a. Two new North American subspecies of *Argynnis,* with some revisional notes (Lepidoptera: Nymphalidae). Am. Mus. Novit. No. 1214, 6 pp., 1 fig., 8 Dec. 1942. Material from Gunder collection and others described as *Argynnis utahensis linda,* n. ssp. (t.l. Heyburn Peak, Sawtooth-Boise, ID, 9500–10,000 ft [2896–3048 m], C. W. Herr); *Argynnis coronis carolae,* n. ssp. (t.l. Charleston Park, Clark Co., NE, E. Schiffel); both holotypes in AMNH; both holotypes figured; *A. pfoutsi* Gunder a synonym of *A. platina* Skinner; *A. albrighti* Gunder appears to be form of *A. mcdunnoughi* Gunder, a subspecies of *A. utahensis* Skinner; *A. semivirida* McDunnough correctly placed with *A. nevadensis* W. H. Edwards, a species distinct from *A. utahensis*; *A. chitone* W. H. Edwards a subspecies of *A. hesperis* W. H. Edwards; *A. snyderi* Skinner not a subspecies of *A. coronis* Behr; *A. monticola* Behr a synonym of *A. zerene* Boisduval; *A. malcolmi* Comstock a race of *A. zerene*; *A. conchyliatus* Comstock might be subspecies rather than form of *A. zerene.*

1943

19. Some new subspecies of *Incisalia* from North America (Lepidoptera, Lycaenidae). Am. Mus. Novit. No. 1230, 5 pp., 1 Jun. 1943. Scudder, not Minot, is author of

Incisalia; type localities fixed for *I. augustus* (Kirby), *I. augustus croesioides* Scudder, *I. iroides* (Boisduval), *I. henrici* (Grote & Robinson), lectotypes designated for these taxa; *Incisalia iroides annetteae*, n. ssp. (t.l. New Mexico, *ex* J. D. Gunder collection); *Incisalia augustus helenae*, n. ssp. (t.l. Doyles Station, Newfoundland, H. McIsaac); *Incisalia henrici margaretae*, n. ssp. (t.l. 8 mi [13 km] E Deland, FL, B. Heineman); all holotypes in AMNH.

20. A new Riodinid record. Can. Entomol. 75:108, Jun. 1943 (23 Jul. 1943). H. A. Freeman furnished 4 specimens of *Apodemia walkeri* Godman & Salvin, Brownsville, TX, 2–9 Jun. 1940, a new U.S. record.
21. A correction. Can. Entomol. 75:178, Sep. 1943 (21 Oct. 1943). In 3 above *Polygonia comma* (Harris) reported from Newfoundland; specimens were *P. marsyas* (W. H. Edwards).

1945

22. Some collections of Lepidoptera. J. New York Entomol. Soc. 53:62, Mar. 1945 (4 May 1945). Since 1935 dos Passos acquired collections of E. H. Blackmore, Victoria, British Columbia; T. E. Bean (IL, Alberta material); M. Rothke, Scranton, PA; R. F. Sternitzky, San Francisco, CA; O. Bryant (including his Arctic material); L. Doerfel, Newark, NJ; most paratypes retained; other types now in AMNH.
23. With L. P. Grey, j.a. A new species and some new subspecies of *Speyeria* (Lepidoptera, Nymphalidae). Am. Mus. Novit. No. 1297, 17 pp., 30 figs., 10 May 1945. Material from various collections described as *Speyeria wenona*, n. sp. (t.l. Cerro Potosi, Municipio de Galeana, Nuevo Leon, Mexico, 12,000 ft [3658 m], R. A. Schneider); *Speyeria cybele letona*, n. ssp. (t.l. City Creek Canyon, Salt Lake City, UT, 4500 ft [1372 m], W. L. Phillips); *Speyeria coronis simaetha*, n. ssp. (t.l. Black Canyon, Cascade Mts., nr. Brewster, WA, J. C. Hopfinger); *Speyeria zerene myrtleae*, n. ssp. (t.l. San Mateo, CA, W. F. Breeze); *Speyeria z. sinope*, n. ssp. (t.l. Estes Park area, Rocky Mt. National Park, CO, 8000 ft [2438 m], R. Weist); *Speyeria z. cynna*, n. ssp. (t.l. Humboldt National Forest, Ruby Valley, Elko Co., NV, E. Schiffel); *Speyeria callippe elaine*, n. ssp. (t.l. Butte Falls, OR, *ex* J. D. Gunder collection); *Speyeria c. sierra*, n. ssp. (t.l. Gold Lake, Sierra Co., CA, C. Hill); *Speyeria c. harmonia*, n. ssp. (t.l. Mt. Wheeler, Snake Range, nr. UT border, NV, 8000 ft [2438 m], *ex* J. D. Gunder collection); *Speyeria montiviga* [sic.] [*montivaga*] *secreta*, n. ssp. (t.l. Estes Park area, Rocky Mt. National Park, CO, 8000 ft [2438 m], R. Weist); *Speyeria hydaspe conquista*, n. ssp. (t.l. Little Tesuque Canyon, nr. Sante Fe, NM, 8000 ft [2438 m], A. B. Klots); *Speyeria atlantis lurana*, n. ssp. (t.l. Harney Peak, Black Hills, SD, A. C. Frederick); *Speyeria a. wasatchia*, n. ssp. (t.l. Payson Canyon, Payson, UT, L. D. Pfouts); *Speyeria a. tetonia*, n. ssp. (t.l. Teton Mts., WY, *ex* J. D. Gunder collection); *Speyeria a. viola*, n. ssp. (t.l. Trail Creek, Sawtooth Mts., ID, 7400 ft [2256 m], C. W. Herr); all holotypes in AMNH; all holotypes figured.
24. With L. P. Grey, j.a. A genitalic survey of Argynninae (Lepidoptera, Nymphalidae). Am. Mus. Novit. No. 1296, 29 pp., 54 figs., 14 Sep. 1945. Genitalia generally discussed, distinctive characteristics given for genera *Boloria* (21 species), *Brenthis* (3 species), *Argynnis* (18 species), *Speyeria* (7 species), *Euptoieta* (2 species); 3 independent genitalic studies of Argynninae conducted (present and those of B. C. S. Warren and F. A. T. Reuss); agreements and disagreements reviewed; *Brenthis* and *Argynnis* should be restricted to Palearctic species; Palearctic *Brenthis* should be set apart from Holarctic *Boloria*, which may require several genera or subgenera; Nearctic *Speyeria* distinct from *Argynnis*; genitalia figured.

1946

25. "1945." The photography of types of Lepidoptera. Bull. Brooklyn Entomol. Soc. n.s. 40:166–169, 4 figs., Dec. 1945 (15 Mar. 1946). Improvement on apparatus of J. D. Gunder described, illustrated; type specimens may be photographed with all their labels, without reflections, shadows; cooperative effort proposed to photograph all types of Lepidoptera.
26. With B. C. S. Warren, s.a., and L. P. Grey. Supplementary notes on the classification

of Argynninae (Lepidoptera, Nymphalidae). Proc. Roy. Entomol. Soc. London ser. B, 15:71–73, 15 Jun. 1946. New tribal division, Boloriidi, proposed to include *Boloria, Proclossiana, Clossiana*; the other tribe, Argynnidi, includes *Brenthis, Yramea, Issoria, Speyeria, Fabriciana, Mesoacidalia, Damora, Pandoriana, Childrena, Argyreus, Argyronome*; Reuss's *Neoacidalia* synonym of *Speyeria.*

1947

27. Notes on Grinnell's types of *Erynnis* Schrank (Lepidoptera, Hesperiidae). Am. Mus. Novit. No. 1337, 3 pp., 24 Feb. 1947. *E. callidus* (Grinnell) should include *E. c. callidus* (Grinnell), *E. c. pernigra* (Grinnell), *E. c. lilius* (Dyar); lectotype designated for *Thanaos callidus* Grinnell.
28. *Erebia youngi* Holland, its subspecies and distribution (Lepidoptera, Satyridae). Am. Mus. Novit. No. 1348, 4 pp., 14 Jul. 1947. *E. herscheli* Leussler a subspecies of *E. youngi* Holland; *Erebia y. rileyi,* n. ssp. (t.l. Mt. McKinley National Park, AK, *ex* J. D. Gunder collection); holotype in AMNH.
29. With L. P. Grey, j.a. Systematic catalogue of *Speyeria* (Lepidoptera, Nymphalidae) with designations of types and fixations of type localities. Am. Mus. Novit. No. 1370, 30 pp., 12 Dec. 1947. 109 names published prior to end of 1946 found attributable to *Speyeria*; these represent 13 valid species; remaining 96 names considered subspecies; 58 synonyms; valid species are *S. diana* (Cramer), *S. cybele* (Fabricius), *S. aphrodite* (Fabricius), *S. idalia* (Drury), *S. nokomis* (W. H. Edwards), *S. edwardsii* (Reakirt), *S. coronis* (Behr), *S. zerene* (Boisduval), *S. callippe* (Boisduval), *S. egleis* (Behr), *S. atlantis* (W. H. Edwards), *S. hydaspe* (Boisduval), *S. mormonia* (Boisduval); checklist followed by catalogue, in which names and citations supplemented by type localities, deposition of types, distribution, references to figures, descriptions of preparatory stages when applicable; *Speyeria mormonia eurynome* ab. *igeli,* n. name (type is type of *Argynnis eurynome* ab. *eris* Igel); *Speyeria mormonia eurynome* ab. *fieldi,* n. name (type is type of *Argynnis eurynome clio* trans. form *gunderi* Field); type localities fixed for *S. diana* (Cramer), *S. c. cybele* (Fabricius), *S. a. aphrodite* (Fabricius), *S. a. alcestis* (W. H. Edwards), *S. idalia* (Drury), *S. n. nokomis* (W. H. Edwards), *S. edwardsii* (Reakirt), *S. c. coronis* (Behr), *S. c. snyderi* (Skinner), *S. c. halcyone* (W. H. Edwards), *S. z. zerene* (Boisduval), *S. z. hippolyta* (W. H. Edwards), *S. z. platina* (Skinner), *S. c. callippe* (Boisduval), *S. c. rupestris* (Behr), *S. c. juba* (Boisduval), *S. c. laurina* (Wright); *S. e. egleis* (Behr), *S. e. adiaste* (W. H. Edwards), *S. a. atlantis* (W. H. Edwards), *S. a. hesperis* (W. H. Edwards), *S. a. irene* (Boisduval), *S. a. electa* (W. H. Edwards), *S. a. lais* (W. H. Edwards), *S. h. hydaspe* (Boisduval), *S. h. rhodope* (W. H. Edwards), *S. m. mormonia* (Boisduval), *S. m. erinna* (W. H. Edwards), *S. m. arge* (Strecker), *S. m. artonis* (W. H. Edwards), *S. m. eurynome* (W. H. Edwards), and in synonymies for *Papilio daphnis* Cramer, *P. daphnis* Martyn, *Argynnis cypris* W. H. Edwards, *A. monticola* Behr, *A. liliana* var. *baroni* W. H. Edwards, *A. wrighti* Wright, *A. nevadensis* r. *meadii* trans. form *gerhardi* Gunder, *A. adiante* Boisduval, *A. montivaga* Behr 1863, *A. montivaga* Behr 1864, *A. astarte* W. H. Edwards 1862, *A. astarte* W. H. Edwards 1864, *A. cornelia* W. H. Edwards, *A. clio* W. H. Edwards, and *A. eurynome* trans. form *brucei* Gunder; types designated in synonymies for *A. astarte* W. H. Edwards 1862, *A. astarte* W. H. Edwards 1864, *A. montivaga* Behr 1864; lectotypes designated for *S. cybele carpenterii* (W. H. Edwards), *S. c. charlottii* (Barnes), *S. aphrodite alcestis* (W. H. Edwards), *S. a. columbia* (Hy. Edwards), *S. nokomis nitocris* (W. H. Edwards), *S. n. coerulescens* (Holland), *S. edwardsii* (Reakirt), *S. c. coronis* (Behr), *S. c. semiramis* (W. H. Edwards), *S. c. snyderi* (Skinner), *S. z. zerene* (Boisduval), *S. z. hippolyta* (W. H. Edwards), *S. z. behrensi* (W. H. Edwards), *S. z. bremnerii* (W. H. Edwards), *S. z. platina* (Skinner), *S. c. callippe* (Boisduval), *S. c. liliana* (Hy. Edwards); *S. c. rupestris* (Behr), *S. c. juba* (Boisduval), *S. c. laura* (W. H. Edwards), *S. c. nevadensis* (W. H. Edwards), *S. c. macaria* (W. H. Edwards), *S. c. meadii* (W. H. Edwards), *S. e. egleis* (Behr), *S. e. adiaste* (W. H. Edwards), *S. e. atossa* (W. H. Edwards), *S. e. oweni* (W. H. Edwards), *S. a. atlantis* (W. H. Edwards), *S. a. hesperis* (W. H. Edwards), *S. a. nikias* (Ehrmann), *S. a. nausicaa* (W. H.

Edwards), *S. a. chitone* (W. H. Edwards), *S. a. irene* (Boisduval), *S. a. lais* (W. H. Edwards), *S. h. hydaspe* (Boisduval), *S. h. rhodope* (W. H. Edwards), *S. h. sakuntala* (Skinner), *S. m. mormonia* (Boisduval), *S. m. bischoffii* (W. H. Edwards); *S. m. opis* (W. H. Edwards), *S. m. washingtonia* (Barnes & McDunnough), *S. m. erinna* (W. H. Edwards), *S. m. arge* (Strecker), *S. m. artonis* (W. H. Edwards), *S. m. eurynome* (W. H. Edwards), and *S. m. luski* (Barnes & McDunnough), and in synonymies for *A. cypris* W. H. Edwards, *A. monticola* Behr, *A. inornata* W. H. Edwards, *A. wrighti* Wright, *A. adiante* Boisduval, *A. montivaga* Behr 1863, and *A. atlantis* ab. *chemo* Scudder; neotypes designated for *S. cybele leto* (Behr), *S. a. aphrodite* (Fabricius), *S. idalia* (Drury), *S. n. nokomis* (W. H. Edwards), *S. coronis halcyone* (W. H. Edwards), and in synonymies for *P. daphnis* Cramer, *P. daphnis* Martyn, *A. aphrodite* f. *arizonensis* Elwes, *A. clio* W. H. Edwards.

1948

30. The eye colors of some *Colias* collected in New Jersey (Lepidoptera, Pieridae). Proc. Entomol. Soc. Washington 50:35–38, Feb. 1948 (27 Feb. 1948). 53% of individuals of *C. philodice-eurytheme* complex collected near Mendham had black eyes, 47% yellow-green when alive; percentages given by sex; no references found to black eyes in complex; yellow-green is normal color.
31. The care of a collection and library. Lepid. News 2:27, Mar. 1948 (6 Apr. 1948). Hints for protection, maintenance of entomological collections, leather bindings.
32. Critics and criticisms. Lepid. News 2:41, Apr. 1948 (7 Jun. 1948). Ethics of scientific criticism, prompted by short critical reviews included in notices of current entomological literature in *News*.
33. Notes on the disappearance of *Polygonia gracilis* at Rangeley, Maine, in 1947. Lepid. News 2:59, May 1948 (30 Jun. 1948). Very wet spring had serious effect on all 3 *Polygonia* species at Rangeley (*faunus, progne, gracilis*); no adults seen during summer; *gracilis*, a rare and local insect, may not reappear.
34. The occurrence of anthoxanthins in the wing pigments of some Nearctic *Oeneis* (Rhopalocera: Satyridae). Entomol. News 59:92–96, Apr. 1948 (2 Jul. 1948). Chemistry of pigments in wings of Nearctic *Oeneis* assists greatly in their systematic arrangement without conflicting with result obtained by genitalic examination; presence of anthoxanthins in scales of *O. uhleri* (Reakirt) and *O. taygete* Geyer groups suggests need for rearrangements; *O. nahanni* Dyar a subspecies of *uhleri* or should be placed next to it; *O. chryxus ivallda* (Mead) should have specific standing; describes test for anthoxanthins not injurious to specimens.

1949

35. New butterflies from Mount McKinley National Park, Alaska, with a review of *Erebia rossii* (Rhopalocera, Satyridae). Am. Mus. Novit. No. 1389, 17 pp., 28 figs., 6 Jan. 1949. *Oeneis mckinleyensis*, n. sp. (t.l. McKinley Park, AK, *ex* C. F. dos Passos collection); holotype in AMNH; holotype, allotype, 3 paratypes figured; subspecies of *E. rossii* (Curtis) reviewed, lectotype designated for *E. r. kuskoquima* Holland; *Erebia r. gabrieli*, n. ssp. (t.l. Mount McKinley Park, AK, 3500 ft [1067 m], *ex* G. P. Engelhardt and C. F. dos Passos collections); holotype in AMNH; holotype, allotype, 2 paratypes figured.
36. The distribution of *Oeneis taygete* Geyer in North America with descriptions of new subspecies (Lepidoptera, Satyridae). Am. Mus. Novit. No. 1399, 21 pp., 16 figs., 26 Jan. 1949. Type locality fixed for *O. taygete*, neotype designated; *Oeneis t. gaspeensis*, n. ssp. (t.l. Mt. Albert, Quebec, A. E. Brower); holotype in AMNH; *Oeneis t. fordi*, n. ssp. (t.l. Kuskokwim River, AK, A. Stecker); holotype in CM; *Oeneis t. edwardsi*, n. ssp. (t.l. San Juan Mts., Hinsdale Co., CO, B. Rotger); holotype in AMNH; holotypes, allotypes figured.
37. [Letter to editor.] Lepid. News 3:19–20, Feb. 1949 (7 Apr. 1949). Actions of Section on Nomenclature and F. Hemming in amending *Règles* at 1948 International Congress of Zoology defended against criticisms of C. W. Sabrosky.

38. The photography of types of Lepidoptera. Lepid. News 3:41–42, 1 fig., Apr.–May 1949 (11 Jul. 1949). Revision and condensation of 25 above.
39. A visit to the home of the late William Henry Edwards at Coalburg, West Virginia. Lepid. News 3:61–62, 1 fig., Jun. 1949 (23 Sep. 1949). Account of visit to State Dept. of Archives and History, Charleston, WV, to consult Edwards' journals, notebooks, other papers; and to house the entomologist built in 1869, where other Edwards manuscripts examined; figure depicts house.
40. Notes on two *Incisalia* types (Lepidoptera, Lycaenidae). Can. Entomol. 81:180–181, Jul. 1949 (25 Oct. 1949). Neotypes designated for *I. hadros* Cook & Watson, *I. henrici* var. *solatus* Cook & Watson.

1950

41. A correction. Lepid. News 4:15, 1950 (20 May 1950). dos Passos erred in note to literature abstract in *News* 3:109; combination *Malacosoma fragile* correct as to gender.
42. Lepidopterology. Butterflies and Moths: Trans. Lepid. Soc. Japan 1:40–42, Aug. 1950.* Summary of current American activity in letter invited by journal editor; translated by him into Japanese.
43. With D. B. Stallings, s.a. The Lepidopterists' Society: Report of the Organization Committee. Lepid. News 4:38, 1950 (16 Nov. 1950). Committee formed to consider proposed constitution and by-laws drafted by dos Passos completed work, submits finished texts for Society ratification; temporary Society officers appointed.

1951

44. The entomological reminiscences of William Henry Edwards with an introduction and annotations. J. New York Entomol. Soc. 59:129–186, Sep. 1951 (23 Aug. 1951). Previously unpublished autobiographical MS written by Edwards in old age, edited and with introduction by dos Passos.
45. On the proposal that the trivial name "*ajax*" Linnaeus, 1758 (as published in the binomial combination "*Papilio ajax*") should be suppressed by the International Commission on Zoological Nomenclature under its plenary powers. [Reference Z. N. (S.) 192.] Bull. Zool. Nomen. 2:349–350, 28 Sep. 1951. In recent years *ajax* used for 2 different Nearctic butterflies which have valid names, *Papilio polyxenes asterius* Stoll and *P. marcellus* Cramer; *ajax* not properly applicable to either; it is desirable to suppress name.

1952

46. Application to the International Commission on Zoological Nomenclature to reconsider and rephrase in part their decision suspending the "Règles" concerning "*Papilio plexippus*" Linnaeus, 1758, insofar as that decision refers to a figure in Holland's "Butterfly book." [Reference Z. N. (S.) 323.] Bull. Zool. Nomen. 6:278–283, 23 Jul. 1952. Original description of *P. plexippus* applies to 2 species, 1 American, 1 Oriental; Commission decided to apply name to the American species, as figured by W. J. Holland in *Butterfly book*; Holland's figure of *Danaus plexippus menippe* (Hübner), so when Opinion is rendered reference should be made to an accurate figure of *D. p. plexippus* (Linnaeus).
47. With L. P. Grey, s.a., and A. B. Klots. The "*niobe/cydippe/adippe*" problem (Class Insecta, Order Lepidoptera, Family Nymphalidae) with suggestions for its solution. [Reference Z. N. (S.) 79.] Bull. Zool. Nomen. 6:323–325, 29 Aug. 1952. *Papilio niobe* Linnaeus 1758 presents no nomenclatorial problem; *P. cydippe* Linnaeus 1761, a synonym of *niobe*, long misdetermined as a different butterfly, the "High Brown Fritillary"; *P. adippe* Linnaeus 1767, a new name for *cydippe* and synonym of *niobe*, also misdetermined as "High Brown Fritillary"; to settle scientific name of latter, Commission should suppress certain usages, validate name *adippe* for insect as from 1775 when used by Denis & Schiffermüller.
48. [Book review.] *Die Schmetterlinge Mitteleuropas*. By Walter Forster & Theodor

A. Wohlfahrt. Lepid. News 6:79–80, 1952 (17 Nov. 1952). First installments of vols. 1 and 2 reviewed.

49. In support of the application to suspend the rules to (a) validate seven generic names of Linnaeus as of 1758, and designate their type species (b) suppress the generic name "*Phalaena*" Linnaeus, 1758, give preference to its typical subgenus "*Noctua,*" declare "Noctuidae" the correct name for the family, and (c) validate one generic name of Linnaeus as of 1767 and designate its type species (Class Insecta, Order Lepidoptera). [Reference Z. N. (S.) 462.] Bull. Zool. Nomen. 9:153–154, 30 Dec. 1952. Generic names in question except *Phalaena* (*Bombyx, Noctua, Geometra, Pyralis, Tortrix, Tinea, Alucita*) in constant use for very long time; to upset their usage would cause greater confusion than uniformity; unfortunate to suppress *Phalaena* but not to do so will result in suppressing almost equally well-known *Noctua*; advisable to settle *Bombyx* and *Pyralis* as generic names as of 1758.

1953

50. [Book review.] *Die Schmetterlinge Mitteleuropas*. By Walter Forster & Theodor A. Wohlfahrt. Lepid. News 7:26, 1953 (20 Apr. 1953). Second installments of vols. 1 and 2 reviewed.
51. Shall the "Règles" be amended so as to regulate the fixation of type localities and if so upon what terms and conditions? [Document 1/58.] Bull. Zool. Nomen. 8:102–108, 25 Jun. 1953. F. Hemming suggested that to reduce instability provisions should be added concerning fixation of type localities; fixation of localities a well-established, desirable practice; rules proposed; some Hemming ideas questioned as basis for discussion of article to amend *Règles*.
52. On the question whether and subject to what conditions the concept of a "neotype" should be officially recognized by an appropriate amendment to the "Règles." [Document 2/13.] Bull. Zool. Nomen. 8:121–127, 30 Jun. 1953. In recent years it has been practice among some zoologists to designate neotypes when types lost or destroyed; arguments presented for recognition of neotypes; rules proposed, comments made on F. Hemming's suggestions regarding neotypes as basis for discussion of article to amend *Règles*.

1954

53. With F. Hemming, s.a. Proposed limitation to the purposes of the law of priority of the suppression of the name "*Argus*" Bohadsch, 1761 (Class Gastropoda) effected in "Opinion" 185, in order to prevent the confusion which would otherwise arise in the Class Insecta, Order Lepidoptera. [Reference Z. N. (S.) 714.] Bull. Zool. Nomen. 9:281–283, 22 Oct. 1954. An Opinion of Commission suppressed for all nomenclatorial purposes generic name *Argus* Bohadsch 1761, and unless action taken, *Argus* Scopoli 1763 becomes available for a genus of Lepidoptera, replacing either *Lysandra* Hemming 1933 or *Polyommatus* Latreille 1804; either result would cause serious confusion; proposals submitted to restrict previous decision to prevent emergence of *Argus* Scopoli.
54. With E. L. Bell, s.a. The lectotype of *Megathymus aryxna* Dyar (Lepidoptera, Megathymidae). Am. Mus. Novit. No. 1700, 5 pp., 20 Dec. 1954. Opinions differ as to what constitutes type series of *M. aryxna* and which specimen is lectotype because Dyar did not designate holotype in description; history reviewed and it is concluded lectotype is specimen figured by H. Druce in Lepidoptera-Heterocera section of *Biologia Centrali-Americana,* ed. F. D. Godman & O. Salvin; this permits recognition of *M. evansi* Freeman as valid name.

1955

55. "1954." [Book review.] *Die Schmetterlinge Mitteleuropas*. By Walter Forster & Theodor A. Wohlfahrt. Lepid. News 8:170–171, 1954 (7 Jan. 1955). Third, fourth, fifth installments of vols. 1 and 2 reviewed.
56. With E. L. Bell, j.a. Request for a ruling as to the specimen to be accepted as the lectotype of "*Megathymus aryxna*" Dyar, 1905 (Class Insecta, Order Lepidoptera).

[Reference Z. N. (S.) 889.] Bull. Zool. Nomen. 11:289–294, 30 Dec. 1955. Bell and dos Passos (54 above) identified lectotype as specimen figured by H. Druce; in same year D. B. Stallings and J. R. Turner identified lectotype as specimen in USNM to which Dyar attached label stating the name *aryxna* was restricted to that specimen; arguments presented against latter conclusion and for former; suggested ruling provided to Commission.

1956

57. A bibliography of general catalogues and check lists of Nearctic Rhopalocera. Lepid. News 10:29–34, 1956 (10 Aug. 1956). "Catalogue" and "check list" defined and discussed in introduction followed by chronologically arranged bibliography of 78 items including "not only the strictly Nearctic works but also all general Palaearctic check lists and catalogues that refer to . . . circumpolar insects."

1957

58. "1955." With L. P. Grey, j.a. A new name for *Argynnis lais* Edwards (Lepidoptera, Rhopalocera). J. New York Entomol. Soc. 63:95–96, 1955 (8 Mar. 1957). *A. lais* W. H. Edwards 1883 a primary homonym of *A. lais* Scudder 1875; insect renamed *Speyeria atlantis helena,* n. name (type is lectotype of *A. lais* W. H. Edwards in CM); question arises whether new name for a homonym should be proposed in original genus in which homonym described or in genus to which homonym transferred, and it would be well to amend *Règles* to cover the problem.
59. A newly discovered announcement of the proposed publication of the *Sammlung exotischer Schmetterlinge* by Jacob Hübner. J. Soc. Bibliog. Nat. Hist. 3:206, 2 pls., Jan. 1957* (date stamps suggest U.S. receipt mid-May 1957). dos Passos' incomplete copy of Hübner's Ziefer volume of text (1805–[1823]) to the *Sammlung europäischer Schmetterlinge* (1796–[1838]) contained 2-page letter press announcement dated 21 Sep. 1806 of proposed publication of the work on exotics; announcement donated to AMNH; plates reproduce the pages.
60. "1956." Additions and corrections to "A bibliography of general catalogues and check lists of Nearctic Rhopalocera." Lepid. News 10:213–214, 1956 (21 Jun. 1957). 14 entries added, typos corrected.
61. "1956." William Phillips Comstock, 1880–1956. J. New York Entomol. Soc. 64:1–5, 1 pl. (portrait), 1956 (23 Dec. 1957). Obituary, bibliography.

1958

62. With A. B. Klots, j.a. Proposal for the amendment of Article 28 of the existing "Règles" as amended at Copenhagen (1953) so as to give preference to the principle of page priority in the selection of generic and specific names and for other purposes. [Reference Z. N. (S.) 1291; Document 15/1.] Bull. Zool. Nomen. 15:285–292, 11 Feb. 1958. Argument in favor of reinstating "page precedence principle" in place of "first reviser principle"; page and line priority objective, while first reviser principle highly subjective; when 2 or more names proposed at same time in same publication for same genus or other taxon, first name published should prevail; text proposed for draft *Règles* which provides page, line, word precedence.
63. *In* W. I. Follett. Views of the committees on nomenclature: (a) of the American Society of Ichthyologists and Herpetologists; and (b) of the Society of Systematic Zoology on the relative status of specific names based on modern patronymics having the terminations "-i" and "-ii" respectively. [Document 32/4.] Bull. Zool. Nomen. 15:677–685, 18 Apr. 1958. Follett publishes statements by 12 taxonomists; dos Passos' opinion (p. 681) is that original spellings whether ending in -i or -ii should be retained without emendation; -i ending should be recommended to authors but if they do not use it their spellings should be valid and not subject to emendation; second similar name in a genus whether ending in -ii or -i or vice versa should be considered junior homonym.
64. With A. B. Klots, j.a. Proposal for the amendment of Article 21 of the "Règles" (i.e. Draft Article 22) so as to make its operation entirely objective in cases where a

person other than the nominal author of the book or paper concerned is responsible for a name and its indication, definition or description. [Reference Z. N. (S.) 1326; Document 34/1.] Bull. Zool. Nomen. 15:695–702, 25 Apr. 1958. Article should state that author of scientific name is person who publishes it in connection with indication, definition, description, unless express statement in same publication that some other person responsible; if 1 person responsible for name and another for rest, that shall constitute joint authorship; text proposed.

65. "1957." [Book review.] *Die Schmetterlinge Mitteleuropas.* By Walter Forster & Theodor A. Wohlfahrt. Lepid. News 11:176, 1957 (13 May 1958). Sixth installment of vol. 2 reviewed.
66. Proposals for the amendment and correction of the draft "Règles" concerning the establishment of neotypes (Article 20). [Document 41/3.] Bull. Zool. Nomen. 15: 816–821, 23 May 1958. Provisions regarding neotypes reviewed, thought too strict, impracticable; language proposed in Bradley draft should be adopted with exception of several provisions, cited but not quoted.
67. Article 22, Section 5(c)(1) and Section 6(b). [Reference Z. N. (S.) 1344; Document 42/1.] Bull. Zool. Nomen. 15:824, 23 May 1958. Regarding draft *Règles,* citation of dates when generic combination changed, dos Passos gives examples of what he considers proper citations; in new combinations author's name only should appear in parentheses, not date.
68. Proposed relaxation of the ban on intemperate language and proposed relaxation of the ban on names calculated to give personal and other types of offence. [Reference Z. N. (S.) 1296; Documents 19/3 and 23/3.] Bull. Zool. Nomen. 15:857, 23 May 1958. Elimination of these provisions may lead some to assume falsely that zoologists have come to feel differently about such matters; matters could be treated as effectively by omitting them from present position in *Règles,* incorporating them in Code of Ethics.
69. Support for the proposal included by Professor Chester Bradley in the suggested annexe to Subsection (6) of Section 4 of Article 7 of the draft "Règles." [Reference Z. N. (S.) 1348; Document 44/1.] Bull. Zool. Nomen. 15:935, 13 Jun. 1958. Regarding status of names in preprints when paper concerned not published later in regular manner, dos Passos agrees with Bradley's addition, suggests it be made to apply after a certain date.
70. Citation of corrected and emended names. [Z. N. (S.) 1269; Document 9/3.] Bull. Zool. Nomen. 15:974, 13 Jun. 1958. Regarding draft *Règles,* when scientific name misspelled or otherwise written incorrectly, all emendations should be noted as such; in appropriate cases incorrect spelling should be placed in synonymy followed by *lapsus calami.*
71. Citation of dates in round brackets for bibliographical references. [Reference Z. N. (S.) 1294; Document 17/4.] Bull. Zool. Nomen. 15:975, 13 Jun. 1958. Regarding draft *Règles,* dos Passos objects to proposed deletion of Article 22, Recommendation 10(B) relating to citation of dates; Paris decisions concise, logical, not restrictive, pedantic; provide instant knowledge where to find a citation.
72. *In* R. V. Melville. [Draft "Règles," Article 28, Section 4(a): The diaeresis symbol, Reference Z. N. (S.) 1013; Document 72/1.] Bull. Zool. Nomen. 15:1158–1162, 2 Jul. 1958. In draft, diaeresis symbol excluded from category of diacritic marks; Melville publishes statements by 3 taxonomists; dos Passos' opinion (p. 1161) is that diaeresis symbol be retained.
73. The Satyrid butterflies of northwestern North America (Lepidoptera: Satyridae). Proc. Tenth Intern. Congr. Entomol., Montreal, August 17–25, 1956 1:673–681, Dec. 1958. Survey of species of *Coenonympha, Cercyonis, Oeneis, Erebia* of AK, Yukon, British Columbia, western Alberta; brief history of collecting in area followed by discussion of each biotic province, catalogue with references.

1959

74. "1958." Frank Edward Watson, 1877–1947. J. New York Entomol. Soc. 66:1–6, Mar.–Jun. 1958 (20 Jan. 1959). Biographical sketch, bibliography.

75. "1958." The dates and authorships of the names proposed in volume 9 of *Encyclopédie méthodique* by Godart and Latreille, 1819–[1824]. Lepid. News 12:119–120, 1958 (26 Jan. 1959). Although title of work dated 1819, only first part published that year; all names in it should be ascribed to Godart; second part published in 1824; some of its names should be ascribed to Godart, others to Latreille; explanatory tables of generic and specific names provided.
76. "1958." The dates and authorships to be ascribed to the generic and specific names proposed by Boisduval and LeConte and by LeConte alone in the *Lépidoptères de l'Amerique septentrionale,* 1829–1833–[1834]. Lepid. News 12:121–122, 1958 (26 Jan. 1959). Discovery of a set of the work in original wrappers and other research resulted in new evidence; tables provide authorship, dates of names.
77. "1958." The authorship of the names proposed in the *Natural history of the rarer lepidopterous insects of Georgia* (1797). Lepid. News 12:191–192, 1958 (30 Apr. 1959). Internal evidence reveals relative roles of J. E. Smith and J. Abbot in producing work; Smith explains he alone responsible for systematic names, definitions, so all names proposed in book can be attributed to Smith alone.
78. "1958." The authorship and dates of publication of the names of some Rhopalocera proposed in the *Reise der oesterreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Wüllerstorf-Urbair,* 1864–1867–[1875]. Lepid. News 12:193–194, 1958 (30 Apr. 1959). Summary of pertinent bibliographical data followed by tables of generic, specific names, dated and ascribed jointly to C. Felder and son R. Felder.
79. "1958." The dates and authorships of some names proposed by Cramer and Stoll in *De uitlandsche kapellen voorkomende in de drie waereld-deelen Asia, Africa en America,* and by Stoll alone in *Aanhangsel van het werk, De uitlandsche kapellen voorkomende in de drie waereld-deelen Asia, Africa en America, door den heere Pieter Cramer* [1775]–1791. Lepid. News 12:195–198, 1958 (30 Apr. 1959). Names cannot be dated from text because many not binomials; specific name often appears alone; names must be dated from indexes (often published later than text) in which generic names appear in conjunction with specific names and references to text figures; table provides pertinent data.

1960

80. "1959." Further notes on the dates of publication of some generic and specific names proposed by Boisduval and LeConte in the *Lépidoptères de l'Amerique septentrionale,* 1829–1833–[1834]. J. Lepid. Soc. 13:212, 1959 (1 Aug. 1960). Information from correspondent about another copy in wrappers (76 above) led to redating a number of names.
81. Taxonomic notes on some Nearctic Rhopalocera. 1. Hesperioidea. J. Lepid. Soc. 14: 24–36, 1960 (15 Dec. 1960). Systematic changes incorporated in forthcoming check-list of Nearctic Rhopalocera explained; contrary to present practice, list will proceed from lower butterflies to higher; result in Hesperioidea is complete reversal of order used by W. H. Evans (1951–55); genera in his work used but there will be changes in systematic arrangement of species; treatment of Papilionoidea will accord more or less with plan of B. C. S. Warren (1947) from lowest to highest; within genera listing of species by J. H. McDunnough (1938) followed except when improvement desirable; most names in recent literature resulting from splitting of genera given subgeneric standing; effort will be made to comply with *Règles* but nomenclature code of N. Banks and A. N. Caudell (1912) preferable to *Règles* in present state, will be followed except when modified by *Règles*; taxonomic notes follow on species within Hesperioidea, in which no new names proposed but some changed in rank or relegated to synonymy, many other corrections made.

1961

82. "1960." [Book review.] *Butterflies of Formosa in colour.* By Takashi Shirôzu. J. Lepid. Soc. 14:243, 1960 (& Sep. 1961).

1962

83. The dates of publication of the *Histoire générale et iconographie des lépidoptères et des chenilles de l'Amerique septentrionale,* by Boisduval and LeConte 1829–1833[–1834]. J. Soc. Bibliog. Nat. Hist. 4:48–56, Jan. 1962* (date stamps suggest U.S. receipt mid-Feb. 1962). Detailed bibliographical summary of work, including information from 3 copies in original wrappers; review of previous relevant bibliographical contributions followed by tables that apply publication dates of livraisons to scientific names.
84. "1961." Taxonomic notes on some Nearctic Rhopalocera. 2. Papilionoidea. J. Lepid. Soc. 15:209–225, 1961 (19 Jun. 1962). Continuation of 81 above; no new names proposed but some changed in rank or relegated to synonymy, many other corrections made; brief supplemental note to part 1 (Hesperioidea) on p. 225.
85. The authorship of three scientific names of Nearctic Rhopalocera variously credited to Boisduval or Lucas. J. Lepid. Soc. 16:45–46, 1962 (30 Aug. 1962). Authorship of *Papilio eurymedon, P. rutulus, P. zelicaon* ascribed to P. H. Lucas, who published names before J. Boisduval.

1963

86. The status of infrasubspecific names. [Reference Z. N. (S.) 1569.] Bull. Zool. Nomen. 20:67–70, 18 Mar. 1963. New article should be added to *Code* to deal with these names; text proposed, practically same as that in Bradley Draft but not adopted in 1958; if proposal adopted, emendations to Articles 1, 15, 17(9), 45c will be necessary.
87. A name first published as a synonym is not thereby made available. Article 11(d). [Reference Z. N. (S.) 1570.] Bull. Zool. Nomen. 20:70, 18 Mar. 1963. *Code* should be amended to state that a name first published as synonym not thereby made available unless prior to 1958 it has been recognized, removed from synonymy, and used as name of a taxon.
88. Neotypes—Article 75. [Reference Z. N. (S.) 1571; Document 17/1.] Bull. Zool. Nomen. 20:71–72, 18 Mar. 1963. Recognition of neotypes by *Code* was step in right direction but some provisions respecting their designation so strict and unnecessary that article will likely be ignored or workers discouraged from designating neotypes; additions, deletions proposed.
89. Form of citation—Article 51b(1). Date in a changed combination—Article 22, Recommendation 22B. [Reference Z. N. (S.) 1576; Document 22/2.] Bull. Zool. Nomen. 20:77–78, 18 Mar. 1963. Article 51b(1) of *Code* should be amended to state that name of subsequent user of a scientific name, if cited, to be separated by comma; Article 22, Recommendation 22B should be repealed because placing date in parentheses when combination is changed can affect and make improper the date citation which in that particular case should be outside parentheses.
90. *Calephelis* Grote and Robinson, 1869, (Insecta, Lepidoptera): Proposed use of the plenary powers to designate a type-species in conformity with current usage [Reference Z. N. (S.) 1563.] Bull. Zool. Nomen. 20:313–320, 12 Jul. 1963. History of uses of generic names *Nymphidia* Boisduval & LeConte, *Calephelis* Grote & Robinson, *Lephelisca* Barnes & Lindsey for North American riodinids reviewed; it is proposed to retain *Calephelis* with type species *Erycina virginiensis* Guérin-Méneville and invalidate others.
91. Supplemental notes to previous taxonomic notes on some Nearctic Rhopalocera. J. Lepid. Soc. 17:103–104, 1963 (8 Nov. 1963). Since publication of 2 papers (81 and 84 above) designed to explain systematic changes incorporated in forthcoming checklist of Nearctic Rhopalocera, communications received from other workers; these, other supplemental matters discussed.

1964

92. *A synonymic list of the Nearctic Rhopalocera.* N. p. [New Haven, CT], 1964. vi, 145 pp. Lep. Soc. Mem. No. 1 (Feb. 1964, *in litt.*). List "almost a catalogue"; effort made to give generic synonymies in addition to specific, and to cite type species of each generic name used; subjective, objective generic synonyms differentiated; taxa

provided with authors' names, publication dates; 687 species numbered; 1002 subspecies recognized, 1 questioned; 96 species asterisked as "of doubtful North American occurrence"; of these, 89 are species in which nominate subspecies not Nearctic but Nearctic subspecies exist; infrasubspecific names included.

1965

93. Peale's *Lepidoptera Americana* (1833). J. New York Entomol. Soc. 73:18–26, 5 figs., Mar. 1965 (19 Apr. 1965). T. R. Peale's work, "the first book begun by an American author on American lepidoptera that was published in this country," discontinued after one number; that part discussed and bibliographically described; 8 copies located; wrappers, subscribers' list illustrated.
94. With H. Ruckes, s.a. In memoriam: Ernest Layton Bell, 1876–1964. J. New York Entomol. Soc. 73:49–56, 1 fig. (portrait), Jun. 1965 (16 Jun. 1965). Obituary, bibliography.
95. Review of the Nearctic species of *Pieris* "*napi*" as classified by androconial scales and description of a new seasonal form (Lepidoptera: Pieridae). J. New York Entomol. Soc. 73:135–137, Sep. 1965 (17 Sep. 1965). As result of B. C. S. Warren's papers on androconial scales and their bearing on speciation in *Pieris*, classification of *P. bryoniae* Ochsenheimer, *P. napi* (Linnaeus), *P. narina* Verity, and subspecies reviewed; *Pieris narina mogollon* gen. aest. *warreni* n. form (t.l. White Mts., AZ, *ex* F. R. Sternitzky collection); holotype in AMNH.
96. With H. Ruckes, s.a. Ernest Layton Bell (1876–1964). J. Lepid. Soc. 19:190–191, 1965 (24 Sep. 1965). Obituary differing from 94 above.
97. Addenda et corrigenda to the "Synonymic list of Nearctic Rhopalocera." J. Lepid. Soc. 19:192, 1965 (24 Sep. 1965). Page laid into later copies of *Synonymic list* sold by Society.
98. With L. P. Grey, j.a. Notes on certain lectotypes designated by the authors in their Systematic catalogue of *Speyeria* (Lepidoptera: Nymphalidae). Trans. Am. Entomol. Soc. 91:351–360, Sep. 1965 (30 Sep. 1965). Continuation of catalogue, prompted by F. M. Brown's study of argynnid names proposed by W. H. Edwards; lectotypes of *S. coronis coronis* (Behr), *S. callippe inornata* (W. H. Edwards), and *S. atlantis hesperis* (W. H. Edwards) redesignated as neotypes; neotype designated for *S. callippe nevadensis* (W. H. Edwards); lectotype redesignated for *S. mormonia artonis* (W. H. Edwards); neotype redesignated for *S. mormonia clio* (W. H. Edwards).

1966

99. The discovery of additional journals of Frank E. Watson. J. New York Entomol. Soc. 74:188, Dec. 1966 (29 Dec. 1966). Entomological journals for 1896–1905, 1914–22, 1926–31, 1934–47 located, donated to AMNH, which now has all Watson journals except those for 1932–33, presumed lost.
100. *Pieris narina oleracera* (Harris) in New Jersey (Lepidoptera: Pieridae). J. New York Entomol. Soc. 74:222–223, Dec. 1966 (29 Dec. 1966). NJ records cited by earlier workers but discounted by later ones as misdeterminations verified by capture of a male by M. A. dos Passos near Springdale, Sussex Co., 8 Jul. 1966.

1968

101. With B. C. S. Warren, j.a. The homonymy of *Papilio aglaja* Linnaeus 1758 (Insecta, Lepidoptera, Pieridae and Nymphalidae): Request for validation. Z. N. (S.) 1791. Bull. Zool. Nomen. 25:68–71, 27 Sep. 1968. Linnaeus named 2 insects *P. aglaja* in 1758 ed. of *Systema naturae*, then in 1767 ed. renamed pierid, retained *aglaja* for nymphalid; pierid usage has 1758 page priority over nymphalid usage which is therefore homonym; this long recognized but recent application seeks to resurrect nymphalid name, recognize 2 uses of *aglaja* in different families; situation brought about by adoption of first reviser rule, repeal of priority rule; Linnaeus not reviser in 1767, primary junior homonym not an available name; consequences of decision recognizing 1767 ed. as revision would be chaotic; Commission asked to deny

application insofar as it seeks to suspend rule concerning homonyms and permit 2 uses of name, asked to recognize specific name *charlotta* Haworth for nymphalid, *aglaja* Linnaeus for pierid, and to take other appropriate actions.

1969

102. A revised synonymic list of the Nearctic Melitaeinae with taxonomic notes (Nymphalidae). J. Lepid. Soc. 23:115–125, 1969 (29 May 1969). 2 revisions, 1st by H. L. Higgins, 2nd by D. L. Bauer, published before *Synonymic list* (92 above) rendered its arrangement of Melitaeinae genera, species somewhat obsolete, but checklist already in press; revised synonymic list of subfamily presented in format of 92; 8 fewer species-level taxa, owing primarily to relegation to subspecies; taxonomic notes follow to explain changes, placement of names.
103. A name for *Polygonia satyrus marsyas* auctorum (Lepidoptera: Nymphalidae). Trans. Am. Entomol. Soc. 95:153–159, 2 figs., Mar. 1969 (6 Jun. 1969). Misled by false locality labels, W. H. Edwards described European *P. c-album* as American species *marsyas* in 1870; *marsyas* usually considered U.S. West Coast population of *P. satyrus* (W. H. Edwards), so desirable to propose new name for that population, *Polygonia s. neomarsyas*, n. ssp. (t.l. Salmon Meadows, Brewster, WA, J. C. Hopfinger); holotype in dos Passos collection but will be deposited in CM; holotype, allotype figured.
104. With B. C. S. Warren, s.a. The homonymy of *Papilio aglaja* Linnaeus 1758 (Insecta, Lepidoptera, Pieridae and Nymphalidae): Request for validation Z. N. (S.) 1791. A further note in opposition to this application. Bull. Zool. Nomen. 26:67–68, 8 Aug. 1969. Further evidence provided to support application has not established that Linnaeus a first reviser in 1767; not conducive to stability of nomenclature to alter long-accepted usages; application and another to same end should be denied.
105. *Lethe eurydice* (Johansson) and *L. fumosus* (Leussler), sibling species (Lepidoptera: Satyridae). J. New York Entomol. Soc. 77:117–122, Jun. 1969 (24 Oct. 1969). *L. eurydice* has been considered single species with 4 subspecies; rather, 2 sibling species involved which occur in different environments, have constant superficial differences, probably different foodplants; bibliographical synonymies provided for *L. eurydice*, *L. fumosus* n. comb.; species discussed; arrangement of names proposed in checklist form.
106. With A. B. Klots, j.a. The systematics of *Anthocharis midea* Hübner (Lepidoptera: Pieridae). Entomol. Am. 45:1–34, 11 figs., 1969 (29 Dec. 1969). Species placed in subgenus *A.* (*Falcapica*) Klots; neotypes designated for 3 species-group names available for species: *genutia* Fabricius, *midea* Hübner, *lherminieri* Godart; systematics, geographic variation discussed; bibliographical synonymies provided for species, nominate subspecies; *Anthocharis midea annickae*, n. ssp. (t.l. West Rock, New Haven, CT, C. L. Remington); holotype in AMNH; life history, foodplants, parasites discussed; relevant types figured including holotype, allotype of *annickae*.

1970

107. A revised synonymic catalogue with taxonomic notes on some Nearctic Lycaenidae. J. Lepid. Soc. 24:26–38, 1970 (26 Mar. 1970). Revision by H. K. Clench appeared when *Synonymic list* (92 above) in press, rendered its arrangement of Theclinae obsolete; revised synonymic list of subfamily presented in format of 92; *Harkenclenus*, n. g. proposed; taxonomic notes follow to explain changes, placement of names.

1972

108. Designation of a lectotype for *Erebia youngi* Holland. Entomol. Rec. J. Var. 84: 238–241, 1 pl. incl. 4 figs., Oct. 1972 (15 Oct. 1972*). Since Holland's description a very similar Asiatic species, *E. dabanensis* Erschoff, discovered in AK, *E. kozhantshikovi* Sheljuzhko may occur there also; necessary to determine genitalically whether these species confused in Holland's type series; on dissection of 2 male syntypes 1 found to be *dabanensis*; 2nd *youngi*, latter designated lectotype; *E. herscheli*

Leussler a local race of *youngi*; *E. youngi rileyi* dos Passos similarly proven to be *dabanensis* so *rileyi* falls as synonym.

1973

109. The great advantages of zoological nomenclature as contrasted with the many disadvantages of popular names!?! News. Lepid. Soc. 15 May 1973*:2–3. In light vein, suggested that many common names more stable than scientific names.
110. The correct name for the subspecies of *Limenitis weidemeyerii* occurring in Arizona (Nymphalidae). J. Res. Lepid. 12:21–24, Mar. 1973 (18 Dec. 1973, *in litt.*) Confusion in literature reviewed; synonymy provided; name *angustifascia* Barnes & McDunnough a jr. synonym of *sinefascia* Dyar et al., the correct name.

1974

111. With W. D. Field, s.a., and J. H. Masters. *A bibliography of the catalogs, lists, faunal and other papers on the butterflies of North America north of Mexico arranged by state and province (Lepidoptera: Rhopalocera)*. Washington, DC: Smithsonian Institution Press, 1974. [ii], 104 pp. Smiths. Contrib. Zool. No. 157 (20 Feb. 1974). 2987 selected publications listed in geographical units (Greenland included) and in supplemental bibliography of items that cover more than 1 state or province.
112. With J. R. Heitzman, s.a. *Lethe portlandia* (Fabricius) and *L. anthedon* (Clark), sibling species, with descriptions of new subspecies of the former (Lepidoptera: Satyridae). Trans. Am. Entomol. Soc. 100:52–99, frontis., 20 figs., Mar. 1974 (16 May 1974). *L. portlandia* has been considered as having 4 subspecies and 1 synonym; rather, 2 sibling species involved: *portlandia*, having 3 subspecies (2 named here), *L. anthedon*; the 2 species occur in different environments, have different foodplants; bibliographical synonymies provided for *portlandia*, its nominate subspecies, for *Lethe portlandia floralae*, n. ssp. (t.l. Rock Springs, Orange Co., FL, S. Roman); holotype in AMNH; and *Lethe portlandia missarkae*, n. ssp. (t.l. 5 mi [8 km] S of Fayetteville, Washington Co., AR, 1300 ft [396 m], J. R. Heitzman); holotype in AMNH; the 2 subspecies discussed; most specimens referred to in literature as *portlandia* are *anthedon*, so bibliography provided; arrangement of names proposed in checklist form; holotypes, allotypes of new subspecies figured, as are other relevant types, some genitalia.

1977

113. "1976." A note on *Oeneis jutta harperi*, its author and date of publication (Satyridae). J. Res. Lepid. 15:211–213, Dec. 1976* (date stamps suggest receipt late Apr. 1977). Previous publications of name *harperi* as subspecies of *O. jutta* (Hübner) invalid according to *Code*; name validly published here as *Oeneis j. harperi*, n. ssp.; t.l. fixed; types mentioned in literature presumably in P. W. Chermock collection.
114. A taxonomic note on *Polygonia faunus arcticus* Leussler (Lepidoptera: Nymphalidae). Pan-Pac. Entomol. 53:179–180, Jul. 1977 (28 Nov. 1977). Leussler's *arcticus* is subspecies of *P. hylas*, not *P. faunus*, as type specimens indicate; name should be written as *Polygonia hylas arcticus* Leussler, n. comb.

1978

115. Correction—Note on *Polygonia faunus arcticus*. Pan-Pac. Entomol. 54:42, Jan. 1978 (26 Apr. 1978). Phrase concerning type locations added to 114 above.

1981

116. A little-known, anonymous work on American and European butterflies and moths (1906), which should be attributed to William Beutenmüller (Lepidoptera: Nymphalidae). J. New York Entomol. Soc. 89:143–145, Jun. 1981 (24 Sep. 1981). Discussion and description of *A manual of American and European butterflies and moths reproduced in natural colors with their common and scientific names*; Mrs. Beutenmüller probably executed plates.

1982

117. "1981." With A. B. Klots, s.a. Studies of North American *Erora* (Scudder) (Lepidoptera, Lycaenidae). J. New York Entomol. Soc. 89:295–331, 34 figs., Dec. 1981 (19 Feb. 1982). Genus *Erora* characterized, discussed, as are *E. laeta* (W. H. Edwards), *E. q. quaderna* (Hewitson), *E. q. sanfordi* dos Passos; early stages, ethology, ecology, geographic distribution of *laeta, quaderna sanfordi* discussed; bibliographical synonymies, lists of distributional records included; early stages, types figured.
118. "1981." Some little-known U.S. publications on Lepidoptera I. [Edited and with abstract and foreword by L. P. Grey.] J. Res. Lepid. 20:111–115, Summer 1981 (20 Sep. 1982). Periodicals *The Lepidopterist* (1916–17), *Lepidoptera* (1918–21), *The Lepidopterist* (1918–31) discussed, known numbers listed with dates of publication, pagination, inclusions.
119. "1981." Some little-known U.S. publications on Lepidoptera II. [Edited and with abstract by L. P. Grey.] J. Res. Lepid. 20:115–122, Summer 1981 (20 Sep. 1982). Information similar to 117 above provided for *The Butterfly Farmer* (1913–14), *Lorquinia* (1916–19), *Southwest Science Bulletin* (1920), *Butterfly Park Nature Club News* (1929–31), *The Lepidopterists' News* (1933), *The Entomologists' Exchange Association* (1936), *The Entomologists' Exchange News* (1937–42), *The Butterfly Club* (1946–47), *Club Notes, Moth and Butterfly Club* (?1947–53), *Notes on Moths and Butterflies* (1953–55), for relevant material in *Sierra Club Bulletin* (1913), *Hobbies* (1936).

1983

120. With C. D. Ferris, s.a., J. A. Ebner, and J. D. Lafontaine. An annotated list of the butterflies (Lepidoptera) of the Yukon Territory, Canada. Can. Entomol. 115:823–840, 6 figs., Jul. 1983 (22 Jun. 1983, *in litt.*) 95 taxa reported including subspecies; some listed as questionable; various species figured.

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BIOLOGY OF *SPEYERIA ZERENE HIPPOLYTA* (NYMPHALIDAE) IN A MARINE-MODIFIED ENVIRONMENT

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ABSTRACT. This paper examines life history and adaptations of *Speyeria zerene hippolyta* (Edwards) along the Oregon and Washington coasts where cold wind, rain, and fog persist during much of the year. The butterfly uses an open grassland habitat on salt-spray meadows and higher headlands adjacent to the ocean, where the larvae feed on the common *Viola adunca* J. E. Smith. Four unusual adaptations to this environment are seen in *S. zerene hippolyta* that are absent from the closely related *S. z. bremnerii* (Edwards) of the inland Willamette Valley: small body size and extensive dark basal suffusion which enhance body heating from solar radiation; normal flight activity under cool, cloudy or foggy conditions; prolonged larval development which coordinates adult emergence with the most favorable weather conditions in late summer and fall; and much individual variation in larval development rate and adult emergence which compensates for variable and unpredictable weather from year to year.

Additional key words: *Speyeria zerene bremnerii, Viola adunca,* adaptation, grassland, coastal habitat.

Speyeria zerene (Boisduval) is a complex polytypic species with 14 recognized subspecies (Grey & Moeck 1962). The subspecies occupy a wide diversity of habitats ranging from coastal rainforests in the Pacific Northwest to arid sagebrush plains in the Great Basin. *Speyeria z. hippolyta* (Edwards), informally known as the "Hippolyta Silverspot" or "Oregon Silverspot", is restricted to a cool, wet, marine-modified environment adjacent to the Pacific Ocean in western Washington and Oregon. This subspecies is of special concern because of its decline toward extinction and its official classification as a threatened species (Hammond & McCorkle 1983).

The closely related *S. z. bremnerii* (Edwards) occupies inland areas of the Pacific Northwest from Vancouver Island S through the Puget Sound trough and Willamette Valley of western Oregon. The primary difference in adult phenotype between these subspecies is the small wing of *S. z. hippolyta* although extinct Oregon populations of *S. z. bremnerii* also differed in having reduced basal suffusion on the dorsal wing surfaces (Fig. 3). In addition, *S. z. hippolyta* differs in several aspects of life history and developmental physiology which appear to be specific adaptations to the coastal environment. An investigation of these characteristics is the subject of the present paper. It should be noted that both Moeck (1957) and Howe (1975) confused this coastal subspecies with a population of dwarfed *S. z. conchyliatus* (Comstock) endemic to the volcanic ash and pumice fields along the E slope of the Oregon Cascade Range.

MATERIALS AND METHODS

Field and museum studies were conducted from 1960 to 1986 together with laboratory rearing of larvae. Most public and many private collections in Washington and Oregon were examined. In 1963 and 1964, one of us (McCorkle) developed a technique for rearing *Speyeria* larvae using a modification of a procedure (Magnus 1958) for the European fritillary *Argynnis paphia* L. A variant of the former technique was described by Mattoon et al. (1971), and was used in the present study, except that larvae were kept over winter in hollow wooden blocks and reared in small jars instead of nylon sleeves.

Capture-recapture studies were done at the Rock Creek study site in Lane Co., Oregon, during 1980 using the 1-2-4-7 marking system described by Ehrlich and Davidson (1961). Sex, wing length, general condition, time, place, and type of activity at time of capture and recapture were recorded.

Voucher specimens are deposited in the Systematic Entomology Laboratory at Oregon State University, Corvallis.

BIOLOGY OF STAGES

Oviposition

Speyeria zerene hippolyta is usually a grassland butterfly that lives on open salt-spray meadows and grassy headlands adjacent to the Pacific Ocean, where the larvae feed on the common blue violet, *Viola adunca* J. E. Smith. Based on more than 100 observations, females oviposit singly among vegetation near host plants. Females are apparently stimulated to oviposit by some volatile compound emanating from violets. We found that females oviposit only in the presence of violets, but that direct physical contact with the host is not necessary. We observed oviposition up to 20 cm downwind of even dried violet leaves.

During oviposition behavior, the butterflies flew near the ground, working their way upwind. When violets were near, they paused to climb in meadow vegetation, probing with curved abdomen until a suitable site was contacted, and an egg deposited. We even observed females crawling into knee-deep layers of grass that overgrew violets by late summer. Oviposition observations and location of larvae indicate that females favor sunny sites, and usually avoid N slopes of steep meadow rises.

Eggs are cream colored when first laid, but if fertile, darken to pinkish tan by the second day. Eggs began to hatch 16 days after oviposition with ambient room temperature varying from 21 to 24°C (N = ca. 1000). A large quantity of lipid is stored in *Speyeria* eggs which appears to serve as a food reserve during larval diapause. This lipid, in the form of a light oil, is readily observed in yolk by dissecting eggs.

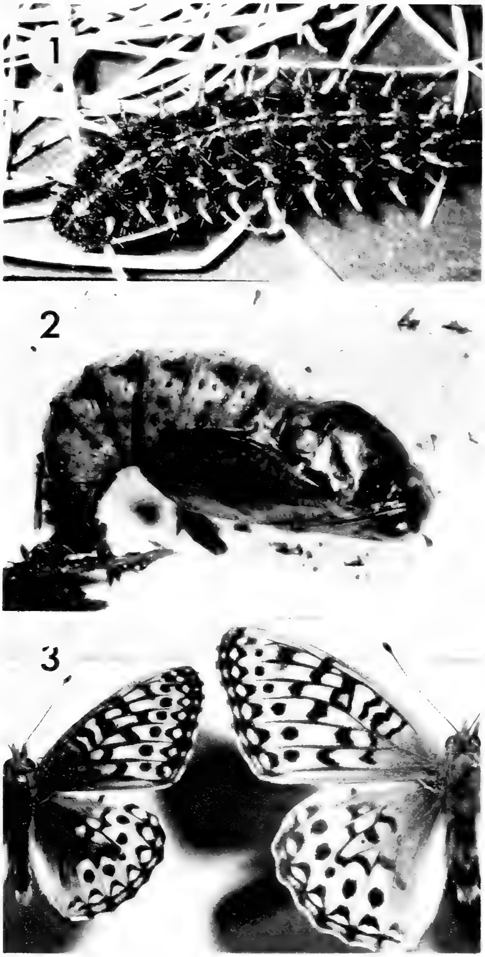
Larva

Newly hatched larvae (N = ca. 1000) usually wander short distances. As in other *Speyeria*, first instar *S. z. hippolyta* soon enter a diapause that lasts over winter. After selecting a suitable site, they spin a thin silk mat on which they rest until spring. Larvae exhibit considerable resistance to desiccation during diapause. In the laboratory, they survived a month or more without moisture, but this stress may diminish survival by spring. Thus, in years with delayed fall rains, the earliest hatched larvae may be at a disadvantage. When moisture is available, laboratory larvae touched their mouths to a wet surface, and some nearly doubled in size within a short time.

The following description of the last (6th) instar is based on larvae from about 10 family lines. The spiny larva (Fig. 1) is dark brown with a pair of pale lines running down the back, each of which has a row of black patches running parallel to it on the outside. These black patches are located on both sides of each body segment adjacent to the pale dorsal lines. Lateral parts of the body are finely and irregularly mottled with pale yellow. The head is mostly black, but the occipital area is yellow. Spine bases, especially those of the lateral rows, are straw colored similarly to the lines on the back. This color pattern resembles that of the inland *S. zerene bremnerii* (Hardy 1958), and blends with dried leaves where larvae take refuge when not feeding.

The first instar possesses unbranched setae or hairs. Later instars bear branched spines in the pattern illustrated by Scott and Mattoon (1982) for *S. nokomis* (Edwards). We reared all 13 species of *Speyeria*, and this setal pattern is consistent throughout the genus. However, it should be noted that a lateral spine is present on the 10th abdominal segment that was omitted from the Scott-Mattoon setal map. Superficially, this spine appears to be on the 9th segment. Spine branches or spinules are attached to the primary shaft in such a way that they can swing in toward the shaft apex when the larva withdraws from an entanglement. When pushed outward, the spinules lock into the outstretched position. In larger larvae, these sharp spines may provide protection from predators such as mice and, perhaps, shrews (unpubl. obs.).

In addition to spines, *Speyeria* larvae possess what may also serve as a defense against predators in the form of a fleshy, eversible osmeterium.



FIGS. 1–3. *S. zerene*. **1,** Mature 6th instar of *S. z. hippolyta*; **2,** Pupa of *S. z. hippolyta*; **3,** Reared males of *S. z. hippolyta* (left) and Willamette Valley *S. z. bremnerii* (right).

Whenever this structure is extruded, a disagreeable musky smell becomes apparent. This odor is faint in the small *S. zerene hippolyta*, but is much stronger in larger-bodied species such as *S. coronis* (Behr) and *S. edwardsii* (Reakirt). Unlike the long dorsal osmeteria of papilionid larvae, *Speyeria* osmeteria are short, wedge-shaped organs located ventrally just behind the head and before the first pair of thoracic legs. In addition, the musky smell of *Speyeria* osmeteria is distinctly different from the more pungent, aromatic smell of papilionid osmeteria.

As with most *Speyeria*, older larvae of *S. z. hippolyta* retreat to shelter sites sometimes several centimeters from host violets. These sites may

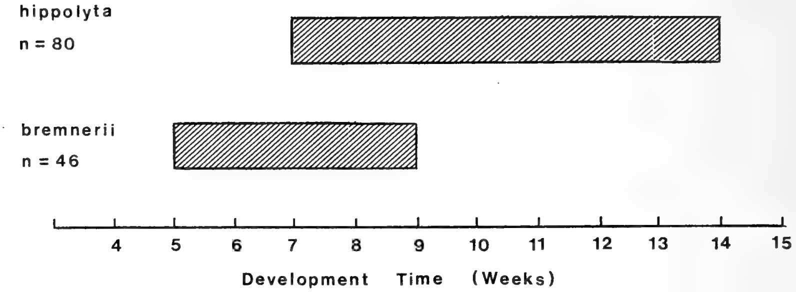


FIG. 4. Laboratory development time from first instar to adult in *S. zerene hippolyta* and *S. z. bremnerii* reared at 22° ± 1°C.

provide thermal advantages as well as cover from predators (McCorkle 1980). Some species may be mostly nocturnal (Dornfeld 1980:75). However, one field larva of *S. z. hippolyta* found during daytime in the present study was feeding, and laboratory larvae of many *Speyeria* feed both night and day. Their feeding is typically rapid so that they are exposed from cover only briefly. In the constantly heated laboratory, larvae probably grow faster than in nature. Their growth rate in the field may be delayed especially by cooler spring weather. Nevertheless, in the laboratory, they still required from one to three months to grow through six instars (Fig. 4, Table 1), and they spent about two weeks in the pupal stage.

Larval feeding signs were evident on violets in the Rock Creek meadow on 15 April 1980, indicating that at least some larvae were well into feeding activity. On 8 May 1986, one early 4th instar was observed. On 5 July, we found one nearly mature 6th instar (not parasitized) and several violets with fresh feeding signs, indicating that at least some larvae were still active. On the same date, however, the first adult male was taken, although normally the males do not begin to eclose until after 10 July with peak emergence in early August. Thus, the minimum natural larval feeding span is from mid-April to mid-June, some two months. It may be that a few larvae continue to feed well into August, producing the fresh adults present in early September.

Pupa and Adult

The pupa (Fig. 2) is smooth, rounded, and mostly dark brown with variable paler areas on abdomen and wing covers, and a dark, transverse band on the anterior edge of each abdominal segment. As in most *Speyeria*, the pupal chamber consists of several leaves drawn together with silk, and the pupa is usually attached in a hanging position to the top of the chamber.

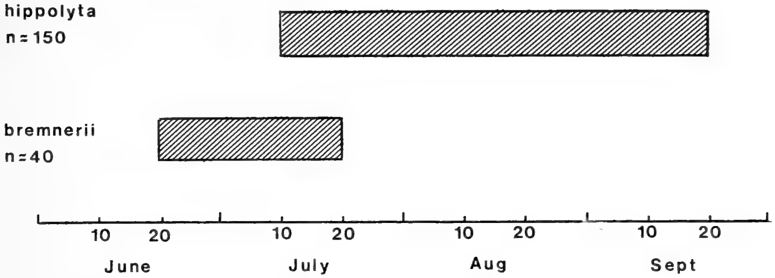


FIG. 5. Time range in field presence of fresh adults of *S. zerene hippolyta* (central Oregon coast) and *S. z. bremnerii* (Willamette Valley).

As noted above, the first adult male was taken on 5 July, and a nearly mature larva was also found on that date. By early August, males were common (Fig. 5) (22 marked 1–3 August), and females had begun to appear (2 marked). Between 20 and 22 August, 22 new males and 7 new females were marked, including several fresh females and a few fresh males. On 4 September, 15 new males and 16 new females were marked. Of these, five females were fresh, three males were fairly fresh, and one very fresh. It is thus apparent that in this colony, males eclosed from mid-July until at least the end of August. The first females eclosed by the end of July, and eclosion continued through August to mid-September, with aging specimens surviving into October. Recapture results (McCorkle 1980) indicate that some adults live for at least three weeks, and disperse widely up to 2–3 km (1–2 miles). Butterflies fly inland and seek shelter along forest margins when strong winds are blowing off the ocean (McCorkle 1980).

ADAPTATIONS TO COASTAL ENVIRONMENT

Both coloration and wing size appear to have a strong genetic determination, since *S. z. hippolyta* differs consistently from the larger and paler Willamette Valley *S. z. bremnerii* both in the field and in laboratory rearings (Figs. 3, 6). The difference between forewing lengths (Fig. 6) is highly significant ($P_t < 0.0001$). Data from Willamette Valley was obtained before the apparent extinction of these populations around 1977 (Hammond & McCorkle 1983).

There is evidence that small size and extensive dark basal suffusion as shown in *S. z. hippolyta* are adaptations to enhance solar heating, as would be needed in a marine-modified environment with persistent cold wind and frequent fog (McCorkle 1980). Butterflies, being heterothermic, usually depend on solar radiation to elevate body temperature sufficiently to allow flight necessary for foraging, mate seeking, escape from predators, and oviposition (Watt 1968, Douglas 1978,

TABLE 1. Time required for larval and pupal development in *Speyeria zerene* populations reared at 21–23°C. Each entry represents progeny of one female, with number of individuals in parentheses.

Subspecies	Locality	No. weeks Males	Females
bremnerii	Benton Co., Oregon	6 (2)	7 (3)
		5–6 (5)	6 (5)
	Thurston Co., Washington	6–7 (3)	8–9 (3)
		6 (2)	7–8 (3)
hippolyta	Pacific Co., Washington	8–9 (3)	9–10 (5)
		8–9 (7)	9 (3)
	Clatsop Co., Oregon	7–9 (11)	8–10 (12)
	Lincoln Co., Oregon	8–9 (9)	9–10 (10)
	Lane Co., Oregon	7–9 (7)	8–10 (9)
hippolyta-like	Del Norte Co., California	9–13 (8)	12–14 (7)
		8–9 (5)	9–10 (7)
		10–13 (6)	11–13 (8)
behrensii	Curry Co., Oregon	7–8 (5)	8–9 (9)
		7–8 (2)	9 (5)
gloriosa	Josephine Co., Oregon	7–8 (11)	8–10 (12)
		7–8 (7)	9–10 (6)
myrtleae	Marin Co., California	7–8 (11)	8–10 (14)
		7–9 (11)	8–10 (10)
		8–9 (12)	8–10 (12)

McCorkle 1980). Rapid ovarian development is also thermodependent (Watt 1968).

Speyeria use a dorsal basking position in which the wings are extended in a horizontal plane from the body, thus exposing the dark basal suffusion to solar radiation. In dorsal basking butterflies, heat first absorbed by the basal part of the wings is then absorbed by the thorax, and usually a thick coat of long hairs serves as insulation for retention of thoracic heat (Douglas 1978, McCorkle 1980). Douglas (1978:43) suggests that large butterflies are at a disadvantage under cool conditions because they heat up more slowly, while smaller butterflies warm quickly to an adequate thoracic temperature. In a cold, windy environment, small butterflies also have a second advantage because the smaller wingspan allows flight closer to the ground where wind velocity is lower. Wind is a problem in maintaining body temperatures because heat is lost from the body surface by forced convection (Douglas 1978:69).

Since most *Speyeria* require high body temperatures for normal activity, they usually fly only in full sunshine, or under cloudy conditions when the air temperature is higher than 21°C (70°F). However, field observations of *S. z. hippolyta* revealed that it engages in normal activity under cloudy or foggy conditions with air temperatures as low as 16°C

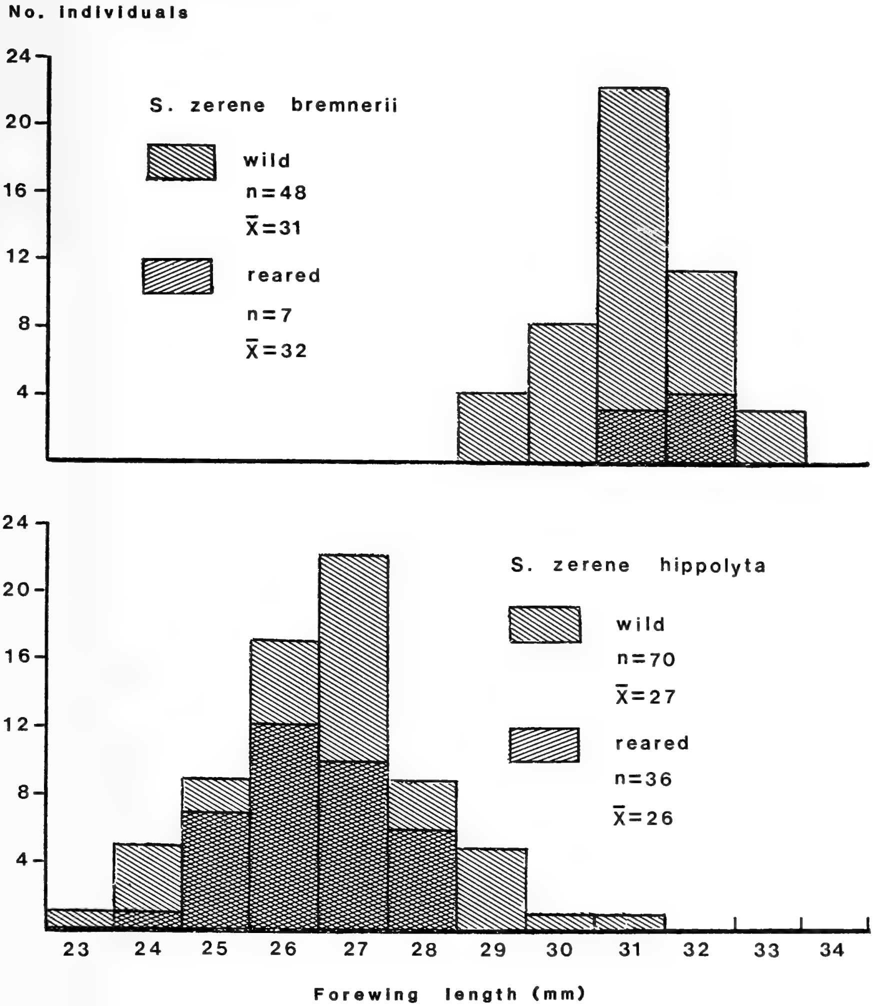


FIG. 6. Frequency distribution of male forewing length in wild and reared *S. zerene hippolyta* (central Oregon coast) and *S. z. bremnerii* (Willamette Valley).

(60°F), although the butterflies retreat to shelter under windy conditions. For example, during early September 1982, we observed approximately a dozen males in mate-searching flight, six males and females nectaring on flowers, and three females engaged in oviposition under windless, cloudy-foggy conditions with air temperature only 16°C (60°F). Similar observations have been made consistently during subsequent years. In sharp contrast, observations of the similarly colored *S. a. atlantis* (Edwards) in the Appalachians of West Virginia during 1977 revealed virtually no evidence of similar activity under cool, cloudy conditions. These adults (N = 100+) engaged in nectaring and flight only in full sunshine, and retreated to shelter in trees when clouds covered the sun at a temperature of approximately 21°C (70°F). In more dramatic contrast, the large *S. idalia* (Drury) favors minimum air temperatures of 24–27°C (75–80°F) for normal flight activities based on observations (N = 100+) in Nebraska during 1983, and continues to fly at temperatures of 41°C (105°F) or more. This species exhibits little basking behavior in the field, and the basal wing areas completely lack dark suffusion. Even the black hindwings of *S. idalia* are mostly pale orange at the wing base.

Because *S. a. atlantis* and *S. zerene hippolyta* are nearly identical in their dark basal suffusion, and are of similar small size, the expected thermal regulation and behavioral activity of these species should be similar. Therefore, the above observations suggest that *S. z. hippolyta* employs an additional mechanism that allows activity under low temperatures and cloudy conditions. This mechanism might include changes in enzyme systems that would allow normal physiological function at low body temperatures, but this possibility has not yet been studied.

Finally, *S. z. hippolyta* along the central Oregon coast is also highly unusual in that adult emergence in the field extends over a long period of some 8 weeks from early July to early September, and it requires 7–14 weeks to complete larval and pupal development in the laboratory (Figs. 4, 5). These developmental patterns appear to be an additional adaptation to the coastal environment. By contrast, most western *Speyeria* emerge over a relatively short period of about three to four weeks in June and July. For example, the Willamette Valley form of *S. z. bremnerii* usually emerged during late June and early July in the field, and required only 5–9 weeks to complete larval and pupal development in the laboratory. As shown in Figs. 4 and 5, the sharp differences in the developmental patterns between *S. z. hippolyta* and *S. z. bremnerii* are maintained consistently both in field and laboratory, suggesting that a strong genetic component is involved.

There are two apparent reasons for these developmental patterns in *S. z. hippolyta*. In most years, adverse conditions of cold wind, fog, and rain persist along the ocean through May, June, and July, and weather more favorable for adult flight usually does not develop until August and September. The retarded larval development of *S. z. hippolyta* coordinates adult emergence with the best weather conditions in the coastal environment. In addition, adverse stormy weather may develop in some years along the coast during either August or September. The great range of individual variation in developmental rate and adult emergence suggests an additional adaptation to variable and unpredictable weather conditions. Thus, early emerging butterflies may be more successful in reproduction one year, and late butterflies the next year, depending on each year's storm patterns. Since coastal weather is so variable from year to year, genes for both early and late emergence (fast and slow development) would tend to be maintained.

During the past 20 years, we have reared most of the geographic subspecies recognized in *Speyeria* under similar laboratory conditions at temperatures of 21–23°C (70–72°F). The fastest rate of larval and pupal development was observed in certain forms of *S. atlantis, S. egleis* (Behr), *S. callippe* (Boisduval), and Oregon *S. zerene bremnerii*, all of which required only five to six weeks for males and six to seven weeks for females. Most subspecies of *S. zerene* and *S. coronis* required six to seven weeks for males and seven to eight weeks for females. These include Sierran-type *S. z. zerene*, Rocky Mountain *S. z. sinope* dos Passos & Grey, and Great Basin *S. z. gunderi* (Comstock). Even very large-bodied species such as *S. c. cybele* (Fabricius), *S. idalia*, and *S. nokomis caerulescens* (Holland) required only a similar amount of time, while *S. nokomis apacheana* (Skinner), *S. diana* (Cramer), and *S. edwardsii* required seven to eight weeks for males and eight weeks for females.

However, except for typical *S. z. bremnerii* itself, all populations of *S. zerene* within the *bremnerii* subspecies group as defined by Grey and Moeck (1962) exhibit a relatively long developmental time of 7–9 weeks for males and 8–10 weeks for females (Table 1). Our field emergence data (Fig. 5), indicate especially long and variable development times for *S. z. hippolyta* populations along the central Oregon coast from Lane Co. N to Tillamook Co.

Hammond & McCorkle (1983) noted *hippolyta*-like populations of *S. zerene* along the coast of Del Norte Co., California, N of Crescent City. These are disjunct from Oregon *hippolyta*, and are separated by intervening populations of an *S. z. behrensii-gloriosa* intergrade in Curry Co., Oregon. Two of three family lines reared from the Del Norte populations exhibited an extended development time of 10–13 weeks for males and 11–14 weeks for females (Table 1). Thus, the extremely variable developmental rates observed in field emergence of *S. z. hippolyta* are also seen in some family lines reared in the laboratory. In sharp contrast, two family lines of *S. z. behrensii* from Curry Co. to the north, and three family lines of *S. z. myrtleae* from Marin Co., California to the south did not exhibit this extended development. Moreover, wild populations of *S. z. myrtleae* usually emerge in the field during early to mid-July, a full month earlier than the *hippolyta*-like populations. The manner in which these emergence patterns relate to respective local weather is undocumented as yet.

There are two close parallels to *S. zerene hippolyta* within the Argynninae that also exhibit adaptations to cold, wet marine-modified grasslands. One is *S. mormonia bischoffi* (Edwards) in coastal S Alaska from the Kodiak region N to Anchorage. The second is *Fabriciana* (*Mesoacidalia*) *aglaja scotica* Watkins in the Hebrides and Orkney Islands N of Scotland. Both species display extensive dark suffusion over much of the dorsal wing surfaces. Ford (1945) indicated that *F. a. scotica* often exhibits reduced wing size on small, wind-swept islands.

In the San Francisco Bay area of California, both *Speyeria c. callippe* and *S. coronis coronis* also have heavy melanic basal suffusion in a cool, foggy coastal environment (Hovanitz 1941), although the California habitat is less severe compared to the northern coastal grasslands occupied by the previous three species.

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MARKING LEPIDOPTERA AND THEIR OFFSPRING: TRACE ELEMENT LABELLING OF *COLIAS EURYTHEME* (PIERIDAE) WITH RUBIDIUM

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ABSTRACT. Trace elements can be used to label lepidopteran eggs via treated adults, but sources and importance of sample variability are relatively unexplored. Female *Colias eurytheme* (Boisduval) reared on rubidium (Rb)-treated foodplants and their eggs were analyzed for Rb by atomic absorption spectrophotometry. Parent (3 untreated and 4 treated females) and mean egg (25/female) element content were significantly correlated. Compared with untreated adults and eggs, treated samples were reliably marked, although significant egg-to-egg variability in Rb concentration was found within and between sib-groups. Analysis-day differences were not significant. Adult sizes and element exposures may have contributed to between-group variance. Maternal and genetic influences were potential sources of within sib-group variance.

Additional key words: alfalfa butterfly, internal marker, adults, eggs, atomic absorption spectrophotometry.

Many methods for marking and monitoring lepidopteran populations have been proposed, tested, and employed with various degrees of success (Southwood 1978). An internal marking method that shows great potential for use in dispersal studies of phytophagous insects is that of trace element labelling (Berry et al. 1972). These labels can be used in concentrations low enough to permanently mark but not adversely affect the insect or its host. The mark can be acquired without handling the insect because it is obtained as the animal feeds on treated plant tissue (Stimmann et al. 1973) or nectaries (Culin & Alverson 1986). Insects in 7 orders, including 10 species of Lepidoptera in 5 families, have been successfully labelled (Hayes & Hopper 1987:table 1). Dispersal tests employing trace elements as adult markers have been conducted with three lepidopteran species: *Heliothis zea* (Boddie) and *Spodoptera frugiperda* (J. E. Smith) (both Noctuidae) (Graham et al. 1978); and *Pectinophora gossypiella* (Saunders) (Gelechiidae) (Van Steenwyk et al. 1978).

One recently revealed advantage of trace element use over external markers of Lepidoptera is that the mark is passed along to reproductive products, including eggs (Legg & Chiang 1984, Hayes & Hopper 1987) and spermatophores (Graham & Wolfenbarger 1977). Detection of a parental mark in the egg or spermatophore provides, much like a genetic marker, a potential means of assessing gene flow in the field. In measuring dispersal, recovery of eggs may prove superior to recovery of adults because the marked adult transmits multiple signals through the distribution of marked eggs (Jones et al. 1980). Also, the possibility of using elemental marking of reproductive products in behavioral, physiological, or developmental studies is suggested, but has not been much explored (Engebretson & Mason 1981).

It remains to be seen whether recovery of marked eggs will prove feasible in large-scale field studies. However, the method has been used successfully to monitor small-scale egg dispersal by *Trichoplusia ni* (Hübner) (Geometridae) to adjacent crops (G. Ballmer pers. comm.). Among the many questions that need to be addressed is that of variability among eggs. Individual variability among adults can arise from exposure differences and differences in size or weight, and can occur through time. It has yet to be determined whether variability is passed along to offspring and whether there are intrinsic differences among eggs from the same female.

To investigate these areas and develop methods for more efficient and possibly expanded utilization of trace-element labelling, we analyzed marked adult *Colias eurytheme* (Boisduval) (Pieridae) and their eggs by atomic absorption spectrophotometry (AAS) for trace-element content. In addition to the parent-offspring relation, we examined egg-to-egg variability within sib-groups and among offspring of different parents. Differences between preparation dates were also considered possible sources of variability. Adult samples were prepared from bodies and head capsules and compared with egg samples to examine cost-effective adult sample preparation procedures.

MATERIALS AND METHODS

Insects. *Colias eurytheme*, the alfalfa butterfly, was used because of its tractability in the laboratory and greenhouse (Taylor et al. 1981), and because it is considered a model system for other Lepidoptera (Watt et al. 1974). Like *Heliothis* spp. and a number of other economically important Lepidoptera, *Colias* spp. are highly mobile, polyphagous, and distribute their eggs individually over a potentially large area (Tabashnik 1980). Experimental insects were obtained from a colony originating from eggs collected in November 1986 on commercial vetch, *Vicia villosa* Roth (Leguminosae), on the grounds of the Jamie Whitten Delta States Research Center, Stoneville, Mississippi.

Treatments. Adults were reared in the greenhouse from eggs or neonate larvae on vetch plants treated with rubidium (in chloride form). Host plants were grown from seed in vermiculite, and treated weekly with 1 g RbCl/l water (1000 ppm), initially by foliar application, then by watering the potting soil after insects were placed on the plants. Freshly treated host plants were provided as needed until pupation. Control insects were reared in a similar manner on untreated plants.

Treated and untreated pupae were placed in separate 2-l cardboard cartons with organdy top cloths and moistened paper towel liners. Eclosing adults were marked on the left hindwing with a felt tip pen (/ = treated; // = untreated), and placed in a mating cage. The cage, a 0.6 × 0.6 × 0.3-m wood frame covered with transparent plastic, was provisioned daily with honey-water (1:3) soaked cotton balls, and held at 12°C without light. To stimulate mating, temperatures were elevated to 30°C and light was provided by two banks of fluorescent lights for 2–4 h/day. The cage was checked at 15–30-min intervals for the occurrence of mating. Pairs were removed and held at room temperature (ca. 25°C) until spermatophore transfer was completed. The males were uniquely marked and returned to the cage. For oviposition, females were placed individually on host plants covered by plastic bags and maintained at room temperature (ca. 25°C) and LD 12:12. Ovipositing females were fed daily with honey-water and transferred to fresh host plants as needed.

Twenty-five eggs from each treated female (N = 4) and each untreated female (N = 3) were collected separately by sib-group, and frozen. Eggs were obtained from day 1–2 of oviposition. When a female died, wings were removed and the body frozen.

Sample digestion. Individual eggs were digested, following the method of Hayes and Hopper (1987), by placing an egg directly into the sample cuvette along with 0.025 ml ultrapure nitric acid (HNO_3), heating by microwave for 8–12 min at a low setting, and then diluting with 0.5 ml deionized distilled water (DDI).

The head and body of each female were placed in separate 7-ml scintillation vials with 0.2 ml and 0.4 ml ultrapure nitric acid, respectively. Digestion was allowed to occur at room temperature for 24 h, then samples were microwaved for 8–12 min. Digested material was then diluted with DDI, 4.0 and 5.0 ml, respectively.

AAS analysis. Samples were analyzed using a Perkin-Elmer 3030 with an HGA 400 graphite furnace and AS-40 autosampler. An electrodeless discharge lamp for Rb was used. Wavelength was set at 780 nm. Char and atomization temperatures were 800° and 1900°C (Slavin 1984). Elements were atomized off the wall of pyrolitically-coated graphite tubes.

Data. Initially, 10 eggs from each female (treated and untreated) were individually digested and analyzed by AAS for presence or absence of a detectable Rb signal (=day 1). To increase the sample size and examine between-analysis-day variability, an additional 15 eggs from each female were prepared and analyzed 14 days later (=day 2). To examine within-preparation variability, two separate aliquots of a single preparation from each head and body were decanted and analyzed on different days. Mean values for head and body samples were used in subsequent analyses since no significant differences were found between dates (Mann-Whitney *U*-test).

Data were analyzed to determine reliability of mark detection for each female and her eggs. Mark thresholds for both eggs and adults (heads and bodies) were determined and compared by two methods: (1) using the high-range value of untreated controls, and (2) using the conservative method of Stimmann (1974), which assumes a normal distribution, three standard deviation units above the mean of untreated control samples. All Rb concentration values are given in units per egg or body part. Variation in egg weight within and between sib-groups was considered negligible for our purposes (mean dry wt = 0.111 mg, SE = 0.0017, N = 10/female). Variation in head and body weight was more extreme (mean dry wt of heads = 0.897 mg, SE = 0.1536; body wt = 16.54 mg, SE = 3.374). Within and between sib-group differences were examined by analysis of variance. Parent-offspring relation was evaluated by correlation of Rb content of a female body or head with the mean Rb content of her eggs. Data analyses were performed using SAS software.

RESULTS AND DISCUSSION

The mean quantity of Rb (in ppm) found in the body, head capsule, and eggs of treated and untreated females is given in Table 1. Samples prepared from the bodies of treated females were found to be 100% reliably marked when compared to thresholds derived from samples prepared from untreated adults. However, only 10–20% of the samples prepared from heads alone produced detectable signals, and head results were not significantly correlated with body results (r = 0.30). It is apparent that detectable quantities of Rb were not evenly distributed throughout the insect's tissues. The time and expense of digesting whole insects makes it advantageous to use the smallest sample that provides consistent results. For *Heliothis* spp. it has been found that a single wing is an adequate substitute for a whole moth (Hayes in press). For butterflies, the wing is not as practical because of large size and the frequent need to retain wings for morph determinations. Thus, *Colias* samples prepared from wingless and headless bodies were used, and they produced reliably detectable signals. If spermatophores are routinely dissected from females, or abdomens are removed for electrophoretic analysis, it would be ideal to be able to rely on a preparation from the thorax alone. However, a feasibility test for use of the thorax has not yet been conducted.

More than 90% of eggs (N = 100; 4 females) were determined to be detectably marked regardless of method used (92% exceeded range of

TABLE 1. Quantity of Rb (mean & range in ppm) in untreated and treated female *Colias eurytheme* (body and head) and their eggs (for 2 analysis days). Mark thresholds, both high range of untreated controls (Mark 1) and Stimmann value calculated from mean of controls (Mark 2), are provided along with mark determination (yes/no) or percentage of marks.

		Rb concentration			
Female no.	N	Mean	Range	Mark 1	Mark 2
Threshold values:					
Body	10			0.0185	0.0309
Head	10			0.0140	0.0213
Eggs (day 1)	30			0.0014	0.0015
(day 2)	45			0.0028	0.0026
			Untreated		
1					
Body		0.0039[a]		no	no
Head		0.0021[a]		no	no
Eggs (day 1)	10	0.0004	0.0000–0.0012	0%	0%
(day 2)	15	0.0011	0.0003–0.0014	0%	0%
2					
Body		0.0182		no	no
Head		0.0046		no	no
Eggs (day 1)	10	0.0006	0.0002–0.0014	0%	0%
(day 2)	15	0.0013	0.0008–0.0022	0%	0%
3					
Body		0.0047		no	no
Head		0.0125		no	no
Eggs (day 1)	10	0.0002	0.0000–0.0006	0%	0%
(day 2)	15	0.0011	0.0004–0.0028	0%	0%
			Treated		
4					
Body		0.0739		yes	yes
Head		0.0208		yes	no
Eggs (day 1)	10	0.0035	0.0011–0.0030	90%	80%
(day 2)	15	0.0038	0.0031–0.0048	100%	100%
5					
Body		0.0999		yes	yes
Head		0.0058		no	no
Eggs (day 1)	10	0.0035	0.0016–0.0160	100%	100%
(day 2)	15	0.0038	0.0030–0.0051	100%	100%
6					
Body	2	0.0378		yes	yes
Head	2	0.0106		no	no
Eggs (day 1)	10	0.0022	0.0011–0.0032	70%	70%
(day 2)	15	0.0045	0.0019–0.0077	73%	73%
7					
Body		0.0995		yes	yes
Head		0.0101		no	no
Eggs (day 1)	10	0.0063	0.0033–0.0169	100%	100%
(day 2)	15	0.0070	0.0049–0.0086	100%	100%

[a] Mean of two aliquots per sample; for further explanation see Materials and Methods.

nonmarks; 91% exceeded Stimmann's value). The proportion of detectably marked eggs per analysis day for each sib-group is given in Table 1. Significant correlation was found on both analysis days between maternal Rb content of the body and mean quantity of Rb in offspring (Table 1; day 1 $r = 0.88$, $P < 0.01$; day 2 $r = 0.84$, $P < 0.01$).

Analysis of variance revealed significant differences between treated and untreated samples ($P < 0.0001$; Table 1). More than 60% of the variance was due to within-sib-group variance, more than 35% to between-group variance, and less than 1% was attributable to analysis-day variance. Low day-to-day analysis difference is reassuring because in field tests large numbers of samples must be processed over several days.

Between-group variance dropped to less than 20% for the untreated sib-groups when treated and untreated groups were analyzed separately. However, within-sib-group variance remained above 60%. Between-group differences could be attributed to differing insect sizes and element exposures. Eggs from a large female or one that has fed consistently on well-treated foliage may show higher levels of Rb than those from a smaller female or one that has fed inconsistently on a treated host plant.

Within-group differences cannot be understood as easily. Each female was mated only once, and use of the first eggs oviposited should lessen age effects. Since Rb is a potassium mimic, results suggest that the female does not supply her eggs with consistently similar quantities of necessary metabolites. Alternatively, inherent differences from egg to egg (genomic differences) may result in the observed Rb content variance. The parent-offspring correlation analysis reveals significant associations which may indicate some degree of inherent relation. Further investigation of these hypotheses could provide valuable insights into development, and might dictate an expanded role for the use of trace elements as an experimental tool.

In the final analysis, specimen-to-specimen, in particular egg-to-egg, variability does not present difficulties for use of this marking technique in field operations. Despite high individual variability, our findings indicate that labelled parents and offspring are readily distinguishable from unlabelled specimens.

Trace element marking has been reported previously with only one other butterfly species, *Pieris rapae* (L.), and then only in the adult stage (Stimmann 1974). The potential to exploit this marking method among all Lepidoptera is great. It seems well justified since mark-release-recapture studies using external markers are commonly used to study pest and nonpest lepidopteran population attributes (Ehrlich & Davidson 1960), but have received considerable criticism (Morton 1984).

Along with problems arising from handling insects, insufficient recapture numbers are a persistent problem. By labelling the egg, the adult signal is amplified, and the concomitant ability to directly assess gene flow is a definite advantage. Increasing the number of unique marks will also improve recapture efficiency per unit area. Along with Rb, other elements such as cesium and strontium are promising adult and possible egg markers.

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ANNOUNCEMENT

JOURNAL COVER ILLUSTRATIONS AND FEATURE PHOTOGRAPHS

Journal submission categories are being broadened to include front cover illustrations and feature photographs. Submissions in these new categories, like all submissions to the *Journal,* may deal with any aspect of Lepidoptera study. Submissions in both categories must be accompanied by brief captions that include scientific names.

Cover illustration subjects are well depicted by past covers created before submissions were invited. Submissions should be no larger than letter size, with the caption for the inside front cover on a separate sheet. Drawings may be more suitable than photographs because drawings can usually better withstand the coarse reproduction necessitated by present cover stock texture. Submissions will be selected for artistry, novelty, and general appeal. There are no author page charges for cover illustrations.

Feature photographs might show unusual behaviors, unusual habitats, type localities, specimens in nature illustrating identifying marks, or other subjects. Photographic submissions should be mounted on white cardboard no larger than letter size, with a brief caption on a separate sheet. Feature photographs must be suitable for reduction to either half or full *Journal* pages (8.5 cm high by 11 cm wide, or 17 cm high by 11 cm wide, caption included). Submissions will be selected for photographic quality, scientific merit, and general appeal. Regular page charges will apply to accepted feature photographs.

Submissions in both new categories should be sent to the *Journal* editor.

WILLIAM E. MILLER, Editor

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AN APPRAISAL OF *GAZORYCTRA* HÜBNER (HEPIALIDAE) AND DESCRIPTION OF A NEW SPECIES FROM ARIZONA AND NEW MEXICO

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ABSTRACT. *Gazoryctra* includes 10 species from North America, and 3 from N Europe and Asia. Seven Nearctic species of *Hepialus* are transferred to *Gazoryctra*: *hyperboreus* Möschler, *lembertii* Dyar, *mathewi* H. Edwards, *novigannus* Barnes & Benjamin, *pulcher* Grote, *roseicaput* Neumoegen & Dyar, and *sciophanes* Ferguson. *Gazoryctra wielgusi* is described based on 94 males from the White Mountains of Arizona and adjacent New Mexico. A checklist of *Gazoryctra* is included.

Additional key words: *Gazoryctra wielgusi, Hepialus,* systematics, Holarctic.

Gazoryctra Hübner are medium-sized swift moths found in high latitudes or alpine habitats of the Holarctic Region. They are handsome moths, with brown, orange, or pinkish forewings and silvery white maculations. Adults of most species fly in late summer or fall. They are exceptionally strong fliers, particularly the diurnal arctic-alpine species. Many have very brief periods of diurnal activity, flying for only 20 or 30 min during evening twilight.

All previously known *Gazoryctra* were described in the nominotypical genus *Hepialus* Fabricius (or *Epialus* Lederer). North American *Gazoryctra* have been referred to as the "*hyperboreus* group" by Barnes and Benjamin (1926) and Ferguson (1979). Members of this group were incorrectly placed in *Phymatopus* Wallengren by Pfitzner (1912, 1937–38). Viette (1949) alone recognized that some Nearctic hepialids should be classified in *Gazoryctra*.

The purpose of this paper is to provide adult, pupal, and larval characters for the recognition of the genus, to clarify which elements of the Holarctic hepialid fauna belong to *Gazoryctra,* to validate nomenclature changes for the North American species, and to describe a new species from the southwestern United States.

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Background

Hübner ([1820]:198) established three genera for the heterogeneous Palearctic swift moth fauna occurring in N Europe: *Gazoryctra, Pharmacis,* and *Triodia.* In his synopsis of the generic classification of European Hepialidae, Viette (1949) designated *Bombyx ganna* as type species of *Gazoryctra.* He characterized *Gazoryctra* as having a lobed valva and a toothlike trulleum in male genitalia, and further noted that small apical tibial spurs were present on middle and hind legs. He transferred to *Gazoryctra* the Palearctic *Hepialus macilentus* Eversmann and the Nearctic *H. confusus* H. Edwards and *H. mcglashani* H. Edwards. Later, Viette (1953) noted that *Gazoryctra* species also had prominent earlike lobes in the intersegmental membrane between abdominal segments 8 and 9 (socii of Robinson 1977, tergal lobes of Nielsen and Kristensen in press), and added a fifth species to the genus, *H. fuscoargenteus* Bang-Haas.

Many lepidopterists have overlooked or ignored the generic concepts of Hübner [1820], Wallengren (1869), Börner (1925), and Viette (1948, 1949), and have continued to treat most Holarctic swift moths as members of the nominotypical genus *Hepialus* (McDunnough 1939, Heath 1976, Ferguson 1979, Davis 1983). In North America, Hepialidae have been classified into two genera: *Hepialus* (type species: *humuli* Linnaeus) and *Sthenopis* Packard (type species: *quadriguttatus* Packard). Most lepidopterists have recognized *Sthenopis* from the time of its proposal in 1865 (Packard 1865, Kirby 1892, Neumoegen & Dyar 1894, Wagner & Pfitzner 1911, Forbes 1923, McDunnough 1939, Davis 1983). However, our studies indicate that *Hepialus humuli* and members of *Sthenopis* (with *Zenophassus* Tindale, *Aenetus* Walker, and perhaps others) have a common ancestor not shared by most other Holarctic Hepialidae. Synapomorphies for these taxa include (1) a metatibial hairpencil in males; (2) swollen metatibiae in males (members of the *Sthenopis regius* group and some *Aenetus* lack hairpencils and swollen metatibiae, but these appear to be reversals within the clade); (3) triangular forewings with falcate apices; (4) forewing scales with rounded apices; and (5) absence (loss) of the epiphysis in all but *Aenetus* and *Sthenopis argenteomaculatus* (Harris). In addition, all members of this group are larger than most other Hepialidae and exoporian Lepidoptera, with forewing lengths typically exceeding 4 cm. Consequently, if *Sthenopis* is to be retained as a distinct genus, then names proposed for more distantly related taxa like *Gazoryctra* warrant at least generic status.

Gazoryctra in North America

So that we could reliably assign the hepialid described here to a genus, we prepared dissections of all the Holarctic hepialid generotypes.

We also examined all North American hepialid extant primary types, and prepared genitalia and wing slides for all named Nearctic and many European species, including all examined by Viette (1949).

In addition to the characters given by Viette (1949), eight others were found to be shared by *Gazoryctra* species: (1) forewing subcosta forked (vein Sc_1 well developed); (2) halves of tegumen meeting dorsoanteriorad, but free over much of midline; (3) dorsal margin of tegumen bearing dense oval patch of spinules; (4) caudal portion of trulleum not fused to tegumen; and (5) pulvilli large and setose. In the larva, (6) claw elongate, with basal tooth ending before ½; (7) D2 and SD setae on prothorax not grouped. In the pupa, (8) caudal band of teeth encircling abdominal segment 7 broken ventrolaterad.

Our studies indicate that *Gazoryctra* is the largest genus of North American Hepialidae. In addition to the two Nearctic species identified by Viette (1949), seven other described hepialids were found to share this list of characters and are transferred here to the genus *Gazoryctra*.

Checklist

In what follows, subspecific names are indicated by a), and are but tentatively recognized. Author names followed by year do not necessarily refer to literature cited in this paper.

Gazoryctra Hübner [1820]
  Gazoryctes Kirby 1892, missp.

  confusa (H. Edwards 1884) (*Hepialus*)
  fuscoargentea (Bang-Haas 1927) (*Hepialus*)
    sordida (Nordstrom 1929) (*Hepialus*), infrasubsp.
   a) *postmaculata* (Landin 1943) (*Hepialus*)
  ganna (Hübner [1810]) (*Bombyx*)
    arctica (Boheman 1848) (*Hepialus*)
    reducta (Deutsch 1925) (*Hepialus*), infrasubsp.
    confluens (Hellweger 1914) (*Hepialus*), infrasubsp.
    chishimana (Matsumura 1931) (*Hepialus*), infrasubsp.
  hyperborea (Möschler 1862) (*Epialus*), **new combination**
  lembertii (Dyar 1894) (*Hepialus*), **new combination**
  macilenta (Eversmann 1851) (*Hepialus*)
    gerda (Staudinger 1897) (*Hepialus*)
   a) *nesiotes* (Bryk 1942) (*Hepialus*)
  mathewi (H. Edwards 1875) (*Epialus*), **new combination**
    matthewi (H. Edwards 1884), missp.
  mcglashani (H. Edwards 1887) (*Hepialus*)
    mcglachanii (Pfitzner 1912), missp.
  noviganna (Barnes & Benjamin 1926) (*Hepialus*), **new combination**
    novigana (Pfitzner 1937–38) (*Hepialus*), missp.
   a) *mackiei* (Barnes & Benjamin 1926) (*Hepialus*)
  pulchra (Grote [1865]) (*Hepialus*), **new combination**
  roseicaput (Neumoegen & Dyar 1893) (*Hepialus*), **new combination**
    mutata (Barnes & Benjamin 1926) (*Hepialus*), infrasubsp.
    demutata (Barnes & Benjamin 1926) (*Hepialus*), infrasubsp.

①

②

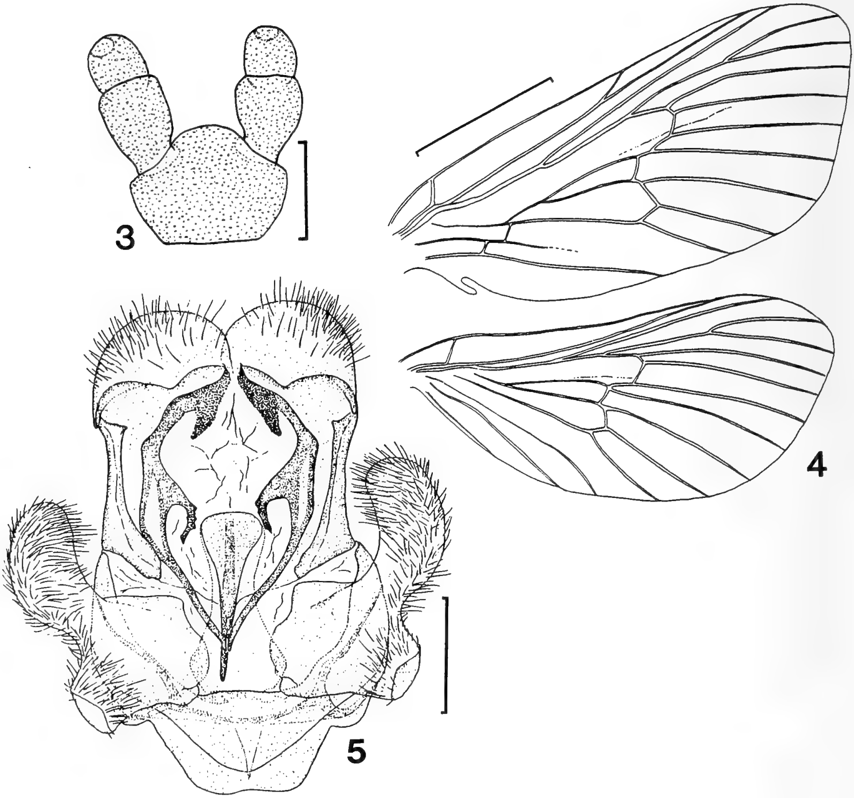
FIGS. 1, 2. *Gazoryctra wielgusi.* **1,** Holotype male; **2,** Paratype males from Ditch Camp. White scales replaced by silvery gray scales in lower right-hand specimen. Label data in text.

sciophanes (Ferguson 1979) (*Hepialus*), **new combination**
wielgusi Wagner & Tindale, **new species**

Gazoryctra wielgusi, new species

This pink and silvery moth is so far known only from a restricted area in the mountains of E Arizona and W New Mexico. Terminology for genital structures follows Birket-Smith (1974), Ueda (1978), and Nielsen and Robinson (1983); for wing veins, Nielsen and Robinson (1983); and for scale ultrastructure, Downey and Allyn (1975) and Kristensen (1978b).

Male (Figs. 1–11). Forewing length 15–18 mm (N = 94). **Head.** Antenna with 29–32 segments (N = 10), flagellomeres slightly compressed with abundant short setose sensory setae (Figs. 6, 7), yellow to orange-brown. Head vestiture dense admixture of buff and darker piliform scales; dark or dark-tipped scales prominent over frons, labial palpus, and ventral region. Labial palpus with 2 subequal segments (Fig. 3), vom Rath's organ dorsosubapical. **Thorax.** Pro- and mesothoracic dorsum with brown-tipped and buff piliform scales intermixed; metathorax buff. Procoxae and pro- and mesofemora dark-scaled. Tibiae and tarsi with elongate salmon-colored lamellar scales and contrasting dark fusiform scales (Fig. 8). **Venation** (Fig. 4). R_{2+3} branched at mid-length; hindwing vein CuP obscure in some specimens, and 2A differentiated from wing cuticle. **Scales** (dorsal surface over median region) (Figs. 10, 11). Broadest beyond middle, apices 3- or 4-toothed; secondary ridges prominent; windows small, circular to elliptical, diameter less than ⅕ interridge distance, surrounded by ring of unmodified cuticle, separated by 1 to 3 transverse flutes; window membrane occasionally present; flutes prominent with perpendicular secondary ribbing between adjacent flutes. Forewing tan or brown to peach or salmon with peppering of darker scales; heavily maculated with silvery white (rarely silvery gray) markings, these outwardly edged with dark scales; submarginal spots nearly always present, occasionally fused with oblique submarginal band; white spots or streaks also along subcosta and base of inner margin. Hindwing uniformly brown with orange or salmon-colored scales along margin, at apex, and extending basally along veins; apex faintly patterned. Fringe of both wings orange or salmon. **Abdomen.** Dorsum of segments 1 and 2 uniformly covered with long pale piliform scales; segments 3 to 8 with both long buff scales and lamellar salmon-colored scales. **Genitalia** (Fig. 5). Tergal lobes prominent, densely setose dorsad and laterad, hemispherical, with ventrolateral digitate lobe extending below margin of tegumen. Caudal margin of tegumen with 2 sets of ventrally projecting, strongly melanized processes, upper pair digitate and angled ventrad, apices with single prominent tooth and several smaller distal teeth; lower pair gradually tapering to



FIGS. 3–5. *Gazoryctra wielgusi.* **3,** Labium: scale = 0.2 mm (DLW Slide 86-63); **4,** Wing venation: scale = 0.5 cm (DLW Slide 86-62); **5,** Male genitalia: scale = 0.5 mm.

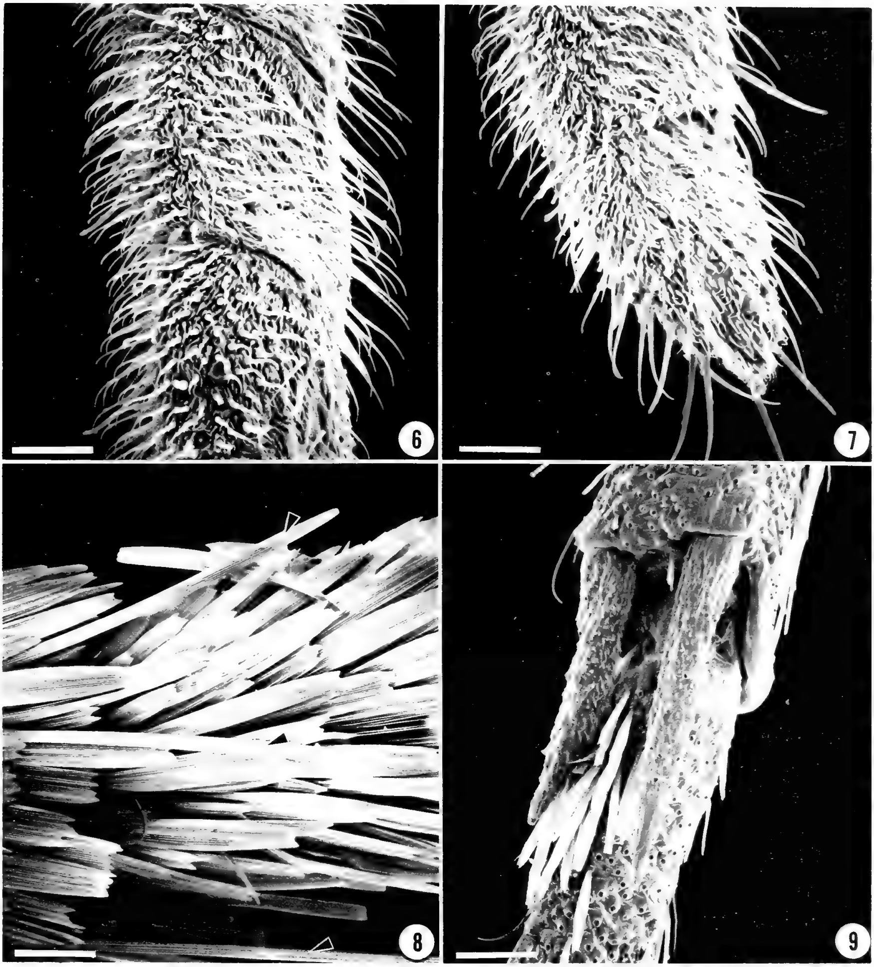
points, apices approximate over midline. Trulleum long, narrow, tapering to strongly melanized spine. Valva densely setose, boot-shaped; lower lobe rounded, curving mesad; inner margin notched above basal articulation. Juxta elongate, constricted in middle; roughly pentangulate. Vinculum often emarginate ventrolaterad.

Female. Unknown.

Diagnosis. A heavily maculated species with silvery white streaks and spots along base of inner margin, subcosta, and termen between medial veins. It can be readily separated from other strongly marked *Gazoryctra—confusa, hyperborea, pulchra,* and *roseicaput*—by its dark brown hind wings with contrasting orange or salmon-colored fringe. The oblique submarginal band is continuous, never broken into separate spots as is often the case in other members of the genus. It is the only salmon-colored *Gazoryctra* in the S Rocky Mountains. Male genitalic characters distinguishing *wielgusi* from at least some other members of the genus follow: tergal lobes nearly as high as broad, valva boot-shaped, vinculum ventrolaterally emarginate, trulleum very elongate.

Distribution. White Mountains of E Arizona and adjacent ranges in New Mexico between 2400 and 2800 m elev.

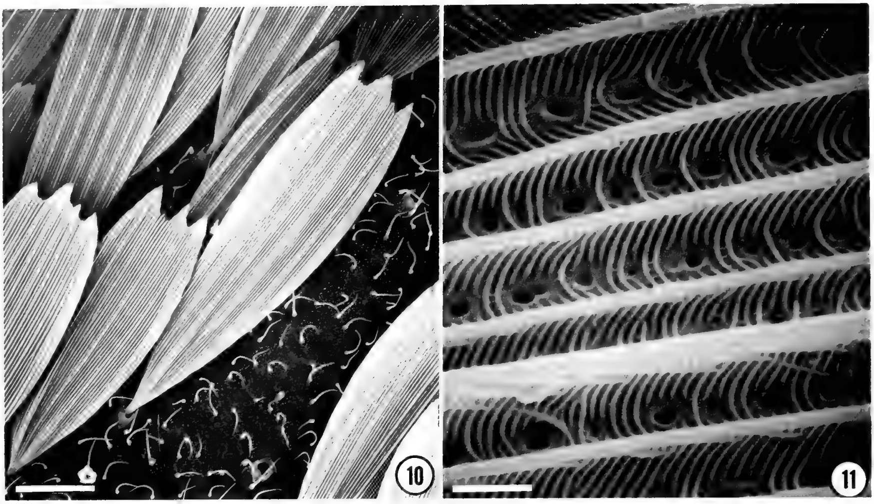
Material examined. 94 males. Holotype: Male, Arizona, Apache Co., 14.4 km E McNary, Ditch Camp, 2400 m, 25-VII-1974, R. S. Wielgus, at ultraviolet and white light, DLW Slide No. 86-66. Deposited in Los Angeles County Museum. Paratypes: Arizona: Apache



FIGS. 6–9. *Gazoryctra wielgusi* male. **6,** Antenna showing abundance of sensory setae and cuticular projections. Scale = 43 μm; **7,** Distal antennal segments. Scale = 43 μm; **8,** Protibia. Fusiform scales (arrows) appear dark and spinelike against salmon-colored squamose scales. Scale = 60 μm; **9,** Metathoracic tibial spurs. Scale = 100 μm.

Co., same data as above, 25-VII/14-VIII-1974/80, R. S. Wielgus, 58 males (Fig. 2), and 26/29-VII-1978, N. B. & M. Tindale, 2 males; White Mtns., Greer, 2600 m, 4-VIII-1962, E. & I. Munroe, 4 males; Greer, 0.8 km S, Government Springs, 6-VIII-1977, R. S. Wielgus, 2 males, and 28/30-VII-1978, N. B. & M. Tindale, 10 males; Greer, 19.2 km SW, Winn Cmpgd., 2800 m, 26-VII-1986, R. Robertson, 12 males; Greenlee Co., Hannagan Meadow, "12-IV-1975", A. Menke, 3 males. New Mexico: Catron Co., Gila Wilderness, along route 78, Willow Creek Cmpgd., ca. 2400 m, 28-VII-1978, 1947 h MST, R. S. Wielgus, 1 male; Indian Creek nr. Gilita Cmpgd., 2400 m, 29-VII-1978, 1948 h MST, R. S. Wielgus, 1 male.

The three specimens of *G. wielgusi* in the USNM bearing the data "CALIFORNIA:



FIGS. 10, 11. *Gazoryctra wielgusi* scales from medial region of male forewing. **10,** Scale showing typical exoporian arrangement of primary and secondary ridges. Scale = 30 μm; **11,** Scale ultrastructure: scutes and flutes well developed. Scale = 1.15 μm.

Greenlee Co., Hannagan MDW., April 12, 1975, A. Menke" are mislabeled as there is no Greenlee Co., California. Moreover, all *Gazoryctra* species are summer- or fall-flyers. Presumably, Menke captured the moths in Hannagan Meadow during a collecting trip to the Southwest in August 1975 (A. Menke pers. comm.).

Paratypes are deposited at Arizona State University, Tempe; Australian National Insect Collection, Canberra; British Museum (Natural History), London; California Academy of Sciences, San Francisco; Canadian National Collection, Ottawa; Los Angeles County Museum, California; South Australian Museum, Adelaide; United States National Museum, Washington, D.C.; University of California, Berkeley and Davis; Zoologische Staatssammlung, Munich.

Biology. *Gazoryctra wielgusi* has a very brief period of adult activity. All specimens have been captured in early evening just after onset of darkness. In late July, the main flight occurs between 1945 and 2000 h MST (N = 17); by mid-August flight starts as early as 1930 h MST (N = 7). All specimens (males) were collected at light; typically they are the first moths to arrive at sheets. Adults are most numerous after afternoon rains and may even fly during strong rains (R. S. Wielgus pers. comm.).

Our records are from mesic areas in conifer forests. The locality at Ditch Camp is an open ponderosa pine forest with abundant grasses in open areas and nearby alders. Higher-elevation localities have more understory shrubbery. Spruce is dominant at the two sites in New Mexico. Nothing is known of the early stages. The larvae presumably are polyphagous, subterranean feeders, as are other Holarctic hepialids (Heath 1976, Wagner 1985, 1987). Recorded hosts for other *Gazoryctra* include *Betula, Phlox, Picea,* and grasses (Wagner 1985, Tham et al. 1985).

Etymology. We name this moth after Ronald S. Wielgus whose seemingly inexhaustible collecting efforts produced most of the known specimens and biological data.

Discussion

Gazoryctra is confined to the Holarctic Region; 10 Nearctic and 3 Palearctic species are recognized. No member is recognized from both faunas, although the markings of both *ganna* and *macilenta* approach those of *hyperborea* from North America.

Gazoryctra appears to represent one of the most primitive genera of Hepialidae. No synapomorphies have been identified that link *Gazoryctra* to other hepialids. In the past, the absence of tibial spurs has been used to define Hepialidae (Borror & White 1970, Kristensen 1978a, Nielsen & Robinson, 1983). Yet members of *Gazoryctra* possess a pair of small tibial spurs (Fig. 9, Viette 1949, Wagner 1985). In addition, the trulleum is free from the tegumen caudad in *Gazoryctra,* but fused in more derived Hepialidae (Nielsen & Scoble 1987).

Both adults and immature stages of *Gazoryctra* are rare in collections. Only three new hepialids have been described from North America since the turn of the century, and all belong to *Gazoryctra.* Moreover no specimens of *sciophanes* and *wielgusi* were known before 25 years ago. The biology is not known in detail for any species.

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TEMPORAL TRENDS IN FREQUENCIES OF MELANIC MORPHS IN CRYPTIC MOTHS OF RURAL PENNSYLVANIA

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ABSTRACT. Five species of moths with recorded melanic forms were light-trapped for 10–16 years during 1971–86 at a remote mountain valley in E-central Pennsylvania. Observed melanic frequencies were: *Biston betularia cognataria* 0.52 (1971–78) and 0.38 (1979–86); *Epimecis hortoria* 0.34; *Phigalia titea* 0.14; *Charadra deridens* 0.64; *Catocala ultronia* 0.001. All but *Biston* showed constant melanic frequencies during their sampling periods.

Additional key words: Geometridae, Noctuidae, *Biston betularia cognataria, Lymantria dispar*.

Many eastern North American nocturnal moths that escape daytime predation by cryptic resting behavior have a moderate frequency of heritable dark forms. A simple working hypothesis to explain the adaptive advantage of this phenomenon is that these are "industrial melanics", favored by industrial and automotive pollutants in the atmosphere (Kettlewell 1973). Such an hypothesis is only vaguely supported in North America because of inadequate records. If trends showing systematic increases or decreases in frequency of melanics can be documented, the causes of such shifts might be found.

A second major body of relevant evidence results when enough localities are sampled for melanic frequencies. With these possibilities in view, I have been obtaining melanism data from daily light trap samples in a rural wooded valley for 16 years. The first eight years (1971–78) of records for *Biston betularia cognataria* (Guenée) (Geometridae) were presented and discussed previously (Manley 1981). In the present paper, data are given for *B. b. cognataria* for the next eight years (1979–86) as well as the first eight, and comparative records are included for *Epimecis hortoria* (F.), *Phigalia titea* (Cramer) (both Geometridae), *Charadra deridens* (Guenée), and *Catocala ultronia* (Hübner) (both Noctuidae). The observed melanic frequencies are compared with each other and with published records from other areas.

MATERIALS AND METHODS

Sampling (dusk to dawn) was conducted nightly from April through early September each year using a fluorescent 15-watt blacklight and a mercury-vapor light trap. The trap was located in an isolated mountain valley 12 km NE of Klingerstown, Schuylkill Co., Pennsylvania. Except

TABLE 1. Melanic frequencies in four species of moths near Klingerstown, Pennsylvania. The two annual broods of *Biston betularia cognitaria* are combined. Dash signifies no observation.

	Biston b. cognitaria		*Charadra deridens*		*Epimecis hortoria*		*Phigalia titea*	
Year	Frequency	N	Frequency	N	Frequency	N	Frequency	N
1971	0.52	588	—	—	—	—	—	—
72	0.51	669	—	—	—	—	—	—
73	0.56	828	0.68	35	—	—	—	—
74	0.52	272	0.58	52	0.47	15	—	—
75	0.52	102	0.62	50	0.35	15	—	—
76	0.53	219	0.80	5	0.38	21	—	—
77	0.51	244	0.67	15	0.33	55	0.14	176
78	0.46	226	0.71	7	0.23	13	0.17	189
79	0.48	452	0.73	11	0.29	68	0.15	148
80	0.52	68	0.86	7	0.25	24	0.17	219
81	0.43	30	0	0	0.14	7	0.20	257
82	0.36	100	0	0	0.22	40	0.15	31
83	0.34	466	0	0	0.42	52	0.15	180
84	0.33	196	0.67	12	0.31	74	0.18	211
85	0.34	239	0.75	4	0.37	87	0.15	93
86	0.38	301	0.75	4	0.38	60	0.10	33
Total	0.47	5000	0.65	202	0.33	531	0.15	1537

for a few open fields, the area is tree-covered. Details of site, sampling methods, and regional sources of air pollution potentially affecting air quality and melanic frequency are given in Manley (1981). Sampling extended over a period of 10 or more years for each species. Specimens were pinned with full data and are part of the Manley Collection, Peabody Museum of Natural History, Yale University.

The data format in Table 1 allows quick comparisons with Owen (1961, 1962), Sargent (1971, 1974), and Klots (1964, 1968). *G*-tests using Williams's correction (Sokal & Rohlf 1981) were employed to test whether melanic frequencies differed from year to year.

RESULTS

Biston betularia cognataria appears to undergo large fluctuations in population density every 4–5 years (Table 1). In 1975, the first brood consisted of 3 trapped specimens followed by a second brood of 99, with the melanic frequency of 0.52 equal to the first 8-year average (Manley 1981). The melanic frequency declined from 0.52 in 1980 to 0.33 in 1984, while numbers trapped rebounded to levels before the population crash of 1980–81. Populations after 1981 show a six-year (1981–86) melanic frequency of 0.34, compared to 0.48 for the 6-year period (1975–80) following the 1975 crash. This contrasts with a frequency of 0.53 for the first 4 years (1971–74).

The 1971–78 trends in *Biston b. cognitaria* were earlier interpreted partly as a gradual decline in melanic frequency (Manley 1981). The new data here strengthen this suggestion (linear regression of melanic frequency against year: slope = -0.016 ± 0.002, $N = 16$, $t = 7.27$, $P < 0.001$). However, an equally plausible explanation is the population crash of 1981 (1971–80 data versus 1981–86 data: $G = 132.47$, df = 1, $P < 0.001$; samples in 1971–80 set are homogeneous, as are samples in 1981–86 set, $P > 0.25$ by G-tests).

Epimecis hortoria (Table 1) exhibits a stable frequency of 0.33 for its melanic form "*carbonaria*" ($G = 9.98$, df = 12, $P > 0.50$). This moth has become increasingly abundant at the light trap since its population crash in 1981. Owen (1961, 1962) reported a 1957 sample of 8 specimens from Westmoreland Co., just E of Pittsburgh, as 100% melanic, and a 1959 sample at Lebanon, Hunterdon Co., New Jersey, as 0.90.

The melanic form "*deplorens*" of *Phigalia titea* is distinct, with no apparent intermediates; it (Table 1) maintained a stable frequency of 0.15 during the sampling period ($G = 3.66$, df = 9, $P > 0.50$). Owen (1961) reported 1960 melanic frequencies in Michigan ranging from 0.11 to 0.14; Sargent (1971) reported 1968–70 melanic frequencies at Leverett, Massachusetts, at 0.20.

My samples of *Phigalia titea* were taken 25 March through 5 May. Since this moth begins flying on warm March nights, a portion of the total possible sample of it was probably not taken. My samples reflect only warm nights in late March with no continuous sampling until April. Nevertheless, there does not appear to be substantive change in melanic frequency of this species.

Melanic frequency for *Charadra deridens* during 1973–86 (Table 1) was stable at 0.65 ($G = 3.89$, df = 9, $P > 0.50$). Klots (1968) at Putman, Windham Co., Connecticut, reported limited 1961–66 samples ($N = 28$) to be 0.89 melanic, and a laboratory reared sample ($N = 39$) to be 2:1 melanic.

Charadra deridens samples have been small since 1981–83, when no moths were taken (Table 1). The 10-year melanic frequency of 0.65 is the highest of any melanic moth sampled to date at this locality.

Catocala ultronia, the most abundant *Catocala* in central Pennsylvania, was sampled during 1968–78. In my sampling, only 2 of 1520 specimens were the melanic form "*nigrescens*", all others being color variants of form "*celia*". Sargent (1974) reported the 1968–74 melanic frequency in Leverett, Massachusetts, to be 0.17 ($N = 586$).

DISCUSSION

Except for *Catocala ultronia*, the species discussed in this paper show strong melanic tendencies. Melanic frequencies differ from those observed at Leverett, Massachusetts (Sargent 1974), even for the same years. Melanic frequency appears to fluctuate independently at least in part among species. Some factors affecting melanic frequencies are presented in Manley (1981).

The 1980–81 season heralded severe reductions in the populations of *Biston, Epimecis* and *Charadra,* whereas *Phigalia* produced the largest sample of its 10-year period, only to be reduced to 31 individuals in 1982. An explanation for the sudden reductions in population densities could in part be local infestation of the deciduous woods by the gypsy moth, *Lymantria dispar* (L.). A partial defoliation in 1980 was followed by severe defoliation in 1981 and aerial spraying with Dylox or Dimilin by the Pennsylvania Department of Forestry. Spraying was discontinued in 1982, and no noticeable defoliation has occurred since.

Four species in this study are polyphagous. More than 50 species of trees and shrubs are recorded for *Biston betularia cognitaria,* with *Salix, Populus, Betula,* and *Alnus* preferred (Rindge 1975, McGuffin 1977). Prentice (1963) lists 25 species of hard and softwoods for *Phigalia titea,* with *Tilia, Ulmus, Betula, Populus, Acer,* and *Quercus* preferred. *Epimecis hortoria* prefers *Liriodendron, Sassafras,* and *Prunus,* and is rarely found on other deciduous trees (Forbes 1948). *Charadra deridens* prefers *Ulmus, Betula,* and *Quercus* (Forbes 1954). Only *Quercus* among the preferred food plants is normally eaten by the gypsy moth. Aerial spraying to control gypsy moth may have been a critical factor in reducing populations of the polyphagous species. The rapid recovery of *Biston* and *Phigalia* following reductions in 1981–82 (Table 1) could be attributed to the wide range of food plants acceptable to these species. Similarly, the preferred food plants of *Epimecis* are not those eaten by larvae of the other species in this study, thus perhaps accounting for a rapid recovery in 1982. *Charadra deridens,* a *Quercus* feeder (Forbes 1954), appears to have been severely reduced in the defoliated area, as none were trapped from 1981 to 1983, and it remains rare in the area (Table 1).

The population reduction of *Phigalia* in 1982 does not coincide with the 1981 reductions of the other species (Table 1) in that the annual sample was taken before the aerial spraying in 1981.

Defoliation by gypsy moth opens the forest canopy, allowing light penetration which could aid predators in finding active adults, especially ovipositing females. The tendency of birds to seek the safety of trees escaping defoliation could increase the density of predators on larvae feeding on those trees, as well as on ovipositing females.

Air pollution over Pennsylvania is often from industrial areas in the Ohio Valley and Gulf Coast (Brown 1987). Local sources of pollution do not greatly increase the quantity of oxides of sulfur and nitrogen in the sampling area, since the area is not industrial. Despite reports of a two- to three-fold increase in ozone and other oxidants in the Appalachians between 1962 and 1976 (West 1977), air pollution may not be a critical factor in fluctuations in melanic frequencies at this site. Despite high levels of polluted air over Pennsylvania, four of the five species sampled in this report have stable melanic frequencies. The determining factors appear to be localized biological factors, like gypsy moth.

The data here suggest that the widespread aerial spraying for gypsy moth control may be having a catastrophic effect on many species of lepidopterous insects in the eastern United States.

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A NEW SPECIES OF *OCALARIA* (NOCTUIDAE: CATOCALINAE) AND ANALYSIS OF SOME MORPHOLOGICAL CHARACTERS USEFUL FOR ELUCIDATING NOCTUID PHYLOGENY

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ABSTRACT. *Ocalaria cohabita* is described from 24 specimens captured on Barro Colorado Island, Panama. A key to adults of *Ocalaria* is provided, followed by a morphological comparison of *O. cohabita, O. oculata* (Druce) and *O. quadriocellata* (Walker). Particular emphasis is placed on characters that may prove useful in elucidating noctuid phylogeny, including features of head, legs, wings, abdominal segments 2 and 8, and genitalia.

Additional key words: morphology, Panama, *Ocalaria oculata, O. quadriocellata,* systematics.

Greig and DeVries (1986) described the gregarious diurnal roosting behavior of a small noctuid moth from Parque Nacional Corcovado in Costa Rica. This moth was an undescribed species of *Ocalaria* Schaus. Adults of this species were subsequently captured near the Smithsonian Tropical Research Institute on Barro Colorado Island, Panama, and sent to me for identification. Comparison with illustrations of Corcovado specimens showed that the Panamanian material was conspecific. The species is described below.

Ocalaria cohabita, new species

(Figs. 1–5, 10, 14, 16, 17, 20, 21, 24, 26)

Diagnosis. Forewing underside discal eyespot with double pupil, smaller pupil surrounded by iridescent deep-blue scales, lacking marginal blue-green scales; hindwing underside with solid brown band between postmedian and subterminal lines; male antenna serrate.

Male. Head. Haustellum unscaled; labial palp mainly dark gray-brown, first segment with some off-white scales dorsally and lateroventrally, smooth-scaled laterally but scales on dorsal and ventral edges projecting as a loose fringe, 2nd and 3rd segments uniformly dark gray-brown, smooth-scaled on all surfaces, subequal in length, elongate, ascending in life, at rest recurved dorsally over head (Greig & DeVries 1986:fig. 4), 2nd segment gibbous; antenna long, almost equal to forewing length, dorsally uniformly scaled dark gray-brown, ventrally serrate, sensory setae distinct, white; eyes large, bulbous, bare, unlashed; frons narrow, unscaled on lower half except for extreme edges, scales on dorsal half projecting anteriorly forming median ridge; frons, vertex, occiput dark gray-brown except for band of off-white scales bordering eye posteriorly. **Thorax.** Patagia, thoracic scaling concolorous with head, tegulae similar but with weak, transverse, median white band. **Legs.** All uniformly dark gray-brown dorsally, off-white ventrally; apexes of tibial and tarsal segments off-white, weakly so on forelegs, more strongly marked on hindlegs; tibiae unspined. **Forewing length** 13.4–16.0 mm (holotype 16.0 mm). **Wings** (Figs. 1, 2). Forewing ground color dark gray-brown, transverse bands pale gray, with weak purple iridescence in oblique lighting; space on forewing enclosed by costa, discal cell, antemedian line pale orange; eyespot black with off-center white pupil, surrounded by ring of pale orange; apical spot black with basal small white spot; ventral pattern similar to upper but more colorful; forewing pale gray, ventral of discal cell as far as postmedian line, eyespot as upper surface but with additional smaller white pupil posterodistal to main pupil, smaller pupil surrounded by deep blue iridescent scales visible only in oblique lighting, area between postmedian and subterminal lines violet-gray with central brown area, anterior part suffused with orange scales; pupil of apical eyespot much larger than on upper surface, rounded or square, subequal to main pupil of discal eyespot; distally veins R_5 and M_1, together with costal area to apical eyespot, orange; hindwing ground color pale gray, suffused costally with brown scales, discal lunule, antemedian, postmedian, and subterminal lines dark gray-brown, distinct; brown band present between postmedian and subterminal lines, bounded basally and distally by pale gray. **Abdomen.** Dorsally and ventrally transversely striped, anterior half of each segment pale gray, posterior half dark gray-brown. **Genitalia** (Fig. 3). Uncus with small apical hook; saccus ovoid; juxta ill-defined; valve simple, lacking appendages, with a strong constriction on the costa basally; aedeagus cylindrical, with bluntly-pointed apical process; vesica without cornuti.

Female. As described for male except antenna filiform, wings broader, more rounded, not as acutely pointed (Figs. 1, 2). Ratio of forewing length to maximum width perpendicular to costa averaging 2.28 in males ($n = 12$) and 2.11 in females ($n = 11$), the 0.17 difference being significant ($P = 0.001$, 1-tailed Mann-Whitney test because larger ratio expected in males). **Genitalia** (Fig. 4). Segment 8 annular; antrum membranous, undifferentiated from ductus bursae; corpus bursae membranous, ovoid, lacking signa; ductus seminalis broader than ductus bursae, arising from posterior end of corpus bursae.

Types. Holotype male: Panama, Barro Colorado Island, 20 May 1986, N. Greig. Paratypes: 1 female: Panama, Barro Colorado Island, 28 May 1986, P. J. DeVries (BMNH noctuid slide #12816); 11 males, 11 females: Panama, Barro Colorado Island, 18 August 1986, P. J. DeVries (BMNH noctuid slides #12803–12815). In British Museum (Natural History).

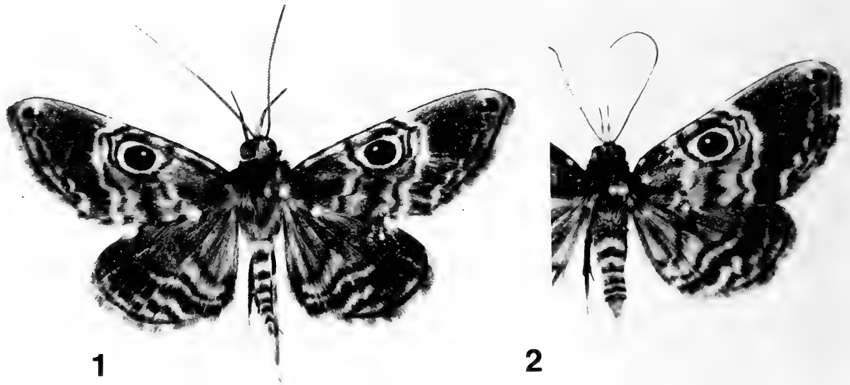
Life history. Nothing is known about the immature stages or larval hosts of any species of *Ocalaria*.

Variation. There is no major variation in wing pattern either between or within sexes. The pale orange forewing costal band may be weakly subdivided medially by ground color scales. However, older moths become worn and faded, eventually presenting a "washed-out" pale coloration. This phenomenon affects wings and body scales equally and appears due to a combination of scale loss and fading of brown pigments.

Key to Adults of *Ocalaria*

Ocalaria currently contains 7 described species (provenances and numbers examined are those of specimens held in BMNH): *dioptica* (Walker) (=*macrops* (Felder & Rogenhofer)) (Brazil: Amazonas, n = 2; Peru: Amazonas, n = 1; Bolivia, n = 2; French Guiana, n = 1), *guarana* Schaus (Brazil: Rio de Janeiro, n = 2; São Paulo, n = 1), *oculata* (Druce) (Guatemala: San Isidro, n = 56), *pavina* Schaus (Brazil: Rio de Janeiro, n = 9), *pavo* Schaus (Costa Rica: Sixola), *quadriocellata* (Walker) (Brazil: Cuiabá, n = 11) and *cohabita*, new species.

The couplet for *O. pavo* is based on a small water-color painting in BMNH, which lacks specimens of this species. This type of painting, probably commissioned by G. F. Hampson, has been found to be realistic and reliable as an identification guide (A. Watson pers. comm.).



FIGS. 1, 2. *Ocalaria cohabita*. **1,** Holotype male; **2,** Paratype female.

1. Discal eyespot on forewing underside with single white pupil (occasionally double in *O. quadriocellata*, not surrounded by deep blue iridescence), marginal iridescent blue-green scales; hindwing underside without solid brown band between postmedian and subterminal lines; male antenna bipectinate 2
   Discal eyespot on forewing underside with double pupil, smaller pupil surrounded by iridescent deep blue scales, lacking marginal blue-green iridescence; hindwing underside with solid brown band between postmedian and subterminal lines; male antenna serrate .... *cohabita*, new species
2. Area between postmedian and subterminal lines on upperside of both wings solid dark brown, edged with continuous pale cream lines .... *pavo* Schaus
   Area between postmedian, subterminal lines on upperside of both wings not solid dark brown, pale line bordering inner edge of subterminal line interrupted 3
3. Discal eyespot on forewing upperside subequal to apical eyespot; brown streak present in discal fold between median and postmedian lines .... *pavina* Schaus
   Discal eyespot on forewing upperside much larger than apical eyespot; brown streak in discal fold between median, postmedian lines absent 4
4. Forewing upperside, distal to discal eyespot, with conspicuous white spot often divided in half by brown scaling along vein M_3 .... *quadriocellata* Walker
   Forewing upperside without such spot 5
5. Forewing underside with white spot or streak below apical eyespot; pupil of apical eyespot small, no more than half width of eyespot in diameter, surrounding black scales conspicuous 6
   Forewing underside without white spot or streak below apical eyespot; pupil of apical eyespot large, subequal in diameter to width of eyespot, almost obliterating surrounding ring of black scales .... *oculata* Druce
6. Ground color dark brown; forewing upperside postmedian line cream, continuous across wing; discal eyespot on forewing underside without diagonal cream line below .... *guarana* Schaus
   Ground color off-white suffused with pale brown; forewing upperside postmedian line indistinct, not continuous across wing; discal eyespot on forewing underside with diagonal cream line below, originating from posterobasal corner of the eyespot .... *dioptica* Walker

Comparative Morphology of *O. cohabita*, *O. oculata*, and *O. quadriocellata*

In a previous cladistic analysis of Plusiinae (Kitching 1987), I described several characters useful in elucidating generic and higher level

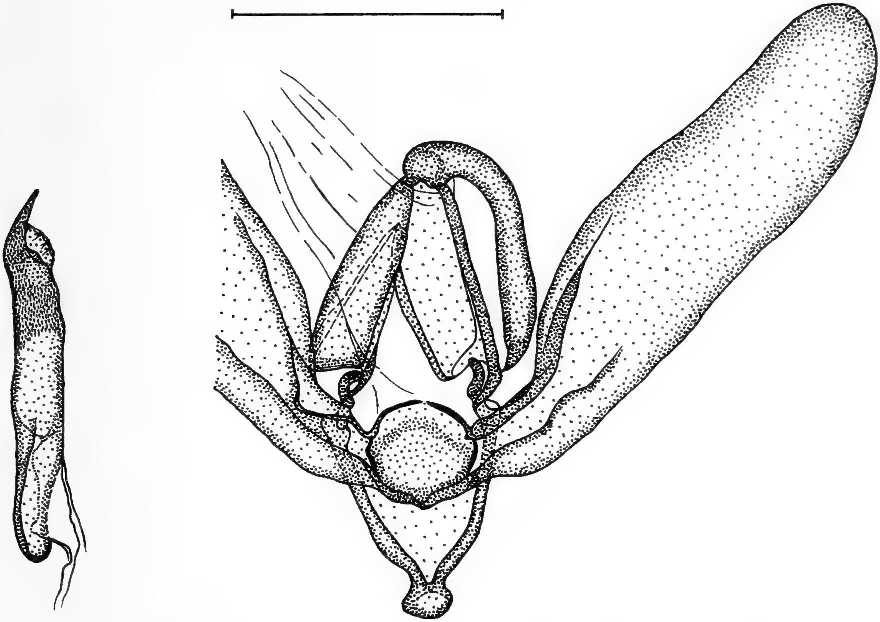


FIG. 3. *Ocalaria cohabita,* paratype male genitalia, BMNH noctuid slide #12804 (genitalia) and #12805 (aedeagus). Scale line = 1 mm.

interrelations on the proboscis, female frenulum, basal abdominal segments and abdominal segment 8. I have examined these structures in three *Ocalaria* (*O. cohabita, O. oculata* and *O. quadriocellata*) and here describe the results to facilitate future analyses of higher classification of Catocalinae. *Ocalaria oculata* and *O. quadriocellata* were chosen for detailed examination because they are well represented in the BMNH collection; the remaining species (several undescribed) were not because it was not my intention to revise the genus. Comparisons are also drawn, where appropriate, with equivalent conditions in Plusiinae and the taxa employed as outgroups in that study.

Labial palps. In all three *Ocalaria* species, the dorsal margin of segment 2 of the labial palp is markedly convex. This feature is more conspicuous in *O. quadriocellata* (Fig. 6) and *O. oculata* than in *O. cohabita* (Fig. 5) but there is no sexual dimorphism. The function of the bulge is unknown; examination at 400× revealed no obvious sensory structures or differential scale arrangements.

Antennae. Female *O. cohabita* have filiform antennae (Fig. 16) with relatively short subventral setae; males have longer, more conspicuous subventral setae, while the ventral surface of each segment is produced into a rounded triangular flange (Fig. 14), giving a serrate appearance

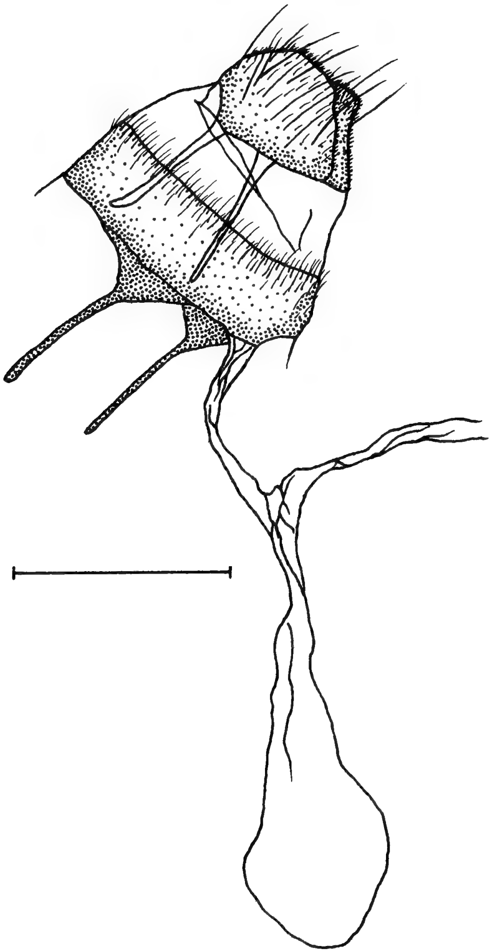
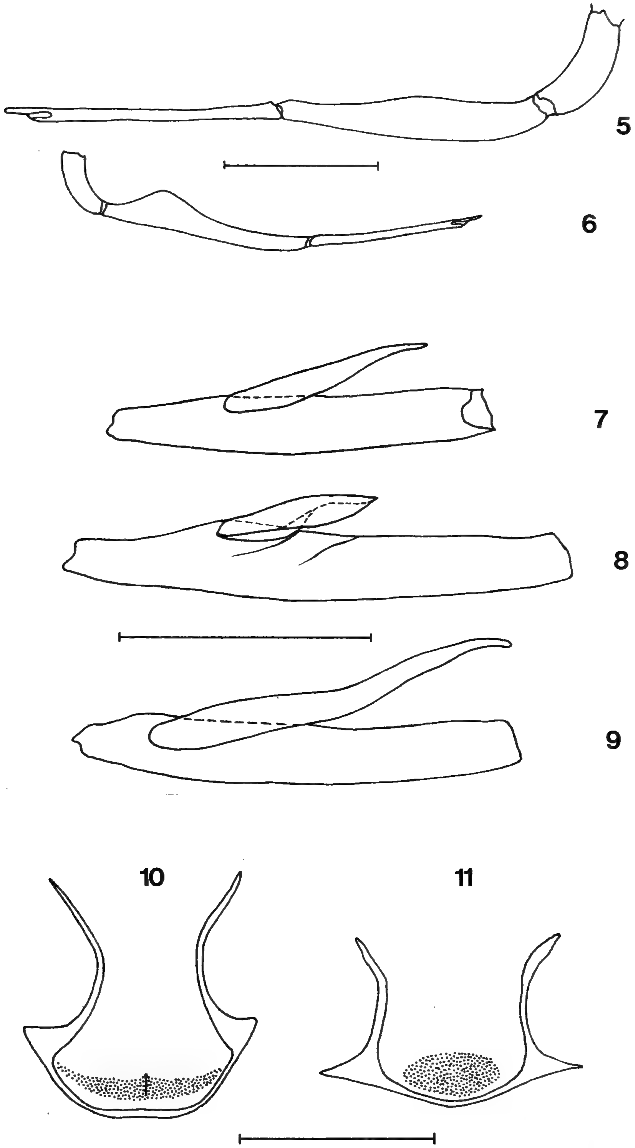


FIG. 4. *Ocalaria cohabita,* paratype female genitalia, BMNH noctuid slide #12816. Scale line = 1 mm.

to the antenna. Apically, this flange bears two setae and a sensillum styloconicum.

Antennae of female *O. quadriocellata* are also filiform, although the segments are longer than in *O. cohabita*. In contrast, male antennae of *O. quadriocellata* are strongly bipectinate (Fig. 12). Each pair of pectinations, which arise at the base of a segment, are long, slender, parallel-sided and bear a strong apical seta. Male *O. oculata* are similar but the pectinations are even longer and thinner (Fig. 15). Female *O. oculata* are unique among the three taxa studied in also having bipectinate



FIGS. 5–11. *Ocalaria* structures. 5, 6. Labial palps. **5,** *O. cohabita* male; **6,** *O. oculata* female. 7–9. Foretibiae. **7,** *O. oculata* female; **8,** *O. quadriocellata* female; **9,** *O. oculata* male. 10, 11. Male sternite 8. **10,** *O. cohabita*; **11,** *O. quadriocellata*. Stippling indicates extent of hairpencil scale insertions. Scale lines = 1 mm.

antennae (Fig. 13), although the branches are shorter than in either male *O. oculata* or *O. quadriocellata.*

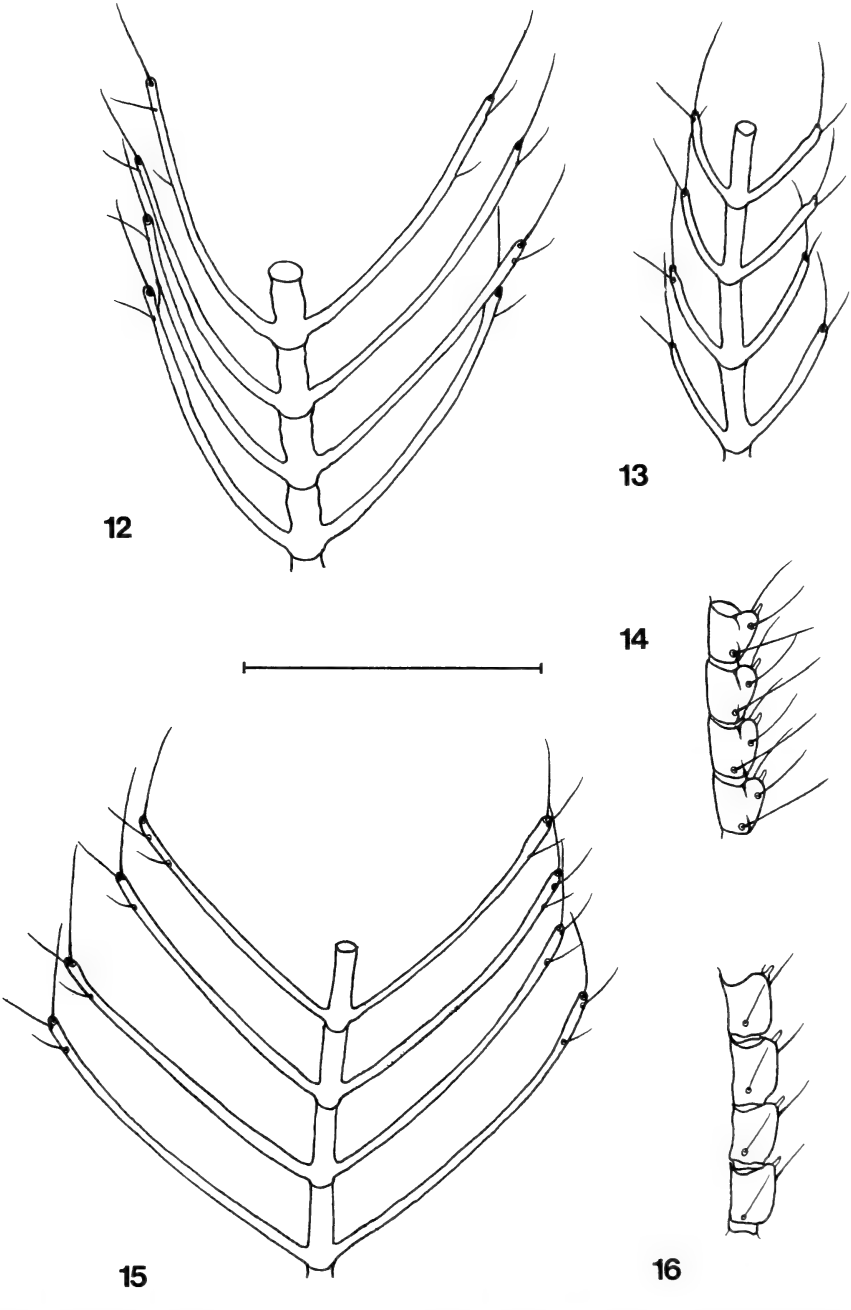
Proboscis. Proboscides in all three species are short, stout, and similar in general appearance to those of such genera as *Oncocnemis* Lederer (Cuculliinae), *Magusa* Walker (Amphipyrinae), *Stictoptera* Guenée (Stictopterinae) and *Paectes* Hübner (Euteliinae). *Ocalaria* also shares with these and other genera a nodular apex to the proboscis and ridged styloconic sensilla (which appear stellate in apical view), all of which suggests that this form of proboscis is plesiomorphic within Noctuidae. Concomitantly, the form of proboscis found in Plusiinae is apomorphic for that subfamily, although certain features appear to have been convergently derived in *Cucullia* Schrank and *Calophasia* Stephens (both Cuculliinae).

Epiphysis. The epiphysis in *Ocalaria* exhibits considerable variation in length. In both sexes of *O. cohabita* and female *O. quadriocellata,* it is small, being only about a quarter the length of the fore-tibia (Fig. 8). However, in male *O. quadriocellata* and *O. oculata,* the epiphysis is highly elongate and often exceeds the fore-tibial apex (Fig. 9). Female *O. oculata,* which have smaller antennal pectinations, also have a shorter epiphysis, but one that is still elongate compared to female *O. cohabita* (Fig. 7). This close correlation between epiphysis length and degree of development of antennal pectinations is strong circumstantial evidence to support the hypothesis that the primary role of the epiphysis is keeping the antenna clean. A long epiphysis is necessary in male *O. quadriocellata* and *O. oculata* to clean the long pectinations efficiently.

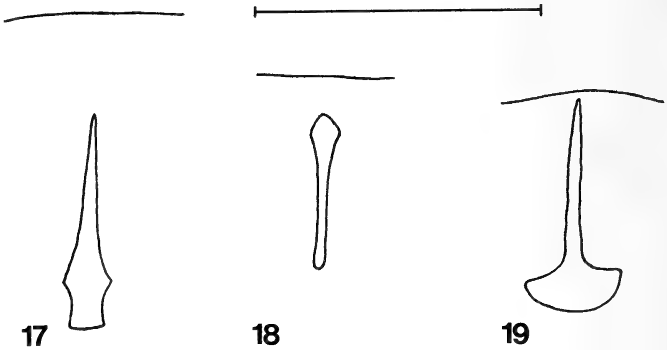
Wings. Venation of *Ocalaria* is typical quadrifine noctuid, although hindwing vein M_2 is somewhat weaker than either M_1 or M_3 and does not arise close to the base of M_3. A potential *Ocalaria* apomorphy in hindwing shape is the shallow concavity just beyond the midpoint of the costal margin, although this is weakly expressed in *O. oculata.* All *Ocalaria* examined have a trisetose female frenulum in which the setae are subequal in length, further corroborating the hypothesis that this state is plesiomorphic within Noctuidae (Kitching 1987).

Abdominal segment 2. In all noctuid genera examined so far, the anterior edge of tergite 2 (T2) bears an inflected flange. At its simplest, the flange is concave, uniformly narrow and difficult to discern in slide-mounted material, as in Stiriinae, Cuculliinae, Heliothinae, and basal plusiine tribe Omorphinini. The more derived Abrostolini display two subdorsal lobes directed medially. These fuse in Argyrogrammatini and Plusiini but leave a central rounded emargination. The ventral edge of the flange in Stictopterinae and Euteliinae is straight, with a median dorsal triangular inflection of T2 itself.

In general, the form of the T2 flange is highly invariant in large



FIGS. 12–16. *Ocalaria* antennae. **12,** *O. quadriocellata* male; **13,** *O. oculata* female; **14,** *O. cohabita* male, lateral view; **15,** *O. oculata* male; **16,** *O. cohabita* female, lateral view. Scale line = 1 mm.



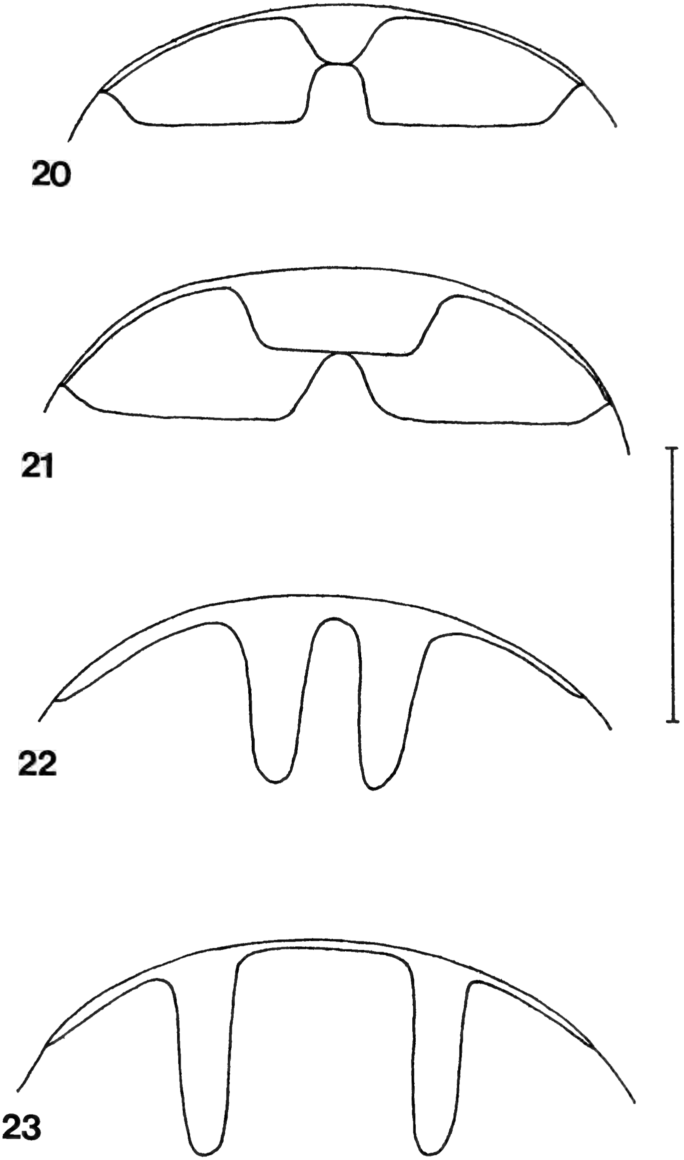
FIGS. 17–19. Male tergite 8. **17,** *O. cohabita*; **18,** *O. oculata*; **19,** *O. quadriocellata*. Posterior edge uppermost, with transverse line marking posterior margin of abdominal segment 8. Scale line = 1 mm.

taxonomic groups, such as tribes or subfamilies. However, in *Ocalaria*, the T2 flange is remarkably variable between species. The putatively basal *O. cohabita* shows a sclerotized dorsal inflection of T2 similar to that in Stictopterinae and Euteliinae, but with the median emargination typical of "higher" plusiines. In addition, the ventral edge of the flange is somewhat cut back laterally. This flange is sexually dimorphic in *O. cohabita*, a feature almost certainly correlated with the dimorphism observed in sternite 2 (St2). The female (Fig. 21) differs from the male (Fig. 20) in that the median emargination is not parallel-sided, while the dorsal inflection is much broader and has a straight ventral edge.

Ocalaria oculata and *O. quadriocellata* differ markedly in lacking the sclerotized dorsal inflection and in the extreme specialization of the flange. *Ocalaria quadriocellata* has a T2 flange formed of two broad, ventrally-directed, well-separated rounded lobes (Fig. 22). This trend is more noticeable in *O. oculata*, in which the lobes are long, narrow, and closer to the lateral edges of T2 than to the center (Fig. 23).

St2 in *O. oculata* and *O. quadriocellata* is typically noctuid in form, with no marked diagnostic features. It is a roughly square sclerite (Fig. 25), with convex lateral and posterior edges. The anterolateral corners are produced into a pair of apodemes, from which a sclerotized bar arises laterally. This passes anteriorly to the counter-tympanal hood. The anterior margin of St2 is broadly U-shaped.

Females of *O. cohabita* have a broadly similar St2, but it is slightly squarer, with marginally concave lateral edges, and the anterior margin is more V-shaped (Fig. 24). St2 of male *O. cohabita*, however, is markedly different (Fig. 26), which may be the first record of sexual dimorphism in this structure in quadrifine noctuids. The whole sclerite



FIGS. 20–23. Tergite 2 flange. **20,** *O. cohabita* male; **21,** *O. cohabita* female; **22,** *O. quadriocellata* male; **23,** *O. oculata* male. Scale line = 1 mm.

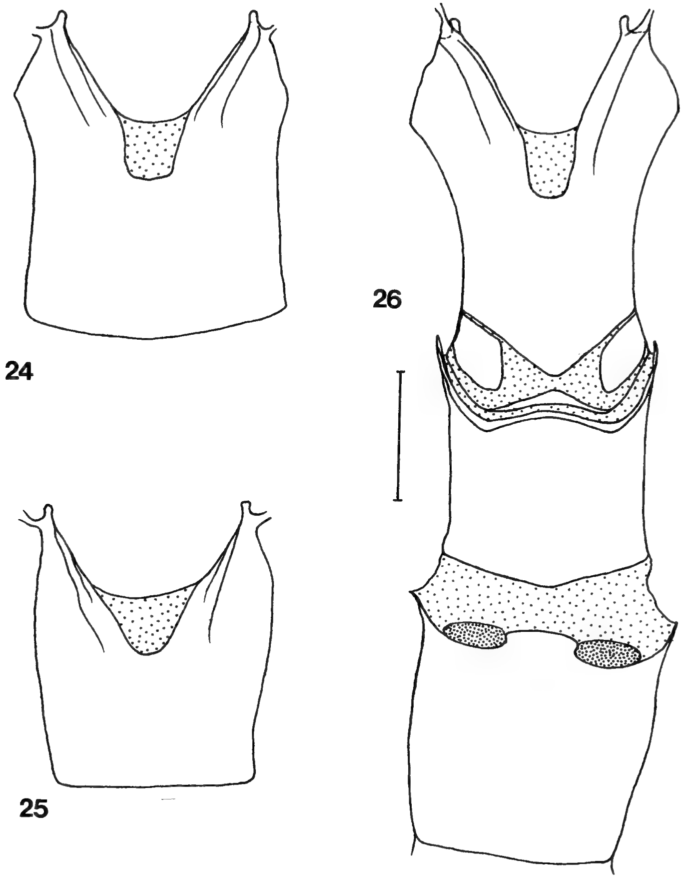
is elongate, with distinctly concave lateral margins. The anterior edge is V-shaped, while the posterior margin is produced as a broad, triangular point. Posterolaterally are two secondary sclerites in the intersegmental membrane between St2 and St3. In addition, the anterior corners of St3 (Fig. 26) are produced around the posterolateral edges of these secondary sclerites, a feature similar to that seen in numerous trifine species, where it is associated with the lever of male basal abdominal hair pencils (Birch 1970). The posterior margin of St3 is also produced to a median point, but is more obtuse than that of St2. Finally, on the anterior edge of St4 (Fig. 26) are two concavities that appear to house shallow glandular pockets. The function of this complex in male *O. cohabita* is a matter for conjecture but suggests that adult biology, particularly courtship, of this species might be usefully studied.

Male abdominal segment 8. The form of the male eighth tergite (T8) and sternite (St8) displays species-level diagnostic features in a number of noctuid subfamilies; for example, Plusiinae (Dufay 1970), Stiriinae (Hogue 1963), Heliothinae (M. J. Matthews pers. comm.). In addition, these sclerites have yielded characters useful in recognizing suprageneric taxa in Plusiinae (Kitching 1987).

The form of T8 in *Ocalaria* is characteristic, consisting of a median sclerotized longitudinal bar tapered posteriorly and expanded anteriorly. The three species differ in minor details: in *O. cohabita,* the bar does not reach the posterior margin of the segment and the anterior expansion has concave margins and a truncate apex (Fig. 17); in *O. oculata,* the anterior expansion is drawn out laterally into narrow points (Fig. 18); while in *O. quadriocellata,* the anterior expansion has a rounded apex (Fig. 19). In all three taxa, there appear to be two shallow pockets associated with the lateral edges of T8 anteriorly.

A8 bears a median weak tuft of hairs, barely differentiated into a pair of hair pencils, arising from a shallow, membranous, ventral pocket. St8 forms a thin sclerotized bar anterior to this pocket, with two concave bars running longitudinally on either side of the hair tuft. The anterolateral corners of St8 are produced as blunt triangular lobes. The form of St8 is similar in all three species, but whereas the anterior bar forms a blunt median point in *O. oculata* and *O. quadriocellata* (Fig. 11), in *O. cohabita,* it is broadly rounded with a somewhat straight central section (Fig. 10).

Male genitalia. *Ocalaria oculata* is very similar to *O. cohabita* (Fig. 3) except that the valve is of more uniform width basally, the saccus is acutely pointed and the aedeagal process is absent. In addition, the spines on the vesica basally are larger and more strongly sclerotized. Genitalia of *O. quadriocellata* are similar to *O. oculata* but the sacculus



FIGS. 24–26. *Ocalaria* sternites. 24, 25. Sternite 2. **24,** *O. cohabita* female; **25,** *O. quadriocellata* male; **26,** Sternites 2–4 *O. cohabita* male. Scale line = 1 mm.

bears a small rounded lobe basally and the saccus forms a less acute point.

Female genitalia. The posterior margin of St8 bears a fringe of persistent, brown, setose scales that may be apomorphic for *Ocalaria*. *Ocalaria oculata* is essentially similar to *O. cohabita* (Fig. 4) but differs in that the corpus bursae is not differentiated from the ductus bursae, being merely a long, slightly broader membranous sac; the ductus bursae is broader with a median annulus of longitudinal ridges and sclerotized granulations; and the ostium bursae is adorned with sclerotized granulations. The anal papillae are diagonally cut back dorsally to the origin of the posterior apodemes. *Ocalaria quadriocellata* is broadly similar to *O. cohabita,* except that the dorsoposterior parts of the anal papillae are drawn out into blunt, slightly downcurved points.

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A NEW *SESIA* CLEARWING MOTH FROM MICHIGAN (SESIIDAE)

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ABSTRACT. *Sesia spartani,* new species was discovered in Michigan (30 males) in traps baited with a sex attractant consisting of 50:50 mixture of (3,13) Z,Z-ODDOH/(3,13) E,Z-ODDOH. The new species is described, illustrated, and compared with *S. tibialis* (Harris). The two differ in structure of male antennae, genital morphology, response to sex attractants, and seasonal occurrence.

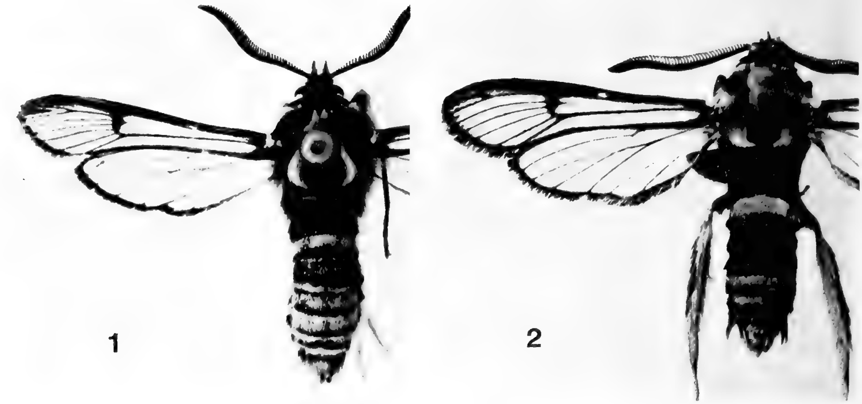
Additional key words: *Sesia spartani, S. tibialis,* attractants.

Use of synthetic sex attractants has resulted in the discovery of several new species of sesiids in the Western Hemisphere (Duckworth & Eichlin 1977a, 1977b, Greenfield & Karandinos 1979, Brown et al. 1985, Eichlin 1986, 1987).

During studies employing sex attractant baits to survey the Sesiidae of Michigan, a new species closely related to *Sesia tibialis* (Harris) was discovered and is described below. Males of *S. tibialis* (Fig. 2) are known to be very responsive to the Z,Z isomer of 3,13-octadecadien-1-ol acetate (Z,Z-ODDA) (Duckworth & Eichlin 1978:28), a major component of many clearwing moth pheromone systems (elucidated by Tumlinson et al. 1974). In Saskatchewan, Underhill et al. (1978) found the best attractant was probably a 80:20 blend of Z,Z-ODDA/Z,Z-ODDOH. The new species was discovered in the Lower Peninsula of Michigan when males were captured in traps baited with sex attractants consisting of a 50:50 mixture of the Z,Z and E,Z alcohols (Z,Z-ODDOH/E,Z-ODDOH). Traps baited with other sex attractants including that known to be effective for *S. tibialis* were deployed in the same areas throughout the collecting season but failed to capture any *S. spartani.*

Sesia Fabricius

Genus *Sesia* is characterized by the following: Head with haustellum reduced, about ⅔ length of labial palpus; antenna strongly clavate, ventrally ciliate-unipectinate on male; horizontal flat plate of scales projecting somewhat over middle of eye. Forewing vein R_4 terminating at apex, R_5 below. Hindwing veins M_3 and Cu_1 joined at corner of cell or very short-stalked. Genitalia unique, generally as shown in Figs. 5 and 6.



FIGS. 1, 2. Adult males of *Sesia* spp. **1,** *S. spartani,* Shiawassee Co., Michigan (holotype); **2,** *S. tibialis,* Isabella Co., Michigan.

Sesia spartani, new species

Male (Fig. 1). Head with vertex brown-black, some white posteriorly; front brown-black; occipital fringe white dorsally, yellow laterally; labial palpus roughened with long hairlike scales ventrally on basal segment, yellow with brown toward base; haustellum short, less than ½ length of labial palpus; antenna brown-black with yellow-orange at tip, unipectinate, individual middle segments with ramus about 3 times as long as the distance between 2 adjacent rami (dorsoapical view of antenna), produced from dorsoapical portion of segment (Fig. 3). Thorax brown-black with yellow behind collar, around wing bases, subdorsally on posterior half of mesothorax, and variously on metathorax. Abdomen brown-black but with broad yellow bands on segments 5, 6, and 7, less so on 4 dorsally; tip of abdomen mostly yellow with anal tuft poorly defined. Wings hyaline; narrow margins and discal spot brown. Wing length 8–9 mm (30 n). Legs with coxae brown-black edged with yellow; femora yellow dorsally, brown-black ventrally; tibiae yellow, hind tibia roughened dorsally by semierect, thin, elongate scales; tarsi yellow-orange. Genitalia as in Fig. 6.

Female. Unknown.

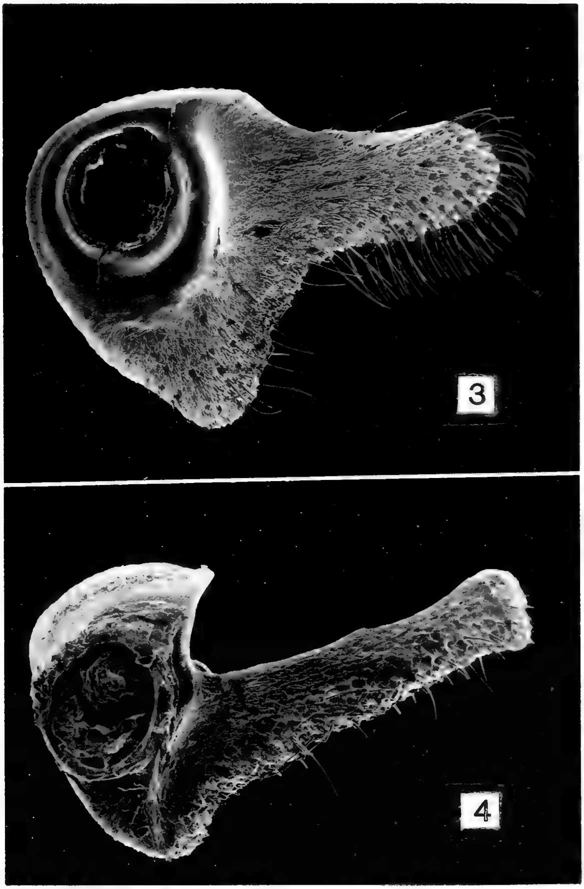
Host. Probably species of Salicaceae, particularly *Populus tremuloides* Micheaux (quaking aspen), based on observed larval damage to trees at the type locality and at other sites where *S. spartani* was collected.

Distribution. *Sesia spartani* has been collected in the Lower Peninsula of Michigan in Clinton, Shiawassee, and Lake counties.

Types. Holotype: Male, MICHIGAN: Shiawassee Co., Bath, 13 June 1987, Coll. William H. Taft; Rose Lake Wildlife Research Area, T5N R1E Sec 20; ZZOH/EZOH, 50:50; deposited in Entomology Museum, Michigan State University, East Lansing (MSU). Paratypes (29 males): 6, Shiawassee Co.: V-29-1987 (1); VI-9-1987 (2); T5N R1E Sec 20, 13 June 1987 (2); same as last except 14 June 1987 (1). 22, Clinton Co.: T5N R2W Sec 31, 13 June 1987 (3); same as last except 14 June 1987 (2); 16 June 1987 (4); 17 June 1987 (7); 19 June 1987 (2); 20 June 1987 (4). 1, Lake Co.: T17N R14W Sec 12, 14 June 1987 (all collected by William H. Taft using traps baited with ZZOH/EZOH 50:50).

Paratypes are deposited in MSU; U.S. National Museum of Natural History, Washington, D.C.; California Department of Food and Agriculture, Sacramento; Canadian National Collection, Ottawa, Ontario; and Field Museum, Chicago, Illinois.

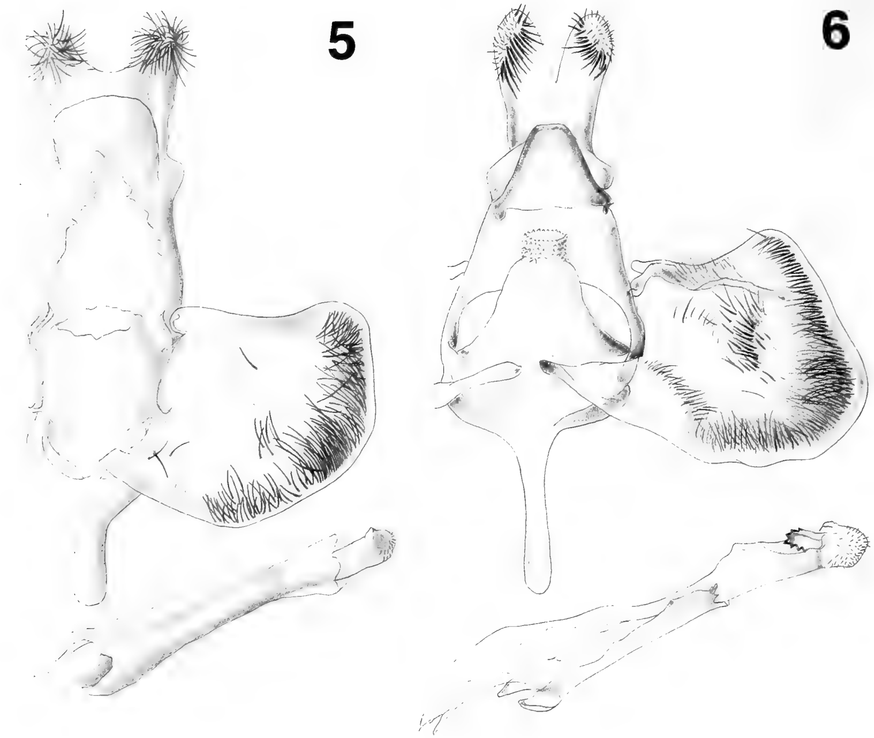
Discussion. *Sesia spartani* is superficially similar to *S. tibialis*. However, male genitalia



FIGS. 3, 4. Segments from near middle of left antennae of *Sesia* spp. as viewed ventrally on proximal surface by scanning electron microscope. **3,** *S. spartani*; **4,** *S. tibialis*.

differ considerably (Figs. 5, 6): *S. spartani* uncus deeply and acutely divided, cleft of *S. tibialis* uncus less deep, broadly rounded; saccus about ½ length of valve, only ⅓ on *S. tibialis*; valve more produced ventroposteriorly and with more thick, dark spines near center than on *S. tibialis*; gnathos narrowing apically and of different form than for *S. tibialis*; and aedeagus with jagged plate posteriorly, *S. tibialis* lacking jagged plate. Some specimens of *S. tibialis* from Michigan (Fig. 2) are nearly lacking yellow dorsally on abdominal segments 4 and 5, while on *S. spartani* segment 5 is mostly yellow, and 4 has some yellow powdering. *Sesia tibialis* from elsewhere usually has yellow banding on all segments.

The collecting sites were low muck soil depressions in scattered locations. These habitats are characterized by large stands of regrowth quaking aspen mixed with willows (*Salix* spp.), elm (*Ulmus* sp.), red maple (*Acer rubrum* L.), and black cherry (*Prunus serotina* Ehrh.). The undergrowth is dogwood (*Cornus* sp.), viburnum (*Viburnum* sp.), and blueberries (*Vaccinium* sp.).



FIGS. 5, 6. Male genitalia of *Sesia* spp. viewed ventrally, left valve removed. **5,** *S. tibialis* (from Duckworth & Eichlin 1978); **6,** *S. spartani.*

The *S. spartani* males were captured in Multi-pher #1® plastic pheromone traps. Collecting dates for *S. spartani* were 29 May–20 June 1987. *Paranthrene dollii* (Neumoegen) was collected with *S. spartani* during late May and early June. At the time of capture, the growing season was 250–300 degree-days (base 50) above normal; consequently, in normal years *S. spartani* may fly later in June or in early July. It appears to fly two weeks to a month earlier than does *S. tibialis* in Michigan. *Sesia tibialis* has not been found in counties where *S. spartani* originated, but has been collected as far south as Newaygo, Isabella, and Midland counties, and is known from Nova Scotia and New England to British Columbia, and from the Rocky Mountains to the Pacific Coast. The Michigan habitats for both species appear to be similar.

This species is named for the Spartans, a nickname applied to Michigan State University athletic teams.

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TWO NEW SPECIES OF *RHYACIONIA* PINE MOTHS FROM MEXICO (TORTRICIDAE: OLETHREUTINAE)

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ABSTRACT. *Rhyacionia cibriani* is described from five males and five females, and *R. rubigifasciola* from one male and one female. The former is differentiated from *R. jenningsi* Powell by genital and other characters including longer antennal pecten. The latter is differentiated from all congeners, none of which it resembles closely, by genital characters including a ridge separating sacculus and valval neck in the male, and an anally emarginate sterigma in the female. *Pinus hartwegii* Lindl. and *P. oocarpa* Schiede are the respective hosts, the larvae boring in branchlets. The new species bring the number of *Rhyacionia* known in Mexico and the Neotropics to nine species.

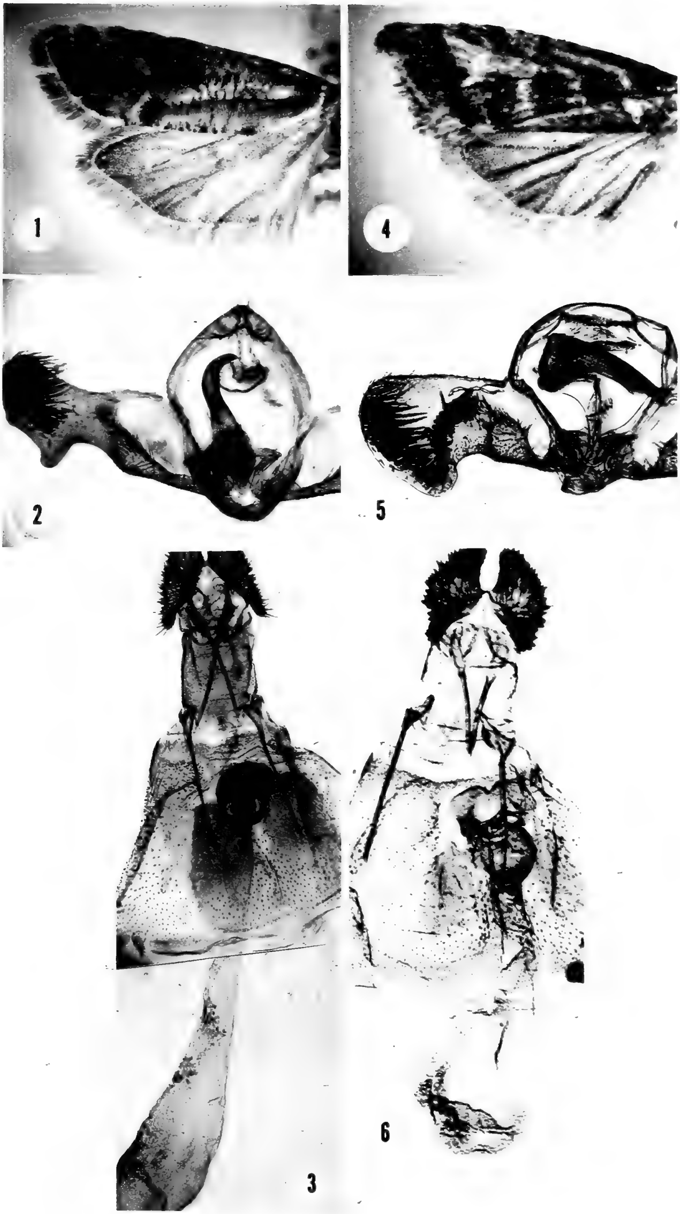
Additional key words: taxonomy, Eucosmini, *Rhyacionia cibriani, R. rubigifasciola,* Neotropics.

Pines, the larval hosts of *Rhyacionia,* are numerous in Mexico, 21 of the 30 pine species occurring there being absent in the U.S. (Critchfield & Little 1966). The 2 new species described here bring the number of *Rhyacionia* known in Mexico and the Neotropics to 9 species (Powell & Razowski in press), and the number described worldwide to 34 (Miller 1985, Obraztsov 1964, Powell & Miller 1978). This is the fourth paper in a series in which I describe new Neotropical olethreutines in various genera whose hosts and modes of feeding make them of economic interest or importance (Miller 1966, 1986, 1987).

In both species described here, hindwing vein M_2 is bent at its base, and hindwing veins M_3 and CuA are either stalked or connate and approximate toward their bases. These character states place the species in Eucosmini (Obraztsov 1958). Features that place them in *Rhyacionia* are italicized in descriptions. Venation was ascertained under a stereomicroscope from temporary preparations made by touching xylol to wings while light passed through them (Zimmerman 1978).

Rhyacionia cibriani, new species
(Figs. 1–3)

Male. Forewing length 11.0 to 12.0 mm (holotype 11.0 mm) (5n). **Head.** Labial palpus clothed with brown-banded white scales, length of 2nd segment 2× eye diam., length of 3rd segment ⅙ that of 2nd; vestiture of vertex similar to that of labial palpus; antennal pecten length 1 to 1¼× flagellar length, 1¾ to 2× flagellar diam. **Thorax.** Dorsal vestiture beige, ventral paler; front and middle leg scaling similar to that of labial palpus, hind leg paler, tarsi indistinctly white-banded; *forewing with veins M_2 and M_3 connate, termen straight or convex, costal fold absent,* upper side yellowish to coppery red, tinged with lavender in cell area, crossed by irregular striae near middle (Fig. 1), underside pale grayish yellow; hindwing upper side gray, underside paler than forewing underside. **Genitalia** (Fig. 2) (3n). *Valva lacking costal hook,* a ridge from sacculus to neck terminating in a nipplelike process at mid-neck, neck constricted to nearly ½ maximum sacculus



FIGS. 1–6. 1–3. *Rhyacionia cibriani* from type locality. **1,** Wings of paratype; **2,** Male genitalia of holotype; **3,** Female genitalia of paratype. 4–6. *R. rubigifasciola* from type locality. **4,** Wings of holotype; **5,** Male genitalia of holotype; **6,** Female genitalia of paratype. Additional information keyed to figure numbers appears in Type Data section. Some negatives reversed.

width, *pollex present* and its length about ¼ maximum cucullus width; *uncus and socii rudimentary or absent*; aedeagus curved and tapering toward apex, vesica with 3 to 4 cornuti.

Female. Forewing length 9.5 to 11.0 mm (5n). Similar exteriorly to male except for shorter antennal pecten. **Genitalia** (Fig. 3) (3n). Sternum 7 emarginate; sterigma nearly square in outline, laterally inflected, with a broad and evenly rounded longitudinal ridge; ductus bursae sclerotized only near ostium bursae; corpus bursae with 1 thornlike signum, sometimes a tiny 2nd one.

Type data. Holotype male, Paso de Cortez, Méx., Mexico, 12 March 1984, No. 1133, *Pinus hartwegii* Lindl., D. Cibrián, genit. prep. WEM 1910844 (Fig. 2), in U.S. National Museum of Natural History, Washington, D.C. Four paratype males, same data as holotype except 5–9 April 1984, 2 genit. preps. WEM 910842 and WEM 84885; 5 paratype females, same data as holotype except 5–16 April 1984 (Fig. 1), 3 genit. preps. WEM 910843 (Fig. 3), WEM 2210841, and WEM 53882, in U.S. National Museum of Natural History; Essig Museum, University of California, Berkeley; University of Minnesota, St. Paul; and Lab. de Entomologia Forestal, Universidad Autonoma Chapingo, Chapingo, Mexico.

Discussion. *Rhyacionia cibriani* most resembles *R. jenningsi* Powell, but differs in size, structure, and forewing pattern as follows. *Rhyacionia cibriani* has a 40% greater average forewing length, 100% greater relative length of 2nd palpus segment, and 350 to 400% longer relative antennal pecten length than *R. jenningsi;* the lavender hue of the *R. cibriani* forewing cell is lacking in *R. jenningsi*; the nipplelike process on the male valva in *R. cibriani* is lacking in *R. jenningsi*; the 7th female sternum is more deeply emarginate in *R. cibriani* and the sterigma more square than in *R. jenningsi.* The foregoing character states for *R. jenningsi* are documented in Powell and Miller (1978).

Pinus hartwegii is classified in *Ponderosae* (Critchfield & Little 1966), a *Pinus* subsection whose members are hosts to several *Rhyacionia* species (Powell & Miller 1978).

The species is named for David Cibrián-Tovar, who reared adults from larvae boring in *Pinus hartwegii* branchlets.

Rhyacionia rubigifasciola, new species

(Figs. 4–6)

Male. Forewing length 8.5 mm (1n). **Head.** Labial palpus clothed with silvery white scales sometimes tinged with orange or gray, length of 2nd segment 1⅓× eye diam., length of 3rd segment ¼ that of 2nd; vestiture of vertex silvery white except for orange near antennal bases; antennal pecten length 0.8× flagellar length, 0.8× flagellar diam. **Thorax.** Dorsal vestiture similar to vertex; front and middle legs orange, banded with white, hind leg paler except for tarsi; *forewing with veins M_2 and M_3 connate, termen convex, costal fold absent,* upper side with 4 orange spindle-shaped fasciae extending from costa to dorsum, 2 less tapered ones from costa to termen, all separated by silvery white (Fig. 4), underside pale gray; hindwing upper side gray, underside paler than forewing underside. **Genitalia** (Fig. 5) (1n). *Valva lacking costal hook,* sacculus separated from neck by a ridge, neck scarcely constricted dorsoventrally, concave anally, *pollex present* but not well defined in outline; *uncus absent*; *socii tiny, inflected, nearly obscured by tergum,* aedeagus apically expanded, forked, with several tiny apical spurs; vesica with 6 cornuti.

Female. Forewing length 8.5 mm (1n). Similar exteriorly to male. **Genitalia** (Fig. 6) (1n). Sternum 7 not markedly emarginate; sterigma rounded in outline, emarginate on anal margin, lamella antevaginalis scoop-shaped; ductus bursae sclerotized in an incomplete ring for a short distance at ⅖ its length from ostium bursae; corpus bursae with 2 thornlike signa.

Type data. Holotype male, Sta. Lucia, Sinaloa, Mexico, 1 July 1981 (Fig. 4), No. 802, *Pinus oocarpa* Schiede, D. Cibrián & T. Méndez, genit. prep. WEM 108842 (Fig. 5), in Essig Museum, University of California, Berkeley. One paratype female, same data and depository as holotype except genit. prep. WEM 234851 (Fig. 6).

Discussion. *Rhyacionia ribigifasciola* does not clearly resemble any congener (Miller 1985, Obraztsov 1964, Powell & Miller 1978). It differs from all in male valval outline and in the ridge separating sacculus and neck; also in shape of the female sterigma with its anal emargination. The larvae bore in *Pinus oocarpa* branchlets.

Pinus oocarpa is classified in *Oocarpae* (Critchfield & Little 1966), a *Pinus* subsection whose members are hosts to only one other *Rhyacionia* species, *R. pasadenana* (Kearfott) (Powell & Miller 1978). The new species does not appear closer morphologically to *R. pasadenana* than to other *Rhyacionia* species, however.

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BOOK REVIEWS

THE BUTTERFLIES OF COSTA RICA AND THEIR NATURAL HISTORY: PAPILIONIDAE, PIERIDAE, NYMPHALIDAE, by Philip J. DeVries (illus. by P. J. DeVries, Jennifer Clark and R. Cubero). 1987. Princeton Univ. Press. xxii + 327 pp. Hardback, ISBN 0-691-08420-3, $60.00; paperback, ISBN 0-691-02403-0, $22.50.

Costa Rica is an exceptionally delightful Central American country with a happy and friendly people (they abolished their military some years ago and used the money recovered for education), gorgeous landscape, and a surprisingly complete complement of beautiful Neotropical butterflies which are ably described, discussed, and made known in intimate detail in this book.

For the three families covered, this is a *very* good book on Neotropical Lepidoptera, and will be most useful (especially at the low price for the paperback edition) to anyone interested in these families from central México southwards. It could be a better book still; it contains a rather high density of errors of nomenclature, fact, writing, and interpretation which should be corrected in the second edition (which surely will be necessary as several thousand copies have already been sold). A list of these has been given to the author; only some more important facets can be commented on here, probably most usefully to those who have already bought the book. If you haven't, you should as soon as you plan to work on the Neotropical fauna in the three families.

DeVries has lived for almost 10 years in Costa Rica, working at the National Museum of Natural History with top Costa Rican scientists, and maintaining ties with many foreign scientists studying natural history in this Country (mostly through the Organization for Tropical Studies; a general volume entitled *Costa Rican Natural History*, edited by Daniel Janzen, recently appeared, and covers many aspects of this work), and also in other Central American countries (especially the Muyshondts, active in El Salvador). He is responsible for the discovery of many species in Costa Rica, verification of their habitats and foodplants, and description of their early stages, and is surely well qualified to produce this book. The text was written mostly during periods in Austin, Texas, and the British Museum; the color plates, of high quality but reduced a little too much for optimal usefulness, were prepared in the latter institution, at times using non-Costa-Rican or older specimens, with faded colors or tattered wings.

Strong points of the book include maps of the Country with roads, cities, topography, and parks (but with a wrong scale; 50 km on the scale given are actually 82 km on the map), a refreshing emphasis on natural history and juvenile biology with much valuable new data, a useful list of butterfly-enemy groups (p. 18), a sensible and eclectic position on systematics (p. 32), a recommendation for taking notes rather than specimens in the field (p. 33) and use of binoculars and simple camera equipment to increase the value and number of observations (p. 37), a good grasp of the Costa Rican faunal regions showing much first-hand experience (though perhaps not enough yet in cloud-infested Atlantic coastal forests), recognition of certain behavioral traits such as "only new males visit wet sand", an excellent job of correlating illustrations with types in difficult groups like *Memphis, Adelpha, Phyciodes* (s.l.), and Euptychiini which will be useful to many (if all are correct), and palatability data on many species. Line drawings of juveniles are strikingly clear and correct.

DeVries' youthful enthusiasm, which made this book possible and contributed greatly to its notable authority, style, grace, and the breadth and interest of its natural history accounts, gets the best of him in diverse parts of the book. His statement in the Preface that, when he began to work in Costa Rica in the 1970's, "nobody was willing to do a detailed study of the Neotropical butterfly fauna" is bound to earn some grumbles from the many "nobodies" who have willingly and tirelessly labored in this task since Müller (1870's) and Moss (1900's) started doing broad work on natural history of Brazilian Lepidoptera; several dozen are now active, many in fact quoted in the large Bibliography (382 references). An unexpected unfamiliarity with recent work in Mexico, such as that on *Parides* (mostly published in the *Rev. Soc. Mex. Lepid.* mentioned on p. 53 but cited only 3 times in the Bibliography), and in South America since Müller and Moss, sometimes leads to unnecessary affirmations or contradictions; in species ranges, 10 genera and 58 species common in southeastern Brazil are indicated as reaching only the Amazon Basin, 10 others have their southern limits shrunken appreciably (sometimes all the way to Central America) and many groups are indicated as "reaching their maximum diversity in the Amazon Basin" when in fact this occurs on the lower Andean slopes (as indicated correctly in *Prepona*)—Amazonian to be sure but only a small, special part of the Basin, over almost all of which butterfly diversity is quite low. Peterson's classic 1948 work on larvae is not mentioned (p. 6), and the list of parasites omits mites (p. 17). The affirmation that "the effects of parasitoids on populations of tropical butterflies are unstudied" (p. 17) makes one wonder what the author accepts as a study (there are dozens of purported scientific papers published in this area). Likewise, the generalization that "toxins in adult butterflies are probably entirely directed at vertebrate predators" (p. 23) is indefensible. That Neotropical diversity "remains one of the great challenges in evolutionary biology" (p. 57) again ignores much serious work done recently by many Neotropical and other scientists. In a perhaps Freudian slip, several medicinal (officinal) plant species are spelled "officionale", and misspelled plant families (new synonyms?) include Vochysiaceae ("Vouchysiaceae", p. 66, 68), Canellaceae ("Cannelaceae", p. 61), Quiinaceae ("Quiiniaceae", p. 109, but correct on p. 112), and Verbenaceae ("Verbenaeceae", p. 76). Ithomiinae venations on p. 215 are so poorly drawn that they will confuse, not help the reader. The late Walter Forster would surely be disappointed at DeVries' summary dismissal of almost all his Euptychiine genera, many of which are sound natural groupings. Nomenclatural corrections and changes necessary (*) or suggested include at least the following (which should be noted also on the check-list, pp. 291 ff):

Page	Name given	Should be	Comments
18	*Tyranidae	Tyrannidae	—
41	**Hamadryas iphtheme*	*H. iphthime*	—
65	**Parides alopius*	(delete)	Nicaraguan record an error.
	**P. dares*	(delete)	A unique hybrid (*photinus* × *montezuma*).
67	**P. arcas*	*P. eurimedes*	*Arcas* a homonym.
69	**Battus belus varus*	*B. latinus*	*B. varus* is Amazonian, female *latinus* monomorphic throughout range.
70	*B. crassus*	*B. crassus lepidus*	Transandean subspecies.
75	*Papilio victorinus, P. cleotas*	(probably one species)	Would be useful to hybridize these in Costa Rica.
77	*Eurytides ilus, E. branchus*	(probably one species)	—
78	**E. protesilaus dariensis*	(includes *E. macrosilaus*)	Should separate.
89	**Archonias eurytele*	*Charonias eurytele*	Well differentiated genera; also Fig. 7.
97	**Perrhybris pyrrha*	*P. pamela*	*Pyrrha* a homonym; also Fig. 7.
99	*Ascia limona*	*A. buniae limona*	Probably conspecific.
113	**Prepona omphale*	(includes *P. laertes*)	Should separate.
115	**P. meander amphimachus*	(two different species)	Separate.
116	*Zaretis ellops, Z. itys*	(probably one species)	Widespread polymorphism all over Neotropics; seasonal.
144, 145	*Dynamine hecuba, D. sosthenes*	(probably subspecies of South American species)	—

	D. glauce	*D. artemisia glauce*	—
142	**Myscelia orisis*	*M. orsis*	—
153	*Eunica venusia, E. augusta*	*E. volumna venusia, E. caelina augusta*	—
154	**Cantonephele*	*Catonephele*	—
161	**Haematera pyramus*	*Callidula pyrame*	Senior synonym, same species.
162	**Pseudonica*	*Nica*	Senior synonym, *Nica* used on p. 156.
163	*Diaethria marchallii*	*D. clymena marchallii*	—
182	**Turnera ulmnifolia*	*T. ulmifolia*	—
183	**Actinote leucomelas*	*Altinote ozomene nox*	Well separated genus, older name.
185	**A. melampeplos, A. guatemalensis*	*A. pellenea* subspecies (both)	—
186	**Heliconius sappho*	*H. sapho*	—
188	*Dione juno*	*D. juno huascuma*	Central American subspecies.
191	**Eueides lybia lybioides* (first mention, (Fabr.))	*E. lybia olympia*	—
193	*Heliconius doris*	*Laparus doris*	Well differentiated genus.
192	**Eueides isabella zoracon*	*E. isabella zorcaon*	—
207	**Napeogenes peredia*	*N. peridia*	See also p. 46, fig. 7.
221	**Callithomia hexia*	*C. hezia*	—
224	**Ithomia diasa*	*I. diasia*	—
226	**Prestonia portabellensis*	*P. portobellensis*	—
230	**Godyris zavaleta sorites*	*G. zavaleta caesiopicta*	Senior synonym.
240	**Hyaliris*	*Hyalyris*	Popular misspelling.
241	*Antirrhaea miltiades, A. tomasia*	(should be one species)	Reason for separation not convincing.
249	*Brassolis isthmia*	*B. sophorae isthmia*	Probably monotypic genus.
257ff	Euptychiini (esp. *Euptychia mollina, Cissia terrestris*)	(many Amazonian names pulled in incorrectly for Central American species. Nomenclature here a big step forward but still lacks refinement)	—
262	**Callitaera* (for *polita*)	*Cithaerias*	Older synonym, correct on p. 260.
275	**Cissia libye*	*C. libyoidea* (Butler) (or *Magneuptychia*)	Transandean species has different chromosomes from Guianan type.
276	**Cissia hesione*	*Pareuptychia ocirrhoe*	*Hesione* a homonym.

Plate errors include illustration of *Papilio paeon* as *P. cresphontes* (Plate 4; *P. paeon* not mentioned in text); inversion of names for *Danaus gilippus* and *D. eresimus* (Plate 33); and illustration of a probable *Caligo oileus* (indicated as "not illustrated" in text) as *C. illioneus* on Plate 46, no. 2. Figure 7 (a "tipped in" plate following p. 26) was missing from the paperback copy purchased for my University library.

A selection of additional irksome errors (unfortunately, there are many more, some quite misleading) includes the following. There is a general lack of detailed information on variation in juveniles (very frequent in my experience), accentuated by sketchy, often inscrutable or generalized, or even wrong (as in *Papilio, Hypothyris*) descriptions, and few mentions of the number of replicates of rearing (thereby many opportunities to help in juvenile field identification lost). There occurs an implicit advocation of collection in nature reserves (p. 33); recent work on endangered species in Brazil suggests that even limited collecting of adults or juveniles of rare or local species in some kinds of habitats can seriously depress subsequent generations. Species lists for the Carrillo Belt are repeated (pp. 47, 49). Many place names mentioned in text are missing from maps (but usually are present in the gazetteer, pp. 285–287, where only one locality—Rincon, Osa—was found misplaced, 160 km to the NW). Data on canopy faunas are anecdotal, and seem overemphasized, or else are much more important in Costa Rican topography than in the flatter Amazon Basin. Diversity comparisons (p. 52) use only two sites in each of the six regions; only near-asymptotic lists, which these are probably not, can give a reliable picture. A number of generalizations presented in family, tribe or generic accounts are not obeyed by many included taxa, such as "tailless and sexually dimorphic troidines" (not *Parides photinus* or *P. montezuma*) with "white woolly scent scales" (not *P. eurimedes*), and "mimetic Dismorphiines" (not the majority listed). Inference of larval host plant from pupal placement for *Papilio cleotas* (*fide* W. Haber) would permit *P. anchisiades* to eat my back door, over 30 m from the nearest *Citrus* they actually fed upon; some go much farther. The book's author doubts that male *Battus* visit sand (normal all over South America), that male *Eutresis* visit pyrrolizidine alkaloid sources (frequent in Venezuela and Colombia), that pterin pigments occur outside Pieridae (present in most butterflies, at times in large quantities), or that mimetic charaxines occur outside *Consul* (he illustrates several without commenting on their mimicry). He mixes up the characters in describing seasonal forms of *Eurema proterpia* (p. 105, compare Plate 10), and uses an-idi ending for "subfamily or tribal status" (p. 127). He indicates 10 species in *Libytheana* (there are 3), 2 in *Baeotus* (there are 3), "a few" in *Eutresis* (probably only 2), 5 in *Brassolis* (probably all 1), 10 in *Cithaerias* (probably 3 or less), 1 in *Dulcedo* (few know about the 2nd high-elevation west Colombian species, *D. mimica*). He restricts *Nessaea* to swamp forests, though it occurs on mesic hillsides in many parts of South America. Female behavior of *Callidula pyrame* ("*Haematera*") is generalized to both sexes. The red basal dots on the ventral hindwing of *Heliconius* are transferred to the forewing. *Microtia* is placed in the Melitaeini on p. 198, in the Phyciodini on p. 205. A dropped line on p. 213 grows wing-pads on *Lycorea* larvae. The interesting mimicry situations involving *Caligo atreus*-*Antirrhaea pterocarpha*-female *Catoblepia orgetorix* and *Drucina leodonta*-*Tithorea tarricina* need comment; the second is simply denied (it occurs in Panamanian Chiriqui), the first involves birds' wariness at the large size and eyespots of *Caligo* who can even keep birds away from their feeders.

These diverse "gripes" could go on, but will tire the reader. They are not intended to subtract from the value of the book, but to add to that of future editions, avoiding a wide circulation of inconsistencies and misinformation. In relation to most current books covering parts of the Neotropical butterfly fauna, this one stands out in general as carefully written, taxonomically accurate, biologically important, ecologically interesting, and sane. This is, in part, a negative reflection on the others.

It seems interesting to compare this book with the only other well illustrated modern single-country butterfly guide for the Neotropics, Barcant's 1970 *Butterflies of Trinidad and Tobago*. Prepared by an amateur and lifetime Trinidad resident, and aimed at nature lovers, children, and collectors, this book received such a negative and unfair review in this journal that its author remained deeply embittered until his death last year. It covered the complete lot of families (with rather inscrutable plates for Lycaenidae and an outdated list for Hesperiidae); its color illustrations were generally of high quality and esthetic balance, showing recently captured specimens with no damage. Emphasis was likewise on natural history, though with less information on juveniles and foodplants, to the point of using an arrangement based on habitat rather than taxonomy; coverage of historical, traditional and folklore aspects was strong, with common names in Trinidad given for many species. Barcant was not familiar with modern ecological patter and theory as is DeVries, which sometimes detracted and other times helped his book (many such aspects have notoriously short half-lives). Both books give many specific details on collecting localities, adult habitats, mimicry, seasonality, physical geography and general methods; Barcant is more "folksy" while DeVries is more "objective".

It is to be hoped that DeVries' book reaches a wider readership today than did Barcant's 18 years ago, and will continue to stimulate and aid those who study the fullness of biological aspects of Neotropical butterflies, and who wish to publish such well illustrated regional accounts in the future. All of these, like the Barcant and DeVries books, should be of immeasurable assistance in biological and ecological studies in the Neotropics, as well as useful and enjoyable to amateurs.

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BUTTERFLIES OF NORTH DAKOTA: AN ATLAS AND GUIDE, by Ronald Alan Royer. 1988. Science Monograph No. 1, Division of Science, Minot State University, Minot, North Dakota 58701. Format 14 × 20 cm, 192 pp., 12 pp. color plates, 1 b/w plate, 30 pp. maps. Plastic spiral binding. Soft cover. $14.95.

The author has brought together in a single volume a guide and atlas which describes with text, color plates, and distribution maps all 142 species of butterflies known to occur in North Dakota. The book succeeds in fulfilling the author's goal of providing access to the Lepidoptera literature for the state.

The book begins with an Introduction which includes an explanation of the binomial system, North Dakota environments, terminology (wing surface and venation), and scope and use of the book. This is followed by the Guide, which includes a narrative for each species. Each species is introduced with the common and binomial name (including full author name), and corresponding plate number. The Atlas includes a State map with counties named followed by a State map for each species with the counties of record spot marked. There are five maps on the left side of each page with space on the right for notes. Plates are 60% natural size photographs of actual specimens. Opposite each plate, the binomial name, sex, view (dorsal or ventral), collection locality, and date collected are arranged according to how specimens appear in the plate. Next is a Hypothetical and Erroneous Records List followed by a list of names and addresses of lepidopterist organizations and suppliers. The Bibliography follows, then a 121 word Glossary, and finally the Index of Butterflies listed by binominal and common names with page numbers for the Guide, Atlas, and Plate sections.

Some of the nice things about this volume have already been mentioned, but still others are obvious when you pick it up—the sturdy binding and quality paper are suited for years of use. The cover is dominated by a photograph of *Hesperia dacotae* (Skinner), a nice touch. Coverage is complete and you could not ask for more information in the species descriptions. The author follows the 1981 Miller & Brown generic naming system, and there are no taxonomic surprises.

The faults with the book are few considering the wealth of information presented. The map in the Introduction shows only the major life zones. A more detailed map should have named the major rivers, drainage systems, and geographical features. Repeating the named counties map would have been helpful, too. Reading this section makes one feel the book was written for North Dakota collectors already acquainted with the State rather than for collectors who find themselves in North Dakota. The terminology section would have benefited with an explanation of how to distinguish the sexes, and with a generalized diagram of external morphological characters. The chapter might also have included a brief discussion of butterfly evolution, clarifying the heirarchy used in the book. There are no keys except one to the Papilionoidea.

Most of my comments concern the Guide and Plates chapters. The desired information is there, but would have been easier to locate if headings such as Description, Similar

Species, Life Cycle, Flight, Habitat, and Range were inserted in bold type in the text. The text is not cross-indexed except for a Plate number with each species description. The Guide, Atlas, and Plates sections should have included page numbers for the corresponding sections which would have helped tie the chapters together. The color plates are of good quality, and my only change would have been to adjust background colors of Plates II and IV to increase contrast. Illustrated specimens should have been numbered, with those numbers repeated in the Plate legend. This would have helped Plate II, as the extreme example, where 56 specimens are pictured, and searching the legend for the binomial name is tedious. A simple checklist at the end would have been useful to some collectors, or perhaps a box to check by each distribution map.

The faults with the book are few, and my criticisms also apply to a number of other popular books and field guides. This book is a valuable source of information. Whether or not you are ever fortunate enough to collect in North Dakota, this handsome book is a must for the naturalist.

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THE MOTHS OF BORNEO: SUPERFAMILY BOMBYCOIDEA: FAMILIES LASIOCAMPIDAE, EUPTEROTIDAE, BOMBYCIDAE, BRAHMAEIDAE, SATURNIIDAE, SPHINGIDAE, by Jeremy D. Holloway. 1987. Southdene Sdn. Bhd., P.O. Box 10139, Kuala Lumpur 50704, Malaysia. 199 pages, 20 color plates. Paperback. About $35.00.

This book deviates from other faunistic treatments by including more detail on phylogeny and ecology, particularly hostplants. The color plates were produced by Bernard D'Abrera, so are predictably of high quality. All known species in these families from Borneo are treated in the text and depicted in color, thus including a considerable portion of the Indo-Australian moth fauna. The text draws from observations and works published in Asia by resident entomologists, and manifests Holloway's own extensive field experience in the region; the result is far beyond what could be produced from study of museum specimens alone. Where new or controversial taxonomic decisions are enacted, the author faithfully provides justification or explanation.

Inclusion of Sphingidae within Bombycoidea is unexpected. Upon reading the discussion of characters to justify this, I was a little disappointed, but apparently seven synapomophies do link sphingids to other bombycoids. Such a large superfamily, now comprising 13 or 14 families worldwide, makes it difficult to designate nomenclaturally the closer relationships within the group; one wishes for a category between superfamily and family levels (or between suborder and superfamily levels) to remedy the situation. Holloway's discussion of the phylogeny of those families makes the book useful to Lepidoptera taxonomists around the world, even to those who profess no interest in moths of southeastern Asia. The book is well done. I found no typographical errors. I believe those who acquire it will wish to purchase other volumes in the series, most of which are as yet unpublished.

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——— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10:165–216.

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The object of the Lepidopterists' Society, which was formed in May 1947 and formally constituted in December 1950, is "to promote the science of lepidopterology in all its branches, ... to issue a periodical and other publications on Lepidoptera, to facilitate the exchange of specimens and ideas by both the professional worker and the amateur in the field; to secure cooperation in all measures" directed towards these aims.

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Cover illustration: Captive female cecropia moth, *Hyalophora cecropia* (L.) (Saturniidae), released to wild and resting on staghorn sumac, *Rhus typhina* L. (Anacardiaceae). Submitted by Monica Miller, 5560 Library Road #201, Bethel Park, Pennsylvania 15102.

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SYSTEMATIC POSITIONS OF *ACENTRIA EPHEMERELLA* (DENIS & SCHIFFERMÜLLER), NYMPHULINAE, AND SCHOENOBIINAE BASED ON MORPHOLOGY OF IMMATURE STAGES (PYRALIDAE)

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ABSTRACT. *Acentria ephemerella* (Denis & Schiffermüller), the one known species of its genus, is sometimes placed in Schoenobiinae, but it lacks three important autapomorphies of that subfamily: larval prothoracic sac, exposed pupal mesothoracic coxae, and deep pitlike pupal mesothoracic spiracle. Apomorphies such as spinelike pupal frontal setae, lack of pupal mesothoracic spiracle, and reduced posterior pupal abdominal spiracles confirm that *Acentria* belongs in Nymphulinae. No larval or pupal characters were found to support *Acentria* as a separate family or subfamily (Acentropidae or Acentropinae). Several synapomorphies suggest Nymphulinae and Schoenobiinae are sister groups. They share long exarate pupal appendages and reduction of larval L2 seta on abdominal segments 1-8. The unisetose L group on abdominal segment 9 in other subfamilies of Crambiformes may be used as a synapomorphy to define a clade separate from Nymphulinae and Schoenobiinae in which the L group is bisetose on segment 9.

Additional key words: larva, pupa, cladogram, systematics.

Acentria ephemerella (Denis & Schiffermüller), formerly *Acentria* (=*Acentropus*) *nivea* (Olivier), has a long and varied systematic history (Speidel 1981, 1984). It was placed in Schoenobiinae because of a reduced proboscis, tubular CuP (1A) forewing vein, and lack of hindwing Cu pecten (hair fringe) (Hampson 1895, Forbes 1926, 1938). Other workers (Marion 1954, Roesler 1973, Leraut 1980, Goater 1986) thought *Acentria* should be in Acentropinae or Acentropidae largely because the adult lacks a praecinctorium. Nigmann (1908) and Speidel (1981) cited enlarged anterior abdominal pupal spiracles as an autapomorphy of Nymphulinae and thus considered *Acentria* to be in this subfamily because of its similar pupa. Larval chaetotaxy confirmed this view. Hasenfuss (1960) placed *Acentria* in Nymphulinae based on a bisetose L group on abdominal segment 9, and unusual arrangement of larval stemmatal (ocular) setae. Speidel (1984) suggested *Acentria ephemerella* is the correct name for *A. nivea* and recommended acceptance of Acentropinae instead of Nymphulinae as the valid subfamily name. The latter change, in agreement with Minet (1982), is not followed here because Nymphulinae has been stable and unambiguous in most checklists. Fletcher and Nye (1984) placed *Acentria* with Nymphulinae in their Pyraloidea catalogue. However, Yoshiyasu (1985) doubted the placement of *Acentria* with Nymphulinae because enlarged abdominal spiracles are also found in some aquatic Crambinae. The possibility remained that enlarged spiracles had arisen in certain species because of aquatic habits instead of common ancestry. Minet (1982, 1985) also considered *Acentria* to be a nymphuline, based on several apomorphies of the tympanum. As was traditional in the U.S., Munroe (1983) listed *Acentria* with Schoenobiinae. Batra (1977), Berg (1942), Buckingham and Ross (1981), Speidel (1981), and Yoshiyasu (1985) either illustrated stages of *A. ephemerella* or discussed its biology.

Only three workers have published Pyralidae cladograms (Fig. 1). Roesler (1973), relying mostly on adult morphology, recognized an Acentropidae-Crambidae complex. Yoshiyasu (1985) doubted the validity of Roesler's characters. He called attention to variability in the Nymphulinae radial vein and maxillary palpi, as well as to the presence of aquatic species in other subfamilies. More importantly, some key portions of Roesler's (1973) cladogram are defined by plesiomorphic features (lack of specialized scales in the male genitalia, for example). Kuznetzov and Stekolnikov (1979) considered Schoenobiinae and Nymphulinae to be unrelated, based almost exclusively on genital musculature. However, they studied very few species and paid only superficial attention to immature stages. Yoshiyasu (1985), considering characters of all stages, linked Schoenobiinae, Nymphulinae, and *Acentria* as sister groups but was unable to place this clade in an overall scheme. Instead, three clades were extended to a single point with dotted lines and a question mark at their bases (Fig. 1A). Thus, convincing evidence from adult (Minet 1982), larval (Hasenfuss 1960) and pupal (Nigmann 1908) morphology suggests *Acentria* belongs with Nymphulinae in spite of recent doubts (Yoshiyasu 1985, Goater 1986).

This paper examines apomorphic larval and pupal characters of *Acentria ephemerella* to provide additional evidence on the systematic position of *Acentria*. The relation of Nymphulinae to Schoenobiinae, and their taxonomic position within Crambiformes are also discussed.

METHODS

Morphological information on pyralid immature stages came from Passoa (1985), literature illustrations, and borrowed material. Unpub-

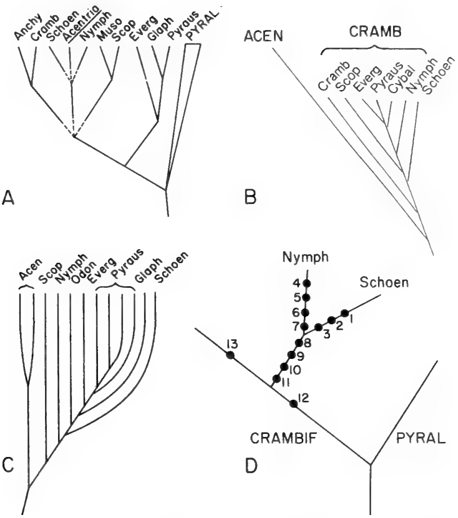


FIG. 1. Systematic position of *Acentria*, Nymphulinae, and Schoenobiinae after various authors. A, Yoshiyasu (1985). B, Roesler (1973). C, Kuznetsov & Stekolnikov (1979). D, Present study, with major apomorphies numbered as follows: 1—larva with prothoracic sac; 2—pupal mesothoracic spiracle pitlike; 3—pupal mesothoracic coxae exposed; 4—stemmatal setae in line with each other; 5—pupal frontal setae enlarged and spinelike; 6—pupal anterior abdominal spiracles enlarged and on conelike projections, posterior abdominal spiracles reduced; 7—pupal mesothoracic spiracle lost; 8—V1 lost on larval thorax; 9—L2 on larval abdominal segments reduced; 10—tegumen-vinculum plate developed, transtilla lost; 11—pupal appendages exarate with metathoracic legs exposed; 12—praecinctorium present; 13—larva with unisetose L group on A9. Abbreviations: ACEN—Acentropidae; Acen—Acentropinae; Anchy—Ancylolomiinae (Anchylolomiinae of Yoshiyasu 1985); CRAMB—Crambidae; Cramb—Crambinae; CRAMBIF—Crambiformes; Cybal—Cybalomiinae; Ever—Evergestinae; Glap—Glaphyriinae; Muso—Musotiminae; Nymph—Nymphulinae; Odon—Odontiinae; PYRAL—Pyraliformes; Pyraus—Pyraustinae; Schoen—Schoenobiinae; Scop—Scopariinae.

lished keys and a data matrix of larval characters by workers at the U.S. National Museum (C. Heinrich, H. Capps, and D. Weisman) ("USNM Tables") provided information on pyralid genera in that collection. Literature on Crambiformes immature stages included general works such as Fracker (1915), Mosher (1916), Peterson (1962), and Neunzig (1987) for the U.S., Hasenfuss (1960) for Europe, Nakamura (1981) for Asia, and Gerasimov (1947, 1949) for the U.S.S.R. Important articles on New World Nymphulinae immatures were selected from Munroe (1981, 1982). Yoshiyasu (1985) published a review on Japanese Nymphulinae and their systematic position. Schoenobiinae immatures were discussed by Passoa and Habeck (1987). Crawford (1961), Mauston (1970), and Tan (1984) provided descriptions of Crambini larvae and pupae. Agarwal and Chaudhry (1966), Passoa (1985), and Rothschild (1967) described Chilini immatures. Works on New World Pyraustinae included Allyson (1981, 1984), and Passoa (1985). Khot'ko and Molchanova (1975) studied Old World species. Some African pyralids were illustrated by Breniere (1979). Indian pyralids were described by Mathur and Singh (1963) and Mathur (1954, 1959).

Preserved larvae, and usually pupae, of the following species were examined:

Nymphulinae

Acentria ephemerella (Denis & Schiffermüller)
Nymphula depunctalis Guenée
N. fluctuosalis (Zeller)
Munroessa sp.
Synclita sp.
Parapoynx diminutalis Snellen
P. obscuralis (Grote)
Neargyractis slossonalis (Dyar)
Petrophila longipennis (Hampson)
P. bifascialis (Robinson)
P. avernalis (Grote)
P. jaliscalis (Schaus)
Usingeriessa onyxalis (Hampson)
Eoparargyractis sp.

Schoenobiinae

Rupela albinella (Cramer)
R. horridula Heinrich
R. leucatea (Zeller)
R. sp.
Scirpophaga (=*Schoenobius, Tryporyza*) *incertulas* (Walker)
S. excerptalis (Walker) (=*S. intacta* Snellen)
Donacaula sp.
D. maximella (Fernald)

This list represents 9 of 16 Nymphulinae genera and 3 of 5 Schoenobiinae genera in the U.S. (Munroe 1983). *Acentria* contains only one species, *A. ephemerella* (Speidel 1984). Larva and pupa terminology follows Stehr (1987) and Mosher (1916). Munroe (1972) and Minet (1982, 1983, 1985) were used to characterize adult subfamilies.

CHARACTER POLARITY

Certain assumptions are necessary before a cladistic study of *Acentria*, Nymphulinae, and Schoenobiinae can proceed. Pyralidae is assumed monophyletic because of apomorphies in the tympanum (Minet 1982, 1983, 1985) and venation (Munroe 1972). All Pyralidae cladograms (Fig. 1) agree there are two lineages, Crambiformes (sometimes called Crambidae) and Pyraliformes (sometimes called Pyralidae in a restricted sense). Crambiformes, which include Nymphulinae, Schoenobiinae, and *Acentria*, are apomorphically defined, in part, by a praecinctorium in the tympanum (Minet 1982). Although tympanic morphology of Midiliformes and other pyralids differ, larval characters, as discussed further on, support Minet's (1982) placement of this taxon within Crambiformes. Pyraliformes, which include all remaining pyralid subfamilies, are the sister group to Crambiformes, and thus comprise the outgroup. Minet (1985) apomorphically defined Pyraliformes by a tympanic "paraspina" and sclerotized pinaculum rings around larval seta SD1. Speidel (1984) mentioned scale morphology, dimorphic labial palps, and reduction of proboscis, ocelli, and leg spurs as apomorphies of *Acentria*. A shortened, stout gnathos, and broad basal portion of the apophysis united *Acentria* and *Kasania* on a single clade.

Unless stated otherwise, Watrous and Wheeler's (1981) method of outgroup comparison was used to polarize characters. This method is especially appropriate when most characters have two states, and relatives are easily defined. In spite of criticisms (Farris 1982, Clark & Curran 1986), outgroup comparison appears to be the most reliable way to determine polarity (Donoghue & Cantino 1984). All morphological features relevant to the systematic positions of *Acentria*, Nymphulinae, and Schoenobiinae are mentioned below even if their polarity is somewhat uncertain. References under each morphological feature usually provide illustrations.

Larval Characters

Stemmatal (ocular) setae. Hinton (1946) considered S1 close to stemmata 3 and 4, S2 level with stemma 5, and S3 below all stemmata as the usual arrangement in Lepidoptera. This trend is also true in Pyralidae where all Pyraliformes and Crambiformes except Nymphulinae show this arrangement (Hasenfuss 1960, Yoshiyasu 1985). Two states occur in Crambiformes: setae in nonlinear arrangement or in line with each other. Since all Pyraliformes (the outgroup) have a nonlinear arrangement, this is considered plesiomorphic. The alternative state in Crambiformes, stemmatal setae in a line with each other, is apomorphic.

Mandible. Based on study of Pyralidae mandibles (Passoa 1985, Neunzig 1987, Peterson 1962), presence of a dentate ridge under the first scissorial tooth is an unusual modification. Inner teeth are sometimes present on the first molar ridge, especially in Pyraustinae (Peterson 1962, Passoa 1985), but in the latter case they do not form a ridge. Two character states occur in Crambiformes: ridge absent or present. Since all Pyraliformes lack a ridge (Passoa 1985), this is plesiomorphic. A dentate ridge, the alternative state, is apomorphic.

Thoracic V1 seta. Hinton (1946) stated V1 was present on all first and last instar Lepidoptera he examined. In Crambiformes, two character states occur: V1 absent (Yoshiyasu 1985) or present (Passoa 1985). Since V1 is present in Pyraliformes (Passoa 1985), this is plesiomorphic. Therefore, loss of this seta is considered apomorphic.

Rothschild (1967) speculated V1 may not be lost in *Tryporyza* (Schoenobiinae) but instead could have migrated to the coxae as in some Tineidae and Psychidae (Hinton 1946). The extreme reduction in body setal length of Nymphulinae and Schoenobiinae (setae may be difficult to see even under a compound microscope), coupled with lack of knowledge about coxal setae and their homologies, makes evaluation of Rothschild's hypothesis impossible at present. In any event, either case would be apomorphic as V1 is not found on the coxa in the outgroup (Pyraliformes).

Prothoracic membranous sac. The Schoenobiinae membranous sac is apparently a unique structure not homologous to other lepidopteran cervical glands (Passoa & Habeck 1987). In Crambiformes, two character states occur: prothoracic sac present or absent. All Pyraliformes lack a prothoracic sac (Passoa 1985). Therefore, presence of a membranous prothoracic sac is apomorphic.

L2 seta on abdominal segments. Hinton (1946) remarked that L1 and L2 are macroscopic and frequently subequal in length throughout Lepidoptera. This is true for all Pyraliformes and Crambiformes except Schoenobiinae (Hasenfuss 1960) and Nymphulinae (Neunzig 1987, Yoshiyasu 1985). Therefore, when L1 and L2 are subequal in length, this is plesiomorphic. A very short, almost microscopic, abdominal L2 seta is apomorphic.

Thoracic L seta. Neunzig (1987) noted that all Pyraliformes have three setae in the L group of mesothorax and metathorax. In Crambiformes, two character states occur: L group bisetose (some Nymphulinae and Schoenobiinae) or L group trisetose (most Crambiformes). Therefore, loss of the thoracic L seta is considered apomorphic.

L2 on A9. All Pyraliformes have L1, L2, and L3 present on A9, whereas L2 is either present (Schoenobiinae and Nymphulinae) or absent (most Crambiformes) in other pyralid larvae (Neunzig 1987, Hasenfuss 1960). L1 is always present in Pyralidae while L3 is always absent in Crambiformes. Because outgroup comparison demands a character distribution in which a feature is present or absent in the group being studied, L2 is the only seta that can be polarized at present. Since L2 is present in the outgroup, the plesiomorphic state within Crambiformes occurs when L2 is present (bisetose condition). In contrast, the apomorphic state occurs when L2 is lost (unisetose condition).

Yoshiyasu (1985) also considered loss of L setae in Crambiformes to be apomorphic but he polarized both bisetose and unisetose conditions as apomorphies. Unfortunately, this idea cannot be confirmed by outgroup comparison until more information is available on the sister group of Pyralidae. If the unisetose condition is apomorphic, the bisetose condition may be part of a trend from trisetose (plesiomorphic state) to a unisetose L group on A9.

Extra pinacula. When present, pinacula are located only around setal bases in Pyraliformes and most other Lepidoptera (Hinton 1946, Passoa 1985). In Crambiformes, two character states occur. There may be extra pinacula (apparently lacking setae) on the thorax and abdomen of Crambinae, a few Pyraustinae, and Scopariinae (MacKay 1972, Passoa 1985) while extra pinacula are absent in Nymphulinae and Schoenobiinae. Therefore, development of secondary pinacula is considered apomorphic. When extra pinacula are lacking, this is plesiomorphic.

Pupal Characters

Frontal setae. Frontal setae are about as thick as other body setae in Pyraliformes (Passoa 1985). In Crambiformes, they are thin in all subfamilies except Nymphulinae (Passoa 1985) and several described Musotiminae (Nakamura 1977, for example). Therefore, thin setae are plesiomorphic while thick spinelike frontal setae are apomorphic.

Mesothoracic spiracle. Outgroup comparison is of limited value here since both clades have equal character distributions. In Pyraliformes, all subfamilies except Galleriinae and some Phycitinae have a mesothoracic spiracle (Passoa 1985). Among Crambiformes, all subfamilies except Nymphulinae have a mesothoracic spiracle. Loss of the mesothoracic spiracle is considered apomorphic by parsimony since three independent losses (Nymphulinae, Galleriinae, and some Phycitinae) is a more likely evolutionary scenario than independent gain of this spiracle many times in other pyralid subfamilies. Moreover, Mosher (1916) found a mesothoracic spiracle on nearly all other Lepidoptera studied. This supports the contention that a mesothoracic spiracle was probably present in ancestors of Pyralidae.

No Pyraliformes examined during this study have a deep pitlike mesothoracic spiracle. In Crambiformes, all subfamilies except Schoenobiinae lack a deep pit. Therefore, a pitlike mesothoracic spiracle is considered apomorphic while absence of a pitlike mesothoracic spiracle is plesiomorphic.

It should be noted that some Pyraustinae (for example, *Spoladea* and *Asciodes*) have pits adjacent to the mesothoracic spiracle while a few Epipaschiinae have the spiracle set in a shallow concavity. This should not be confused with the situation in Schoenobiinae where only a deep pit can be found and no trace of the spiracle is visible inside the pit.

Anterior abdominal spiracles on A1–3. All Pyraliformes lack enlarged anterior abdominal spiracles set on conelike projections (Passoa 1985). In Crambiformes, two character states exist. Nearly all species of Crambiformes except Nymphulinae (Speidel 1984) and *Thopeutis forbesellus* (Fernald) (Crambinae) lack enlarged anterior abdominal spiracles set on conelike projections. Therefore, lack of enlarged anterior abdominal spiracles is plesiomorphic while their presence on conelike projections is apomorphic. Speidel (1981) also considered enlarged anterior abdominal spiracles of Nymphulinae pupae to be apomorphic.

Posterior spiracles. All Pyraliformes examined during this study have anterior and posterior spiracles subequal in diameter. In Crambiformes, two character states exist. Most species, except Nymphulinae and a few Pyraustinae, have spiracles subequal in diameter throughout the abdomen. This is considered plesiomorphic. Reduced posterior spiracles are considered apomorphic.

Mesothoracic and metathoracic coxae. All Pyraliformes and all Crambiformes except Schoenobiinae have hidden mesothoracic and metathoracic coxae. Thus, exposed mesothoracic and metathoracic coxae are apomorphic while hidden coxae are plesiomorphic. Davis (1986) noted that only the forecoxa is exposed in higher Lepidoptera, and thus he considered exposed mesothoracic coxae to be apomorphic.

Metathoracic legs. All Pyraliformes have obtect appendages; the metathoracic legs, if not hidden, have only their tips exposed. This is also true of most Crambiformes, except Nymphulinae and Schoenobiinae which have exarate appendages with metathoracic legs clearly exposed. Fully exposed metathoracic legs and exarate appendages are considered apomorphic while partially hidden metathoracic legs are plesiomorphic.

Adult Characters

Proboscis. Most pyralids have the proboscis well developed and scaled but some Crambiformes (Schoenobiinae) and Pyraliformes (Peoriinae) lack a proboscis (Munroe 1972). This character distribution (present or absent in each clade) limits the usefulness of outgroup comparison. Instead, a reduced proboscis is considered apomorphic by parsimony since two independent reductions are more likely than many acquisitions.

Forewing CuP. Forewing CuP is another difficult character to polarize by outgroup comparison since it may be either a fold or a tubular remnant in each clade of Pyralidae (E. G. Munroe pers. comm.). Perhaps a fully developed vein was gradually lost until only a tubular remnant remained at the distal end of the forewing. This reduction of CuP continued so only a fold now marks its former position. Since Common (1970) noted a trend in higher Lepidoptera where anal and radial veins are gradually lost in advanced forms, reduction of CuP to a fold is tentatively called apomorphic. Further studies on Pyraloidea ancestors would help polarize this character, but dugeoneids, which Minet (1982) believed could be the sister group of the Pyralidae, have CuP developed.

Another possibility, independent reacquisition of CuP in Schoenobiinae, some Nymphulinae and some Pyraliformes, is equally parsimonious with the reduction of CuP in most Crambiformes, most Pyraliformes, and some Nymphulinae. CuP reduced to a fold would be plesiomorphic while gain of a tubular remnant would be apomorphic. This polarization of CuP is especially attractive if morphological studies show the sister group of Pyralidae is not Dugeoneidae (dugeoneids have CuP developed).

Praecinctorium. The praecinctorium is either present (Crambiformes) or absent (Pyraliformes) in Pyralidae. Dugeoneidae, a tentative sister group of Pyralidae, lacks a praecinctorium. Thus, presence of a praecinctorium is apomorphic whereas its absence is plesiomorphic.

Acentria probably lost the praecinctorium secondarily because it may be vestigially present in the tympanum (Minet 1985). Given presence of a praecinctorium as a groundplan apomorphy of Crambiformes, absence or extreme reduction of praecinctorium must be an apomorphic reversal.

Tegumen-vinculum plate. All Pyraliformes lack the t-v plate (Yoshiyasu 1985). This is also true for all Crambiformes except Nymphulinae and Schoenobiinae (Yoshiyasu 1985). Therefore, presence of the t-v plate is considered apomorphic.

Cu hindwing pecten. Munroe (1972) noted that cubital pecten occurs in both Crambiformes and Pyraliformes, and this limits outgroup comparison as a method of analysis. However, parsimony would indicate that several independent gains of cubital pecten are more likely than numerous losses. This suggests that presence of pecten is apomorphic while its absence is plesiomorphic. Roesler (1973) also considered presence of pecten to be apomorphic.

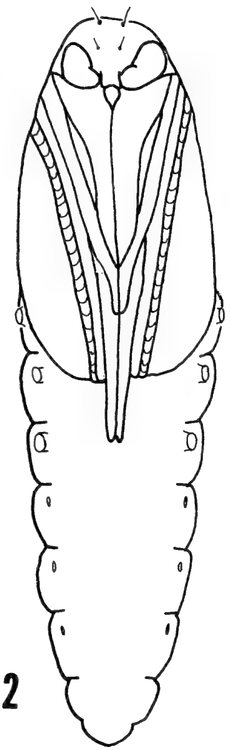
BIOLOGY

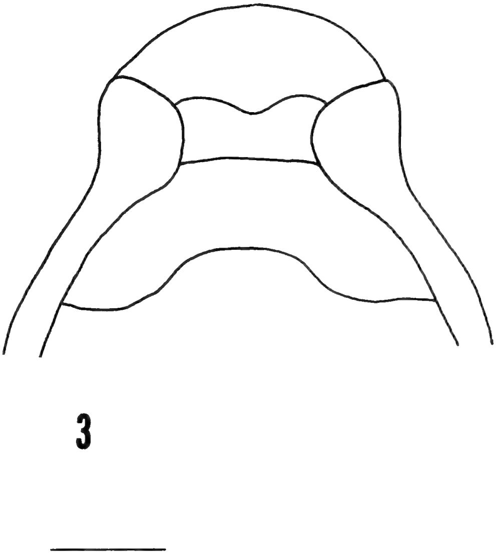
Aquatic habitat. Nearly all Pyraliformes are terrestrial, and do not form cases entirely of leaf fragments. This is true of all Crambiformes except Nymphulinae. When restricted to exclude Musotiminae, Nymphulinae include species which are always aquatic and frequently form cases. Thus, aquatic habit is apomorphic while terrestrial living is plesiomorphic. Speidel (1981) also considered aquatic living to be apomorphic.

TAXONOMIC AFFINITIES OF *ACENTRIA*

The above characters and their polarities provide additional information on the systematic position of *Acentria ephemerella.* Schoenobiinae larvae are apomorphically defined by a membranous prothoracic sac (Hasenfuss 1960, Passoa & Habeck 1987), which is absent from *Acentria* (Yoshiyasu 1985). *Acentria* also lacks the pitlike mesothoracic spiracle and exposed mesothoracic coxae (Figs. 2, 3) that apomorphically define Schoenobiinae pupae (Passoa & Habeck 1987). Therefore, immature stages of *Acentria* demonstrate the genus is misplaced in Schoenobiinae. Hampson (1895) and Forbes (1938) claimed affinity between *A. ephemerella* and Schoenobiinae because of a reduced proboscis, tubular forewing CuP, and absence of hindwing cubital pecten. Lack of cubital pecten is plesiomorphic; thus absence of this feature does not indicate relation (individuals sharing symplesiomorphies may not be relatives). The tubular forewing CuP may be apomorphic, but this character is found in both Nymphulinae and Schoenobiinae (Munroe 1972), and thus does not clarify the systematic position of *Acentria.* The single apomorphic adult character that *Acentria* and Schoenobiinae have in common, a reduced proboscis, perhaps arose through convergence since both taxa are associated with a similar (moisture-rich) aquatic environment. Although a reduced proboscis is usually considered characteristic of Schoenobiinae (Forbes 1938), some Nymphulinae also have the proboscis reduced (Yoshiyasu 1985), so a species with reduced mouthparts could be a member of either subfamily. Adult morphology, like that of immatures, provides little evidence that *Acentria* belongs in Schoenobiinae.

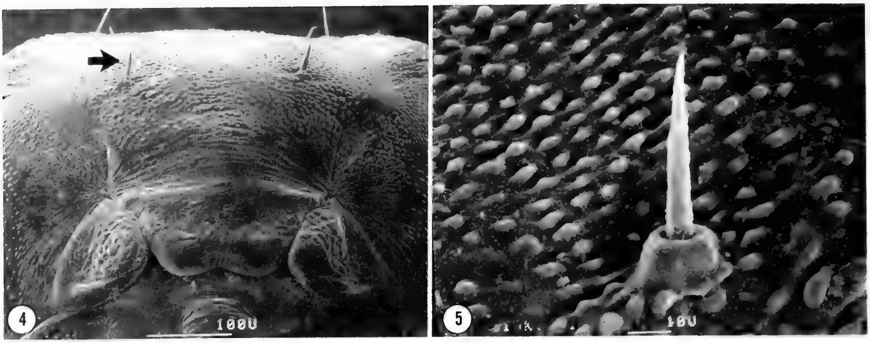
As mentioned earlier, there may be strong selection for enlargement of anterior abdominal spiracles in pupae of aquatic pyralids. These spiracles were considered autapomorphic for Nymphulinae (Speidel 1984), but they also occur in some aquatic Crambinae of Asia (Yoshiyasu 1985), *Thopeutis forbesellus* (Fernald) of the United States, and a few terrestrial Pyraustinae genera such as *Lygropia, Microthyris, Spoladea,* and *Marasmia* (Passoa 1985). Nevertheless, other pupal apomorphies indicate *Acentria* is related to Nymphulinae. Enlarged spinelike frontal setae are found on most Nymphulinae pupae (Yoshiyasu 1985), and are apomorphic for this subfamily. *Acentria* has these enlarged setae (Figs.





FIGS. 2, 3. **2,** Ventral view of *Acentria ephemerella* pupa. Scale line = 0.8 mm. **3,** Dorsal view of *Acentria ephemerella* pupal antenna and thorax. Scale line = 0.25 mm.

4, 5) which indicates a close relation to Nymphulinae. In addition, very few pyralid subfamilies (Galleriinae, Nymphulinae, and some Phycitinae) lack a mesothoracic spiracle (Passoa 1985). Among Crambiformes, only Nymphulinae show this loss. *Acentria* has no mesothoracic spiracle (Fig. 3) and, as is typical for Nymphulinae, has enlarged anterior abdominal spiracles set on conelike projections (Fig. 2). This spiracular arrangement, when combined with much reduced posterior spiracles, is autapomorphic for Nymphulinae. *Thopeutis forbesellus* (Crambinae) has anterior abdominal spiracles set on weak conelike projections, but the abdominal spiracles are all equal in diameter. Some Pyraustinae have enlarged anterior abdominal spiracles (Passoa 1985), but unlike Nymphulinae, lack conelike projections and have posterior spiracles at least half the diameter of anterior ones. These examples show, as Yoshiyasu (1985) suspected, that convergence has produced enlarged spiracles and conelike projections in other Crambiformes.



FIGS. 4, 5. **4,** Micrograph of *Acentria ephemerella* labrum, pillifers, frons, and vertex. Arrow points to spinelike frontal seta. Scale line = 100 microns. **5,** Micrograph of *Acentria ephemerella* spinelike frontal seta. Scale line = 10 microns.

However, it still remains possible to define Nymphulinae pupae easily by their frontal setae and other spiracular modifications.

Besides the aquatic habit (Nigmann 1908) and stemmatal setal arrangement (Hasenfuss 1960), another larval apomorphy may help resolve the systematic position of *Acentria ephemerella*. Many Nymphulini have a dentate ridge on the mandible (Yoshiyasu 1985, "semicircular arrangement" of Lange 1956) which also occurs in *Acentria* (Yoshiyasu 1985). This contrasts with Argyractini larvae which have the mandible more elongated, flattened, and usually without the dentate ridge (Lange 1956). Other characters (Lange 1956, Speidel 1984) such as diet of submerged plants, prothoracic shield chaetotaxy, ability to make cases of leaf fragments, lack of gills on body, lack of palmate setae on labrum, and three enlarged pupal spiracles would indicate *A. ephemerella* lacks apomorphies of Argyractini and belongs in Nymphulini as defined by Lange (1956). Speidel (1984) did not use mandibles, pupal spiracles, or labral setae in his Nymphulinae cladogram. Since the tribal classification proposed by North American workers can be difficult to apply to certain Asiatic genera, for example *Nymphicula* (Yoshiyasu 1980), these features merit further attention.

In summary, *Acentria* is misplaced in Schoenobiinae because immature stages radically differ. In spite of some morphological specializations, there seems little reason to consider this genus separate from Nymphulinae. Placement of *Acentria* in its own family or subfamily was based, in part, on lack of a praecinctorium which is unusual among Crambiformes. Minet (1985), while studying the tympanum, found a possible praecinctorium vestige, and thus placed *Acentria* in Nymphulinae. No characters in immature stages were found to exclude *Acentria* from Nymphulinae as a separate taxon, although crochet arrangement is somewhat unusual. Since differences between the tympanum of *Acentria* and other nymphulines may not be as great as previously thought, and several additional larval and pupal apomorphies confirm its relation to Nymphulinae and exclude it from known Schoenobiinae, there seems little doubt that transfer of *Acentria* to Nymphulinae by Hasenfuss (1960) was correct.

It is worth noting that *Neoschoenobia decoloralis* Hampson, another disputed taxon placed in Nymphulinae (Inoue 1982, cited by Yoshiyasu 1985) and Schoenobiinae (Lewvanich 1981), might be a member of Schoenobiinae because it has exposed pupal coxae and lacks enlarged pupal spiracles and stemmatal setae in a straight line. Since illustrations by Yoshiyasu (1985) do not show a mesothoracic spiracle or a larval prothoracic sac, it seems wise to retain this species in Nymphulinae, although preserved specimens should be examined for these features.

RELATION BETWEEN NYMPHULINAE AND SCHOENOBIINAE

Historically, the systematic position of Schoenobiinae has been debated. Börner (cited by Munroe 1958) thought Crambinae and Schoenobiinae were close relatives. Roesler (1973) considered them unrelated based on maxillary palpi and cubital pecten. Kuznetsov and Stekolnikov (1979) included Crambinae, Schoenobiinae, and Nymphulinae as the most primitive members of their Crambidae.

Larval and pupal features indicate Crambinae and Schoenobiinae are not closely related phenetically or cladistically. Crambinae larvae have a unisetose L group on A9, and well developed extra pinacula on both thorax and abdomen (Passoa 1985, Tan 1984). Schoenobiinae larvae, in contrast, frequently have a bisetose L group on A9 and no pinacula (Passoa & Habeck 1987). Pupal structure is also radically different. Crambinae pupae either have a well developed cremaster (Crambini) or processes on the head or body (Chilini). Metathoracic legs are not exposed or are barely visible. Schoenobiinae pupae, in contrast, always have exposed metathoracic legs, and never have a cremaster or appendages on the head or body. In fact, it is difficult to find any synapomorphies in immature stages to link these two groups.

Immature stages do support the hypothesis of Passoa (1985) and Yoshiyasu (1985) that Schoenobiinae and Nymphulinae are related. Bollman (1955) and Allyson (1976) distinguished Schoenobiinae by their reduced L2 seta, but minute L setae are common on many Nymphulinae (Yoshiyasu 1985, Neunzig 1987). Additional apomorphies to unite Schoenobiinae and Nymphulinae include fully exposed metathoracic legs and exarate appendages. Other synapomorphies listed by Yoshiyasu (1985) are V1 lost on the larval thorax, and absence of transtilla with development of the t-v plate in male genitalia. One exception is *Rupela albinella* (Passoa & Habeck 1987) which has V1 present, but this may merely represent a reversion to the primitive state. All other known species in both subfamilies lack V1, so loss of this seta is probably a groundplan apomorphy. Finally, several characters merit further investigation as synapomorphies of the Nymphulinae–Schoenobiinae clade. These are mesothoracic pupal spiracle (does the pit in Schoenobiinae contain a spiracle, or is the pit the spiracle itself); absence of pupal cremaster (unknown polarity); L setae of thorax bisetose (apomorphic but its distribution within the clade needs study); loss of pinacula (unknown polarity); and CuP tubular at margin (unknown polarity). In addition, a bisetose L group on A9 was thought characteristic of only Nymphulinae (Yoshiyasu 1985, Hasenfuss 1960, Bollman 1955) but this condition is also found in several Schoenobiinae genera (Passoa & Habeck 1987). Some illustrations show a unisetose L group on A9 in Schoenobiinae (Hasenfuss 1960) but these probably represent cases where L2 was overlooked. Chaetotaxy of Schoenobiinae larvae is difficult to study without slide mounts of larval skin. Further study may also show the bisetose L group on A9 is a synapomorphy of the two subfamilies.

RELATIONS OF NYMPHULINAE–SCHOENOBIINAE CLADE IN CRAMBIFORMES

Relation of the Nymphulinae–Schoenobiinae clade to other subfamilies has been unclear. Yoshiyasu (1985) defined a clade uniting all Crambiformes, except Pyraustinae and its relatives, by a reduced transtilla. However, certain exceptions to this generalization limit its use as a synapomorphy. Yoshiyashu (1985) characterized Pyraustinae and Glaphyriinae by their well developed transtilla, but E. G. Munroe (pers. comm.) stated that the transtilla varies widely in these groups. One alternative to a clade defined by transtilla morphology, with far fewer exceptions, involves L setae on A9. The Nymphulinae–Schoenobiinae clade is separated from remaining Crambiformes by the number of L setae on A9. Other Crambiformes subfamilies, without exception, have a unisetose L group on A9 (loss of seta L2 is an apomorphy), which defines them as a monophyletic group. This seta is present (bisetose condition) in nearly all Nymphulinae (restricted sense) and Schoenobiinae larvae. Although the above phylogeny accepts some parallel evolution with the presence of a unisetose L group in a single Nymphulinae species (Yoshiyasu 1985) and in published figures of some Schoenobiinae (if these figures are correct), this represents only a very small number of species. Parallel evolution appears to be normal in the evolution of both Macrolepidoptera (Michener 1949) and Microlepidoptera (Kristensen 1984), so perhaps pyralids have also followed this trend. It seems unrealistic to expect a group with thousands of species to be defined by a single trait without parallelisms, so choice of a clade based on the L setae may represent the case with minimum homoplasy. Use of the unisetose L group on A9 as a synapomorphy supports Minet's (1982) contention that Midiliformes belong in Crambiformes since a *Midila* larva in the U.S. National Museum has a unisetose L group on A9. Moreover, separation of Musotiminae from Nymphulinae is supported by the fact that *Musotima* has a unisetose L group on A9 (Nakamura 1977) unlike the bisetose L group of other Nymphulinae (Hasenfuss 1960).

In conclusion, this study calls attention to the role of immature insects on Pyralidae classification and phylogeny. Modifications of pupae are especially diverse and in need of study. Future studies will probably use more larval and pupal characters, especially if the sister group of Pyralidae can be confirmed.

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EFFECT OF LARVAL PHOTOPERIOD ON MATING AND REPRODUCTIVE DIAPAUSE IN SEASONAL FORMS OF *ANAEA ANDRIA* (NYMPHALIDAE)

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ABSTRACT. In experiments conducted under simulated field conditions in Baton Rouge, Louisiana, laboratory-reared summer-form female *Anaea andria* Scudder from 13- and 14-h larval photoperiods underwent oocyte maturation and mated within two days of eclosion. Laboratory-reared winter-form females from 13-h larval photoperiods did not mate, and showed little oogenesis 20 days after eclosion in simulated field conditions. Data from field-collected specimens numbering 55 winter forms and 26 summer forms support the experimental results, and indicate that female winter forms remain unmated and in reproductive diapause in the fall. Results suggest that larval daylength, by determining adult seasonal form, also regulates reproductive diapause and mating in *A. andria*.

Additional key words: Charaxinae, *Croton capitatus*, seasonal dimorphism.

Anaea andria Scudder (Nymphalidae: Charaxinae) is distributed from Texas to Nebraska, E to West Virginia, Georgia, and the Florida panhandle (Opler & Kriezek 1984). It is common in the southern Mississippi basin and Gulf Coast where it occurs with its primary host plant, *Croton capitatus* Michx. (Euphorbiaceae), an annual herb.

Adult *Anaea andria* are characterized by distinct seasonal wing dimorphism induced by larval photoperiod (Riley 1980, 1988). Winter-form butterflies emerging in fall and surviving until the following spring are characterized by apically acute and falcate forewings, well developed hindwing tails and anal angle projections, and brighter and more contrasting coloration than summer-form butterflies. Summer forms have non-falcate forewing apices, reduced tails and anal-angle projections on hindwings, and lighter overall coloration. Photoperiods of 14 h or more result primarily in summer-form adults. Decreasing photoperiods result in a greater percentage of winter-form individuals (Riley 1988).

In Louisiana, summer-form *A. andria* occurs from May to September when actively growing host plants are available. The winter form begins to appear in late August, and survives until June of the following year. Its appearance in the fall is followed shortly by the beginning of *Croton capitatus* senescence.

The occurrence of two distinct seasonal forms, one when food plants are abundant, and another when they are in decline, suggests that a corresponding difference in female reproductive status may also occur. In this paper, effects of larval daylength on reproductive diapause and mating in laboratory-reared seasonal forms of *A. andria*, and the mating and reproductive status of field-collected seasonal forms are reported.

METHODS

Experimental insects were collected in East Baton Rouge and East Feliciana parishes, Louisiana. Larvae were collected from host plants in the field, or reared from eggs deposited on container-grown host plants by reared and field-collected butterflies confined in 2-m^3 Saran® screen outdoor cages (Chicopee Manufacturing Co., Cornelia, Georgia 30531). Adults were collected using traps similar to those described by Rydon (1964) baited with bananas.

Larvae were reared in clear plastic 26 × 20 × 10-cm boxes containing a raised 3-mm mesh metal grid to prevent undue larval contact with feces. Larvae were fed fresh *Croton capitatus* leaves, and the boxes cleaned daily or as needed. Pupation occurred on tops and sides of the boxes and on plant material.

Seasonal forms of *A. andria* were produced by rearing the third instar in environmental chambers with controllable photoperiods. To obtain summer-form butterflies, 14 h of light was used. Winter and summer forms were obtained using a 13-h photoperiod. Temperature in the chambers was 27°C during the experiments.

Laboratory-reared males and females of each seasonal form were maintained in separate outdoor cages. Eight hours after eclosion, females were numbered with permanent ink on the underside of a hindwing and released into the cages. Males were also caged eight hours after eclosion, and remained in the cages until death. Virgin females were always caged with males of equal or greater age.

Well-ripened bananas were provided for adult food. Cage location provided exposure to full sun 6 h/day. One cage corner was covered with plywood to provide a shaded resting area for the butterflies. The experiment was conducted from 1 June to 31 October 1986; consequently, insects were exposed to a changing natural photoperiod. Each seasonal form was caged during the time of year when each can be found in the field, summer forms from 1 June to 23 September, winter forms from 6 August to 31 October.

Stage of oogenesis, number of mature eggs, and mating status were determined by dissection and examination of the female reproductive system. Summer forms were dissected 2 and 3 days after eclosion, and winter forms 10 and 20 days after eclosion. Stage of oogenesis is described using a scale of 0–5, 0 denoting no evident oocyte development, and 5 the presence of mature eggs (further explained in Table 1). Insects were judged to be in reproductive diapause if oocyte development 10

TABLE 1. Percentage mated, stage of oogenesis, and number of mature eggs/female in 2- and 3-day-old mated and unmated laboratory-reared summer-form *A. andria* under simulated field conditions.

Age (days)	N	Percent mated[1]	Mean stage of oogenesis[2,3]	No. mature eggs/female Mean[3]	 Range
2	18	83.3a	4.1a	0.6a	0–4
3	44	90.9a	4.9b	44.2b	0–82

[1] Not significant according to Fisher's Exact Test.

[2] 0–5 scale. 0 = no visible oocyte formation; 1 = beginnings of oogenesis; 2 = slight enlargement of oocytes; 3 = some oocytes 50% mature; 4 = greater oocyte enlargement, no oocytes at median oviduct; 5 = mature oocytes at median oviduct.

[3] Means in columns followed by the same letter do not differ significantly according to *F*-test ($P < 0.01$).

days after eclosion was rated <2.0. Mated status of females was determined by spermatophore presence in the bursa copulatrix.

Percentage mating was analyzed using Fisher's Exact Test; all other variables were subjected to analysis of variance (SAS Institute 1985).

Voucher specimens are in the Louisiana State University Entomology Museum.

RESULTS

Laboratory-reared butterflies. Winter-form butterflies resulted only from the 13-h photoperiod. Twenty-seven females and 30 males were reared. Twelve females were dissected after 10 days, and 15 dissected after 20 days of caging with winter-form males. None of the female winter forms had mated, and none of their ovarioles showed any sign of oogenesis. No courtship behavior or mating attempts were seen. It was therefore concluded that winter-form females remain in reproductive diapause for at least 20 days after eclosion. Male mating behavior and female attractiveness may also be inhibited in winter forms.

Summer-form butterflies resulted from both photoperiods, 40 females and 41 males from the 14-h, and 22 females and 25 males from the 13-h. Comparison of summer-form data from both photoperiods indicates that oogenesis, number of mature eggs/female, and mating were not significantly affected by these larval photoperiods.

Age was the most important factor affecting stage of oogenesis and number of mature eggs per female in recently eclosed summer forms. Two-day-old females showed significantly less oogenesis ($F = 31.51$; df = 1, 58; $P < 0.01$), and carried fewer mature eggs ($F = 59.18$; df = 1, 58; $P < 0.01$) than 3-day-olds (Table 1). The age × photoperiod interaction was not significant.

Percentage of mated 2- and 3-day-olds did not differ (Table 1). In several instances, courtship of virgin females was observed within hours of their release into the outdoor cage. Although age of the males involved was not known, it was concluded that mating behavior of male and female summer forms is not suppressed in recently eclosed butterflies. These observations suggest that most female summer forms are mated within a few days of emergence.

Among unmated summer forms, four were three days old, and three were two days old. Mean number of mature eggs/female for the 3-day-olds was 23.5 (range 0–48) while none of the 2-day-olds contained mature eggs, evidence that oogenesis in summer forms progresses with age, independent of mating.

Field-collected butterflies. Forty-two winter-form females were trapped during September–November 1984 and September 1985. They showed little evidence of oogenesis, and all were unmated (Table 2). Thirteen overwintered winter forms trapped in April and May 1985 were mostly mated and contained fully mature eggs (Table 2).

Summer-form females, collected in September 1984 and June to mid-September 1985, all carried fully mature eggs and all were mated (Table 2).

DISCUSSION

Laboratory results and field observations indicate that newly eclosed summer-form females undergo rapid oogenesis and are mated within two days of emergence. This enables summer forms to immediately begin ovipositing and larvae to complete development before onset of unsuitable environmental conditions. Conversely, winter-form females remain unmated and in reproductive diapause for a considerable time after adult eclosion. They are thus relieved of the physiological burden of producing and carrying mature or maturing eggs when environmental conditions are not favorable for oviposition and larval development. Reproductive status appears to be linked to adult seasonal form since summer forms from both 13- and 14-h photoperiods underwent rapid oogenesis while winter forms from the 13-h photoperiod remained in diapause.

Field observations of courtship, mating, and feeding behavior in *A. andria* support these conclusions (unpubl. data). No courtship activity has been seen in winter forms during fall. However, newly eclosed male and female winter forms are readily attracted to fermented fruit baits, indicating a possible feeding response linked to preparation for overwintering. In spring, winter-form males have been observed exhibiting strong territorial behavior, chasing other males, patrolling along forest edges and then returning to the same perch, engaging in courtship behavior, and attempting to mate with females. Baits placed near male territories and perches in spring have proven relatively unattractive and trapping ineffective. These observations lend support to the ex-

TABLE 2. Collection month, percentage mated, and stage of oogenesis in female *A. andria* collected 1984–85 in East Baton Rouge and East Feliciana parishes, Louisiana.

Month collected	Seasonal form	N	Percent mated	Mean stage of oogenesis[1]
September	Winter	18	0.0	0.0
October	Winter	23	0.0	0.5
November	Winter	1	0.0	1.5
April	Winter[2]	5	80.0	5.0
May	Winter[2]	8	100.0	5.0
June though September	Summer	26	100.0	5.0

[1] Same scale as in Table 1.
[2] Overwintered butterflies.

perimental results and suggest different behavioral priorities in winter forms before and after overwintering. Factors initiating oogenesis and mating in winter forms that have overwintered are unknown.

My experience with bait traps during summer in Louisiana and Missouri, and that of Vernon Brou, Abita Springs, Louisiana, who operates bait traps year-round, indicate that summer forms are both trapped and collected less frequently than winter forms. They are also less common in collections. The total number of field-collected summer forms in collections of the author, V. Brou, and the Louisiana State University Entomology Museum is 77 compared to 241 winter forms (Riley 1988). This discrepancy may be due to collecting bias, but may also indicate greater behavioral priority for reproduction vs. feeding in summer forms, similar to winter-form behavior in the spring. These observations along with the experimental results suggest that larval daylength, by determining adult seasonal form, is also a major factor regulating mating and reproduction in recently emerged *A. andria*.

Photoperiod is well documented as a diapause inducing and regulating stimulus for insects (Beck 1980, Danilevsky et al. 1970, Tauber et al. 1986). It is an ideal environmental cue for *A. andria*. The nymphalid *Polygonia c-aureum* L. is very similar in its response to daylength (Hidaka & Aida 1963, Fukuda & Endo 1966, Endo 1970, 1972). In *P. c-aureum*, reproductive diapause and seasonal wing dimorphism are determined by photoperiod but are under independent neuroendocrine control. Pheromone production and mating receptivity of female *P. c-aureum* are also hormonally regulated and under photoperiodic control (Endo 1973). The results presented here suggest that a similar interaction between daylength and neuroendocrine system could be controlling wing dimorphism, diapause, and mating in *A. andria*.

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SYSTEMATIC STATUS AND DISTRIBUTION OF THE LITTLE-KNOWN CHARAXINE *PREPONA WERNERI* HERING & HOPP

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ABSTRACT. *Prepona werneri,* hitherto of uncertain systematic status, and since 1925 recorded from only the holotype male, is authenticated from eight additional specimens. Genitalia dissection and review of characters defining *Archaeoprepona* Fruhstorfer and *Prepona* Boisduval indicates *werneri* belongs in *Prepona sensu stricto.* Most specimens are from hydric forest habitat in the Chocó and Cauca areas of endemism, Colombia, but one has data indicating occurrence southward in the upper Rio Putumayo region. The disjunct distribution is probably relict, reflecting former wider occurrence of perhumid biomes.

Additional key words: Apaturidae, *Archaeoprepona,* Neotropics, biogeography.

Of all "Prepona" butterflies, *P. werneri* Hering & Hopp (1925) has been the most problematical. Previously recorded only from the holotype male (Hering & Hopp 1925, Le Moult 1932–33), its melanic appearance, unusual under-surface wing pattern, and hitherto unexamined genitalia have made it a taxon of uncertain status. The most recent treatment of Neotropical Nymphalidae (D'Abrera 1987) does not mention the species. From fieldwork and survey of public and private collections, we recently located eight additional specimens of *P. werneri.* Only two of these were collected since 1929, and it appears unlikely that more specimens will soon be available for study. We therefore summarize below our current determinations of the taxonomic status, biology, and biogeography of this seldom-collected charaxine butterfly.

Taxonomy of "Prepona" Butterflies

Despite accumulation of specimens in private and public collections, there has not been wide agreement on the systematics of "Prepona" butterflies. Because of overall similarity in the striking blue and black markings of the wing upper surfaces, many authors have treated "Prepona" as a monophyletic group (Comstock 1944, Barcant 1970, Brown & Heinemann 1972, Riley 1975). However, as early as 1915, Fruhstorfer defined two subgroups of "Prepona". One he described as genus *Ar-*

chaeoprepona (type species *demophon* Linnaeus) (Fig. 2C), which he regarded as "primitive" (Fruhstorfer 1915). The other, including taxa placed with Boisduval's (1836) *Prepona* (type species *demodice* Boisduval) (Fig. 2D), he noted as sharing all morphological characters with *Agrias* Doubleday, from which it differed only in wing pattern. Le Moult (1932–33) also noted the heterogeneity of the group and proposed *Pseudoprepona* (type species *demophon* L., a junior objective synonym of *Archaeoprepona*). The above distinctions were followed by a number of authors (Orfila 1950, Rydon 1971, Descimon et al. 1973–74, Johnson & Quinter 1982).

As defined hitherto in the literature, some obvious phenetic differences separate *Archaeoprepona* from *Prepona* (Table 1). Authors recognizing these differences have considered both groups as genera (Stichel 1939, Papworth 1982) and even tribes (Rydon 1971) (Table 1). Our concern when considering the taxonomic status of *werneri* has been whether *Prepona* and *Archaeoprepona* are monophyletic groups. Our unpublished numerical cladistic analyses on taxa placed in these groups (Table 1), including outgroups *Charaxes, Polyura, Palla, Euxanthe* and Comstock's (1961) *Anaea sensu lato,* do not conflict with generic usage of *Prepona* and *Archaeoprepona* as reviewed in Table 1. Therefore, based on male genitalia (Fig. 2A, B) and historical usage, *P. werneri* can be reliably placed in *Prepona sensu stricto.*

Prepona werneri Hering & Hopp
(Figs. 1A, B, C, 2A)

Diagnosis. Male. Upper surface of wings: ground darker black-brown than congeners, with blue stripes of deeper azure color (not silverish or blue-green) restricted thinly caudad the forewing discal cell and in a median arc across hindwing. Under surface of wings: hindwing with variably suffused median band, area basad discal band variously marked with dark blotches, two large eyespots each submarginal in cells RS and CuA1 (or a third in cell M3), forewing with disjunct or continuous apical and postmedian lines. **Genitalia** (Fig. 2A). Typical of general configuration of *Prepona sensu stricto* (Fig. 2D).

Female. Unknown.

Distribution. Principally Chocó and Cauca regions (region names follow areas of endemism postulated by Brown 1976, 1982), Colombia, with a single specimen having data indicating upper Putumayo region.

Known specimens. In addition to the type male (Zoologisches Museum der Humbolt Universität zu Berlin, ZMH), labelled "Origin, *Prepona werneri* Hering & Hopp, Rio Micay, Columbien, Februar 1925, 1000m" (Fig. 1A, B, C), eight male specimens are reported here for the first time: (1) Rio Guayabal, Colombia, February 1929, anonymous private collection (examined by first author); (2) Rio Bravo, Prov. Valle, Colombia, March 1985, anonymous private collection (noted by collector as only specimen taken at locality in many years of collecting, examined by David Matusik, Field Museum of Natural History, FMNH, photograph examined by us); (3) Frontino, Colombia, no other data, anonymous private collection (photograph furnished to first author), one male; (4) Cisneros, Colombia, 6 May 1928 (purchased from Le Moult collection February 1968 for Niedhoffer collection), Milwaukee Public Museum (MPM) (photograph examined; genitalia dissected, illustrated in Fig. 2D); (5) Rio Micay, Cordillera Occidentale, Colombia,

TABLE 1. Main characters in literature differentiating *Archaeoprepona* and *Prepona.*

Character location (authors)	*Prepona*	*Archaeoprepona*
Wing upper surface (1–6)	Androconia well-defined, brush-like, with rigid setae	Androconia diffuse, softly hairy
Hindwing under surface (1–6)	Eyespots large, usually two, postmedian to marginal, cells RS and CuA1	Eyespots small, undifferentiated, marginal, cells RS to CuA2
Male genitalia (1, 3–5)	Slender in all parts (especially uncus and valvae); gnathos rod-like, with prominent radial spines	Stout in all parts; gnathos flat, without spines
Female genitalia (3, 7)	Sterigma Y-shaped	Sterigma circular

Taxa included: *Prepona amesia* Fruhstorfer, *brooksiana* Godman & Salvin, *deiphile* Godart, *demodice* Godart, *dexamenes* Herbst, *eugenes* Bates, *garleppiana* Staudinger, *gnorima* Bates, *laertes* Hübner, *omphale* Hübner, *pheridamas* Cramer, *praeneste* Hewitson, *pylene* Hewitson, *neoterpe* Hewitson, *xenagoras* Hewitson, *Archaeoprepona amphimachus* Fabricius, *camilla* Godman & Salvin, *chalciope* Hübner, *demophon* Linnaeus, *demophoon* Hübner, *licomedes* Cramer, *phaedra* Godman & Salvin, *meander* Cramer (Rydon 1971 included *chromus* Guérin-Méneville and *priene* Hewitson in his genus *Noreppa* and treated genera as tribes).

Authors: (1) Fruhstorfer (1915, 1916)*,**; (2) Stichel (1939)**; (3) Orfila (1950)*,**; (4) Rydon (1971)*,**; (5) Descimon et al. (1973–74)*,**; (6) Papworth (1982)**; (7) Johnson and Quinter (1982)*. * Emphasized certain characters, ** grouped taxa based on these characters.

February–April 1928, collector Kruger, sold by Niepelt 31 May 1928, in Biedermann Collection, Zurich, Switzerland (examined by second author); (6) Cisneros, Rio Dagua valley, 1000 m, 28 February 1928, collector Hopp, sold by Staudinger 15 May 1928, in Biedermann Collection (examined by second author); (7) Queremal, Colombia, November 1986, collector Julian Salazar, Manizales Museum (K. S. Brown Jr. pers. comm., sole South American deposition known to him); (8) Upper Rio Putumayo valley, 1981, local collectors, obtained by David Matusik (FMNH), deposited in American Museum of Natural History (AMNH) (Fig. 1D).

No specimens were located at Allyn Museum of Entomology (AME), British Museum (Natural History) (BMNH), Carnegie Museum of Natural History (CMNH), Field Museum of Natural History, Rijkmuseum van Natuurlijke Historie (Leiden, Netherlands) (RMNH), Museum National d'Histoire Naturelle (Paris), National Museum of Natural History (Smithsonian Institution).

Variation. Variation in the Chocó and Cauca samples appears slight (Fig. 1C), but the single Putumayo specimen (Fig. 1D) is distinctive, as follows: hindwing with emphatic medial band, area basad discal band with heavy blotched markings, three large submarginal eyespots (cells RS, M3, CuA1), and forewing with subapical stripe connected to postmedian stripe across vein M3.

Biology. The few acquirers of *P. werneri* provide the only sources of information about the butterfly's biology. Most specimens now in public (6) or private (3) collections derive from the pre-World War II era of highly financed butterfly sampling in the Neotropics. Initially, commercial interest prompted collection of *P. werneri* at several localities on the Pacific slopes of the Colombian Cordillera (mostly Chocó region). These sites proved extremely inhospitable (Hering & Hopp 1925), being rain forest with extraordinarily high precipitation; Gentry (1982) cites Chocó as the rainiest tropical forest in the world. Consequently, commercial interest in the insect waned, and only one specimen has since been recorded from the region (specimen 6 above). Specimens are so few that most private owners, to avoid deluges of buy offers, request anonymity.

Biogeography. Most specimens of *P. werneri* are from the Chocó region, though one (Queremal, Colombia) is near its eastern margin with the Cauca region. Very likely the extremely hydric Chocó region was a "forest refugium" during Pleistocene glaciations

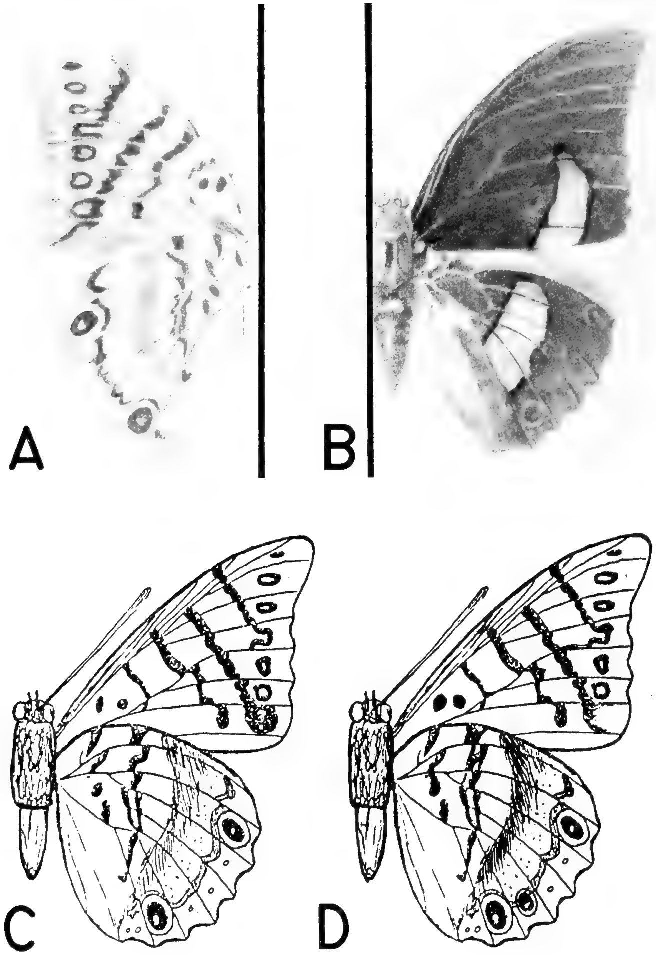

FIG. 1. *Prepona werneri*. A, B, Le Moult's (1932–33) figure of the holotype of *P. werneri*. A, Under surface. B, Upper surface. C, Reproduction of Hering and Hopp's (1925) original figure of holotype (showing distinctive markings characterizing Chocó and Cauca specimens). D, Drawing indicating distinctive markings on divergent specimen from upper Rio Putumayo region.

(Brown 1976, 1982), explaining the occurrence of a number of highly insular and seldom collected butterflies in it and immediately adjacent areas. Brown emphasizes the close geographic proximity of the Chocó and Cauca regions, and includes them in his "Northwestern Region" cluster (Brown 1976). He notes zones of hybridization between their taxa. If represented only by Chocó and Cauca specimens, *P. werneri* might be characterized as a seldom collected, insular cis-Andean species, typifying limited hydric habitat. However, a larger view of its taxonomy and biogeography is necessitated by specimen 8 above from the upper Putumayo region of south-central Colombia. This collection is

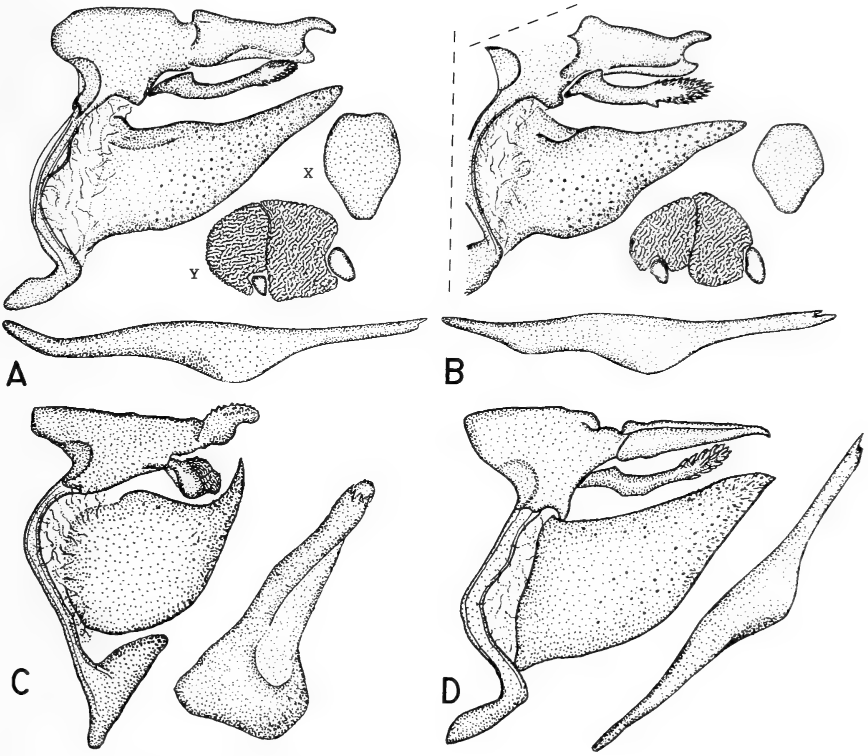

FIG. 2. Male genitalia of *Archaeoprepona* and *Prepona*, and male genitalia and abdominal androconia of *P. werneri*. A, Topotypical *P. werneri*, lateral view of genitalia with aedeagus removed (aedeagus, lateral view, beneath) and (x) ventral view, juxta, (y) lateral view, abdominal androconia at first and second abdominal spiracles. B, *P. werneri* specimen from upper Rio Putumayo region (dashed lines indicating areas of genitalia not available for study because of prior damage to abdomen). C, *Archaeoprepona*, type species *demophon*, Rio de Janeiro, Brazil, same format except for x and y. D, *Prepona* type species *demodice*, Rio de Janeiro, Brazil, same format except for x and y. Females of *Archaeoprepona* and *Prepona* are illustrated in Orfila (1950).

particularly striking, since the Andes are usually considered as a very efficient barrier against faunal exchange. The Putumayo region is located disjunctly southwest of the Chocó and Cauca regions and included in Brown's (1976) "Andean Foothills" cluster. Brown notes very little hybridization between taxa of the Putumayo and Chocó-Cauca regions. Faunal elements of the Putumayo region are mostly trans-Andean. Thus, occurrence of *P. werneri* in the Putumayo region appears biogeographically significant. It seems likely that disjunct distribution in *P. werneri* is relict, reflecting former more widespread occurrence of perhumid biomes. Compared to the rest of the Andes, uplift of its northern elements was relatively recent (Gansser 1973). Consequent separation of *P. werneri* into cis-Andean and trans-Andean nuclei associated with general climatic drying appears more likely than dispersal across the Andes in present or recent times. If further documented, the Putumayo *P. werneri* could be construed as a subspecies.

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A NEW *EUPTYCHIA* SPECIES FROM NORTHWESTERN MEXICO (SATYRIDAE)

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ABSTRACT. A new euptychiine satyr, *Euptychia rubrofasciata*, is described based on 15 males and 4 females from NW Mexico, and compared with other similarly red-suffused species. A possible *Selaginella* foodplant association is discussed, and a mimetic assemblage involving satyrids is suggested.

Additional key words: Euptychiini, *Euptychia rubrofasciata*, mimicry, *Selaginella*.

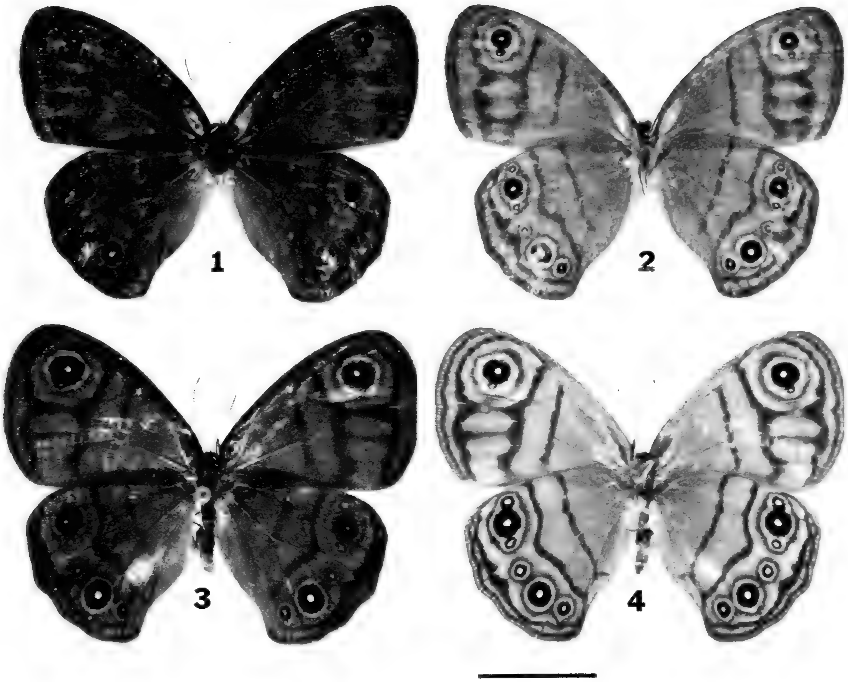
Mexican and northern Central American euptychiine Satyridae are unusual in that several species are strongly laved with red on the upper surface. This condition is shown in such diverse species as *Euptychia fetna* Butler, *Megisto rubricata* (W. H. Edwards), a few species of *Cyllopsis* (L. Miller 1974) and *Paramacera* (L. Miller 1972), *Cissia pellonia* (Godman & Salvin), and *C. cleophes* (Godman & Salvin). These red-patterned elements are rare in Euptychiini, and they are almost unknown in members of the tribe outside Mexico and northern Central America. Recently, Douglas Mullins showed us a series of a red-patterned species from Sonora, Mexico, that is totally unlike any other in this complex of "look alikes". Later, James Brock and Jerry Powell sent additional specimens. This insect is the most ornate of the Mexican red-laved euptychiines, and is undescribed. A name for it is required for Brock and Mullins's forthcoming book on the butterflies of Sonora.

Euptychia rubrofasciata L. & J. Miller, new species
(Figs. 1–9)

Male (Figs. 1, 2). Head clothed with fuscous dorsal setae and somewhat paler hairs ventrad; area immediately behind eye narrowly white. Eyes rich brown, only slightly hirsute. Antennae plain brown above, light brown and narrowly ringed on shaft, dark brown beneath; tip black. Palpi clothed with long fuscous ventral setae and short lateral white hairs. Thorax and abdomen clothed with short fuscous dorsal and gray-brown ventral hairs. Legs clad with short gray-brown hairs.

Upper surface of forewing fuscous, grayer and paler distad of cell, with a darker fuscous submarginal shade and a single smooth, dark fuscous marginal line; wing laved with brick-red in posterior part of cell and just posteriad of cell, and with a darker red fascia from end of cell to middle of Cu_2–2A, a blackish fuscous subapical black ocellus in M_1–M_2, and a smaller one in M_2–M_3, each with a single silver pupil and narrow, dull ocherous ring. Upper surface of hindwing also fuscous, slightly paler subapically, with submarginal darker fuscous shade and a double dark fuscous marginal line. Wing laved with brick-red just outside and posteriad of cell, a red fascia outside cell from apex to near inner angle, blackish fuscous ocelli in Rs–M_1 (large and diffuse), M_1–M_2 (very small, almost a point and occasionally absent), and a well-defined, quite large ocellus in Cu_1–Cu_2, all ocelli consisting of a white pupil and a narrow, dull ocherous iris.

Under surface of forewing light gray-brown slightly shaded with red in and just posteriad of cell, with three brick-red fascia from near costa to inner margin, one across



FIGS. 1–4. *Euptychia rubrofasciata.* **1, 2,** Holotype ♂, upper (1) and under (2) surfaces. **3, 4,** Paratype ♀, upper (3) and under (4) surfaces. Scale line represents 10 mm.

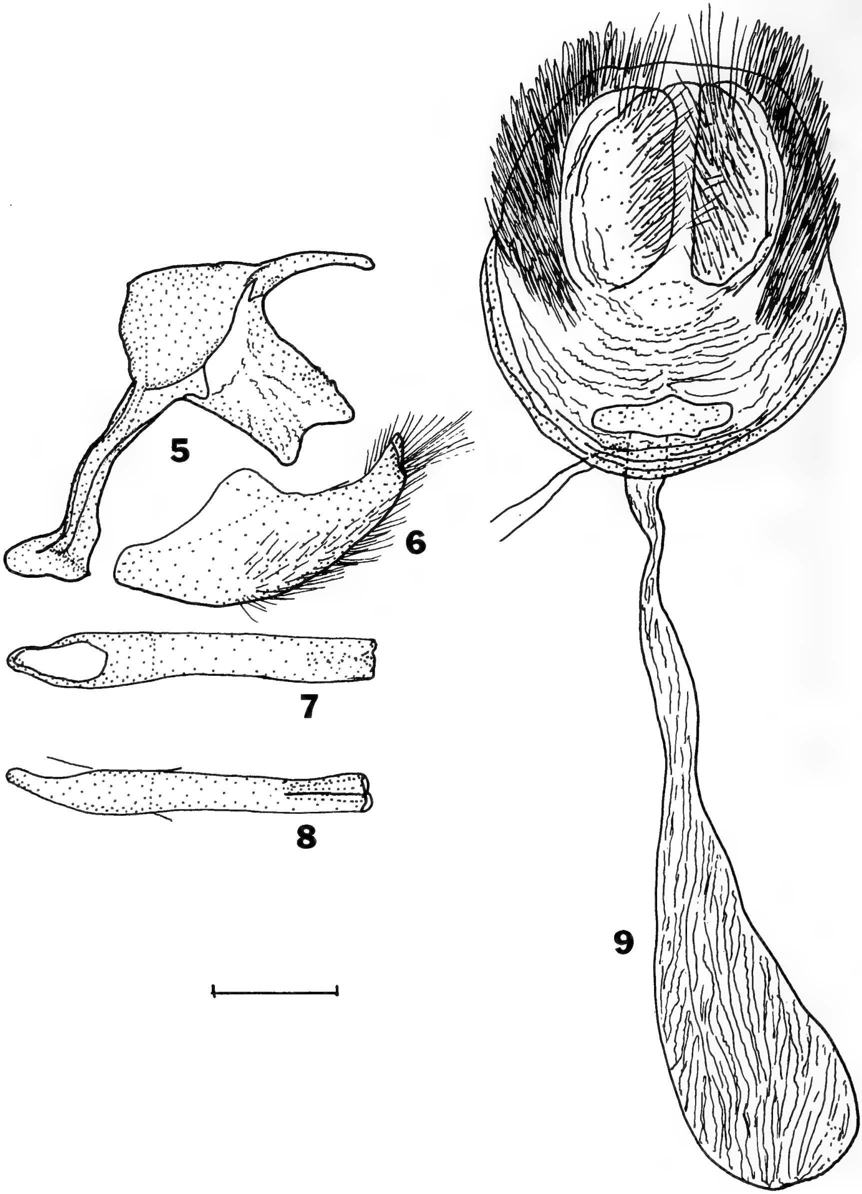
cell, one just outside cell, and one beyond ocelli, the last two connected by brick-red streaks between veins from M_3 to 2A; ocelli as on upper surface, but black with silver pupils and ocherous then fuscous rings surrounding both (not individual rings). Under surface of hindwing likewise gray-brown with three reddish fascia as described for forewing, and dark brown double marginal lines; six black ocelli with silver pupils and ocherous and fuscous rings from $Sc+R_1$ to Cu_2–2A, the ones in Rs–M_1 and Cu_1–Cu_2 large and prominent, the one in Cu_2–2A of moderate size, the others quite small; ocelli in anterior three cells with rings coalesced.

Forewing length of holotype ♂ 17.6 mm, of the 14 ♂ paratypes 17.3 to 19.2 mm, averaging 18.0 mm.

Male genitalia (Figs. 5–8) simple and lightly sclerotized; no superuncus as in most *Euptychia* (comparative illustrations in Forster 1964:81); uncus only slightly curved ventrad; brachia represented by only a very narrow sclerotized ring completely surrounding anus; valvae relatively unadorned, curved dorsad; penis short and straight with no obvious adornment.

Female (Figs. 3, 4). Head, thorax, abdomen, and appendages as in ♂, except thorax and abdomen below somewhat tanner.

Upper surface of forewing somewhat lighter than that of ♂ and more extensively laved with reddish fulvous, rusty fascia across cell and just beyond it, reddish streaks between veins from M_3 to 2A, a fuscous submarginal fascia and double marginal fuscous lines; blackish-brown coalesced ocelli with silver pupils in M_1–M_2 (large and prominent) and M_2–M_3 (very small) with coalesced narrow ocherous and fuscous rings. Hindwing above with similar ground color, red shading slightly more extensive than in ♂, and white-



FIGS. 5–9. Genitalia of *Euptychia rubrofasciata*. 5–8, Holotype ♂. **5,** Uncus, tegumen, saccus, and associated structures, left lateral view. **6,** Right valva, internal view. **7,** Penis, dorsal view. **8,** Left lateral view. **9,** Paratype ♀, ventral view, genit. prep. M-7336-6 (J. Y. Miller). Scale line represents 0.5 mm.

pupilled fuscous ocelli in Rs–M_1 (large), M_3–Cu_1 (very small, not present in all specimens), Cu_1–Cu_2 (large), and Cu_2–2A (small and absent in one specimen), each with ocherous and fuscous rings; red-brown submarginal fascia, two fuscous marginal lines.

Under surface of forewing somewhat less gray than in ♂ with similar markings except ocelli. Under surface of hindwing also less gray than in ♂, but marked similarly with larger ocelli and more prominent ocherous rings.

Forewing length of the 4 ♀ paratypes 17.6 to 20.0 mm, averaging 19.2 mm.

Female genitalia (Fig. 9) very lightly sclerotized with 8th segment heavily clothed in scales; papillae anales densely setose with 6–10 elongated setae posteriad; sterigma simple, lamella postvaginalis membranous with numerous folds, and lamella antevaginalis indicated by a lightly sclerotized plate; ductus bursae and corpus bursae membranous and strongly folded; attachment of ductus seminalis near atrium.

Described from 15 males and 4 females from the Sierra Madre Occidental of Sonora and Chihuahua, Mexico.

Holotype ♂ (Figs. 1, 2). MEXICO: Sonora, 13 mi (21 km) E El Novillo, 12 August [19]85 (J. P. Brock); ♂ genitalia preparation M-7341-v (Lee D. Miller).

Paratypes. All MEXICO: Sonora, 8 ♂, 1 ♀, same data as holotype, 1 ♀ (Figs. 3, 4), Rte. 16, 10 mi (16.1 km) E Trinidad, "Cypress" Canyon, 7 August [19]86 (D. D. M[ullins]); 2 ♂, 2 ♀, San Nicholas-Yecora Rd., 4.1–10.3 mi (5.6–16.5 km) E Santa Rosa, 7.viii.1986 (J. P. Brock) (1 with ♀ genitalia preparation M-7346-v (J. Y. Miller); 3 ♂, creek at 3000 ft (909 m), 6 mi (9.6 km) W Yecora, 31.vii.1984 (J. P. Brock); Chihuahua, S[ierra] Madre Occid[ental], Yepachic Rd., Canyon Rio Tomochic (oak/grass hillside), 31 July [19]84 (D. D. M[ullins]); Sinaloa, 1 ♂, 2 mi (3.2 km) SW Potrerillos, 4200′ (1280 m) viii.7/8.[19]86 (J. Brown & J. Powell).

Disposition of type-series. Holotype ♂, 2 ♂ and 1 ♀ paratypes in Allyn Museum of Entomology; 1 ♂ paratype in collection of California Insect Survey; remaining 11 ♂ and 3 ♀ paratypes to be returned to J. P. Brock and D. D. Mullins for eventual distribution to other collections.

Etymology. The name refers to the unique brick-red fascia on both surfaces of all wings.

Discussion. That this insect proved to be a member of *Euptychia* came as a surprise. It is the largest known *Euptychia*, and superficially more closely resembles *Cissia*. However, the ♂ genitalia are unmistakably *Euptychia*, the abbreviated brachia fused with the tegumen. The ♀ genitalia are simple and very lightly sclerotized, this also in keeping with the apomorphic condition for *Euptychia*.

The only published life history information about *Euptychia sensu lato* is that by Singer et al. (1971) who found the white congener, *E. westwoodi*, feeding as a larva on the lycopsid *Selaginella*. Those authors suggested that *Selaginella* might have "rather potent biochemical defenses," since few herbivores attack them, and that these defenses might convey some protection to *Euptychia*. These toxic chemical defenses have yet to be proven (J. Beckner pers. comm.), but seem reasonable. The Mexican *E. fetna* feeds also on *Selaginella* (J. Llorente and others pers. comm.). *Euptychia westwoodi* appears to be in a mimetic complex involving lycaenids and riodinids (Singer et al. 1971:1342).

We suggest that *E. rubrofasciata* also feeds as a larva on *Selaginella*. This is supported by Brock (pers. comm.), who writes ". . . nearly all the *Euptychia* were found on a shady [canyon] wall loaded with a *Selaginella* species." He further mentioned that he identified the *Selaginella* because it was so abundant and conspicuous at the spot where the new species was most abundant. Mullins (pers. comm.) independently confirms this habitat preference.

Assuming the above foodplant and its toxicity to predators, the present new species and *E. fetna* may be Muellerian mimics, and the other red-laved euptychiines (and perhaps other butterflies) could be Batesian mimics of them.

ACKNOWLEDGMENTS

We thank D. D. Mullins for sending the first specimens of this insect for description, and J. P. Brock and J. A. Powell for additional ones. Thanks are due J. Llorente for discussions concerning *E. fetna* and to J. Beckner for discussions about the properties of *Selaginella*.

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A NEW SPECIES OF *ETHMIA* FROM THE FLORIDA KEYS (OECOPHORIDAE: ETHMIINAE)

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ABSTRACT. *Ethmia powelli* is described from Upper Matecumbe Key based on 123 specimens. It is related to *E. humilis* Powell and *E. julia* Powell, in the *confusella* species-group, by genitalic characters, and is distinguished from *E. farrella* Powell by the small wingspan and fewer forewing black spots.

Additional key words: *Ethmia powelli, E. farrella.*

The genus *Ethmia* was monographed for the known New World fauna by Powell (1973). In Florida seven species are now recorded (Florida Lepidoptera Survey), mostly being Caribbean elements present in southern Florida. The new species was collected after the publication of Powell's (1973) monograph and is described here to make the name available for a revision of Kimball (1965). Description of the species has awaited collection of more specimens, but only recently has one additional individual been collected. Capuse (1981) reviewed the Cuban ethmiines but did not include the species described from Florida. Specimens are deposited with the Florida State Collection of Arthropods (FSCA) and my own collection (JBH), with paratypes distributed to the University of California, Berkeley (UCB), and the National Museum of Natural History, Washington, D.C. (USNM).

Ethmia powelli Heppner, new species
(Figs. 1–4)

Forewing length 4.0–4.7 mm (N = 100) (male); 4.1–4.9 mm (N = 23) (female).

Male (Fig. 1). **Head.** Silvery gray-white with black central mark on vertex; labial palpus silvery gray-white with lateral black mark on each segment and black laterally near base. **Thorax.** Silvery white; legs white, with fore- and mid-tibiae and tarsi marked with black; hind legs white. **Forewing.** Ground color silvery white with numerous black spots (costal spots at base and ⅓ from base; cubital area with elongated spots near base and at hindwing, with a small round spot near dorsal margin; a large elongate spot mid-wing and another along tornus); terminal black spots extending along costa on apical ¼; fringe silvery; venter silvery gray. **Hindwing.** Unicolorous pale gray with dark gray at margin; fringe gray; venter similar. **Abdomen.** Silvery white with darker gray dorsum. **Genitalia** (Fig. 3). Tegumen with slightly bulbous terminal points; vinculum rounded, without saccus; valva subquadrate with prolonged distal end having 3 large spines and 2 smaller truncated central spines, with a large curved hooklike process on dorsal margin near apex; anellus an elongated tube (troughlike), dorsally open; aedeagus similar to that of *E. humilis*, with bulbous phallobase; cornutus indistinct.

Female (Fig. 2). Similar to male; forewing terminal black spots slightly larger on average than in male. **Genitalia** (Fig. 4). Setose ovipositor; posterior apophyses 3× length of anterior apophyses; sterigma composed of fused anterior apophyses extensions; ductus

FIGS. 1, 2. *Ethmia powelli* paratypes, Islamorada, Monroe Co., Florida. **1,** Male, **2,** Female.

bursae with sclerotized collar at ostium, then spiralled to ovate corpus bursae; signum a small sclerotized depression.

Type material. Holotype: male, 1 mi [1.6 km] SW Islamorada, Upper Matecumbe Key, 23-VI-1974, J. B. Heppner (slide JBH 1773) (FSCA). Paratypes: 99 males, 23 females, same data as holotype. Paratypes distributed to FSCA, UCB, USNM, and author's personal collection. Additional specimen: Key Largo, Monroe Co., 30-VIII-1986 (1 male), L. C. Dow (FSCA).

Hosts. Unknown. One species in the *confusella* species-group feeds on *Bourreria ovata* (Boraginaceae).

Remarks. Thus far, *Ethmia powelli* has been collected only twice in the Florida Keys. There are no records of it from any Neotropical locality; thus, the species may be native to Florida. Relations of *E. powelli* by some genital characters appear nearest to *E. humilis*

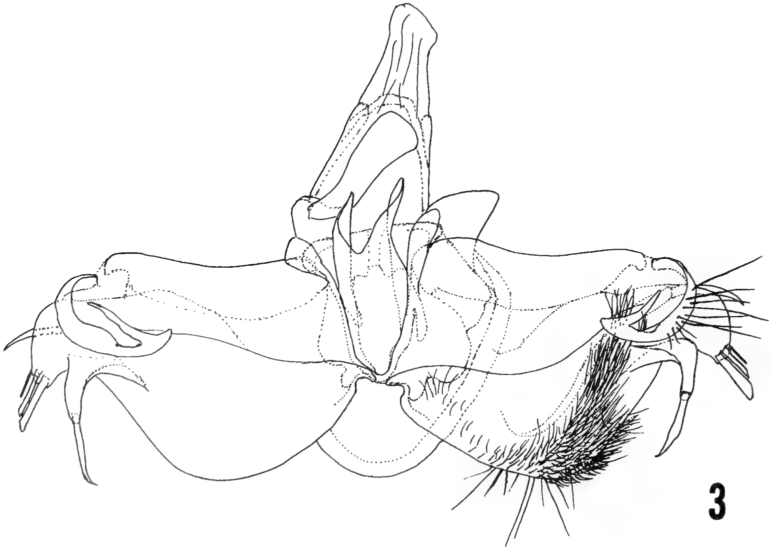

FIG. 3. *Ethmia powelli* male genitalia, aedeagus omitted (JBH 1773).

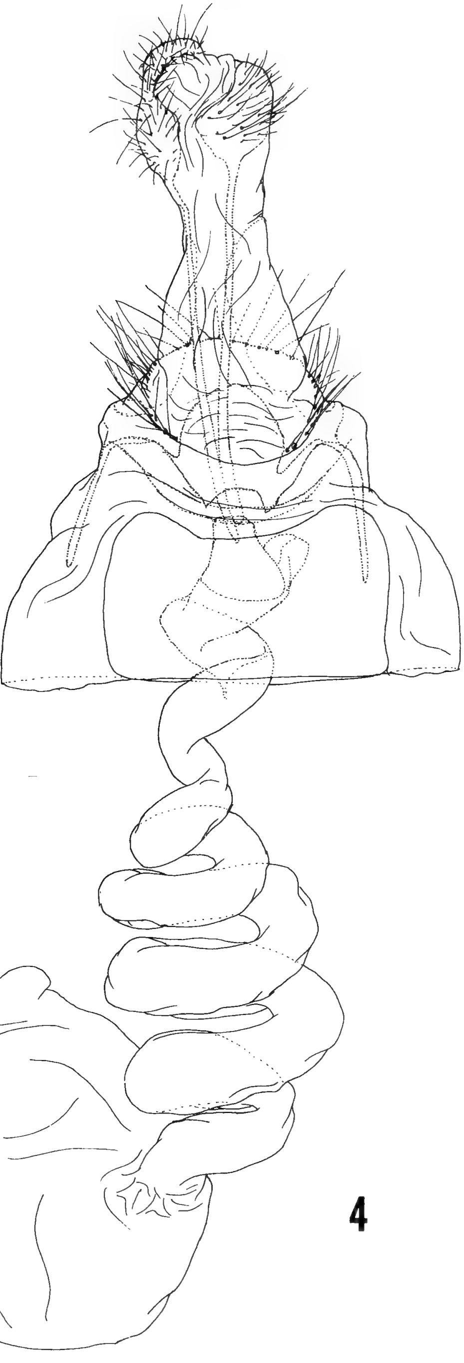

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FIG. 4. *Ethmia powelli* female genitalia (JBH 1774).

Powell and *E. julia* Powell in the *confusella* species-group. This is a primarily tropical group with several species also occurring in S Florida (includes records of West Indian species recently found in the Florida Keys). Forewing maculation, however, is more similar to *E. farrella* Powell. In the key to species in Powell (1973), *E. powelli* keys to couplet 118, differing from *E. farrella* in having fewer black spots on the forewings, and in being significantly smaller, 4.0–4.9 mm versus 6.5–7.0 mm for *E. farrella.* The male genitalia are particularly diagnostic, having 5 spines on the distal end of the valva, and the central 3 of these being truncated; *E. humilis* has only 3 curved spines on the valva, likewise for *E. julia.* Female genitalia are not very similar to the other species; the sterigma is most similar only to the Central and South American *Ethmia catapeltica* Meyrick. The female ductus bursae in *E. humilis* is not coiled as in most *Ethmia* species and the sterigma is very different in *E. farrella.*

Ethmia powelli appears to be one of the smallest species in *Ethmia.* The species is named in honor of Professor J. A. Powell, University of California, Berkeley.

ACKNOWLEDGMENTS

Reviewer comments and study of the L. C. Dow Collection, Largo, Florida, are appreciated. Contribution No. 640, Bureau of Entomology, Florida Department of Agriculture & Consumer Services.

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LARVAE OF NORTH AMERICAN *LEUCONYCTA* (NOCTUIDAE)

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ABSTRACT. Mature larvae of *Leuconycta diphteroides* (Guenée) and *L. lepidula* (Grote), the only known members of *Leuconycta,* are illustrated, described, and diagnosed based on eight specimens of the former reared from ova on *Solidago* sp. and two specimens of the latter reared from ova on *Taraxacum* sp. Although resembling one another in coloration and structure, larvae of the two species can be distinguished by characters in the hypopharyngeal complex.

Additional key words: Acontiinae, *Leuconycta diphteroides, L. lepidula,* hypopharyngeal complex.

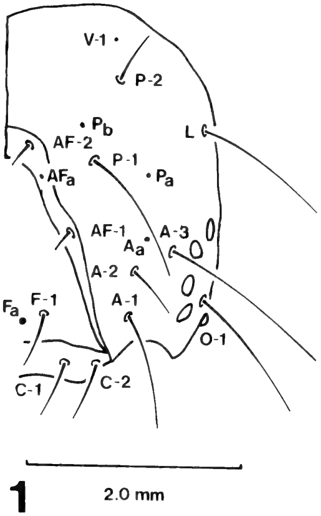
The North American noctuid genus *Leuconycta* Hampson (Acontiinae) contains two species, *L. diphteroides* (Guenée) and *L. lepidula* (Grote). Larval systematic and life history information has been presented by Dyar (1898), Forbes (1954), and Crumb (1956). Crumb was unable to find color or structural differences by which to separate larvae of the species of *Leuconycta.* The purpose of this paper is to more fully describe and diagnose mature larvae, especially with respect to mouthparts and chaetotaxy, which have been shown by Godfrey (1972) to be of taxonomic value.

Leuconycta diphteroides and *L. lepidula* are common and widely distributed in North America, both ranging from Nova Scotia S to North Carolina, and W to Manitoba, Kansas, and Colorado (Forbes 1954). Larvae of *L. diphteroides* have been recorded feeding on *Solidago* sp. (Dyar 1898), and those of *L. lepidula* on *Taraxacum* sp. (Forbes 1954).

Terminology and abbreviations here follow Godfrey (1972). Specific collecting localities and dates are provided in individual descriptions.

Genus *Leuconycta* Hampson
(Figs. 1–14)

Diagnostic description (diagnostic characters in italic). Head 1.6–2.5 mm wide, total body length 25.8–32.2 mm (N = 10). *Head and body smooth. Body broad at middle, tapering slightly anteriorly and posteriorly. Prolegs present on abdominal segments (Ab) 3–6, size increasing posteriorly; those of Ab6 twice size of those on Ab3. Crochets uniordinal. All setae simple.* **Coloration of living material.** Head green, no lines or markings present. Body green, darker at edges of mid-dorsal and subdorsal lines and ventral edge of subdorsal area; ventral area lighter green; mid-dorsal and subdorsal lines white, the latter wider and more irregular; spiracular line greenish white, more whitish on dorsal and ventral edges and bordered dorsally by a narrow red line on thoracic segments (T)1 and 2. Cervical and anal shields concolorous with trunk, the latter with a white medial and two white lateral lines. Pinacula white, the dorsal pinacula larger than lateral and ventral pinacula. Spiracles yellow with black peritremes. True legs greenish, slightly brown distally. Proleg shields concolorous with trunk. **Coloration of preserved material.** Head and body light cream color. Lines and pinacula concolorous with body.



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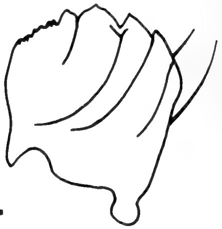

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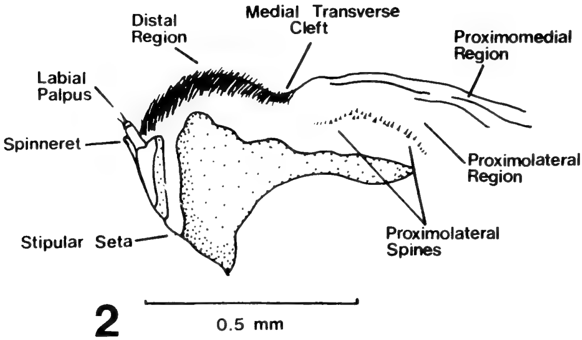

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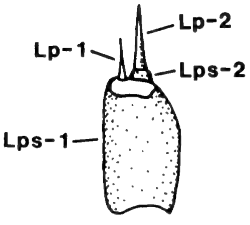

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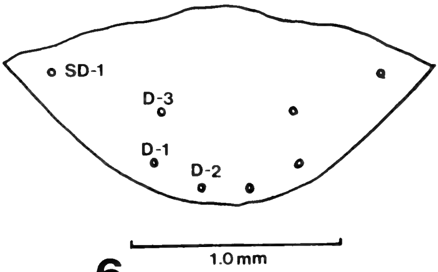

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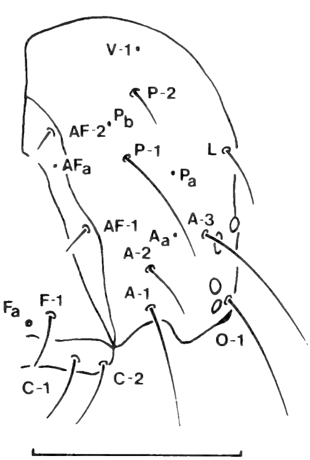
FIGS. 1–6. *Leuconycta diphteroides* larval structures. **1,** Head, frontal view. **2,** Hypopharyngeal complex, left lateral view. **3,** Labial palpus, lateral view. **4,** Left mandible, oral surface. **5,** Left mandible, outer surface. **6,** Anal shield, dorsal view.



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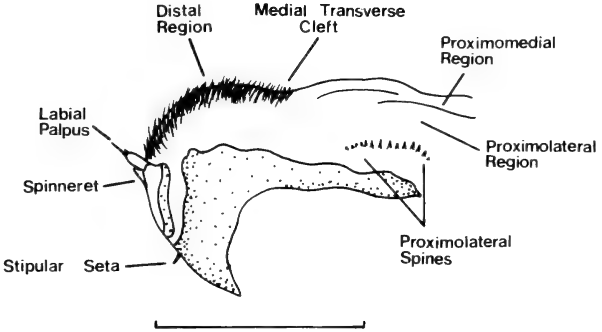

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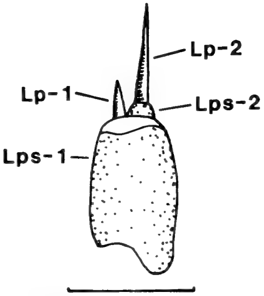

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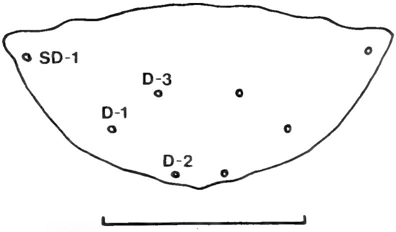

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FIGS. 7–12. *Leuconycta lepidula* larval structures. **7,** Head, frontal view. **8,** Hypopharyngeal complex, left lateral view. **9,** Labial palpus, lateral view. **10,** Left mandible, anal surface. **11,** Left mandible, outer surface. **12,** Anal shield, dorsal view.

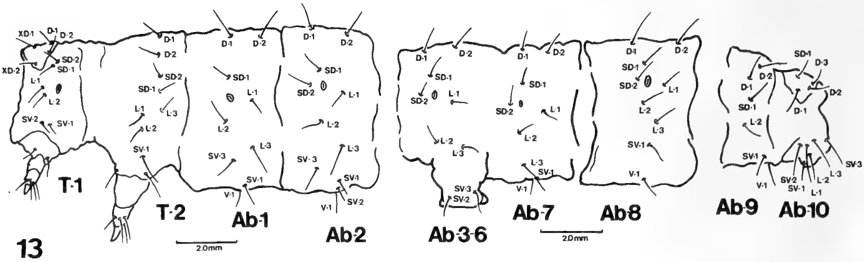

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FIG. 13. *Leuconycta diphteroides*. Dorsal and lateral chaetotaxy of prothoracic (T1), mesothoracic (T2), and abdominal segments (Ab1–3, Ab6–10).

Spiracles white, peritremes dark brown. *Head* (Figs. 1, 7). Cervical indentation shallow; adfrontal sutures terminating at epicranial suture; epicranial suture longer than height of frons; frons slightly higher than its basal width. Adfrontal setae (AF)2 above, and posterior head setae (P)1 below, even with, or slightly above apex of frons; anterior head puncture (Aa) below a straight line between posterior head puncture (Pa) and anterior head setae (A)3. P2, P1, and AF1 in a straight line, Aa closer to A3 than to A2, A1–A3 forming an obtuse angle at A2; lateral head seta (L) even with or slightly below juncture of adfrontal ecdysial lines. Distance between ocelli (Oc)2–Oc3 greater than Oc1–Oc2 and Oc3–Oc4. **Mouthparts.** Hypopharyngeal complex (Figs. 2, 8): *Spinneret short and broad. Stipular setae varying from extremely short to slightly less than ⅓ length of 1st segment of labial palpus (Lps1). Labial palpi* (Figs. 3, 9) *with length of segments variable. Distal and proximal regions of hypopharyngeal complex separated by shallow medial transverse cleft; distal region of hypopharyngeal complex covered with spines which are long, slender, shorter proximally; proximolateral region with spines small, triangular, numbers variable.* **Mandible** (Figs. 4, 5, 10, 11). Two well separated outer setae present; *inner surface with 3 distinct ridges, the last short; outer margin with 12 teeth, the 1st small, 2nd to 4th well developed and angular, 5th to 12th small and angular.*

Thorax. Prothoracic segment (T1) (Figs. 13, 14): Shield smooth and weakly sclerotized, subdorsal body setae (SD)1 and 2 separated from prothoracic shield, setae SD1 and lateral body seta (L)2 fine, hairlike, and with a thickened sclerotized annulus at base; major axis of prothoracic shield passing behind SD1 and SD2, and between subventral body setae (SV)1 and 2; spiracle broadly elliptical, height less than twice its width. **T2–3** (Figs. 13, 14): SD1 fine, hairlike, with a thickened sclerotized annulus at base. Tarsal claws with basal angles acute. Metathoracic coxae contiguous. **Abdomen.** Dorsal and lateral chaetotaxy of Ab2–6 with 3 SV setae; SV1 and SV2 setal insertions well separated. Ab7–8 with 1 SV seta. Ab9: SD1 fine, hairlike, with a thickened annulus at base. Ab10: Anal shield as in Figs. 6 and 12. Dorsal margin convex, posterior margin entire; subanal setae widely separated.

Leuconycta diphteroides (Guenée)
(Figs. 1–6, 13)

Head 2.2–2.5 mm wide, total length 25.8–31.0 mm (N = 8). Larva as described above except: Hypopharyngeal complex (Fig. 2) with spinneret about ½ length of 1st segment of labial palpus (Lps). Labial palpus (Fig. 3) with Lps1 about 3 times length of seta borne by 1st segment of labial palpus (Lp), 13 times length of Lps2, 2 times length of Lp2. Lps2 less than ⅓ length of Lp1. Stipular setae very short, about ⅕ length of Lps1, less than ¼ length of Lp1, subequal to Lps2. Proximolateral spines small, 10–14 small triangular spines.

Material examined. 8 specimens: New Minas, Kings Co., Nova Scotia, reared on *Solidago* sp. from ova obtained from a female collected 19 June 1985. Moth collected,

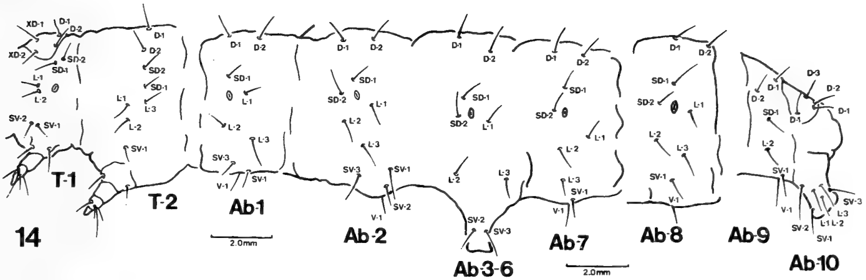

FIG. 14. *Leuconycta lepidula*. Dorsal and lateral chaetotaxy of prothoracic (T1), mesothoracic (T2), and abdominal segments (Ab1–3, Ab6–10).

determined, and larvae reared by author. All specimens in Nova Scotia Museum collection, Halifax, Nova Scotia.

Leuconycta lepidula (Grote)
(Figs. 7, 12, 14)

Head 1.6–1.8 mm wide, total length 31.3–32.2 mm (N = 2). As described for genus except: Hypopharyngeal complex (Fig. 8) with spinneret slightly less than ½ length of Lps1; labial palpus (Fig. 9) with Lps1 slightly less than 5 times length of Lp1, 12 times length of Lps2, less than 2 times length of Lp2. Lps2 about ½ length of Lp1. Stipular seta slightly less than ⅓ length of Lps1, longer than Lp1, and about twice length of Lps2; proximolateral region with 10–14 triangular spines; spines larger than in *L. diphteroides*.

Material examined. 2 specimens: Chicago, Illinois, reared on *Taraxacum* sp., 24 June 1934, A. K. Wyatt. Specimens in U.S. National Museum, Washington, D.C.

Discussion

Larvae of *L. diphteroides* and *L. lepidula* resemble one another closely, but can be separated by the following mouthpart characters: In *L. diphteroides*, the stipular seta is ⅟₁₅ the length of Lps1 compared with *L. lepidula* in which this seta is slightly less than ⅓ length of Lps1, and proximolateral spines are larger in *L. lepidula* than in *L. diphteroides*.

Franclemont and Todd (1983) placed *Leuconycta* in Acontiinae, whereas Forbes (1954) and Crumb (1956) placed it in Amphipyrinae. The latter two authors considered larval characters; those such as the open silk pore on the spinneret, presence of five pairs of abdominal prolegs and two SV setae on Ab1 strongly indicate Amphipyrinae, but resolution of the discrepancy should be based on a wider range of material than examined here.

ACKNOWLEDGMENTS

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42(4), 1988, 291–292

GENERAL NOTES

NEW DISTRIBUTION RECORDS AND A PROBABLE NEW LARVAL HOST PLANT FOR *PHILOTES SONORENSIS* (LYCAENIDAE) IN KERN AND TULARE COUNTIES, CALIFORNIA

Additional key words: Sierra Nevada, *Dudleya calcicola,* Crassulaceae.

Philotes sonorensis (Felder & Felder) is of limited distribution, known only from Sierra Co. in north-central California S to Cedros Island, Baja California Norte, Mexico (John W. Brown pers. comm.). Published distribution records do not include Kern and Tulare counties, California (Langston, R. L. 1963, J. Lepid. Soc. 17:201–223; 1965, J. Lepid. Soc. 19:95-102; 1969, J. Lepid. Soc. 23:49–62; Shields, O. 1973, Bull. Allyn Mus. 15:1–16; Shapiro, A. M. 1974, Pan-Pac. Entomol. 50:442–443). Recently, *P. sonorensis* was discovered at scattered locations in these two counties and in the southern Sierra Nevada. New distribution records (Fig. 1) are as follows:

Kern Co.: Pleito Creek and Canyon (located nr. Mt. Pinos at S end of San Joaquin Valley), 1 ♂, 16 IV 81 (W. D. Patterson). Laura Peak ("Rock Tip" on some maps) in Piute Mts. E of Lake Isabella; adults found by author in canyon on S slope nr. rocky outcrops at 3600–4600 ft (1097–1402 m) elev. on this peak of 5260 ft. (1603 m), 2 ♂, 28 III 87; 3

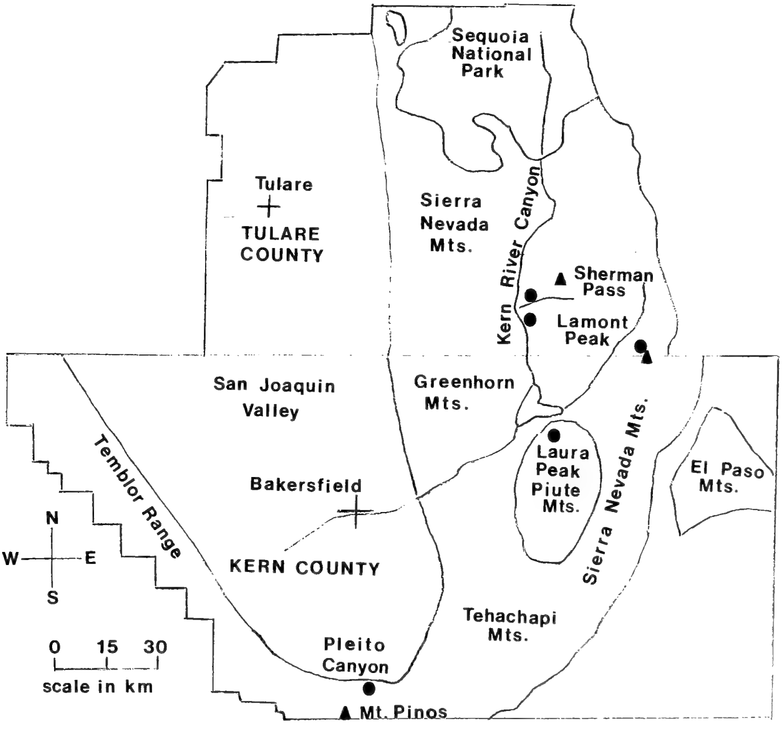

FIG. 1. Map of Kern and Tulare counties, California, showing new localities for *Philotes sonorensis* (black dots). Triangles represent nearby mountain peaks important as reference points. Cross marks represent major cities.

♂, 29 III 87, 2 ♂, 14 IV 87. The latter locality is dry grassland with some junipers on steep rocky slopes. The dry streambed probably carries water for short periods following rainfall.

Tulare Co.: Canyon 1.6 km N of Lamont Peak S of Chimney Peak Road, 3 ♂, 10 IV 85 (K. Davenport). Canyon N of Sherman Pass Road 5.6 km E of Kern Canyon Road, 5 ♂, 2 IV 87 (Davenport); 1 ♂, 5 IV 87 (R. Meyer); 2 ♂, 1 ♀, 14 IV 87 (Davenport & K. Richers). Kern River Canyon 1 km N of Roads End at dam, in side canyon E of road, 4 ♂, 1 ♀, 2 IV 87 (Davenport); 1 ♂, 1 ♀, 5 IV 87 (Meyer); 2 ♂, 14 IV 87 (Davenport & Richers), 8 ♂, 1 ♀, 9 III 88 (Davenport).

The Tulare Co. colonies are in rocky canyons of limestone or granitic composition with small streams between 3000 and 5000 ft (914–1524 m) elev., in chaparral and foothill woodland.

The host plant of *P. sonorensis* in the southern Sierra Nevada (including Laura Peak in the Piute subrange) is likely *Dudleya calcicola* Bartel & Shevock (Crassulaceae), which occurs locally "on pre-Cretaceous limestones within chaparral or pinyon-juniper woodland at 850–1700 m" (Bartel, J. A. & J. R. Shevock 1983, Madroño, 30:210–216), and is limited in distribution to Kern, Tulare, and extreme SW Inyo counties (J. A. Bartel pers. comm.). Adults are closely associated with *calcicola* (no other *Dudleya* spp. present) at the new localities. All known hosts are in the genus *Dudleya* (Shields, O. 1973, Bull. Allyn Mus. 15:9–11). Collections and identifications of *Dudleya* at the new localities were made by J. F. Emmel, J. A. Bartel, and J. R. Shevock. No larvae were collected or reared, and oviposition was not observed. The discovery of *Philotes sonorensis* on Laura Peak was made using herbarium records of *Dudleya calcicola* provided by Emmel.

Eight voucher specimens of *Philotes sonorensis* representing each of the four new Sierran localities have been deposited in the Natural History Museum of Los Angeles County, Los Angeles, California. Remaining specimens are in private collections.

I thank J. A. Bartel, J. W. Brown, J. F. Emmel, R. Meyer, K. Richers, J. R. Shevock, O. Shields, and W. D. Patterson for records and assistance.

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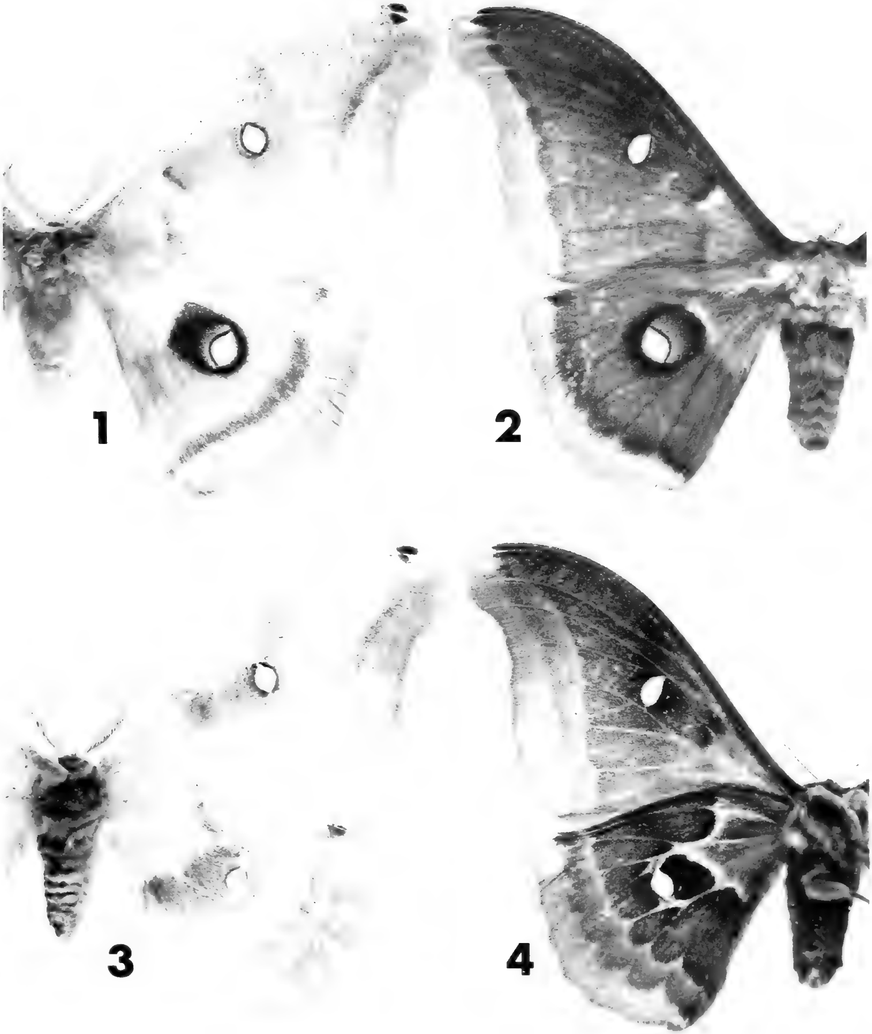
A MELANIC MALE OF *ANTHERAEA POLYPHEMUS POLYPHEMUS* (SATURNIIDAE)

Additional key words: Canada, New Brunswick, light trap.

W. B. Preston and W. B. McKillop (1979, J. Lepid. Soc. 33:147–148) summarized the known information about melanic *Antheraea polyphemus polyphemus* (Cramer), and published the first illustration of a melanic specimen. Our specimen appears to be the fourth ever collected.

On the night of 30 June–1 July 1986, we collected a melanic male of *A. p. polyphemus* on a white sheet illuminated by a 250-W M-V bulb, at the edge of a sphagnum bog in the Acadia Forest Experiment Station, 20 km E of Fredericton, New Brunswick. Dorsally, this male (Fig. 2) differs from typical *A. p. polyphemus* (Fig. 1) by having a dark chocolate ground color. Prothorax and costal edge of upper forewings are black so that the apical and subapical forewing spots are not discernible as distinct spots. However, the grayish lilac dash from the subapical spot toward the forewing apex is still present. In typical specimens, prothorax and costal edge are whitish gray. The blackish component of the submarginal band on fore- and hindwings is exaggerated, obliterating the pinkish shading beyond it on the hindwings but leaving it just discernible on the lower half of the forewings.



FIGS. 1–4. Males of *Antheraea polyphemus polyphemus* (Cramer) from New Brunswick. **1**, Typical dorsum. **2**, Melanic dorsum. **3**, Typical venter. **4**, Melanic venter.

The discal spots on both fore- and hindwings are typical, with the transparent center surrounded by an ocher-yellow ring, edged outwardly with a black ring. The whitish-blue semicircle that outwardly edges the black ring on the proximal side is still discernible on the forewing and very extensive on the hindwing. The black component of the hindwing submarginal band is conspicuously recurved along the outer margin of the wing. The outer margin of both wings beyond the submarginal band is of the usual bright ocherous tawny brown, giving the specimen a distinctive bicolored appearance.

On the underside, the wings are uniformly dark chocolate (Fig. 4), and the markings contrast less than those of a typical specimen (Fig. 3). Costal regions of both fore- and hindwings are dark, as is the basal area of both wings.

The specimen is in the senior author's private collection.

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BOOK REVIEWS

THE MONARCH BUTTERFLY: INTERNATIONAL TRAVELER, by Fred A. Urquhart. 1987. xxii + 232 pp., 24 pp. color photographs. Nelson-Hall, Chicago. Hard cover. $31.95.

To his everlasting credit Fred A. Urquhart showed that the monarch butterfly migrates from Canada to overwintering sites in Mexico. In his most recent book Urquhart gives an enlightening account of his pioneering investigations of North America's most famous butterfly, including its morphology, development, behavior and ecology.

Urquhart documents the migration of the monarch butterfly in historical and personal terms. He writes in the first person and selects information intended for a popular audience. The result is informative and exciting. He describes how he developed the tagging technique for following monarchs. He reveals the clues that ultimately led to the discovery of the Mexican overwintering sites. His conversational, informal style allows him to include anecdotal digressions that enrich the factual account.

Often when writing about the biology of the butterfly, Urquhart poses a simple question and then describes an experiment which he conducted looking for answers. What determines which trees monarch butterflies choose for roosting? Do pheromones help monarch butterflies aggregate? How does a monarch caterpillar which has fallen off a milkweed plant find its way back to that plant or another? The question-and-experiment format generates a certain suspense and captures the reader's attention. The experiments are intriguing even when inconclusive.

Few entomological authors dare to write about the emotions which their love of insects arouses. Scientific papers require a tone of objectivity, and expressions of pleasure come as a surprise. In this book Urquhart overcomes the inhibitions which desiccate more scholarly treatises. Urquhart understands that his audience wants to know why a person would go to the extremes he did in pursuit of a common butterfly (p. 153):

> Those who have had a dream and have lived to see that dream come true will have some conception of my feelings when I first entered the Mexican forest and there, before my eyes, was the realization of a dream that had haunted me since I was a lad of sixteen.

On the negative side, Urquhart's personal approach overemphasizes his own work at the expense of others. For example, in the opening chapter about the monarch butterfly's foodplant, he ignores the ecological chemistry of milkweeds. Later he alludes to the transfer of milkweed toxins to monarch butterflies, but only to dismiss its importance.

Urquhart's failure to recognize the work of others leads him to farfetched speculation. His attempt to explain control of sexual maturation of migrants is an example (p. 121):

> As our small planet earth travels in its elliptical orbit around the sun, it is possible that twice each year it passes through an area rich in some sort of radiation that impinges upon animal life. The radiation cycle might affect in some manner the cells of the body, causing reproductive organs to abort in the fall and develop in the spring and to initiate the migratory response. Perhaps our astronomy researchers may add a missing part to the migration puzzle. Perhaps animal life on our earth is being controlled by what is happening in outer space more than we now consider feasible. . . .

Urquhart could have avoided this fantasy if he had discussed hormonal control of monarch butterfly development, and photoperiodic regulation of the timing of this development (reviewed in Rankin, M. A., M. L. McAnelly & J. E. Bodenhamer 1986, The oogenesis-flight syndrome revisited, pp. 27–28 *in* Danthanarayana, W. (ed.), Insect flight: Dispersal and migration, Springer-Verlag, Berlin, 289 pp.).

Urquhart makes generalizations that violate basic biological principles. He writes (p. 194): "The characteristics of size, shape and color that we now see in different species of butterflies were indelibly fixed in the hereditary gene complex millions of years ago and have persisted to the present time." It is doubtful whether any trait can be "indelibly fixed," since genes are neither indelible nor fixed. Urquhart implies that evolution of butterfly coloration eons ago stopped. The fossil record does not answer the question, but industrial melanism demonstrates that, at least for some Lepidoptera, such evolution continues. When Urquhart does address the literature, he becomes polemical (p. 190):

> The scientific literature abounds with attempts to justify the mimicry theory as it applies to birds feeding on butterflies. These papers contain an impressive array of tables, charts and graphs resulting from experiments carried out in the crowded confines of cages in a laboratory. By the use of abstruse terminology the research assumes an aura of highly qualified investigations, but, when carefully analyzed, contains nothing of real value and no meaningful conclusions.

Much of the information Urquhart presents may be found in his earlier book (Urquhart, F. A. 1960, The monarch butterfly, Univ. Toronto Press, Canada, 361 pp.). That work contains an extensive bibliography, which the current book lacks. More recent findings are described in Urquhart's other publications, which he lists in his current book.

Fred A. Urquhart made perhaps the most spectacular discovery in the field of lepidopterology this century. This book will interest anyone who wonders what he has to say about monarch butterflies and his studies of them. However, to find out what others have to report about this species, readers will have to consult sources other than Urquhart's book.

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THE GEOMETROID MOTHS OF NORTH EUROPE (LEPIDOPTERA: DREPANIDAE AND GEOMETRIDAE), by Peder Skou. Translated from Danish edition by Elisabeth Folino. Entomonograph Vol. 6. 1986. 348 pp., 24 color pls., 358 figs. E. J. Brill/Scandinavian Science Press, Leiden & Copenhagen. 17 × 25 cm, hard cover. $100.00.

This book covers all moths of the families Drepanidae, Thyatiridae, and Geometridae known from Norway, Denmark, Sweden, and Finland. After a brief section introducing categories of information to follow, the author moves directly to species treatments. These consist of scientific name, author and year citation, plate and figure references, description, range, habitat, flight period, and biology. Descriptions are usually brief, with emphasis on variation. The color plates are among the best I have seen in sharpness and color value, comparing favorably with those in Skinner's 1984 *Moths of the British Isles.* Color plates include both sexes and sometimes additional varieties; they accomplish well the identification of most species. Genitalia drawings for some species are included, especially in difficult genera such as *Eupithecia.* Similar species are discussed when separation is difficult, and the author has added text figures showing useful body parts such as wing patterns, heads, and abdomens, with arrows pinpointing diagnostic features.

The worldwide range for each species is given, followed by detailed locality information for the four countries featured. The habitat section gives variably detailed characteristics of known sites, with black-and-white photos of typical habitats for many species. Flight periods are general ("From late April until mid-May."), and the biology section features larval foodplants, time of year in larval stage, place of pupation, and other information. Larvae and pupae are not described, but the book is generously illustrated with large black-and-white photos of the caterpillars, usually on their foodplants. A final line tells how the adult is best collected (at light, usually).

Following the species treatments are a selected bibliography and a table of distribution for all species in the four northern countries.

The arrangement of taxa anticipates a new catalogue of European moths in preparation by K. Schnack. Thus Thyatiridae are treated as a subfamily of Drepanidae. The subfamilies of Geometridae are named as we now recognize them in the North American fauna, but they are arranged in the same order as in the McDunnough 1938 *Check List*: Archiearinae, Oenochrominae, Geometrinae, Sterrhinae, Larentiinae, and Ennominae. The Hodges et al. 1983 *Check List* is the same except that Ennominae are moved to a position between Oenochrominae and Geometrinae.

This book builds on several previous works, and appears to be an excellent identification guide for species. Taxa above species are not described or defined, and there are no keys. Recent expansions of European species to North America were missed (the establishment of *Hemithea aestivaria* (Hübner) in Canada was published in 1979); so range information outside Scandinavia and Finland is questionably thorough.

The English composition is awkward in only a few places—forgivable, considering the nationalities of the book's producers. Some typographical errors were found; and a number of words were broken in mid-syllable—irritating to a former English teacher! The print on coated paper is generally sharp, but there are numerous poorly impressed or broken characters which marr an otherwise lavishly produced book.

The expense of this book will unfortunately preclude its addition to the bookshelves of many amateur lepidopterists in North America and other parts of the lepidopterological world outside Europe. This is sad because it is a first-rate work, and is just one of many fine works on European moths that have recently come out. Those who specialize in Geometroidea should certainly find it a valuable investment.

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42(4), 1988, 297

NOCTUELLES ET GÉOMÈTRES D'EUROPE. DEUXIÈME PARTIE. GÉOMÈTRES. Volume IV—1919–1920. Jules Culot. Reprint edition, 1987. Apollo Books, Svendborg, Denmark. Order from: Apollo Books, Lundbyvej 36, DK-5700 Svendborg, Denmark. Vols. III–IV, DKK 1380.00; Vols. I–IV, DKK 2550.00.

This is the fourth and last volume of the set, with 167 pp. and color plates 38–70 (Figs. 772–1403). It covers part of Larentiinae (beginning with *Eupithecia*) and Ennominae, although neither of these subfamily terms are used, much less defined. Having worked with *Eupithecia* of North America and Chile, I found the 45 pages and 140 figures devoted to this group particularly frustrating, as there are no descriptions or figures of genitalia; to me, a study of these structures is almost a necessity to correctly name many of the species. The same can be said about the species grouped together in *Boarmia*; in this case a number of different generic names are in use today.

Having reviewed Vol. III (J. Lepid. Soc. 41:239), I need not repeat comments made there, except to add that the text is in French in the entire set. This volume can be useful to determine some of the more obvious and distinct species, but the scientific names date from 1901. Much more up-to-date works are available and, to me, they could very well prove more useful than the volumes of this set.

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——— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10:165–216.

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Cover illustration: Male of the primitive ithomiine *Tellervo zoilus zoilus* (Fabricius) feeding from *Stachytarpheta cayennensis* (Rich.) Vahl (Verbenaceae). Illustration based on observation of three of the butterflies persistently attracted to this plant which was growing on a pebbled stream-bank in a clearing of dense rainforest at Mission Beach, northern Australia. Feeding was confined to leaf surfaces and stems. Submitted by Andrew Atkins, 45 Caldwell Ave., Dudley, N. S. W. 2290 Australia.

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SUNDRY ARGYNNINE CONCEPTS REVISITED (NYMPHALIDAE)

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ABSTRACT. Suggestions for revisions in the Argynninae section of the 1981 Miller and Brown checklist are presented, the taxa principally discussed being *Semnopsyche, Boloria, Proclossiana,* and the *Speyeria* species *nokomis, zerene, adiaste, callippe, hydaspe, atlantis,* and *mormonia*. For the genera, hitherto undescribed characters are noted as reasons for retaining *Boloria* while synonymizing *Proclossiana* and *Semnopsyche.* Within the *Speyeria* species, several type locality changes are recommended and new synonymies proposed. While most *Speyeria* "subspecies" intergrade extensively, the category has appealed to many as a useful one, providing convenient tags for geographically localized color forms. Despite lack of definitives, suggesting need for further studies, no immediate drastic curtailing of subspecific listings is recommended.

Additional key words: *Speyeria, Semnopsyche, Boloria, Proclossiana,* North America.

Comments, corrections, and suggested emendations to the Argynninae section in the Miller and Brown (1981) checklist are detailed under the following headings. References for taxa mentioned herein are available in that checklist if not found in the literature citations appended.

Speyeria versus *Semnopsyche*

Miller and Brown (1981) correctly place *Semnopsyche* as a synonym of *Speyeria* although giving no reason for doing so. I recently made dissections that settle this matter unambiguously. To my embarrassment I find that the species *idalia* (Drury) has a "secondary" bursal sac in female genitalia. This was the character used by dos Passos and Grey (1945) in delimiting *Semnopsyche.* But since *idalia* is the generotype of *Speyeria, Semnopsyche* perforce becomes a junior synonym thereof. Perhaps, then, some future splitter will want to categorize separately those speyerians which have a simple, long ovate bursa, as described by dos Passos and Grey (1945), a refinement which would seem undesirable since that type of bursa is usual in argynnines worldwide. Thus, it is an exception worth noting that a bursa almost exactly like that of *idalia* may be seen in the Eurasiatic *Mesoacidalia charlotta* (Haworth) (described by Haworth 1803). The latter's bursa is longer and pointing more dorsad than usual in argynnines, terminating in a definite constriction, followed by enlargement to a small round sac. Comparison of the *Speyeria* generotype with *charlotta* should be of incidental interest since it adds hitherto unpublished evidence supporting the idea that Nearctic argynnines placed in *Speyeria* are closest in phylogeny to *Mesoacidalia*, as various students have speculated when judging by wing facies and as Warren (1944) deduced from features of male genitalia.

Boloria and *Proclossiana*

Studies of bolorian genitalia have lead me to conclude (reluctantly) that generic restriction of *Boloria* Moore to *pales* (Denis & Schiffermüller) and the other species placed in that genus by Warren (1944) probably should stand. This, however, is only because Miller and Brown do not use subgenera. It is fairly certain that many, given the opportunity to study the surprisingly little-varied genitalia of females, plus the invariably bifid uncus of males, would want to place all of the world bolorians in a single category. Nevertheless, in the *pales* group as defined by Warren (1944), the generic diagnosis fails to mention a heavily spiculate uncus, and this, so far as I have seen, is a unique feature in the bolorians, an extreme divergence of probable phylogenetic significance further supporting Warren's categorical treatment.

There is less chance for divided opinions when reviewing *Proclossiana* Reuss. The variety of characters in male genitalia of bolorians may be seen in dos Passos and Grey (1945:figs. 1–21). It would seem to be in violation of consistency and parsimony to accord the single species *eunomia* (Esper) a separate category when the male genitalia appear no more distinctive than in the group now lumped in *Clossiana*. Genitalia of *eunomia*, accredited to the then-prevailing taxon *aphirape* Hübner, are illustrated by dos Passos and Grey (1945:fig. 10). Additionally, when reviewing female genitalia of world bolorians (unpubl. studies), I found only slight distinctions in *eunomia*, nothing to suggest any degree of phylogenetic divergence above the species level. Therefore, I recommend placing *Proclossiana* in synonymy under *Clossiana*.

Neotype and Type Locality of *Speyeria nokomis nokomis* (W. H. Edwards)

A neotype for *S. n. nokomis* was fixed by dos Passos and Grey (1947). It was a specimen purportedly collected by Oslar in the Mt. Sneffels area of Ouray Co., Colorado. That action was criticized both in Miller and Brown (1981) and in Brown's (1965) monumental work on W. H. Edwards types. The historical improbability of Mt. Sneffels as the exact type locality of *nokomis* may be granted, but one source of doubt has been removed: the butterfly does occur there, as has been verified by Richard L. Klopshinske, of Olathe, Colorado. Vouchers, five pairs taken at Mt. Sneffels *leg.* Klopshinske, are in the American Museum of Natural History. I think our neotype designation meets even the rigid Code requirements of today, since the very muddled history of this taxon, as related by Brown (1965), has to be taken into account. The true type locality promises to remain forever obscure, and, therefore, objections could be raised against any other fixation whatsoever. As it stands, the name is tied satisfactorily to all essential requirements of the original description, namely, the neotype is from the "Rocky Mountains" and it has a "cinnamon brown" disk. I therefore reaffirm the earlier (1947) designation of neotype and type locality as having been an acceptable solution to an admittedly murky problem.

Revisions Required in *Speyeria zerene* (Boisduval)

The "Yosemite" type locality chosen for *S. z. zerene* by dos Passos and Grey (1947) is invalid in view of Lorquin's itinerary as traced by Masters (1979). Masters designated a type locality to conform thereto, namely, Agua Fria, which is just west of Mariposa and about 56 km from Yosemite. Evidently Masters concluded that the regional variation was such that taxonomic concepts would remain unchanged.

The taxon *gunderi* (Comstock) is incorrectly placed as a subspecies under *S. coronis* (Behr). Field evidence was discussed by Grey (1975) to this effect: Intensive collecting in the Warner Mountains of California reveals a massive regional phenotypic fluctuation in the species *zerene* because of a collision between a yellow and a red subspecies in a "Basin-Sierran" tension zone. Some resulting individuals have yellow disks, others have pallid greenish disks, yielding very close matches with the type material of *gunderi*, which was beautifully depicted by Comstock (1927:plate 27). In contrast, the species *coronis*, although here strictly sympatric, is relatively little-varied and never appears to verge toward the facies of *gunderi*. This appears to be sufficient proof for the combination *S. zerene gunderi*.

Removal of *gunderi* from *coronis* to *zerene* necessitates putting *cynna* dos Passos & Grey as a junior synonym of *gunderi*. Both taxa apply to the same concept, that is, to a pallid yellow-disk subspeciation of *zerene*.

Speyeria z. pfoutsi (Gunder) is a junior synonym of *S. z. platina* (Skinner), and should be so listed. The reasons why Gunder became confused in this instance are detailed by Grey (1969).

Specific Recognition for *Speyeria adiaste* (W. H. Edwards)

Contemporary students, including the Emmels (1973) and Howe (1975), recognize *adiaste* as a distinct species. This change should be made in the Miller and Brown checklist. Evidence for the subspecific association was circumstantial, and is now outweighed by other considerations, particularly the electrophoretic study by Brittnacher et al. (1978). Students will have to continue to marvel at the narrow distribution of the *adiaste* subspeciation in southern California, which is a huge anomaly in Nearctic argynnine speciations, and something of a world wonder in Argynninae.

Subspeciation of *Speyeria callippe* (Boisduval) in the Sierra Nevada

Reexamination of the lectotype of *S. c. juba* (Boisduval), and comparison with the holotype of *S. c. sierra* dos Passos & Grey suggests treating *sierra* as a junior synonym of *juba*. Variation of *callippe* in the California mountains near Lake Tahoe has bewildered many collectors; the name *sierra* was advanced to be descriptive of the yellowish and greenish-disk variants, associating them with the proper species, *callippe*. The lectotype of *juba* appears to be within bounds assignable to the diversity in the region from whence *sierra* derived. With the apparent need to cut back on subspecific nomenclature, as discussed later on, this would be a good place to start. Variation usually assigned to *S. c. inornata*, centering more southerly in the Sierra, now appears to me to be very distinct from *juba*. Perhaps *inornata* (W. H. Edwards) should be resurrected from synonymy. Despite recent work by Arnold (1983, 1985), the whole Sierran *callippe* subspeciation badly needs further study. Earliness of its flight season can be allowed for, and it appears that colonies are far more numerous than might appear from available records.

Type Locality of *Speyeria hydaspe rhodope* (W. H. Edwards)

Brown (1965) asserted that the type locality of *rhodope* should be restricted to the "Fraser River Lowlands", rejecting the dos Passos and Grey (1947) restriction to the Cariboo District of British Columbia. Three of the four recognized syntypes bear "Cariboo" labels. But Brown found a letter to Edwards from Crotch, the original collector, stating that ". . . the small Argynnis with purple beneath . . ." was taken in an area that Brown interprets to have been in a westerly direction from 100-Mile House, whereas the Cariboo District lies easterly from there.

Based on my visits in 1973 and 1975 to the approximate region suggested by Brown, the habitat appears unsuitable to support any *hydaspe* subspecies. Remaining undisturbed areas are mostly in dry lodgepole pine forest. Going easterly, however, the foothill spruce-fir forests of the Cariboo District present suitable habitat, and specimens of *rhodope* were collected. To my knowledge there are no records of this insect from the Frazer River lowlands, and very few from the Cariboo area, suggesting that it is quite locally restricted.

Discrepancies between Brown's conclusions and my findings could be eliminated by postulating that the reference in Crotch's letter was not to *rhodope* but to *Clossiana titania* (Esper). In the terminology of that day this bolorian would have been called a "small Argynnis" and it also displays "purple beneath". The habitat preferences of *titania* vs. *rhodope* would support that alternative, *titania* being locally abundant in the region where Brown would place *rhodope*. A return to the "Cariboo" type locality for *rhodope* would make syntype labeling consistent with field evidence.

Type Locality and Status of *Speyeria mormonia mormonia* (Boisduval)

The lectotype of *mormonia* is from the Boisduval Collection *leg.* Lorquin, and bears a "Lac Sal" notation on a label. This, conjoined with the name, plus the impression from facies that the specimen might have derived from Utah, led dos Passos and Grey (1947) to designate Salt Lake City as type locality.

A key bit of data, then unpublicized but now well known, is that Lorquin did cross the Sierra from somewhere in northern California, and probably collected as far east as extreme western Nevada.

My recent reinspection of the *mormonia* lectotype suggests that this specimen originated in or closely adjacent to the Sierra Nevada of California. That conclusion would be hard to prove because, as is so often the case in *Speyeria*, it comes down to subtle nuances in color and pattern. But aside from the *ipse dixit*, others whose opinions I value, such as John Emmel and Paul Hammond, apparently have concurred that the specimen obviously is "sierran".

Placement of the original *mormonia* in Utah resulted in *S. m. arge* Strecker being applied to the California subspeciation. To accord with the revised status of *S. m. mormonia*, *arge* becomes a junior synonym thereof.

Miller and Brown (1981) recognized both *m. arge* and *m. mormonia* as valid subspecies, and for the latter, proposed a type locality restriction to Pyramid Lake, Nevada. Some historical justification was adduced for that action, and undoubtedly it is close to the mark in a geographical sense. Since I have never seen *mormonia* material from Pyramid Lake, I would be curious, as others might be, to learn what is available and where it is deposited, and especially how well it matches the lectotype.

Status of *Speyeria mormonia opis* (W. H. Edwards)

This taxon is known from three syntypes, two described by Brown (1965:322), and another in the Smithsonian which, like the first two, appears derived from "Bald Mt." *leg.* Crotch. These specimens support the concept of *opis* as a subspecies of *mormonia,* and all three are similarly characterized by small size and dorsal melanic pattern, being ventrally sordid yellowish and unsilvered.

The Bald Mountain upland is in the Cariboo District of British Columbia, south of Barkerville (in the same area where I think *rhodope* probably originated). In 1981, Edward Peters collected the first contemporary series of topotypical *opis,* 40 specimens, which he kindly allowed me to examine and select 23 examples for deposit in the American Museum of Natural History. Variation in this sample is far greater than in the above-noted syntypes, proving that in the Bald Mountain population there are individuals which, compared to the syntypes, are larger, smaller, lighter, darker, are silvered and unsilvered in about equal proportions, and thus encompass the whole range of *mormonia* variation in British Columbia.

This extensive variation at the type locality necessitates broadening the concept of *opis,* and one result must be to synonymize *jesmondensis,* described by McDunnough (1940), and considered in Miller and Brown (1981) as validated by and attributable to dos Passos and Grey (1947). The population represented by *jesmondensis* overlaps *opis* extensively in variation, and also yields brown-disk forms reminiscent of the Oregon subspecies *m. erinna* (W. H. Edwards). In addition, occasional specimens are like *m. washingtonia* (Barnes & McDunnough), less melanic and light yellowish to pale greenish discally, this being a form dominant in the Okanagan region of British Columbia as well as in Washington.

It was a welcome surprise to find that the legendary *opis* is similar to *jesmondensis* in being a hodgepodge of color forms, thus further justifying suspicions that expanding nomenclature is not likely to promote better understanding of northwestern *mormonia,* which, in itself, is a sharply discrete entity.

Type Locality of *Speyeria mormonia bischoffii* (W. H. Edwards)

The involved history of the taxon *bischoffii* was exhaustively summarized by Brown (1965:316–321), who recommended that Sitka, Alaska, be regarded as type locality. Nothing in the original description supports that conclusion, and a dissenting criticism by dos Passos and Grey (1965) has been reinforced by subsequent events. A colony of *mormonia* has been discovered at Anchorage, far north of records extant in 1965, at a logical spot for a mainland landfall by a sailing vessel operating in the vicinity of Kodiak Island, that is, substantially where dos Passos and Grey had conjectured. Even more persuasive, the Anchorage melanics match the Edwards Kodiak neotype better than any other Alaskan material I have seen. I therefore propose that the Sitka type locality restriction be withdrawn in favor of Anchorage. This will bring the original description, the neotype, and extant material into better agreement. Vouchers, taken in the "Ski Bowl" near Anchorage, *leg.* Bond Whitmore, are presently in the collection of Donald Eff, Boulder, Colorado.

Subspecies in *Speyeria*

In earlier days it was easier to define subspecies of *Speyeria*. For the most part they were distinctive in facies and well separated geographically. Advent of the automobile changed all that: road networks expanded, collectors travelled more, and geographic coverage burgeoned. Consequently, gaps between named subspecies have been partly or wholly bridged by intermediates, giving rise to much name-shuffling and even to questions about the validity of subspecies as a category.

Speyerian populations are notoriously varied in single localities, including type localities. From this it follows that judgments made as to what is "typical" of particular taxa, if based on samplings from type localities, are subjective in presuming a local norm, or are inadequate if based on a single holotype specimen. Still worse, most speyerian subspecies are insufficiently isolated to prevent occasional straying. The variety of local color forms in topotype populations can thus disperse, mingle, and blend with others similarly afflicted. Where then, and how, should subspecific lines be drawn?

A comment by Rindge (1987) gives one answer, and it carries the weight of having resulted from surveying 37,500 specimens of *Speyeria* during geographical rearrangement of series in the American Museum of Natural History. He says: ". . . it quickly became apparent to me that the majority of subspecific names proposed in this genus are, at best, but random points on or at the end of clines, and hence are of little or no scientific value. There appear to be very few completely allopatric populations to which legitimate names might be attached."

In a similar vein, Arnold (1983, 1985) recognized only 3 *callippe* subspecies of 16 accepted in Miller and Brown (1981). I heartily subscribe to the idea that the majority of subspecific names in *Speyeria* could be dropped; they are essentially undefinable. However, I have one major question concerning Arnold's methodologies: As one well acquainted with *callippe* variation in all the geographical regions Arnold sampled, I can only wonder how through any mathematical legerdemain the large brown-disk *callippe callippe* of the San Francisco

Peninsula can be directly associated with, say, the smaller, often yellow-disk "sierra" of Plumas Co.? Or the red-disk silvered *elaine* of southern Oregon with the sordid yellowish and unsilvered *laurina* of the Greenhorns? Also, retention of *semivirida* as one of the three recognized subspecies invites the criticism that *semivirida* in itself is a catchall, beginning in the Tahoe region with creeping intrusion of brown into the green-disk series, and culminating in British Columbia (for example near Jesmond) with individuals nearly black discally. So why is *semivirida* singled out, except in a vague regional sense, from the other intergrading forms that were synonymized?

These are relatively minor quibbles. A measure of how far I agree in principle with Arnold is that I think ambiguities will persist until all trinomials are discarded, and *callippe* is allowed to stand alone as a distinct, nonoverlapping entity. But even the "rigidly definable species" is by no means easily attained, as confirmed in a paper by Ferris (1983) mentioned below. Before ending discussion of Arnold's *callippe* study, however, a serious objection must be stated, namely, that his methodology would seem destined to fail where most needed, namely in determining what are to be accepted as valid *Speyeria* species. The problem here would be with the many local parallels that blur superficial distinctions among species. In many places the differences in facies between species widely agreed to be valid, can be, and often are, fewer and more subtle than among the *callippe* subspecies Arnold synonymized.

This allied and more vital problem of delimiting species amid the welter of subspecific variations is exemplified in Ferris (1983). No better statement of the often confusing impressions conveyed by field-collected series can be found in the literature; this reference should be consulted by everyone interested in sympatry as a means of defining species. It would be hard to dispute Ferris's tentative hypothesis that two sibling species may be involved in the Colorado "*atlantis*" material; this would apply even more certainly to some of the Canadian series. On the whole, however, it probably would require a hand-pairing breakthrough such as Ferris envisions to decide among alternatives. The moral of Ferris's work perhaps is not to worry unduly about subspecies until we can say more precisely what species to recognize. A recent paper by Scott (1988) suggests a fairly objective and practicable way to assess conflicting data in sympatrisms. He studied the situations in *atlantis* described by Ferris. By rearing broods from areas where *hesperis* predominated over *atlantis* and vice versa, Scott obtained enough intermediates to incline him toward the single polytypic entity theory.

The one thing certain from all this is that speciation and subspeciation in *Speyeria* will continue to fuel debate and taxonomic disagreements. Revising this section of Miller and Brown will be an unenviable chore.

So far as I would venture recommendations, I think the species, aside from the elevation of *adiaste*, are standing the test of time.

The status of presently listed subspecies in Miller and Brown (1981) is problematical. While I would retain most of the subspecific taxa, it seems to me a distinction should be made between the utility of these names versus their reality in nature as definable biological units. Lafontaine (1987) retained certain *Euxoa* "subgenera" by the device of a distinct typeface; strictly speaking they are synonyms but practically speaking they are helpful in classifying that difficult genus. The situation in *Speyeria* is analogous: variation is huge and not well understood, sure to be further exploited since furnishing so many exciting possibilities for geneticists and other students of evolution. It would be convenient, then, to have discriminant tags available, and indeed there is something to be said for their "reality"—they enable succinct reference to color forms which students can see actually do prevail in certain geographical areas. For that reason, if for no other, I suspect they will refuse to die even if formally synonymized.

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PHYLOGENY AND ZOOGEOGRAPHY OF THE BIGGER AND BETTER GENUS *ATALOPEDES* (HESPERIIDAE)

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ABSTRACT. What makes *Atalopedes* bigger and better is the addition of two tropical species, *A. clarkei*, new species and *A. bahiensis* (Schaus), and the subtraction of another, *nabokovi* (Bell & Comstock), which belongs in *Hesperia*. Comparison of genus *Atalopedes* with its sister *Hesperia*, using characters of size, antenna, facies, stigma, and, especially, male and female genitalia, precedes comparisons among the species of *Atalopedes*, using these same characters. The five species form three highly distinct groups, whose phylogenetic sequence is (1) *A. campestris* (Boisduval), which ranges from equator to USA; (2) the *mesogramma* group—*A. mesogramma* (Latreille), on most Greater Antilles, Isle of Pines, and some Bahama Islands including New Providence, and *A. carteri* Evans, New Providence Island; and (3) the *clarkei* group—*A. clarkei*, Margarita Island, Venezuela, plus Cartagena, Colombia, and *A. bahiensis*, coastal central Brazil. The far-out *clarkei* group has switched its ecologic niche to seashore grass; habitat is very restricted. The older the species of *Atalopedes*, the wider its geographic range.

Additional key words: genitalia (male and female), *Hesperia*, *H. nabokovi*, taxonomy, evolution.

What makes *Atalopedes* bigger and better is the addition of two tropical species, an undescribed one plus its misplaced sister, and the subtraction of another, *nabokovi* (Bell & Comstock), which belongs in *Hesperia* (Burns 1987).

Because the five resulting species form three highly distinct clusters, *Atalopedes* seems riddled by extinctions—far more than sister genus *Hesperia*, which, with four times as many species, is still relatively compact.

Atalopedes is American; *Hesperia*, mostly so—but it also spans the Palearctic, an extension of range considered rather recent (Scudder 1874, MacNeill 1964). Though basically northern in modern distribution, *Hesperia* turns out, with the inclusion of *H. nabokovi*, to be lowland Hispaniolan as well as Holarctic, which raises questions about area of origin, particularly since *nabokovi* is among the oldest species of *Hesperia* (Burns 1987). The idea that *Hesperia* may have arisen in the Neotropics becomes less astonishing in light of the fact that sister *Atalopedes* occurs from the middle of South America to the middle of North America and in much of the West Indies.

As currently known, the few species of *Atalopedes* tend to replace one another geographically. The only species in the continental United States is widespread and weedy and thus (for a skipper) familiar. *Atalopedes campestris* (Boisduval) ranges from about the equator, through northern South America (up to at least 3100 m in Colombia), through Central America, and through Mexico, to most of the United States below Canada. Across the southern United States, this multivoltine grass-eater flourishes, especially in disturbed open habitats, becoming scarcer toward higher latitudes and altitudes. It commonly invades various northern states in which it fails to overwinter: records typically reflect the mid- to latter warm season. To many temperate lepidopterists (such as Clark & Clark 1951, Shapiro 1966, 1974, Opler & Krizek 1984), this mobile skipper is a classic immigrant.

Three of the four remaining species of *Atalopedes* are emigrants, wholly or partly on islands. Only one has much of an insular distribution: *A. mesogramma* (Latreille) extends through all the Greater Antilles except Jamaica, as well as south of Cuba to the Isle of Pines and north of it to some of the Bahama Islands. By contrast, *A. carteri* Evans occurs on New Providence Island in the Bahamas; and *A. clarkei*, new species, on Margarita, an island (68 km east to west) roughly 25 km north of the Venezuelan mainland and 250 km west of Trinidad.

Beyond that, this new skipper hails from the Caribbean coast of Colombia (Cartagena); and its sister, *A. bahiensis* (Schaus), from the Atlantic coast of central Brazil (Bahia and Espirito Santo)—though, surely, neither is quite so localized.

The last reviser of *Atalopedes* (Evans 1955) saw one species, *A. mesogramma*, as polytypic. Two subspecies, *A. m. mesogramma* and *A. m. apa* Comstock, are real, but apparently minor, differentiates of no special concern here: the latter (with broader light markings that make it brighter overall) occurs on Puerto Rico and Hispaniola; the former (with narrower light markings that leave it darker), to the west. But what Evans (1955:339) described as a third subspecies, *A. m. carteri*, differs more sharply from the others in both size and facies; and, to quote Evans, it "occurs [at Nassau on New Providence in the Bahamas] with *mesogramma*, which probably is a visitor from Cuba, while *carteri* breeds locally." Presumably taking this as evidence of sympatry between differentiates without breakdown of their sizeable differences, Riley (1975:186) called *carteri* a full species. The situation points to double invasion, with complete speciation on the part of the first invader (see Mayr 1963:504–507 for discussion of multiple invasions).

The sistership of *Atalopedes* and *Hesperia* (Burns 1987) has mostly been missed. Lindsey (1921) and Lindsey et al. (1931), in treating the skippers of North America north of Mexico, inserted one genus (*Hylephila*) between *Atalopedes* and *Hesperia*; and Evans (1955), in treating the entire New World fauna, five (*Appia*, *Linka*, *Polites*, *Wallengrenia*, and *Pompeius*), though all these workers, in attempting to characterize *Atalopedes*, compared it with *Hesperia*, Evans (1955:338) even going so far as to say, "Palpi as *Hesperia*. . . . Resembles *Hesperia* in facies." MacNeill (1975) set the two genera side by side, noting a relation. Yet, in the subsequent spate of North American butterfly books and checklists, only Stanford (1981) and Pyle (1981) followed his arrangement (both consulted MacNeill).

Atalopedes vis-à-vis *Hesperia*

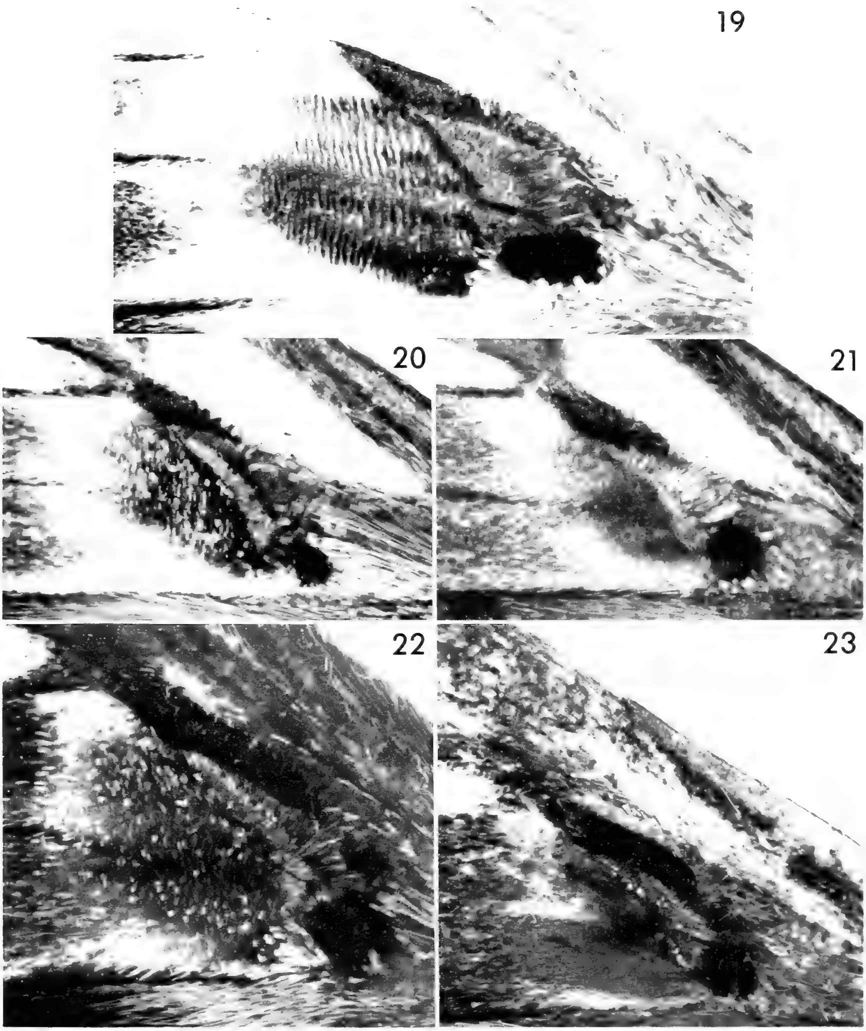
On the whole, *Atalopedes* (Figs. 1–18, 42, 43) is very like *Hesperia,* but less sexually dimorphic with respect to wing shape (in *Hesperia,* females have much more rounded wings than males). The few departures in *Atalopedes* from an intergenerically shared pattern are on the ventral secondary, which is not surprising since this is the surface a resting individual shows the world (Figs. 42, 43): most extreme is a vertical pale stripe down the middle of a dark wing from vein 8 to mid-space lc in *A. mesogramma* (Figs. 8, 18) and *A. carteri* (Fig. 10). *Atalopedes* is more variable in size, with *A. mesogramma* (Figs. 7, 8, 17, 18) averaging larger than any species of *Hesperia* (except *H. nabokovi*!) and *A. clarkei* (Figs. 3, 4, 13, 14) and *A. bahiensis* (Figs. 5, 6, 15, 16), smaller. In both genera, the antenna and its apiculus are relatively short, and the club, stout; but the apiculus is a bit longer in *Atalopedes.*

The stigma (Figs. 19–23)—an elaborate communicative device spreading over the dorsal primary of the male from the junction of veins 3 and 4 inward and downward to vein 1—resembles that of *Hesperia* but clearly differs from it. The central, dustlike microandroconial mass (terminology of MacNeill 1964) is more or less open to view, not neatly enclosed by flanking rows of large, wide, silvery-gray scales as it is in *Hesperia.* The dark brown apical and lower brush patches are more developed, more conspicuous, than they are in *Hesperia,* although the scales comprising them are narrower. The poststigmal patch, too, is well developed and dark, contrasting with adjacent areas of the wing. Altogether, the stigma of *Atalopedes* looks less linear and more massive than that of *Hesperia.*

Parts of the male (though not the female) genitalia of *Atalopedes* hint at those of *Hesperia.* In both genera the valva ends in two large, pointed, more or less dorsally-directed projections whose bases join on the lateral valval surface by way of a smooth, U-shaped edge. This U, narrow in *Atalopedes* (Figs. 24–33), varies from narrow to wide in *Hesperia.* The more distal projection is the more complex, almost always extending forward, medial to the proximal projection. In both genera the aedeagus is slender and comparatively simple—quite unlike the formidable one bristling with bizarre, often outsized, titillators and cornuti in such related genera as *Yvretta, Polites, Ochlodes, Poanes,* and *Paratrytone.*

Many genitalic features divide *Atalopedes* from *Hesperia* (Burns

FIGS. 1–18. Adults of *Atalopedes* (all ×1) (in USNM unless otherwise indicated): **1–10,** males; **11–18,** females; odd numbers, dorsal views; even numbers, ventral views. **1, 2,** *campestris*, Charleson St., Annandale, Fairfax Co., Virginia, USA, 1 September 1979, J. M. Burns; **3, 4,** *clarkei*, El Morro, Margarita Island, VENEZUELA, 12 February 1985, J. F. G. Clarke; **5, 6,** *bahiensis*, holotype, Bahia, BRASIL; **7, 8,** *mesogramma,* Tánamo, CUBA, March 1902; **9, 10,** *carteri,* Nassau, BAHAMAS, 1 February 1898, H. G. Dyar; **11, 12,** *campestris,* Austin, Travis Co., Texas, USA, 3 June 1967, J. M. Burns; **13, 14,** *clarkei*, Cartagena, COLOMBIA, 14 July 1969, J. Herrera (collection of C. D. MacNeill); **15, 16,** *bahiensis*, Conceição da Barra, Espirito Santo, BRASIL, 25 March 1969, C. & C. T. Elias (collection of O. H. H. Mielke); **17, 18,** *mesogramma,* Matanzas, CUBA, October.



FIGS. 19–23. Stigmas on the dorsal left primaries of the *Atalopedes* males in Figs. 1–10. **19,** *campestris*; **20,** *clarkei*; **21,** *bahiensis*; **22,** *mesogramma*; **23,** *carteri*.

1987). The aedeagus is longer than the rest of the intact genitalia in *Atalopedes* (Figs. 25, 27, 29, 31, 33) but not in *Hesperia*; and it bears either two multidentate cornuti (Figs. 24, 25) or none (Figs. 26–33) in *Atalopedes* compared with a single bidentate cornutus in *Hesperia*. Paired prongs projecting forward from the front end of the juxta are short and stout in *Atalopedes* (Figs. 25, 27, 29, 31, 33) but long and delicate in *Hesperia*. The valva is elongate and its top and bottom about

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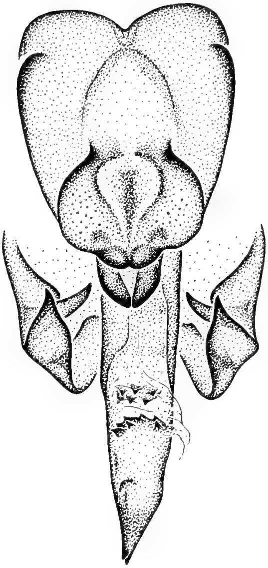

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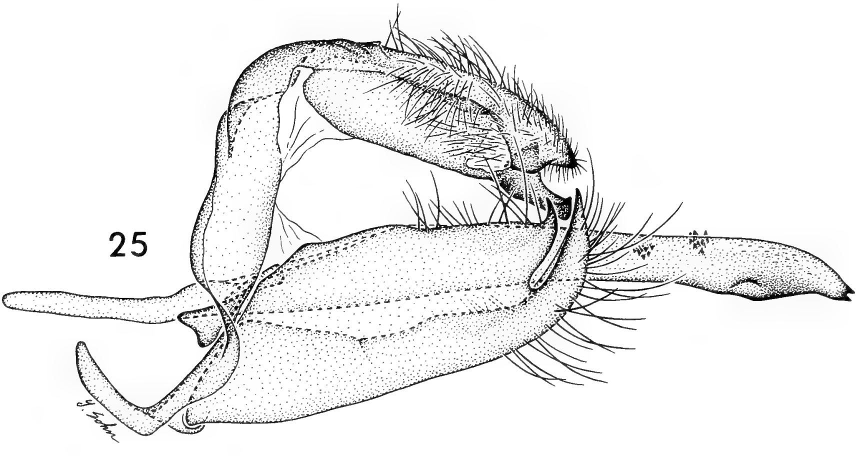

FIGS. 24, 25. Male genitalia of *Atalopedes campestris* from Skippers, Greensville Co., Virginia, USA, 25 July 1983, J. M. Burns (genitalic dissection no. X-2107). **24,** Tegumen, uncus, gnathos, distal ends of valvae, and distal end of aedeagus in dorsoposterior view; **25,** Complete genitalia (minus right valva) in left lateral view.

parallel in *Atalopedes* (Figs. 25, 27, 29, 31, 33), whereas the top of the valva is usually quite humped in *Hesperia*; and the distal projection of the valva, apart from its one (Figs. 24, 25) or two (Figs. 26–33) big points, is smooth along its dorsal edge in *Atalopedes* (Figs. 24–33) rather than serrate, as it is in *Hesperia*. The dorsal tegumen forms a more or less raised sac in *Atalopedes* (Figs. 24–33) but not in *Hesperia*. The uncus, always short and blunt in *Atalopedes* (Figs. 24–33), ranges from a roughly similar state to long and pointed in *Hesperia*. The gnathos, which may be well developed (Figs. 24, 25), reduced (Figs. 30–33), or vestigial (Figs. 26–29) in *Atalopedes,* is always well developed in *Hesperia*. (For figures of male genitalia of *Hesperia,* see Scudder 1874, 1889, Skinner & Williams 1924, Lindsey et al. 1931, Lindsey 1942, MacNeill 1964, and Burns 1987.)

Female genitalia of the two genera are thoroughly distinct. A midventral prong projecting backward and downward from the back part of the lamella postvaginalis (Figs. 34–41) marks *Atalopedes*. The body of the lamella postvaginalis in *Atalopedes* consists of midventral sclerotization (extending the roof of the ductus bursae to the base of the prong) flanked by surfaces (curving upward and outward) that may be entirely (Figs. 34, 35, 40, 41) or scarcely (Figs. 36–39) sclerotized. In ventral outline the simpler lamella postvaginalis of *Hesperia* approaches a rectangle. The ductus bursae is more or less symmetric in *Atalopedes* (Figs. 34–41) but asymmetric in *Hesperia,* where it begins with a caudal chamber on the right and then slants to the left. Sclerotization of the ductus bursae stops before the junction of the ductus seminalis in *Atalopedes* (Figs. 35, 37, 39, 41) but after its junction in *Hesperia*. And the ductus bursae connects with the corpus bursae by means of a dorsal jog in *Atalopedes* (Figs. 35, 37, 39, 41) but not in *Hesperia*. The corpus bursae itself is essentially cylindrical in *Atalopedes* (Figs. 34–41), spherical in *Hesperia*. (For figures of female genitalia of *Hesperia,* see mainly MacNeill 1964 but also Gillham 1954 and Burns 1987.)

Additions to *Atalopedes*

Full and formal treatment of all included species (which would swell an ordinary taxonomic text) is not essential. I have introduced them all already by way of their peculiar distributions and gone on, in connection with strict definition of the genus, to provide comparative figures of their facies, stigmas, and genitalia—a wealth of information useful at the specific level, as well as above. The species are few enough and diverse enough to stand out. Their characters flood the upcoming discussion of phylogeny anyway. Ritual is therefore restricted to the two species in nominal need.

These, the South American sisters, are the most southern in distribution and the smallest in size. Because the sample of the new species is far larger than that of the old—37 males and 3 females as opposed to 1 male and 1 female—and because a larger sample affords a better description, the new species comes first.

Atalopedes clarkei, new species
(Figs. 3, 4, 13, 14, 20, 26, 27, 36, 37, 42, 43)

Length of right primary (mm).

Sample	Sex	N	Range	Mean ± SE	SD	CV
Margarita I., Venezuela	♂	28	11.0–13.4	12.28 ± 0.09	0.46	3.70
	♀	1	12.7			
Cartagena, Colombia	♂	8	11.0–13.0	11.88 ± 0.27	0.78	6.53
	♀	2	13.2–14.0			

Antenna. Club shorter and thicker in males than in females; anterodorsally, from base to (or close to) start of apiculus, club scaled orange in males, blackish brown in females. (This marked sexual dimorphism involving size, shape, and color of the antennal club is of general occurrence in *Atalopedes*—not to mention *Hesperia* and some other genera—though details of expression can vary between species: for instance, the anterodorsal orange stripe of males extends farther out the club in *A. clarkei* and *A. campestris* than it does in *A. mesogramma* and *A. carteri.*) Nudum usually 7/5: of 34 specimens with at least one antenna intact, 3 are 7/4; 27, 7/5; and 4, 7/6. (Nudum usually 7/7 in *campestris,* 8/8 in *mesogramma.*)

Facies. Much as in *campestris* (compare Figs. 3, 4 with 1, 2; and 13, 14 with 11, 12) except for the ventral secondary, where a yellow ray from the cell through most of spaces 4 and 5 divides two yellow spots in spaces 2 and 3 from a third (not always present) in space 6 (Figs. 4, 14, 42, 43). This distinctive ventral secondary relates readily to that of many *campestris* males (compare Figs. 4 and 2) but not to that of *campestris* females (compare Figs. 14 and 12). (It suggests the ventral secondary of marsh-dwelling species of *Poanes.*) Spots of the primary (which become hyaline in females of *campestris* and *mesogramma*) opaque in both sexes.

Stigma. Well developed (Fig. 20) but not hypertrophied as it is, slightly, in *mesogramma* (Fig. 22) and, grossly, in *campestris* (Fig. 19).

Male genitalia. Valva similar to that of *mesogramma* and *carteri* (compare Figs. 26, 27 with 30–33), with the more distal of the two large, terminal projections expanded into two major, dorsally directed points just mediad of the one-pointed proximal projection. Tip of uncus broadly notched (Fig. 26) and roughly textured (Figs. 26, 27). Gnathos vestigial (Figs. 26, 27). No cornuti, but tooth present on left side of aedeagus before the single, backward pointing, terminal tooth (Figs. 26, 27).

Female genitalia. Midventral prong projecting from back of lamella postvaginalis short (compare Figs. 36, 37 with 34, 35 and 40, 41). Much of lamella postvaginalis unsclerotized (Figs. 36, 37). Simple, sclerotized ductus bursae modestly and rather evenly tapered from ostium bursae forward (Fig. 36).

Material examined. Holotype: Male. VENEZUELA, [Nueva Esparta], Margarita I[slan]d, El Morro, [ca. 4 km E Porlamar], on seashore grass, 12 Feb[ruary] 1985, J. F. G. Clarke. Deposited in National Museum of Natural History, Smithsonian Institution (USNM).

Paratypes (39): 27 males with same data as holotype, plus 7 genitalia dissections (USNM). 1 male, 1 female, VENEZUELA, Nueva Esparta, Margarita Island, near Pampatar, between Playa Moreño and Playa El Angel, 19 August 1987, J. Glassberg & J. Scott, plus 2 genitalia dissections (USNM). 2 females, COLOMBIA, Cartagena, 14 July 1969, J. Herrera, plus 2 genitalia dissections (collection of C. D. MacNeill). 8 males with same data except 15 July 1969, plus 4 genitalia dissections (collection of C. D. MacNeill).

Atalopedes bahiensis (Schaus), new combination
(Figs. 5, 6, 15, 16, 21, 28, 29, 38, 39)

Thymelicyus [sic] *bahiensis* Schaus (1902:436).

[The brief, verbal original description of nothing but facies and wing-spread is so vague that Evans (1955:337) questioningly assigned *bahiensis* to the synonymy of *Pompeius amblyspila* (Mabille).]

Length of right primary (mm). Male, 11.8; female, 13.2; so probably about as in *A. clarkei*.

Antenna. [Male, missing.] Female, club scaled blackish brown anterodorsally; nudum 7/5 or 7/6 (count equivocal owing to incomplete suture).

Facies. Reminiscent of *clarkei* but darker, without the pale ray (parallel to veins through the middle of the ventral secondary) characteristic of that species (compare Figs. 5, 6 with 3, 4; and 15, 16 with 13, 14); chiefly in female, brown background encroaches upon pale pattern elements (compare Figs. 15, 16 with 13, 14). Spots of the primary opaque in female as well as in male, as in *clarkei* (but not *campestris* and *mesogramma*).

Stigma. Similar to that of *clarkei* (Fig. 20), but lower brush patch perceptibly larger and poststigmal patch, smaller (Fig. 21).

Male genitalia. Overall, very like those of *clarkei*, but with scattered differences (compare Figs. 28, 29 with 26, 27). In lateral view (Fig. 29 versus 27), one-pointed, laterally placed, proximal terminal projection of valva more nearly horizontal, extending farther back to about end of valva; two-pointed, medially placed, distal terminal projection of valva with its proximal point higher than its distal point, rather than the reverse; posterior edge of valva not curved prominently backward the way it is in *clarkei*; anterior end of tegumen more angular, less rounded. In dorsoposterior view (Fig. 28 versus 26), tegumen-uncus usually narrower; left lateral tooth near end of aedeagus longer and basally much broader.

Female genitalia. Similar to those of *clarkei*, but midventral prong projecting from back of lamella postvaginalis even shorter, lamella postvaginalis still more narrowly sclerotized, and ductus bursae more (and more abruptly) flared around level of ostium bursae (compare Figs. 38, 39 with 36, 37).

Material examined. Male. Holotype: Bahia, Brazil; Collection W. Schaus; *Thymelicus Bahiensis* Sch[au]s Type [handwritten in black]; Type No. 5999 U.S.N.M. [label red]; Genitalia No. X-2357 J. M. Burns 1987.

Female. Conceicao [da] Barra, E[spirito] S[anto], Brasil, 25 March 1969, C. & C. T. Elias; DZ 3081; Genitalia No. X-2390 J. M. Burns 1987; [collection of O. H. H. Mielke].

Niche Switch to Seashore Grass

Atalopedes is a genus of multivoltine grass-eaters. One or, more likely, both additions to it have made a striking ecologic shift analogous to those of marsh-dwelling species of *Euphyes*, *Poanes*, *Ochlodes*, *Problema*, and *Panoquina*. *Atalopedes clarkei* lives in a peculiar and relatively simple community dominated by short grass growing in sand behind sandy marine beach (Figs. 42–44). This physically harsh environment may offer fewer biotic pressures. At any rate, as in marsh-dwelling skippers whose foodplant is local but sometimes locally abundant, populations can be extremely local (and thus hard to find), but the density of a population can be high. It was certainly high at El Morro on Margarita when J. F. G. Clarke found *A. clarkei* (see Material examined). In that area, man is the worst enemy of *A. clarkei* now because he is rapidly wrecking its limited seashore habitat with hotels and such (J. Glassberg pers. comm.).

The habitat must have been basically similar, and the population density more or less high, when J. Herrera found *A. clarkei* at the Colombian seaport of Cartagena (see Material examined). During his

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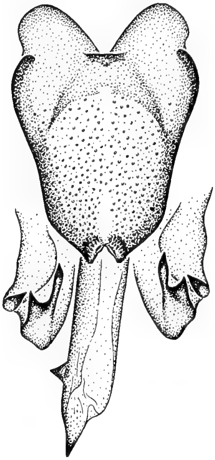

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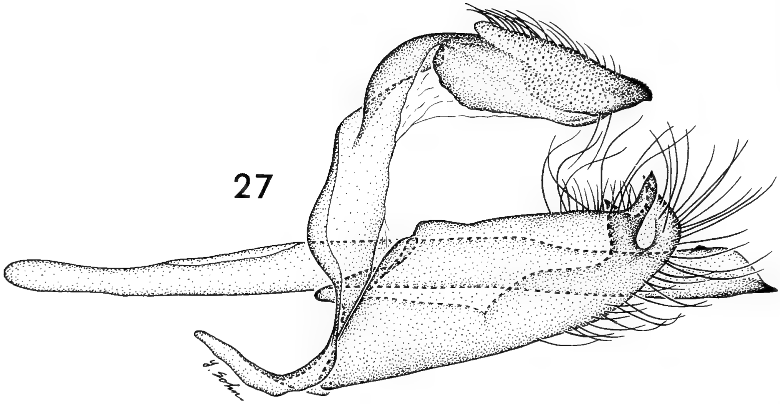
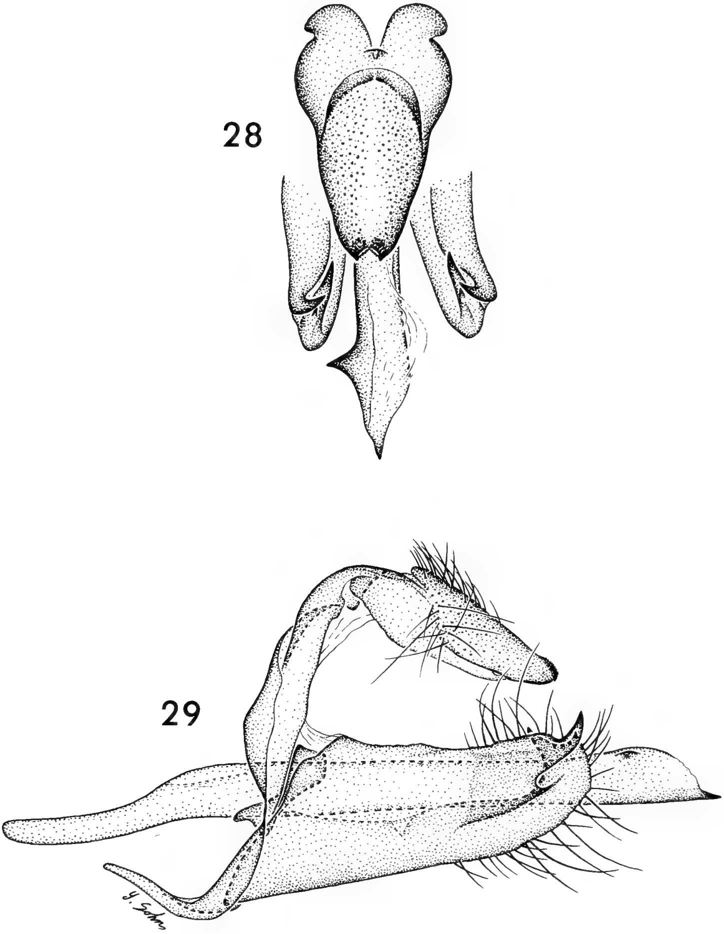


FIGS. 26, 27. Male genitalia of *Atalopedes clarkei* from El Morro, Margarita Island, VENEZUELA, 12 February 1985, J. F. G. Clarke (X-2104). **26,** Tegumen, uncus, distal ends of valvae, and distal end of aedeagus in dorsoposterior view; **27,** Complete genitalia (minus right valva) in left lateral view.

brief time in Cartagena, Herrera collected at the airport, which is right by the water (C. D. MacNeill pers. comm.).

Indirect evidence suggests that seashore grass is also the habitat of *A. clarkei*'s close Brazilian sister. The female of *A. bahiensis,* taken rather recently, is without question from a town on the coast. The male, collected before 1902, is labelled "Bahia Brazil" which may mean the large coastal state of Bahia but probably refers to its capital, a seaport

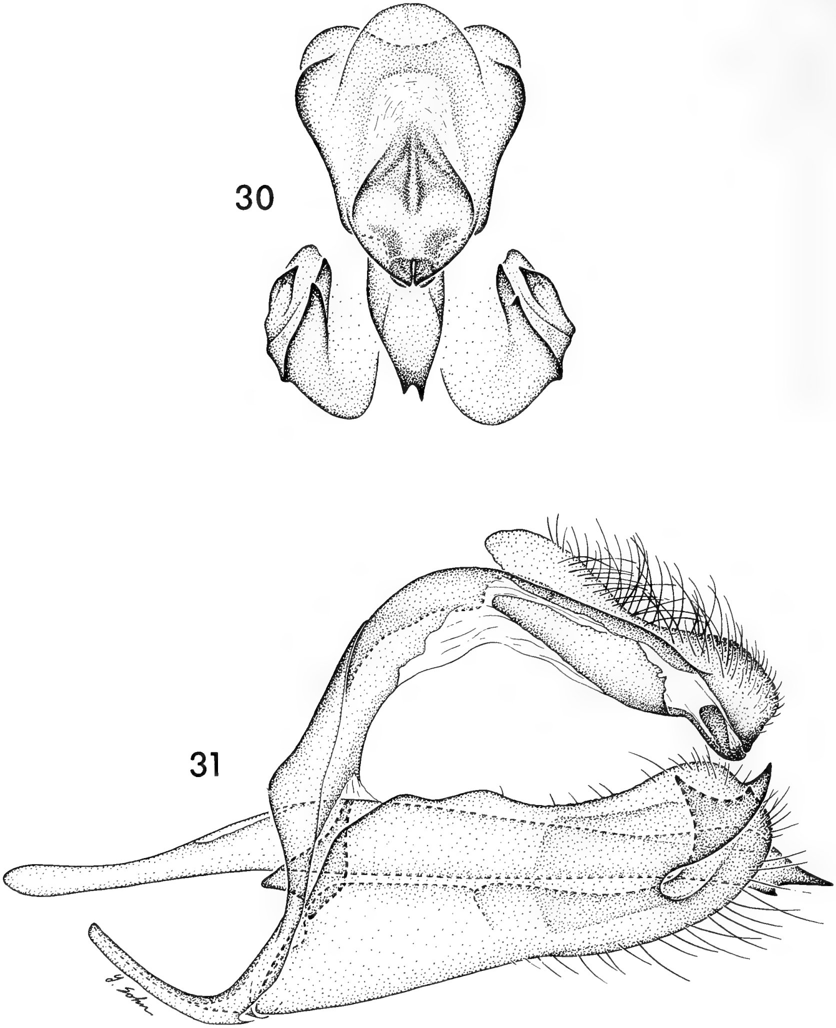


FIGS. 28, 29. Male genitalia of *Atalopedes bahiensis*, holotype, from Bahia, BRASIL (X-2357). **28,** Tegumen, uncus, distal ends of valvae, and distal end of aedeagus in dorsoposterior view; **29,** Complete genitalia (minus right valva) in left lateral view.

now called Salvador but formerly called Bahia. Restriction to special habitat could explain the scarcity of the skipper in collections.

Phylogeny of *Atalopedes*

The species of *Atalopedes* form three obvious groups: (1) *campestris*, (2) *mesogramma* and *carteri* (the *mesogramma* group), and (3) *clarkei* and *bahiensis* (the *clarkei* group). Between these groups, differences are large; within them, small—so small that, when I think about the



FIGS. 30, 31. Male genitalia of *Atalopedes mesogramma* from Guantánamo Bay, CUBA, 14 September 1943, W. H. Wagner (X-2115). **30,** Tegumen, uncus, gnathos, distal ends of valvae, and distal end of aedeagus in dorsoposterior view; **31,** Complete genitalia (minus right valva) in left lateral view.

genus as a whole, it comes down to a trio of widely spaced points, which beg for connection. Drawing those real but unseen lines of phylogenetic relationship (Fig. 45) is trying.

Though extinction seems to have obliterated most of the record so that the surviving species groups stand out and apart from one another,

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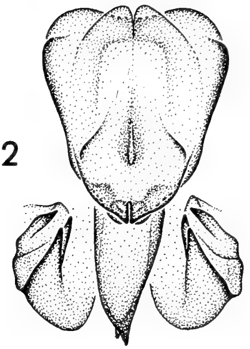

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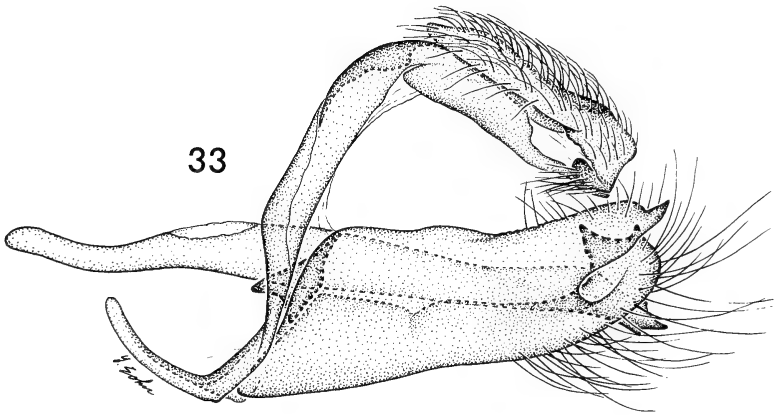
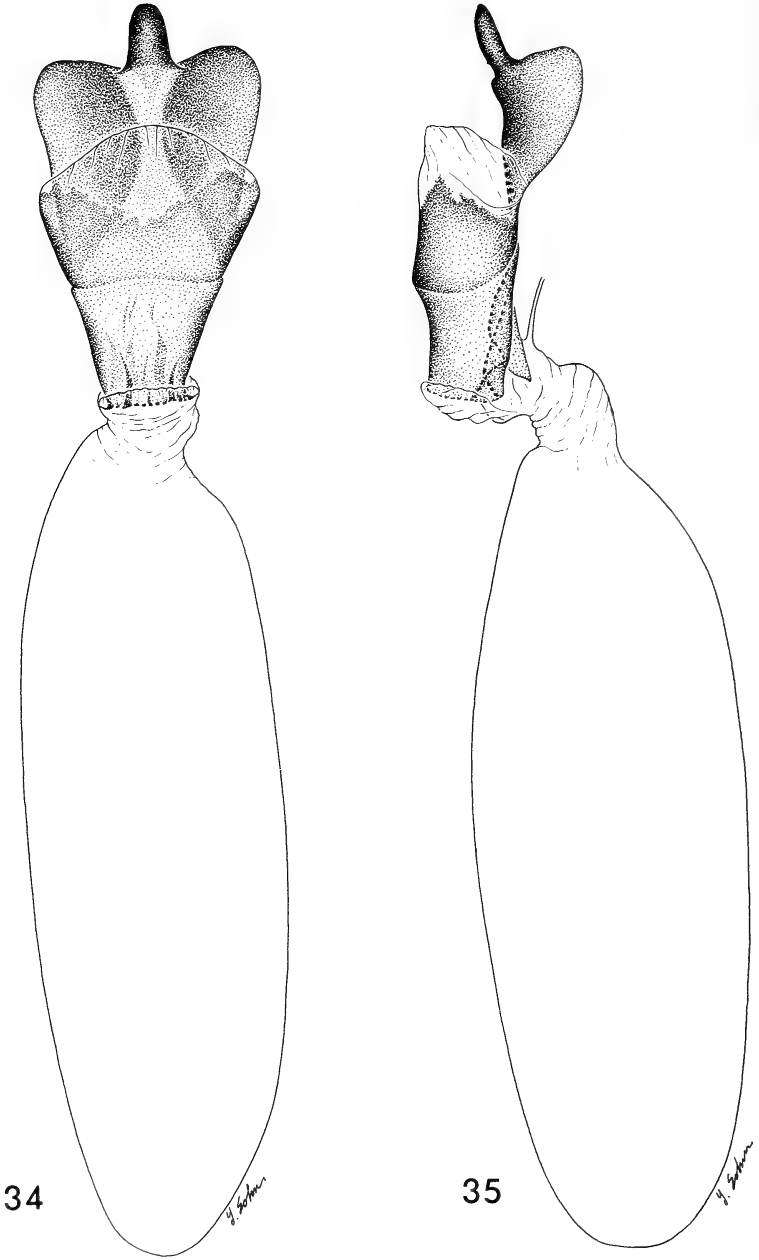


FIGS. 32, 33. Male genitalia of *Atalopedes carteri* from Nassau, BAHAMAS, 1 February 1898, H. G. Dyar (X-2116). **32,** Tegumen, uncus, gnathos, distal ends of valvae, and distal end of aedeagus in dorsoposterior view; **33,** Complete genitalia (minus right valva) in left lateral view.

there is no problem uniting them, using a diversity of characters, in a well-defined, monophyletic higher group distinct from *Hesperia* and sister of it (see *Atalopedes* vis-à-vis *Hesperia*). But within *Atalopedes*, it is unfortunate (from a phylogenetic viewpoint) that many character states are unique to each group and that, where they are shared, it is hard to peg them as primitive or derived.

The gnathos of the male genitalia becomes critical. Despite a hypertrophied stigma (Fig. 19), the most primitive species of *Atalopedes* must be *campestris* because its gnathos is fully developed (Figs. 24, 25) as it is in every species of sister genus *Hesperia*. In the remaining species of *Atalopedes*, the gnathos is reduced—less severely in *mesogramma*



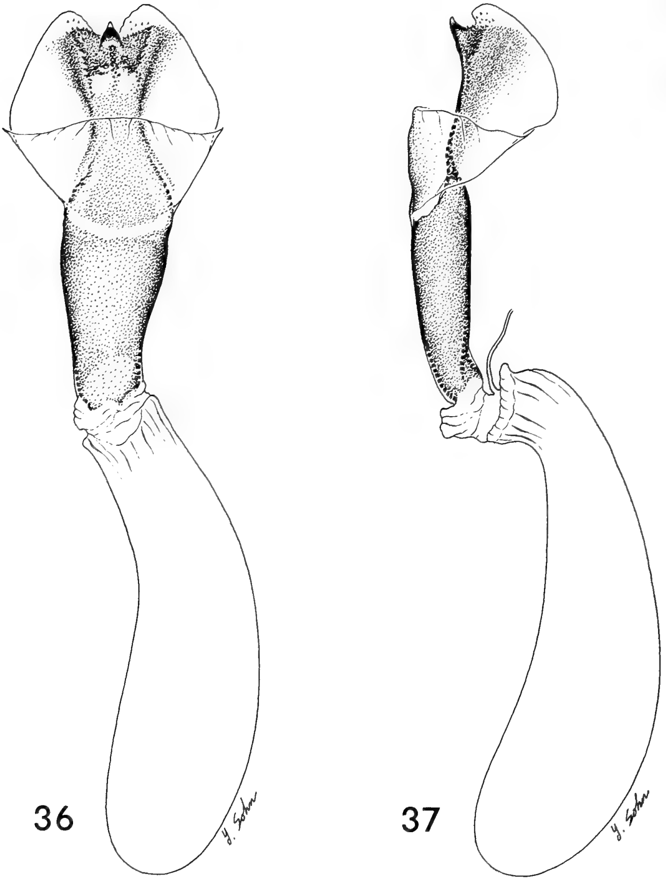
FIGS. 34, 35. Female genitalia of *Atalopedes campestris* from Skippers, Greensville Co., Virginia, USA, 30 September 1981, J. M. Burns (X-2169). **34,** Sterigma and bursa copulatrix in ventral view; **35,** The same, plus part of the ductus seminalis, in right lateral view.

and *carteri* (Figs. 30–33) than in *clarkei* and *bahiensis* (Figs. 26–29)—so that these two groups must be derived, and in that order.

The notion of a gradual and progressive trend toward elimination of the gnathos is entirely different from abrupt total suppression of secondary sex characters like the costal fold, metatibial tufts plus metathoracic pouch, or stigma of male skippers. I hypothesized long ago that presence or absence of those elaborate odor-disseminating structures could have a simple genetic basis such that they might easily reappear in a descendant species after having been switched off in an ancestor (Burns 1964:196–197). Where reversals of that kind are likely, establishing a sequence can be difficult. But in *Atalopedes*, parsimonious interpretation of its three discrete levels of gnathos expression yields the main lines of Fig. 45.

Two more features of the male genitalia lend what may be flawed support to the argument that *campestris* is the most primitive species. First, cornuti occur in *campestris* (Figs. 24, 25) but in no other species of *Atalopedes* (Figs. 26–33). The weakness here is that even though all species of sister *Hesperia* have a cornutus, it is always single and usually bidentate and hence may not be strictly homologous with the paired multidentate cornuti in *campestris*. Second, the distal terminal projection of the valva comes to a single, dorsally directed point in *campestris* (Figs. 24, 25) but broadens to two conspicuous, dorsally directed points (medial to the proximal projection) in all other species of *Atalopedes* (Figs. 26–33). However, since the latter configuration more nearly resembles the distal, terminal valval projection in all species of *Hesperia*, it may be primitive and the one-pointed projection of *campestris*, derived.

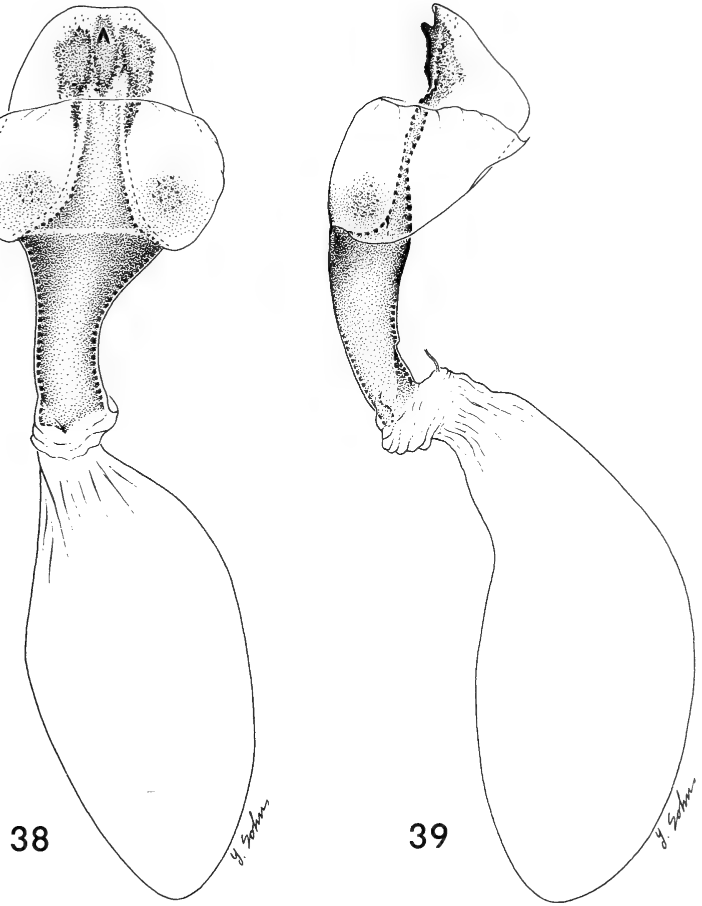
Other male genitalic characters bolster the sequence that puts the *mesogramma* group between *campestris* and the *clarkei* group. The strangely protuberant uncus of the *mesogramma* group (Figs. 30–33) relates clearly to that of *campestris* (Figs. 24, 25), though differing in many details and appearing, as a whole, rather less extreme. (Among the figures just cited, the protuberance shows better in the dorsoposterior views.) The protuberance is wanting in the *clarkei* group (Figs. 26–29). On the other hand, the posterior tip of the uncus is more deeply notched in the *mesogramma* group (Figs. 30, 32) than it is in *campestris* (Fig. 24); and the deep notch persists in the *clarkei* group where, moreover, its sides diverge widely (Figs. 26, 28). The very tip of the aedeagus is finely dentate in *campestris* (Figs. 24, 25) and more coarsely bidentate in the *mesogramma* group, where, in addition, one tooth is decidedly more anterior than the other (Figs. 30–33); in the *clarkei* group, the anterior tooth appears to have moved upward and forward along the left side of the aedeagus and to have grown bigger still (Figs. 26–29).



FIGS. 36, 37. Female genitalia of *Atalopedes clarkei* from Cartagena, COLOMBIA, 14 July 1969, J. Herrera (X-2267) (collection of C. D. MacNeill). **36,** Sterigma and bursa copulatrix in ventral view; **37,** The same, plus part of the ductus seminalis, in right lateral view.

All parts considered, the male genitalia set the *clarkei* group farthest out (which is reasonable from an ecologic perspective, considering the shift to seashore grass). Admittedly, some far-out facies mark the *mesogramma* group (compare Figs. 7–10, 17, 18, particularly the ventral secondaries, with Figs. 1–6, 11–16, and the entire genus *Hesperia*); but facies can be much more labile even than genitalia. When such data conflict, favor the genitalia.

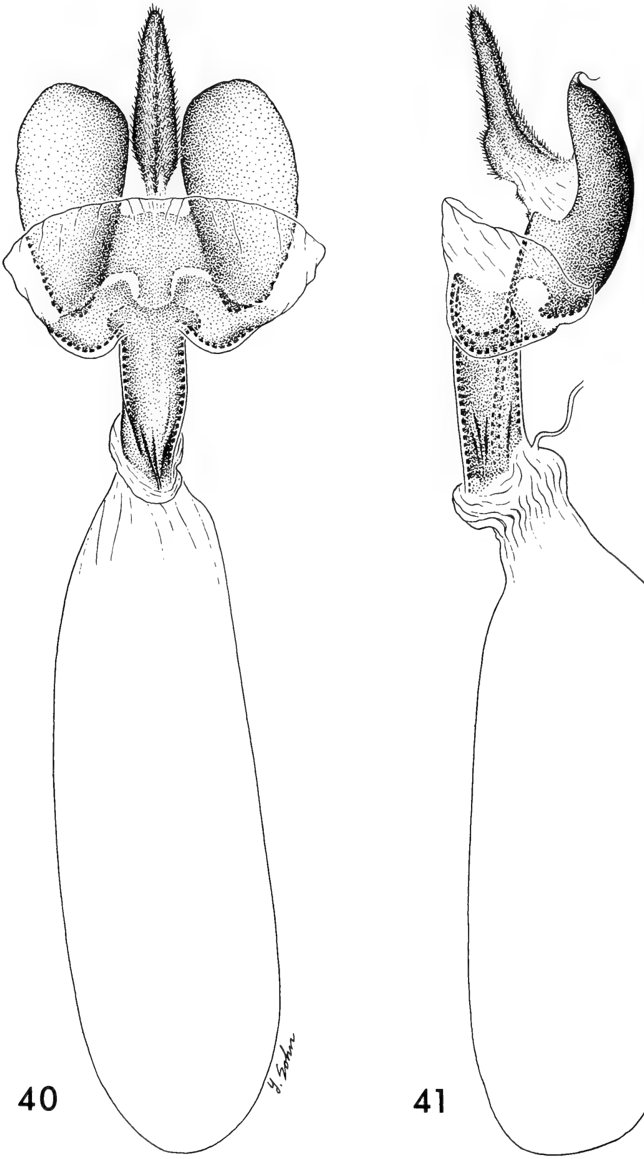
Size is another labile character of little value in working out low-level skipper phylogeny. In *Atalopedes* size varies from medium in



FIGS. 38, 39. Female genitalia of *Atalopedes bahiensis* from Conceição da Barra, Espirito Santo, BRASIL, 25 March 1969, C. & C. T. Elias (X-2390) (collection of O. H. H. Mielke). **38,** Sterigma and bursa copulatrix in ventral view; **39,** The same, plus part of the ductus seminalis, in right lateral view.

campestris (Figs. 1, 2, 11, 12) to large in *mesogramma* (Figs. 7, 8, 17, 18) but small in *carteri* (Figs. 9, 10) and, independently, to very small in *clarkei* (Figs. 3, 4, 13, 14) and *bahiensis* (Figs. 5, 6, 15, 16).

Female genitalia neither help nor hurt the case built from male genitalia, except that *campestris* does seem to reflect a more generalized morphology from which the disparate expressions of the *mesogramma* and *clarkei* groups could readily come. In *campestris* (Figs. 34, 35) the midventral prong projecting backward and downward from the back of the lamella postvaginalis is of medium length, the whole sterigma is



FIGS. 40, 41. Female genitalia of *Atalopedes mesogramma* from Guantánamo Bay, CUBA, 15 September 1943, "caught laying eggs on *Poa* lawn," W. H. Wagner (X-2172). **40,** Sterigma and bursa copulatrix in ventral view; **41,** The same, plus part of the ductus seminalis, in right lateral view.

FIGS. 42, 43. Fresh and worn individuals of *Atalopedes clarkei* perched, larger than life, on flower heads amid the seashore grass in Fig. 44 on 19 August 1987.

well sclerotized, and the sclerotized ductus bursae is short, wide, and evenly tapered. In *mesogramma* (Figs. 40, 41) the midventral prong is hypertrophied, sclerotization of the sterigma is reduced medially but not laterally, and the sclerotized ductus bursae is fairly short, narrow, and parallel-sided. Conversely, in the *clarkei* group (Figs. 36–39) the prong is atrophied, sclerotization of the sterigma is much reduced lat-

FIG. 44. Seashore grass habitat of *Atalopedes clarkei* between Playa Moreño and Playa El Angel, near Pampatar, Margarita Island, Nueva Esparta, VENEZUELA, 19 August 1987. Caribbean Sea shows at upper right through crescentic gap in barrier dune.

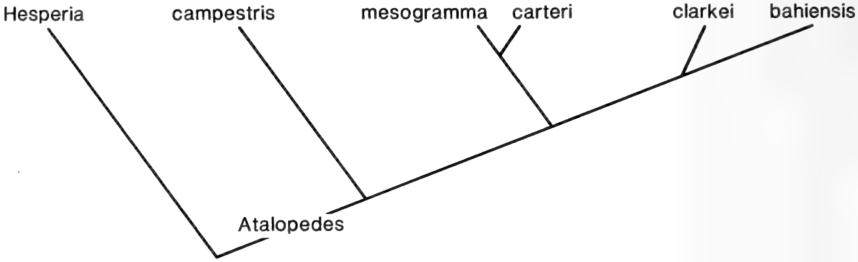


FIG. 45. Phylogeny of the bigger and better genus *Atalopedes*.

erally but not medially, and the sclerotized ductus bursae is long, wide, and tapered.

Within each group of two species, which species is primitive and which derived? Geographic distribution indicates that *mesogramma* must have given rise to *carteri*: *mesogramma* is complexly widespread (Puerto Rico, Hispaniola, Cuba, Isle of Pines, and some of the Bahamas, including New Providence) whereas *carteri*, so far as known, is limited to one small, low island (New Providence); furthermore, *mesogramma* is somewhat differentiated across its discontinuous range. I should note tangentially that *mesogramma* may be even more widely distributed: Evans (1955) lists one female in the British Museum (Natural History) from Costa Rica, and I find in the National Museum of Natural History, Smithsonian Institution, one male labelled "Mex" and three males labelled "Yucat."—but all of these mainland records need verification. Except for its small size and reduced pattern elements, daughter species *carteri* (Figs. 9, 10, 23) is very like mother *mesogramma* (Figs. 7, 8, 17, 18, 22). I have seen only one example of *carteri*, a male whose genitalia (Figs. 32, 33) are essentially those of *mesogramma* (Figs. 30, 31; Comstock 1944:606, pl. 1, fig. 4)—the slight differences between figures may reflect nothing more than individual variation.

Ancestral-descendant relations in the *clarkei* group (whose species differ more from each other) are not obvious. To judge from genitalic form, *clarkei* (Figs. 26, 27, 36, 37) probably preceded *bahiensis* (Figs. 28, 29, 38, 39). In the male the narrow tegumen-uncus and the enlarged anterior tooth of the aedeagus that mark *bahiensis* (Fig. 28) appear more derived. In the female the more atrophied midventral prong of *bahiensis* (Figs. 38, 39) seems farther out.

Zoogeography

Geographically, too, it is the derived species of each two-species group which is farther out—in this case from some generic center of distribution at about the north end of South America: *carteri* is to the far side of Antillean *mesogramma*, on a small island on the northern edge of the latter's range; *bahiensis*, on the central coast of Brazil, is far to the southeast of coastal Colombian and Venezuelan *clarkei*.

The older the species of *Atalopedes* (Fig. 45), the wider its geographic range: *campestris*, the oldest, has much the widest range (equator to USA), even when the vast area temporarily taken by immigrants is discounted; *mesogramma*, the second oldest, is second most widespread (Greater Antilles plus); *clarkei* (Cartagena to Margarita) is third; *bahiensis* (coastal central Brazil), fourth; and young *carteri* (New Providence Island), a distant fifth.

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TERRITORIAL BEHAVIOR AND DOMINANCE IN SOME HELICONIINE BUTTERFLIES (NYMPHALIDAE)

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ABSTRACT. By marking and systematically observing activities of focal individuals of *Heliconius sara, H. leucadia,* and *Eueides tales* at six trailside sites at Serra dos Carajás, Pará, Brazil, we found that resident male butterflies returned daily during 1–3-h periods to patrol and defend fixed 10–15-m-long sunny corridors against conspecific males. Defenders expelled intruders about once every 5–20 min, and unoccupied territories were taken over by vagrant males in about the same time interval. Marked primary residents of the two *Heliconius* species won all 149 combats observed with encroachers, and could evict newcomers settling on territories left temporarily vacant. Resident *E. tales* were more than 95% victorious. Besides fleeing vigorously from residents, trespassing *H. sara* and *H. leucadia* frequently departed slowly from territories when accompanied by the resident from below and behind. Resident *H. sara* flew erratic blocking patterns underneath slowly departing invaders, although a trespasser sometimes avoided immediate expulsion by diving to soil level and flying in circles too close to the ground for the accompanying resident to get under it. These ground-circling flights of *H. sara* appear to be contests to decide territory ownership whereas the peculiar slow exits of desisting *H. sara* and *leucadia* apparently function as appeasement behavior that bridles territorial aggression. *Eueides tales* sometimes followed one another through several steep glides (interpreted as ritualized chases) during territorial encounters. Territories seem to be rendezvous sites attractive to receptive females, although *E. aliphera* may defend emergence sites.

Additional key words: appeasement behavior, *Eueides tales, Heliconius leucadia, H. sara,* mate location.

Territorial behavior gains its advantage by permitting the preferential use of resources in restricted areas (Brown & Orians 1970). Territorial defense has been reported repeatedly in temperate-zone butterflies (Powell 1968, Baker 1972, Wellington 1974, Douwes 1975, Davies 1978, Bitzer & Shaw 1980, 1983, Lederhouse 1982, Dennis 1982, Alcock 1983, 1985, Knapton 1985, Wickman 1985a, Dennis & Williams 1987), where, so far as known, males defend probable mate encounter sites against other males (Baker 1983).

Defended encounter sites are frequently defined by landmarks, such as hilltops (Shields 1968, Alcock & O'Neill 1986) and other landscape features that reliably bring the sexes together (Parker 1978). Thus, butterfly territories may occur along flyways (Baker 1972, Bitzer & Shaw 1983) or occupy sheltered sites offering favorable conditions until matings occur (Knapton 1985, Wickman 1986). Oviposition sites frequented by gravid females (Baker 1972) and female emergence sites

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(Dennis 1982) may also be defended. Territorial males often return to defend the same place over a period of days or weeks (L. E. Gilbert *in* Maynard-Smith & Parker 1976, Lederhouse 1982, Alcock 1983, Knapton 1985, Wickman 1985a).

Territorial interactions in butterflies may be characterized by their greater duration (Wickman & Wiklund 1983, Wickman 1985a) and by the peculiar combat behavior of residents (Fitzpatrick & Wellington 1983, Wickman & Wiklund 1983). Territorially related dominance hierarchies and appeasement behavior, although present in other non-social insects (Ewing 1972, Raw 1976), are apparently unreported for Lepidoptera.

Recently Baker (1983) suggested that tropical *Heliconius* butterflies are territorial. Indeed, Seitz (1913) reported seeing male heliconiines ". . . showing some characteristic defect, daily during four weeks flying at about the same place . . . up and down in that characteristic fashion . . . called 'promenading,'" and added, "this habit of flying for hours or half days at a time up and down for a certain distance, turning sharply around at a certain point and returning the same way . . . is nowhere quite so distinct as in the genera *Eueides* and *Heliconius*." On the other hand, Crane (1957) found no evidence for territorial behavior or social hierarchies during insectary studies of six species of Trinidad heliconiines. Murawski (1987), however, observed territory-like stationary defense of flowers by *Heliconius* when floral resources were scarce.

The "large scale promenading" reported for several *Heliconius* (Brown & Mielke 1972, Brown 1972, Cook et al. 1976, Mallet & Jackson 1980) refers to the repeated use of flyways within daily activity ranges, and does not correspond to the behavior reported by Seitz (1913).

We report here observations on male *Heliconius sara thamar* (Hübner), *H. leucadia pseudorhea* Staudinger, *Eueides tales pythagoras* Kirby and *E. aliphera* (Godart) patrolling and expelling conspecifics from territories. Results show that defense is often achieved through specialized ejection behavior, and that invaders rapidly occupy vacant territories. Notes are given for other heliconiines indicating that similar behavior may occur widely in these insects.

STUDY SITES AND METHODS

Systematic observations were undertaken during the austral dry season (July) of 1986 and 1987 in the Serra dos Carajás near Serra Norte, Pará, Brazil (6°03′S, 50°07′W), at sites occupied by promenading (*sensu* Seitz 1913) heliconiine butterflies. *Heliconius sara* (Fabr.), *H. leucadia* Bates and *Eueides tales* (Cramer) were observed along trails near Caldeirão (5°53′S, 50°27′W), an abandoned mineralogical camp at 210 m elev. by State Road PA-275 where it crosses the Rio Itacaiúnas. A second site, with only *H. sara*, was at 650 m on an abandoned spur of PA-275, 2 km N of the iron ore outcrop called "N-1" (5°59′S, 50°16′W). In 1987, males of *H. sara* held territories at three points 100–200 m apart at Caldeirão, here referred to as Areas 1, 2, and 3, and 3 others—4, 5, and 6—arranged linearly 75–100 m apart at the N-1 site. Only Caldeirão was worked in 1986 where *H. sara* territories were observed at Areas 1 and 2. *Heliconius leucadia* was observed only in 1987 defending territories at Areas 1 and 3. *Eueides tales* defended in both years at Area 1. Observations on territorial *H. sara* totaled 1194 min, on *H. leucadia* 664 min, and on *E. tales* 627 min. Notes on territorial *Eueides aliphera* were mostly taken in Costa Rica.

The climate at Carajás is moist tropical with mean annual rainfall 2100 mm (CV = 23%) and mean temperature between 24° and 26°C, depending on altitude. Temperatures and relative humidities during observation periods at Caldeirão were typically near 24°C and 90–95% at 0930 h and 30°C and 75% at 1130 h. Most days were cloudless or with scattered clouds only appearing at the ends of observation periods.

Net-captured butterflies were marked using colored porous-point pens or by cutting notches from wing margins. Individually recognizable animals were merely netted to establish positive species identification. Sex, wing length, and wing damage and wear indicative of age were noted. Behavioral observations were made from trailsides with the aid of a stopwatch and binoculars. In territorial interactions, sex of unmarked nonresident butterflies was inferred from their behavior using Crane (1957) and observations on marked intruders of known sex. Male *Eueides tales* were distinguished from females by their narrower wings. During 1987 observation periods, specific activity of focal individuals (Altmann 1974) was monitored continuously or noted every 15 sec for time budgets. For measured variables we give arithmetic means and use standard deviations (SD) to describe data variation.

RESULTS

Territoriality in *Heliconius sara*, *H. leucadia*, and *Eueides tales* is broadly similar. Defending males divided their time between perching and promenading over 10–15-m-long territories situated in sunlit vegetation corridors. Territory cores were normally delimited by conspicuous features such as overhanging limbs or jutting bushes, and were adjoined by less frequently visited peripheral areas of 5–30 m at one or both ends. Males did not feed when engaged in territorial activity nor were host-plants or other resources consistently present on territories. *Heliconius leucadia* and *H. sara* flew irregular paths 1–2 m wide, usually staying within 1–2 m of neighboring vegetation whereas *E. tales* tended to occupy the center of the approximately 5-m-wide trail clearing. A complete circuit of a core area took approximately 10–15 sec when butterflies did not tarry in localized circling. In all three species, conspecific males were challenged when approaching within 2–3 m of a resident. Pursuing residents normally followed intruders well beyond the patrolled area where they broke off the chases.

Territorial behavior. Discounting courtships and matings, approximately 100 conspecific interactions were observed in each of the three main heliconiine species studied (Table 1). These were almost always lengthy, and continued until one butterfly was either driven from the territory or was able to evade the other.

In *Heliconius sara*, a resident male often followed, rather than chased, a male encroacher, and attempted to get below it. Eighteen of 32 interactions observed in 1986 began with downward flight that tended to bring the two butterflies to ground level (the other 14 were rapid, straightforward chases). In five of these chases, the insects descended almost to the ground, and in two, terminating in relatively open undergrowth, the butterflies flew 5 to 15 cm above the ground, and circled and weaved back and forth over contiguous areas 30–40 cm in diam.

We have observed such ground circling behavior on many additional occasions. Circling may last from a few seconds to a minute or more, after which normally the interloper begins flying upwards with the resident joining to accompany it from below and behind. Low flight apparently prevents the dominant butterfly from getting under and expelling the subordinate. On occasion, and despite apparent attempts to block it, an intruder may slip past a resident and initiate another bout of circling. One series of interactions of this type observed in 1987, involving several individuals, went on for 15 min.

Once the resident succeeded in getting under the trespasser, a characteristic ascending ejection generally followed. Initially, when flying through vegetation, if the intruder became separated from the resident by more than 30–40 cm, the latter usually dashed in the interloper's direction until again immediately below and behind. Once free of confining foliage, an intruder tended to fly slowly upwards, almost hovering, with the resident darting erratically back and forth almost directly underneath it. Ejections gave the impression of the invader being driven upwards by the resident, and in one instance the lower butterfly was seen to dart several times at a subordinate that was ascending at an abnormally slow pace. Butterfly pairs habitually rose 15 m or more to pass over vegetation bounding the territory, and could wander as far as 40 m laterally before the resident disengaged. Expulsions sometimes ended with the intruder bolting away with the resident in pursuit. Territory holders returned from such excursions

TABLE 1. Summary of observations on four species of territorial heliconiine butterflies. SD and number of sample days in parentheses; SD of times in min. Caldeirão (Cald) and N-1 are in the Serra dos Carajás, Pará, Brazil.

Species	Site, area no., year	Marked**	Time elapsed in min, no. days obs.	% time in flight*	Hour of: Arrival	Hour of: Departure	No. territorial expulsions	No. expulsions/h*
Heliconius sara	Cald, 1, 86	No	178, 2	—	1003 (5.7; 2)	1121 (6.4; 2)	26	7.6 (1.4; 2)
	Cald, 2, 86	Yes	92, 2	—	0935 (—; 1)	1107 (17.7; 2)	6	3.9†
	Cald, 3, 87	Yes	294, 3	42.8 (4.8; 3)	0940 (12.2; 3)	1203 (—; 1)	36	7.0 (1.7; 3)
	N-1, 4, 87	No	207, 2	53.1 (9.3; 2)	0927 (21.5; 3)	—	15	4.4 (3.1; 2)
	N-1, 4, 87	Yes	237, 2	42.7 (3.5; 2)	—	—	10	2.6 (0.25; 2)
	N-1, 5, 87	No	154, 2	40.3 (5.0; 2)	—	—	11	4.3†
H. leucadia	Cald, 1, 87	Yes	384, 6	62.5 (12.6; 5)	0943 (12.6; 4)	1057 (18.8; 4)	50	8.8 (4.2; 6)
	Cald, 3, 87	Yes	263, 6	72.3 (5.0; 5)	1000 (14.4; 6)	1047 (29.0; 6)	47	12.8 (2.4; 4)
Eueides tales	Cald, 1, 86	No	321, 3	93.6 (—; 1)	1058 (27.8; 5)	1238 (15.5; 3)	41	7.5 (3.5; 3)
	Cald, 1, 87	Yes	183, 3	95.7 (1.8; 2)	1053 (28.2; 3)	1209 (19.1; 2)	33	12.6 (4.8; 3)
	Cald, 1, 87	No	87, 1	84.4 (—; 1)	1105 (26.3; 3)	1232 (17.4; 3)	23	15.9†
E. aliphera	Costa Rica, 67	No & yes	113, 3	—	0830#	1404 (36.4; 3)	11	5.1†

* Only days with ½ h or more of observation used to estimate means.
** Observations on unmarked butterflies may have included more than 1 individual.
† Expulsion rate calculated as No. territorial expulsions/time elapsed.
# Time of earliest observed patrolling; no arrivals observed.

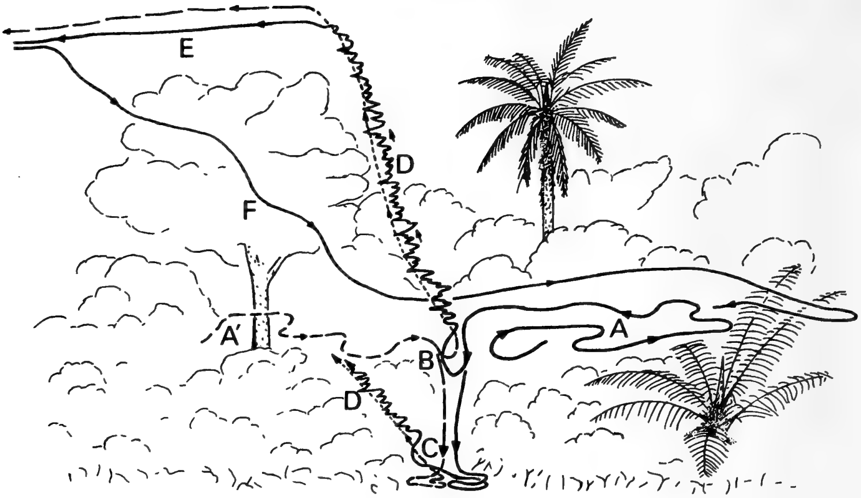

FIG. 1. Typical territorial interaction in *Heliconius sara* at Serra dos Carajás, Pará, Brazil. Resident *H. sara* (solid line) promenades (A) or perches on territory while intruder (broken line, segment length approximately proportional to intruder velocity) patrols along forest margin (A'). One or both butterflies attack, with resident attempting to get below invader (B) and both butterflies sometimes diving to ground where they circle adjacent to one another (C). Intruder starts flying slowly upwards with resident darting back and forth below and behind it (D) until reaching tree-top level where invader may dash away with resident in pursuit (E). Resident returns to territory where it flies briskly over core and peripheral areas as it resumes promenading (F).

generally after a few 10s of seconds, flying briskly over the core and peripheral areas before resuming usual patrolling. Fig. 1 schematizes an ejection sequence in *H. sara*.

Evasive diving in intruding *H. sara* typically led to ground circling, which we interpret as an endurance contest to determine territorial possession. Although in the sequences we observed, territorial residents seemed always to expel invaders, extended contests, sometimes involving several butterflies, were witnessed just before and after changes in ownership. Twice in 1986 and once in 1987, an intruding *H. sara* was seen to attack a promenading resident which dove into the undergrowth. In each of these cases, the trespasser shortly left the area, and the submissive individual resumed patrolling, suggesting that downward dives may also aid less capable males in retaining territories, at least temporarily.

In *Heliconius leucadia*, agonistic territorial behavior seems less complex than in *H. sara*. After the initial rush at an intruder, the resident may expel it by simply following it off the territory from approximately ½ m below and behind. These tandem flights were often leisurely, and

TABLE 2. Behavior of *Eueides tales* during territorial interactions at Serra dos Carajás, Pará, Brazil during 1986 (n = 44) and 1987 (n = 31).

	Behavior of intruder			
	Interaction initiated by resident		Interaction initiated by intruder	
Behavior of resident	Slow departure	Rapid departure	Slow departure	Rapid departure
Chase or following	9	49	1	9
No chase or following	0	1	1	5

normally passed over bounding vegetation, sometimes attaining a height of 15–20 m before the resident suddenly and spontaneously disengaged. At Area 3 one resident often returned to the vicinity of its territory by means of spectacular 40-m-long glides.

Although more or less rapid, apparently aggressive expulsions were common in each of the three main species studied here, we did not observe spiraling pursuits of the type reported for other Lepidoptera (Baker 1983, Fitzpatrick & Wellington 1983). In *H. leucadia*, vigorous circular chases were accompanied by sounds of wing contact indicative of physical combat.

The leisurely exit of trespassing *H. sara* and *leucadia*, when being conducted from a territory by its owner, is almost certainly a form of appeasement behavior, behavior functioning to "inhibit or reduce aggression . . . where escape is impossible or disadvantageous" (McFarland 1981:17). Territorial defense in butterflies typically consists of direct combat, with the dominant positioning itself above its opponent and striking at it with its wings (Fitzpatrick & Wellington 1983, Wickman & Wiklund 1983). In the *Heliconius* studied by us, rapidly flying invaders may be vigorously pursued and perhaps hit by territory holders. In contrast, the slow ejections of heliconiines involve neither aggressive pursuit nor physical combat, and slow intruder movements, perhaps in concert with other behavior, seem to signal submission and stimulate "escort" behavior. Serious challenges are apparently resolved by endurance contests (within a context of appeasement) in *H. sara* and by brief but violent combats in *H. leucadia*.

Trespassing *Eueides tales* usually fled from a territory with the resident in pursuit, although often an intruder left slowly with the resident merely following (Table 2). Less commonly, intruders initiated interactions by flying at residents, but these were usually attacked in return or withdrew rapidly without being chased or followed. When a trespasser being followed from a territory got more than about ½ m ahead of the resident, or entered into foliage, the owner normally dashed after it, which at times provoked a high-speed chase.

Intruding male *E. tales* sometimes evaded pursuit by alighting on leaves. In the seven instances of landing by escorted butterflies, the resident flew agitatedly around the point of last contact. However, only once did the resident find the perched intruder, and in this case dislodge it, apparently by butting and landing on it. In two instances, landing intruders succeeded in fleeing unmolested, and in four, they returned to the territory where the resident found and expelled each once again.

On five occasions an attacked butterfly, rather than flee or retaliate against its aggressor, assumed a descending gliding flight with its wings partially folded. This posture, apparently starting with the attacked individual, seemed to be copied by the attacker which trailed about 20–40 cm above and behind in descending flight. As the butterflies drifted downwards, the lead individual sometimes switched places by darting swiftly behind the trailing one, or one chased the other back up to patrolling altitude, initiating another descent, or chased it off the territory in an expulsion. Although sample sizes are small, data from 1987 suggest that glide chases may occur more frequently when invaders challenge residents (3 times in 7 attacks) than the converse (2 times in 25 attacks). One of the two observed cases of a resident *E. tales* losing its territory to an intruder followed an intruder-initiated attack and 4–5 glide sequences. Glide chases in *E. tales* seem to be ritualized territorial pursuits and, like ground circling in *H. sara*, may constitute assessment behavior that helps resolve disputes in lieu of potentially injurious combat.

Territorial defense. Territorial defense in the heliconines studied at Carajás was concentrated in the late morning (Table 1) with *Eueides tales* and exceptional *Heliconius sara* continuing as late as 1245 h. At Area 1 where territorial males of all three species flew, *H. leucadia* promenaded somewhat lower (about 3–4.5 m from the ground) than *H. sara* (4–5 m) and *E. tales* (5–6 m). The percentage of time spent in promenade flight ranged from less than 50% in *sara* to more than 90% in *tales* (Table 1). *Eueides tales* seemed to glide more than the two *Heliconius* species, perhaps assisted by its smaller size and the generally stronger breezes higher up and around mid-day.

During defense, territory owners typically clashed with conspecifics from 3 to 12 or more times/h, depending on the frequency of intrusions (Table 1). Intruders were almost always successfully intercepted; we have only one record of a probable intruder *H. leucadia* crossing a territory apparently unseen by the perched resident.

Each species had territory holders that rarely lost contests. In *H. sara*, one territory owner marked in 1986 and two marked in 1987 were observed to win all of their 52 conflicts with intruders (Table 1). One of these (1987, Area 4) additionally ejected another male that had set up a territory during a temporary absence. A resident briefly observed at Area 5 also dispossessed a newcomer that took over its territory after it was captured for marking. The two individually recognizable *H. leucadia* won the 97 clashes with trespassers, and in addition, each twice evicted newcomers that took up residence when the owner was away. A marked *E. tales* won 33 of its 34 territorial clashes, and of the 23 conflicts involving unmarked butterflies in 1987, only 1 was for certain lost by the resident butterfly. Reconquest of territories from subsidiary residents was not observed in *E. tales.*

The two *Heliconius* species usually returned to defend the same territory on successive days. The marked *H. leucadia* at Area 1 was observed defending on all nine visits over 19 days, and the Area 3 resident on all six visits over the last eight days we were at Carajás. The latter stayed in Area 3 at least 20 days after marking. On the last day of observation, the Area 3 resident patrolled for only 7 min, and the Area 1 butterfly did not appear. The *H. sara* at Area 3 defended on all seven visits made over the 11 days following marking. An *H. sara* at Area 4 apparently abandoned the territory after being marked, but returned in the role of owner 10 and 11 days later. Similarly, a butterfly at Area 6 took up residence 15 days after it was marked. The marked *E. tales* that returned to defend the Area 1 territory in 1987 was among the defenders present during visits made on three of the four days following marking. On day 4 it was evicted by an intruder and did not reappear on day 5.

The limited nature of territories is indicated by the rapidity with which newcomers reoccupied those left vacant. Three *Heliconius sara* removed from territories at Areas 4, 5 and 6 at N-1 were replaced in 3, 11, and <30 min, respectively. Three others taken from territories at Areas 1 and 2 were replaced by unmarked *H. sara* on the same or following days. On 7 of the 15 occasions in which an identifiable *H. leucadia* left or was removed from a territory (including final daily departures), another individual took up patrolling within 10 min. On the five occasions in 1987 that a *Eueides tales* territory became vacant before noon, a new resident took up promenading within 7 min. Territorial *E. tales* netted in 1986 were also rapidly replaced by newcomers.

The similarity in time intervals between expulsions and that required to reoccupy a vacant territory suggests that most intruders are floating males seeking territories. Intrusion rates in *H. sara* and *H. leucadia* seemed to decline during the morning (Figs. 2 and 3), perhaps because floaters took up searching for mates in other habitats.

Territorial heliconiines usually dashed after any large butterfly passing by. With non-conspecifics, chases normally terminated when the owner came within 10–30 cm of the intruder. Butterflies pursued in this manner included a number of heliconiines, including the other territorial species, and pierids. Heterospecific interactions between similarly patterned *H. sara*, *H. leucadia* and *H. wallacei* Reakirt often included mutual "on-and-off" chasing that, in the first pair of species, sometimes occurred across a territorial boundary in Area 3. We interpret this case of interspecific territoriality as a nonadaptive result of imperfect species recognition (Murray 1971). The *H. sara* and *H. leucadia* at Area 1 simultaneously occupied broadly overlapping territories without markedly interfering with one another. Both *E. tales* and *H. sara* darted after falling leaves, and one of the latter pursued a large bee, and another flew 8–10 m upwards eight times in succession in the direction of lesser yellow-headed vultures (*Cathartes burrovianus* Cassin) gliding low overhead. Apparently a combination of color, apparent size, form, and movement stimulates inspection flights in *H. sara* without the intervention of physical proximity or chemical stimuli.

In 1987, the marked territorial *H. sara* at Areas 3 and 4 each once courted and was rejected by a female, and a marked male patrolling Area 5 was seen to chase a probable female. Before systematic observations were begun, a recently emerged female *H. sara* was found copulating in undergrowth immediately adjacent to Area 5. The marked *H. leucadia* at Area 3 was also observed courting a female. In one encounter, which may represent a courtship flight, the other marked *H. leucadia* at Area 1, rather than follow the intruder from behind, flew 30 cm almost directly below it with rapid wing beats and darting flight reminiscent of the ascending expulsion flight of *H. sara*. The pair rose approximately 20 m directly overhead before drifting out of sight behind trees. The resident returned 14 min later, ousted an unmarked individual that had taken up promenading in the meantime, and resumed patrolling. In 1986 a courtship involving a male *E. tales* of unknown status was observed at Area 1.

Territoriality in other heliconiines. Territorial behavior in *Eueides aliphera* was noted in 1967 in a weedy coffee field 5 km S of San Vito, Puntarenas Province, Costa Rica. One of the several *E. aliphera* present on 27 April, flying about 1 m above the vegetation, seemed especially pugnacious, and dashed after *Heliconius charitonia* (L.), *Hypanartia lethe* (Fabr.), and on three occasions after other *E. aliphera*, in 18 min of observation. A male *E. aliphera* color-marked at the site 5 days later was re-encountered defending a territory at the same place on the six visits made over the next 19 days. This *E. aliphera* won all combats with natural intruders (Table 1) in addition to one with an apparently territorial male that was experimentally herded onto the marked butterfly's territory. The resident attacked and chased this insect into the underbrush. In encounters with other species, the territorial *E. aliphera*

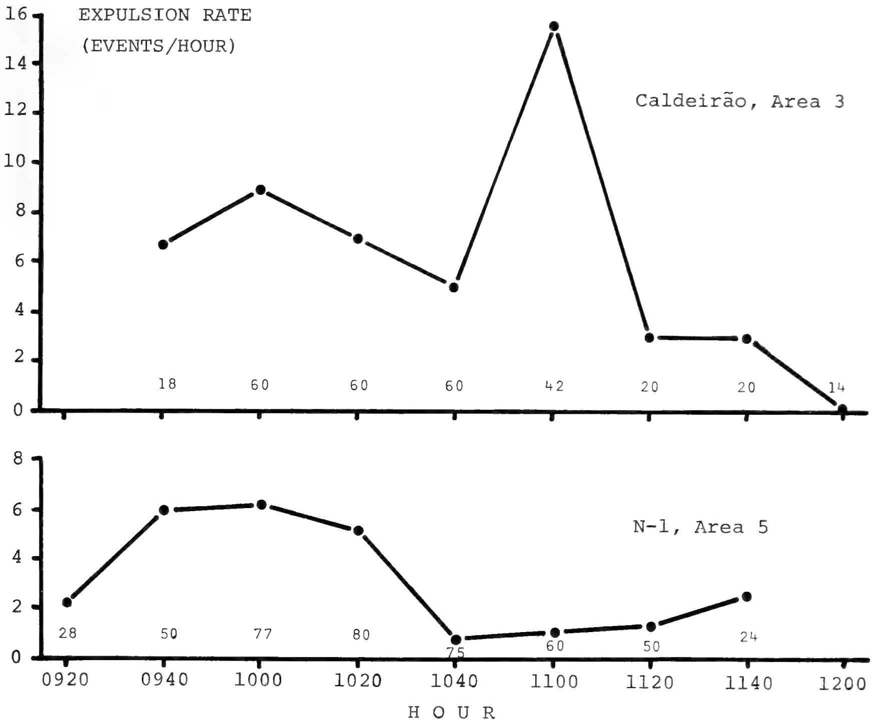

FIG. 2. Expulsion rates for territorial *Heliconius sara* at Serra dos Carajás, Pará, Brazil. Results grouped for intervals of 20 min. Numbers above abscissa show minutes of observation in time interval.

immediately turned away; however, conspecifics were vigorously pursued with pairs usually rising 10–15 m into the air and speeding off the territory. After flying well outside the patrolled area—pairs sometimes flew out of sight—the resident disengaged and returned to the territory. All chases were energetic, and "escorting" analogous to that recorded in other heliconiines was not observed.

The marked butterfly arrived on the territory as early as 0830 and 0910 h, and departures were as late as 1433 h during sunny weather. On one afternoon, the *E. aliphera* flew off the territory and over the canopy of neighboring forest about 50 m away three times during cloudy periods, and returned to patrol during intervening sunny spells.

The territory of the marked *E. aliphera* contained larval food-plant (*Passiflora oerstedii* Mast. *in* Mart.) with immature stages. An *E. aliphera* observed in August 1985 near Serra Norte, Brazil, promenaded above a roadside tangle of *Passiflora* vines on which *E. aliphera* larvae were also feeding. The territories of other heliconiines studied at Cal-

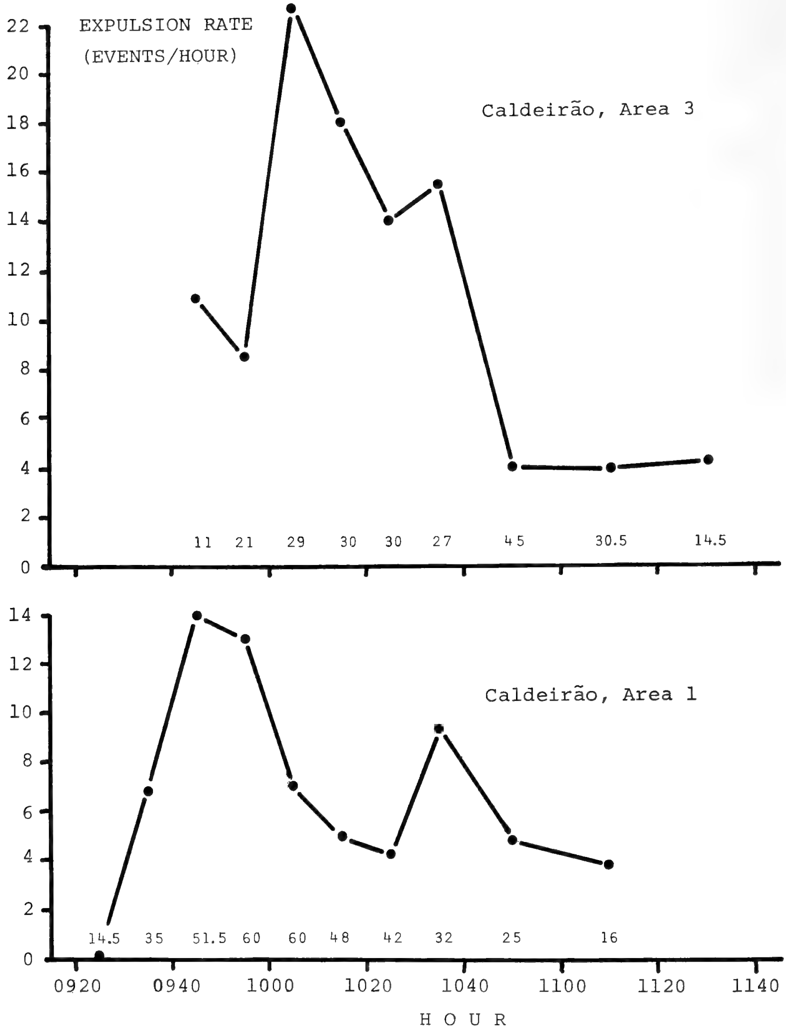

FIG. 3. Expulsion rates for territorial *Heliconius leucadia* at Caldeirão, Serra dos Carajás, Pará, Brazil. Results grouped for intervals of 10 or 20 min. Numbers above abscissa show minutes of observation in time interval.

deirão lacked larval food-plants, although at N-1 an *H. sara* host, *Passiflora* (*Astrophea*) sp., was abundant next to Area 5. This situation seems fortuitous.

Territoriality probably occurs in other heliconiines. In January 1968 near Huixtla, Chiapas, Mexico, two well separated *Eueides isabella* (Cramer) were briefly observed while tracing 10–15-m-long paths over low vegetation in a roadside ravine. Each shared its space with a single similarly behaving *E. aliphera*, although the latter flew somewhat lower (1 m vs. 2 m) above the vegetation. On approaching within 2–3 m of each other, one butterfly would occasionally dash at the other without chasing it. *Heliconius ricini* (L.) promenades in Trinidad (W. W. Benson field notes), and at Caldeirão appears to defend spaces over the forest canopy. *Heliconius antiochus* (L.) at Caldeirão is both aggressive and site-tenacious, and may be territorial. However, *Eueides vibilia* (Godart) promenading near N-1 did not fight or expel closely approaching conspecifics. Seitz (1913) reported promenading to be especially well developed in *E. aliphera, E. isabella* and *Philaethria dido* (L.). We have detected no sign of promenading or area defense in *Heliconius erato* (L.), *H. melpomene* (L.), *H. wallacei, Eueides lybia* (Fabr.), or *Dryas iulia* (Fabr.) at any locality.

DISCUSSION

The heliconiines studied here are clearly territorial. Conspecific males rarely remained together in a promenade area longer than the few seconds necessary for the resident to find and expel the encroacher. In the absence of an owner, territories were rapidly taken over, and the time for this to occur was comparable to the average interval between intrusions, suggesting that most intruders are territory-seekers. In three species, both residents and invaders seem to possess a repertory of species-specific behaviors for use during territorial confrontations.

Territoriality in butterflies seems based on male defense of encounter sites where chances of mating are high (Baker 1983, Wickman 1985b, Courtney & Anderson 1986). The territorial heliconiines studied by us probably also defend rendezvous points. Although we observed few courtships and no matings by known territorial males, female heliconiines seem often to mate only once (Crane 1957, Gilbert 1976), and their rarity is expected in long-lived insects that mate infrequently (Alcock 1983). The places defended by *Heliconius sara, H. leucadia* and *Eueides tales* are humid, sunny, and seem protected from wind, and possibly attract receptive females. *Eueides aliphera* defends more exposed sites, and its territoriality may be in part based on the despotic control of host-plant patches where females are likely to emerge.

Territorial combat in heliconiines contrasts greatly with courtship. In *Heliconius sara* and related species, courting males hover above and in front of females (Crane 1957, pers. obs.). Territorial males fly below intruders or harass or "escort" them from behind. Owner behavior seems adaptive since intruders are denied searching foliage for receptive mates, taking the profit out of trespassing. However, trespassing and skirmishing may still benefit interlopers in assessing vacancies and discovering weak residents (Lederhouse 1982, Wickman & Wiklund 1983, Grafen 1987).

Promenading heliconiines fly slowly and seemingly with little effort through their territories. Butterflies are conspicuously exposed under such circumstances, and aposematic unpalatability in *H. sara* (Brower et al. 1963), and probably the other species studied, must compensate for much of the added risk of predator attack. Butterflies that are profitable prey may be selected to reduce conspicuousness by perching more, or to reduce catchability by patrolling territories using energetically costly acrobatic flight, or both.

Recent works on territoriality (Bitzer & Shaw 1983, Wickman 1985a, Dennis & Williams 1987, Shreeve 1987) equate Scott's (1974) terms "perching" and "patrolling" with territorial and nomadic mating strategies, respectively. Although this terminology is misleading when applied to a species such as *Eueides tales,* which spends more than 90% of its time in patrolling flight and combats, it is probably too intrenched to change. Promenading, *sensu* Seitz (1913), may be a useful alternative to designate site-faithful patrolling.

Given the prowess of resident *Heliconius sara* and *H. leucadia* in rivalries, unrestrained fights may be risky. The fact that intruders often flee, flying at what seems to be maximum speed, suggests that some chance of injury exists. The submissive stance of many intercepted intruders is noteworthy, and, combined with a less aggressive dominance of the resident, results in slow but safe and effective expulsions. To our knowledge these are the first reports of stereotyped appeasement behavior in butterflies, and one of the few among nonsocial insects (Fitzpatrick & Wellington 1983). They are also apparently the only known cases of relatively pacific dominance relations inserted in territorial behavior sequences.

The ground-circling behavior of *H. sara* seemed to help submissive individuals avoid ejection, and may be, as appears with the glide chases of *E. tales*, a ritualized contest used to decide territorial ownership. Whatever their precise origins and functions, these behaviors are clearly tied to presumably adaptive defense of territory.

Territoriality in *Heliconius sara* and *H. leucadia* is not simply explained by current hypotheses. In general, female attraction to encounter sites (and competition for them by males) is thought to stem from male rarity and the increased speed of mating permitted by their use (Shields 1968, Lederhouse 1982, Alcock & O'Neill 1986). However, nonterritorial male *H. sara* and *H. leucadia* were common in our study, and *sara* is frequently abundant throughout its range, suggesting that isolated females would be quickly found and mated and that rendezvous sites may be superfluous. On the other hand, the known territorial

Heliconius lay eggs in batches that give rise to synchronously developing groups of larvae. It seems likely that emergence of large broods of females in these species may commonly overtax mating capacity of local males and result in pulses of virgin females that might profitably seek mates at encounter sites. The importance of intrasexual competition among females is manifest in the use of what is apparently an aggregating sex pheromone by female pupae of *H. sara* (W. W. Benson field notes), similar to that of the related *H. charitonia* (Edwards 1881, Gilbert 1975) and *H. hewitsoni* Staudinger (J. T. Longino *in* DeVries 1987). Pupal pheromone production may aggravate mate shortages by concentrating males at pupation sites well ahead of mating. We believe that common heliconiines that lay solitary eggs would tend to have a more uniform production of, and a more assured rapid mating of, receptive females, and thus tend not to be territorial. Territoriality in *Eueides tales* and *E. aliphera* may be explained by current theory.

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REPRODUCTIVE TRACT DEVELOPMENT IN MONARCH BUTTERFLIES OVERWINTERING IN CALIFORNIA AND MEXICO

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ABSTRACT. Reproductive organs of male and female monarch butterflies captured in December, February, and March in overwintering colonies in both Mexico and California were examined as soon as possible after capture. In addition, response of such organs to incubation in summer-like conditions was determined for animals from both locations in all three months. Results demonstrated numerous similarities between the two populations, indicating comparable stages of reproductive tract development in the two locations. However, a higher percentage of mating was recorded in Californian females, and data obtained after incubation indicated that diapause might last longer in both sexes of Mexican monarchs.

Additional key words: Nymphalidae, *Danaus plexippus*, diapause, overwintering.

North American monarch butterflies (*Danaus plexippus* L.) aggregate in two major overwintering locations. One is California, where several colonies form each winter (Lane 1984). The other is in the mountains of the states of Michoacan and Mexico in Mexico, where multiple overwintering colonies have now been located (Calvert & Brower 1986). The Mexican colonies are principally aggregations of monarchs that emerge in the eastern United States and Canada, while the Californian colonies are the major overwintering sites for monarchs originating west of the Rocky Mountains. Although it might be reasonably assumed that overwintering monarchs from both locations were in similar reproductive states, direct comparative evidence concerning the reproductive status of such animals is not available. To obtain such evidence, we weighed reproductive organs in both sexes collected in December, February and March from colonies in both locations. Additionally, we compared such weights to those found at eclosion, and to those found when animals from both locations were exposed to summer-like environments. Our data demonstrate striking similarities, and some differences, between the two populations.

MATERIALS AND METHODS

Butterflies came from three localities. Those providing data on eclosion values and prediapause (Herman 1981) response to summer-like conditions were obtained from larvae reared outdoors on *Asclepias syriaca* L. in June and July in Minnesota. Larvae were collected as first instars immediately after hatching from eggs laid by wild-caught females. Eclosion data came from adults dissected on the day of emergence. Prediapause response to summer-like conditions was measured by holding newly emerged adults, fed daily with 30% honey, in incubators at 25°C on a 16-h photophase for 10 days before dissection. Californian monarchs were airmailed to Minnesota from the Natural Bridges colony near Santa Cruz. These insects were either dissected immediately upon arrival or incubated as above before dissection. Animals from California were examined in three separate years (1977–79), and all results were pooled. Diapause values (Herman 1981) were obtained by holding animals captured during the principal portion of the diapause period (September–November) in summer-like conditions for 10 days before dissection. Diapause data were also obtained over a 3-yr period from animals captured in both Minnesota (September) and California (October–November), and the results were pooled. Mexican animals were collected during 1983–84 at the Chincua and Herrada colonies in Michoacan and Mexico, respectively, and airmailed (in three separate shipments) to Minnesota as soon as possible (within eight days) after capture. These adults were either dissected immediately or incubated as above before dissection.

Anatomy of the reproductive tracts of both monarch sexes, and terminology applied to the tracts, is discussed elsewhere (Urquhart 1960, Herman 1975). Reproductive organs were dissected, cleaned of fat body, blotted to remove excess saline, and weighed to the nearest 0.01 mg. Mature oocytes, defined as oocytes with chorionic ridges, were counted in both ovaries in all females. Mated females were those with sperm in the spermatheca, which in monarchs is that portion of the receptable gland proximal to the common oviduct. Rear-wing maximal length was measured to the nearest 0.5 mm with a ruler. Data were analyzed with Student's *t*-test. In this report "significant" refers to statistical significance at the $P \leq 0.05$ level. All data are presented as mean ± SE. Some of the reproductive tract weight data obtained at eclosion, in prediapause, and in diapause have been reported earlier (Herman 1981, 1985, Herman et al. 1981) but this report includes new data from additional animals.

RESULTS

Wing lengths. Females had rear wing lengths of 37.7 ± 0.1 mm ($n = 145$) and 37.8 ± 0.1 mm ($n = 201$) in the Minnesotan and Mexican populations, while males had significantly larger wings (38.1 ± 0.1, $n = 145$ and 38.2 ± 0.1, $n = 188$) in the two populations, respectively. Monarch wings examined at eclosion were not significantly different from those of the Minnesotan and Mexican populations. Animals obtained from California in October–November had significantly smaller wings than those from Mexico or Minnesota: 37.5 ± 0.1 mm (n = 161) and 37.9 ± 0.1 mm (n = 141) for females and males, respectively. In addition, Californian adults of both sexes exhibited significant declines of wing length in February–March, to 37.0 ± 0.2 mm (n = 114) and 37.6 ± 0.1 mm (n = 201) for females and males, respectively. These latter values were the lowest recorded during this study.

Reproductive organ weights. Mexican and Californian females showed no significant weight differences in the ovaries (OV) and colleterial glands (CG) on arrival in either December or February, but both organs were slightly and significantly heavier in Californian females in March (Fig. 1). The OV and CG weights of Mexican animals on arrival never exceeded the eclosion values, but those of the Californian adults in March were significantly heavier than at emergence. Mature oocytes (MO) were never observed on arrival in females from either location.

Response of the OV and CG to summer-like conditions was qualitatively similar, but quantitatively different, in the two groups of females (Fig. 1). Incubated Californian females in all three months had final organ weights significantly above the diapause value, generally comparable to or above those in prediapause females, and larger than those of incubated Mexican females. Mexican females exhibited OV and CG weights after incubation that were close to the diapause values in December, but well above those values in February and March. Mating was more often observed in Californian animals, with 29%, 37%, and 96% mated in December, February and March, respectively, while Mexican females exhibited only 17%, 8%, and 15% mating, respectively, in the same months.

Accessory glands (AG), tubular glands (TG), and ejaculatory ducts (ED) were typically heavier than at eclosion in males examined on arrival (Fig. 2). There were no significant differences in gland weights on arrival in December or March between the Californian and Mexican males, but all three glands of Californian males were significantly heavier in February. After incubation, all three glands of Californian males exhibited responses significantly above those of diapause males, and similar to prediapause animals, in all three months (Fig. 2). Mexican male glands showed lesser responses only in December and February, and the December response of TG and ED approached the diapause value. All three male glands exhibited the same level of development in both groups of incubated males in March.

On arrival, testes (TE) in both populations were always smaller than at eclosion, while seminal vesicles–vas deferens (SV) complexes were always larger (Fig. 3). In addition, Californian males had comparable TE, but significantly smaller SV, in all three months. Incubated Cali-

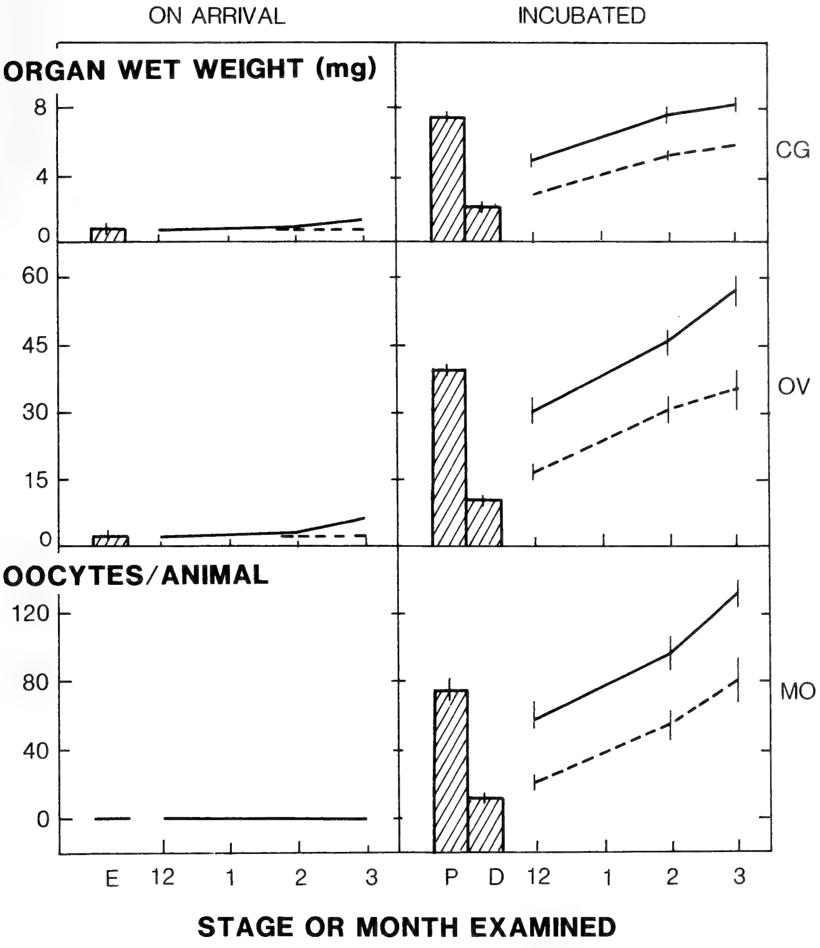

FIG. 1. Wet weights of colleterial glands (CG) and ovaries (OV), and total number of mature oocytes (MO) in females collected in Californian (solid lines) and Mexican (dashed lines) overwintering colonies. On-arrival data obtained from at least 17 animals/data point, and incubated data obtained from at least 18 animals/data point. E = organ weights at eclosion (n = 26), P = organ weights from prediapause animals (n = 47), and D = organ weights from diapause animals (n = 85); 12 = December, 1 = January, 2 = February, and 3 = March. Vertical lines indicate SE; negligible values are omitted.

fornian males consistently had both TE and SV near the diapause level, while Mexican animals exhibited slightly smaller TE and significantly larger SV (Fig. 3).

Receptacle glands (RG) and bursae copulatrix (BC) showed little variation from eclosion level in Mexican females on arrival, as did RG and BC of December females from California (Fig. 3). Both organs

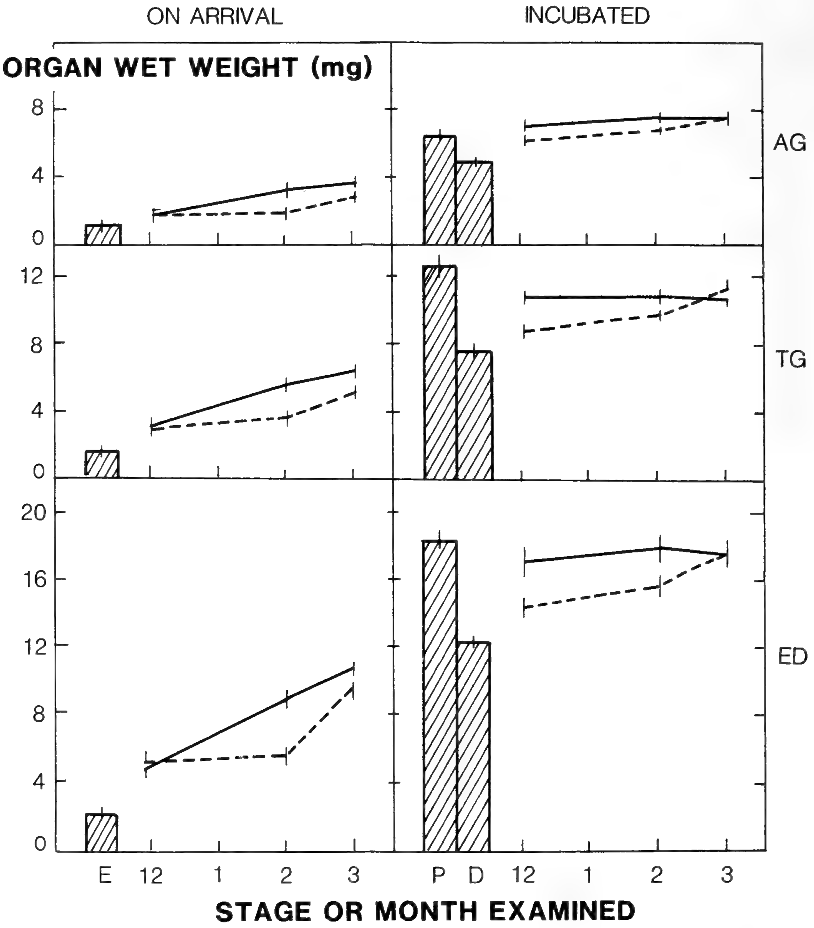

FIG. 2. Wet weights of accessory glands (AG), tubular glands (TG), and ejaculatory ducts (ED) from monarch males collected in Californian and Mexican colonies. On-arrival data obtained by dissection of at least 27 animals/data point, and incubated data obtained from at least 24 animals/data point. Data presentation and other abbreviations as in Fig. 1. Values of n for E, P, and D were 35, 59, and 79, respectively.

exhibited weights significantly above eclosion values in Californian animals examined on arrival in both February and March. Incubation reduced RG size to similar values in both groups of females (Fig. 3), and caused little BC weight change.

DISCUSSION

Our data show major similarities and some differences in the reproductive tracts of monarch butterflies from the Mexican and Californian

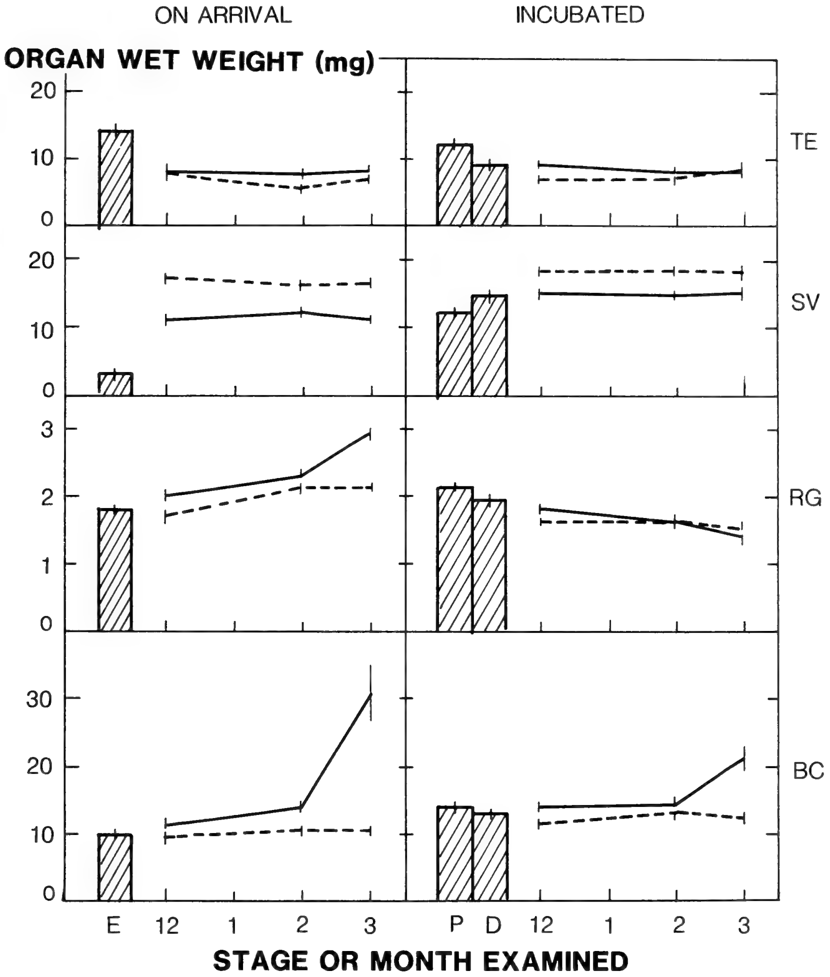

FIG. 3. Wet weights of testes (TE) and seminal vesicles–vas deferens complexes (SV) from males, and of receptacle glands (RG) and bursae copulatrix (BC) from females, collected in Californian and Mexican colonies. Other abbreviations, data presentation, and n values in Figs. 1 and 2.

overwintering colonies. Females from both populations possess OV and CG that are nearly identical in December and February, and only slightly different in March. In addition, these two organs are indistinguishable in December and February, in both groups of monarchs, from those of insects emerging in summer in Minnesota. Female RG and BC are also indistinguishable in December and similar in February in the two populations, but both are larger in Californian females in March.

We believe the differences noted in weights of the female reproductive organs of the two groups in March may be due to a higher percentage of mating in the Californian animals. This conclusion is supported by reports that mating increases juvenile hormone levels in female monarchs (Herman & Barker 1977), and that juvenile hormone stimulates the development of all four organs in this species (Herman 1985). Moreover, the considerable difference in BC weights appears to be due principally to the greater number of Californian females carrying spermatophores in their BC.

Female OV and CG also exhibit qualitatively similar responses to incubation in summer-like conditions, that is, both groups of animals exhibit their lowest response in December and their highest in March. Again, we believe the best explanation for the quantitatively greater response of these organs in Californian females is the higher percentage of mated females in the Californian colonies. Response of female RG to incubation mimics that of posteclosion animals in both groups, that is, the glands diminish in weight after exposure to summer-like conditions for 10 days (Herman et al. 1981). Response of BC in both groups is comparable to that of both prediapause and diapause monarchs: the weights of these organs after incubation are usually slightly above those recorded at eclosion. The relatively high weight of BC in incubated Californian females we again attribute to a higher proportion of mated females.

For most of the overwintering period, the tracts of both groups of females resemble those of females at eclosion in Minnesota. Both groups of monarchs also show remarkable similarity in the response of the female reproductive tract to incubation. Our data do suggest, however, that diapause may last longer in Mexican females than in Californian, since a response of the OV and CG to incubation similar to that of diapause animals is found only in Mexican females in December.

Males from the two colonial sites also exhibit strong similarities and some differences. Both groups of animals have AG, TG and ED of similar size and significantly above eclosion values in both December and March. However, the increased weight noted in Californian males in February was delayed until March in Mexican males. On arrival, both groups also possessed TE that were comparable and smaller than those of newly emerged males. The SV of Californian animals were significantly smaller on arrival, perhaps resulting from the additional mating occurring in the Californian colonies.

The response of male organs to incubation was also similar in both groups. AG, TG and ED exhibited pronounced responses that were comparable in February and indistinguishable in March. Mexican males, however, exhibited a reduced response of those three organs in December, suggesting that male diapause might also last somewhat longer in the Mexican colonies. No striking changes were observed in the TE or SV from either group after incubation. Thus, male monarchs from the two colonial locations exhibited only minor differences in the weight of their reproductive organs on arrival, and in the response of those organs to incubation. The organs were, with the notable exception of the SV, frequently indistinguishable on arrival and they normally exhibited similar responses to summer-like conditions.

The above differences in Californian and Mexican monarchs do not appear to be due to size differences of monarchs in the two populations. As indicated by our data on wing length, Mexican monarchs were somewhat larger than Californian, but exhibited similar or smaller reproductive organs on arrival.

We conclude that overwintering monarchs of both sexes in both California and Mexico maintain similar and low levels of reproductive tract development through most of the overwintering period, and that monarchs from both populations become more responsive to summer-like conditions as the overwintering period progresses. The data suggest that the postdiapause response of the reproductive tract to summer-like conditions may be delayed in both sexes in Mexico, that is, reproductive diapause may last longer in monarchs in the Mexican colonies. The observed quantitative differences in the condition of the tracts, and of their responses to incubation, may be due principally to the greater percentage of mated females observed in Californian animals. Why such a difference in mating exists in the two locations remains to be determined.

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INSTAR NUMBER AND LARVAL DEVELOPMENT IN *LYCAENA PHLAEAS HYPOPHLAEAS* (BOISDUVAL) (LYCAENIDAE)

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ABSTRACT. The arctic-alpine butterfly *Lycaena phlaeas hypophlaeas* (Boisduval) may have either four or five larval instars, the number apparently being fixed at oviposition. Factors affecting instar number were investigated in a laboratory colony of *L. p. hypophlaeas* from the White Mountains of California. Adults in oviposition cages were subjected to outdoor ambient conditions of day-length and temperature, but larvae were reared indoors under nearly constant conditions (ca. 16 h light, 25°C). Larvae with five instars predominated when oviposition occurred during short days (<11 h light) and low maximum diurnal temperatures (ca. 22°C). When oviposition occurred during longer days (>12 h light) and higher mean diurnal temperatures (ca. 33°C) most larvae had four instars. Larvae having five instars required about 70% longer to mature than larvae having four instars. Although diapause is not obligate, overwintering probably occurs as larvae, which are more resistant to cold than are pupae and adults.

Additional key words: diapause, Lycaeninae, *Oxyria digyna*.

The primarily holarctic lycaenid butterfly *Lycaena phlaeas* (L.) inhabits a wide range of habitats from sea level to ca. 4000 m elevation. Various subspecies of *L. phlaeas* in Asia, Europe, and eastern North America are multivoltine, polyphagous (primarily on *Rumex* species), and common at low elevations. However, *L. p. hypophlaeas* (Boisduval) of western North America is univoltine, apparently monophagous on *Oxyria digyna* (L.) Hill, and confined to arctic-alpine habitats (Ferris 1974). This subspecies occurs in isolated colonies above 3000 m in the central Sierra Nevada (Bishop Pass to Sonora Pass) and White Mountains of California; collection records indicate a flight period from mid-July to early September (Shields & Montgomery 1966, Ferris 1974). Its habitat is one of extreme (especially cold) and unpredictable weather for much of the year; even in summer there may be frost and occasional snow. The restricted range of this subspecies is puzzling since suitable hosts (*Rumex* spp.) are widespread at lower elevations in California where they are utilized by other *Lycaena* species (Ballmer & Pratt, 1988). Also puzzling is the fact that, unlike other California Lycaeninae, *L. p. hypophlaeas* may have either four or five instars (Ballmer & Pratt, 1988). Investigations reported here concerning the biology of *L. p. hypophlaeas* were undertaken primarily to clarify instar number under controlled environmental conditions. Additional observations on growth rate and cold tolerance of stages may help explain the ability of this butterfly to survive in the arctic-alpine zone.

MATERIALS AND METHODS

A laboratory culture of *L. p. hypophlaeas* was derived from progeny of a single female captured in the White Mountains (California, Mono Co., White Mt., elev. ca. 4000 m, 26 July 1987) by J. F. Emmel. A single mature larva was also found on *Oxyria digyna* (same data) by G. F. Pratt. No other likely host was encountered at the collection site, although at a lower elevation (3300 m) a few km away, *Rumex paucifolius* Nutt. ex Wats. was abundant and utilized as a larval host by *Lycaena cupreus* (W. H. Edwards) and *L. editha* (Mead). One of us (G.F.P.) has also found larvae of *L. p. hypophlaeas* on *Oxyria digyna* in the nearby Sierra Nevada (Mono Co., Mt. Dana, elev. 3600 m, 7 August 1985). *Oxyria digyna* is also a host for other arctic-alpine populations of *L. phlaeas* in North America (Ferris 1974, Harry 1981).

In captivity, adult butterflies were confined with *Rumex crispus* L. and *R. acetosella* L. in a screened cage (0.3 m × 0.3 m × 0.3 m) for mating and oviposition. The cage was outdoors in a sheltered location with partial sun exposure. Ova were brought indoors and larvae were reared in quart (0.95-l) plastic food containers on leaves of both *R. acetosella* and *R. crispus*. Pupae were transferred to the screened cage for eclosion.

Nineteen neonatal larvae from ova produced during the first week of September (long-day ova) were placed individually in 7-dram (25-ml) plastic vials and reared on leaves of *R. crispus*. Leaves were replaced as needed (usually every 2–3 days for young larvae and daily for last instars). A second group of 23 neonates from ova produced at the end of October (short-day ova) was reared under slightly different conditions. These larvae were kept individually in 25-dram (90-ml) plastic vials with two 25-mm-diam. screened ventilation openings, and fed leaves of *R. crispus*. A small hole in each lid allowed the leaf stem to protrude for immersion in water contained in a second vial; this permitted leaves to remain fresh longer while the ventilation prevented mold which occasionally appeared in the smaller nonventilated vials used earlier. All larvae were reared indoors at 25 ± 3°C (brief temperature fluctuations resulted from operation of indoor heating and cooling equipment). Larvae were inspected daily for signs of ecdysis. Dates of ecdysis were recorded for each larva, and head capsules were measured using a microscope and ocular micrometer.

Total illumination from indirect natural daylight and artificial lighting from overhead fluorescent lamps exceeded 16 h per day. Only adults and ova were exposed to natural (outdoor) diurnal photoperiods and temperatures. There were 12.5 h of daylight (sunrise to sunset) on 10 September, the mean eclosion date for long-day ova, and 10.75 h of daylight on 3 November, mean eclosion date for short-day ova; the effective period of daylight on both dates may have been somewhat longer. Mean maximum and minimum diurnal temperatures for the seven days preceding mean eclosion dates were 33.3°C and 13.3°C, respectively, for long-day ova and 21.5°C and 12.8°C, respectively, for short-day ova.

Four mature larvae from long-day ova were preserved and the remainder allowed to pupate. Four pupae were refrigerated at 5°C for 28 days to test the effect of mild but prolonged chilling. All larvae from short-day ova were reared to adults without chilling.

Other experiments tested the effect of extreme chilling on additional larvae, pupae, and adults. Ten second instars and 12 fourth instars (all destined to have 5 instars) were removed from the colony during December (from short-day ova) and placed in 25-dram (90-ml) ventilated vials, as described above, with fresh host leaves.

Vials were refrigerated (5°C) for 21 days, then wrapped in damp paper towels and placed inside larger sealed jars which were kept at −7°C for 28 days. After the freezing treatment, jars were allowed to thaw at 5°C for 24 h; the vials were then removed, larval condition was assessed, and survivors were given fresh host leaves; rearing continued at 25°C. Ten pupae were similarly treated (7 days at 5°C followed by 28 days at −7°C).

While refrigerated at 5°C, second instars fed considerably, but fourth instars did not feed. Leaves damaged by feeding were dried in a press, weighed, and photocopied. The paper images were cut out and weighed; then their feeding-damaged portions were cut out and weighed to determine percent of feeding damage. The latter values were then used to calculate quantity of leaf tissue eaten per larva.

On several occasions it was noted that brief periods (1–6 h) of exposure to −7°C were not lethal to adults; but death usually occurred after 2–3 consecutive exposures of such duration. The effect of milder but more prolonged exposure to cold was tested by refrigerating 13 freshly eclosed adults at 5°C for 30 days. Adults were placed individually in 25-dram (90-ml) ventilated vials which were then placed inside plastic bags with damp paper towels and refrigerated.

Statistical significance of differences in head size and instar duration was determined by *t*-tests.

RESULTS

Instar number and duration. Mean duration of each larval instar and overall larval and pupal stages are presented in Table 1. Only one male and six females from long-day ova are included owing to loss of gender data for the remainder; therefore, discussion of sex-correlated differences in development rates is restricted to larvae from short-day ova. In general, females developed more rapidly than males, especially in the third and 'extra' instars (fourth instar of five-instar larvae). Sex-correlated differences in development times among larvae from short-day ova were most significant for third instars (P = 0.02 and 0.051 for four- and five-instars, respectively); for other larval instars P ranged from 0.13 to 0.84. Mean larval stage duration of five-instar larvae was greater than that of four-instar larvae; the difference for males (ca. 35% greater) is not significant (P = 0.08), but for females (ca. 49% greater) it is (P = 0.008).

Most larvae from long-day ova (17 of 19) had four instars, and required a mean of 23 days to pupate (both sexes combined); one larva had five instars, and another, which died of a whitish fungal infection in the fourth instar, would have molted again judging from its head size had it survived. Short-day ova produced mostly five-instar larvae (17 of 23), and required a rounded mean of 27 days to pupate (both sexes combined); remaining larvae had five instars and required a rounded mean of 41 days to pupate. Nevertheless, there was considerable individual variation and some overlap in developmental time ranges. It is remarkable that among both four- and five-instar larvae, some individuals remained as larvae about twice as long as others; range of larval duration for all larvae was 13–59 days. No significant differences in pupal duration were found with respect to sex, number of larval instars, or day length.

Head size. Measurements of head widths indicate no significant sex-related differences (P = 0.47, 0.21, 0.40, and 0.55 for instars 1, 2, 3, and 4, respectively, of five-instar larvae from short-day ova). There were also no significant differences in mean head size between four- and five-instar larvae from short-day ova for instars 1, 2, and 3 (P = 0.39, 0.54, and 0.78, respectively). Therefore, data were pooled for all larvae in comparing head sizes of first, second, third, and 'extra' instars of larvae conceived under long- and short-day conditions (Table 2). Since most larvae were reared to pupation, and the last-instar head capsule was invariably deformed at pupation, the head widths of last-instar larvae included in Table 2 are based primarily on preserved larvae reared concurrently. The mean first-instar head width of larvae from short-day ova was slightly but significantly (P = 0.015) larger than that of long-day ova. The head size of the 'extra' (fourth) instar of five-instar larvae was intermediate between that of third and last instars; thus, some growth occurred in all instars.

Values presented here for head size should not be considered typical of all populations of *L. p. hypophlaeas*. The mean last-instar head width

TABLE 1. Larval and pupal duration of *Lycaena phlaeas hypophlaeas* indoors at 25°C.

Sex	No. larval instars	N	Mean no. days ± SD of larval instars					Mean larval stage (days ± SD)[1]	Mean pupal stage (days ± SD)
			First	Second	Third	'Extra'	Last		
					Long-day ova				
Male	4	1	4.0	6.0	8.0	—	5.0	23.0	8.0
Female	4	6	3.3 ± 0.5	6.0 ± 1.7	5.2 ± 1.5	—	6.0 ± 1.3	20.5 ± 4.0	8.2 ± 1.2
					Short-day ova				
Male	4	2	4.5 ± 0.7	7.0 ± 0	13.5 ± 0.7	—	7.5 ± 0.7	32.5 ± 0.7	8.0 ± 0
Female	4	4	5.0 ± 2.2	6.8 ± 1.9	6.0 ± 2.6	—	6.3 ± 1.0	24.0 ± 6.1	7.8 ± 0.5
Male	5	12	4.5 ± 0.7	7.8 ± 1.9	13.2 ± 1.8	11.1 ± 6.7	7.3 ± 1.8	43.8 ± 8.2	8.8 ± 1.0
Female	5	5	4.2 ± 0.5	8.0 ± 1.2	11.2 ± 1.6	6.2 ± 3.2	6.2 ± 0.8	35.8 ± 3.4	8.2 ± 0.8

[1] Egg hatch to pupation.

TABLE 2. Mean head width of *Lycaena phaeas hypophlaeas* larvae reared indoors at 25°C.

Oviposition day length	Mean head width ± SD of larval instars									
	First	N	Second	N	Third	N	'Extra'	N	Last	N
Long	0.24 ± 0.01	14	0.43 ± 0.02	17	0.72 ± 0.06	18	0.89 ± 0.01	2	1.25 ± 0.04	8
Short	0.26 ± 0.01	21	0.43 ± 0.02	23	0.72 ± 0.03	23	0.87 ± 0.03	17	1.22 ± 0.04	5

(1.46 mm) of 10 *L. p. hypophlaeas* larvae from Mount Dana in the Sierra Nevada is 17% larger than that of 13 larvae from the White Mountain colony (1.24 mm); this difference is highly significant ($P = 0.00002$).

Cold exposure. The mortality rate from freezing was similar for second- and fourth- ('extra') instar larvae. Six (of 10) second instars exposed to −7°C for 30 days survived, as did 7 (of 12) fourth instars exposed to the same conditions. During 21 days of exposure to 5°C (before freezing), second instars consumed a mean 0.47 cm^2 (0.002 mg, dry wt.) of leaf tissue.

Adults and pupae were less tolerant of cold. Although all 4 pupae exposed to 5°C for 28 days survived and produced adults, only 1 of 10 pupae frozen (−7°C) for 28 days eclosed, and it was unable to properly expand its wings. All 13 adults refrigerated at 5°C for 30 days perished.

CONCLUSIONS

Instar number in *Lycaena p. hypophlaeas* is variable; four instars are prevalent under warm, long-day (late summer) conditions while five instars predominate when days are cooler and shorter in fall. Number of instars is apparently fixed at oviposition. Developmental time is greater for five-instar larvae than for four-instar larvae. Similar lengthened larval development and extra molts, but without apparent growth, in response to short day-length have also been reported in the multivoltine *L. p. daimio* Seitz of Japan (Sakai & Masaki 1965, Endo et al. 1985).

The greater development time required for *L. p. hypophlaeas* larvae produced under short-day conditions is probably important in winter survival. Unlike at least most other California *Lycaena* species, *L. p. hypophlaeas* does not have an obligate diapause. However, an extended larval duration induced by short day-length and further promoted by reduced activity due to cold fall and winter temperatures reduces the possibility of premature maturation and subsequent exposure of the less cold-tolerant stages to winter conditions. The great variability in development time probably also contributes to survival, since it ensures that some individuals are likely to be in the most cold-tolerant (larval) stage at all times of the year.

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GENERAL NOTES

STATUS OF THE PAPILIONID TYPES *PAPILIO STEWARTI* AVINOFF AND *P. MORRISI* EHRMANN

Additional key words: taxonomy, Neotropics.

Recently we reviewed the types and some newly acquired specimens of several papilionid taxa of uncertain taxonomic status known only from extremely small samples (Johnson, K., R. Rozycki & D. Matusik 1985, J. N.Y. Entomol. Soc. 93:99–109, 1986, 94:

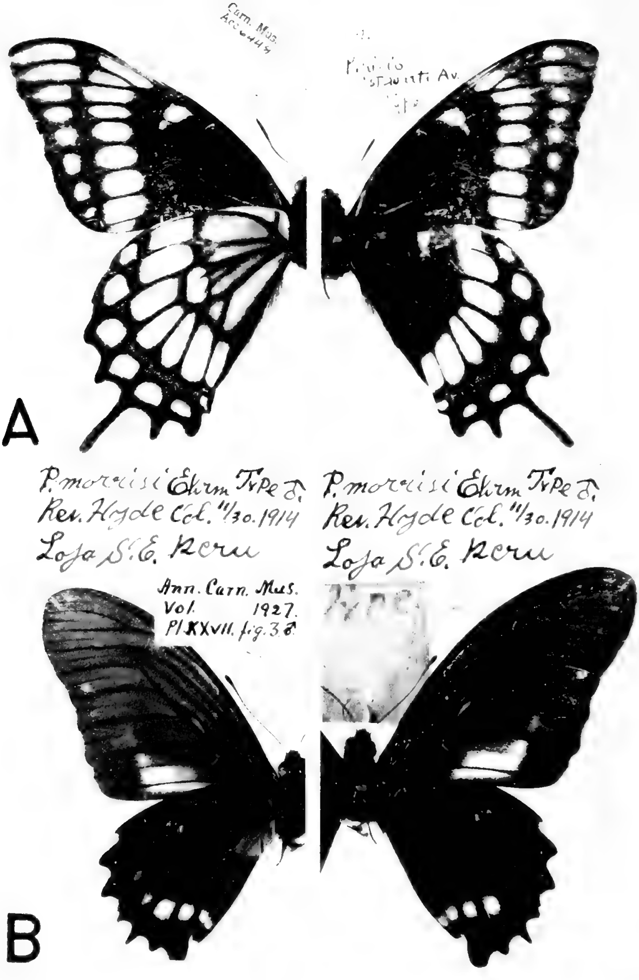

FIG. 1. *Papilio* holotype males. **A,** *P. stewarti,* upper surface on right, under on left; forewing expanse, base to apex, 50.0 mm; **B,** *P. morrisi,* as above; forewing expanse 40.0 mm.

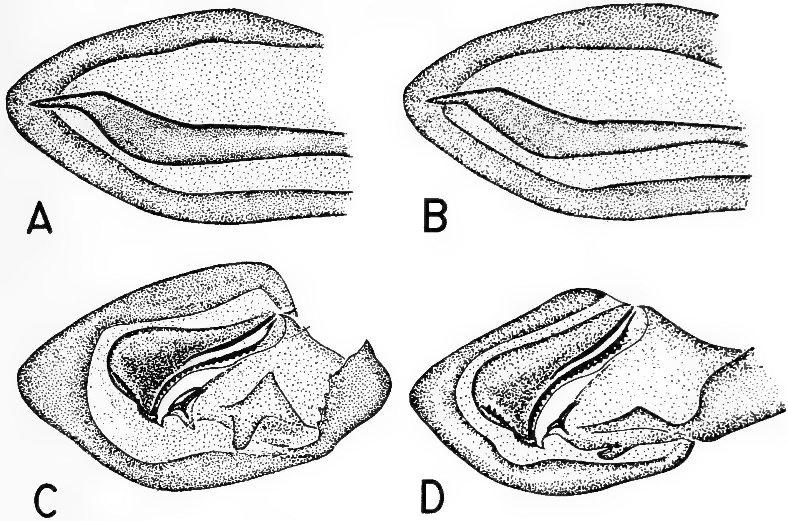

FIG. 2. Papilionid male genital valves, inner lateral view. **A,** *Papilio stewarti* holotype male; **B,** *P. scamander joergenseni,* Tucumán, Argentina (David Matusik Collection); **C,** *P. morrisi* holotype male; **D,** *Protesilaus xenaides,* Rio Pastaza, Ecuador (Am. Mus. Nat. Hist., New York).

383–393; Johnson, K. & R. Rozycki 1986, J. N.Y. Entomol. Soc. 94:516–525; Johnson, K., R. Rozycki & D. Matusik 1986, J. Lepid. Soc. 40:65–66; Johnson, K. & D. Matusik 1987, J. Lepid. Soc. 41:65–69, 108–113; Johnson, K., D. Matusik & R. Rozycki 1987, J. Res. Lepid. in press). The status of two other papilionid taxa, *P. stewarti* Avinoff and *P. morrisi* Ehrmann, are of interest to South American colleagues preparing a study of Neotropical Papilionidae (K. S. Brown Jr. pers. comm.). These taxa, originally described as species from one, or very few, specimens (types at Carnegie Museum of Natural History, Pittsburgh, CMNH), have had little subsequent report in the literature, and their genitalia have hitherto not been examined.

Papilio stewarti (Avinoff, A. 1926, Ann. Carnegie Mus. 16:355–375, type locality, TL, Samaipata, Bolivia). The holotype male (Fig. 1A) indicates *P. stewarti* belongs to the "*scamander* Group" of *Pterourus* (tribe Papilionini) (*sensu* Hancock, D. L. 1983, Smithersia 2:1–48), and is a synonym of the tailed subspecies *P. scamander joergenseni* Röber (Röber, J. K. M. 1925, Entomol. Mitteil. 14:85) which occurs commonly southward in Bolivia and northwestern Argentina (D'Almeida, R. F. 1965, Catalogo dos Papilionidae Americanos, Sociedade Brasileira de Entomologia, 366 pp.). Male genitalia of *P. stewarti* (Fig. 2A) differ negligibly from *P. s. joergenseni* (Fig. 2B) and nominate *P. scamander* (Johnson, Matusik & Rozycki 1985, above:fig. 2A).

Papilio morrisi (Ehrmann, G. A. 1921, Lepidoptera 5(2):17, TL of original description "Peru" but TL of holotype "Loja, S.E. Peru" [sic]). The holotype male (Fig. 1B) indicates *P. morrisi* belongs to the "*lysithous* Group" of *Protesilaus* (tribe Leptocircini) (*sensu* Hancock 1983, above), and, more specifically, the "*harmodius* cluster" (*sensu* Johnson, Rozycki & Matusik 1986, J. N.Y. Entomol. Soc. 94:383–393; 1987, above). Wing characters (Fig. 1B), genitalia (Fig. 2C), and locality data (other *P. morrisi* specimens labelled "Rio Bamba, Ecuador") indicate *P. morrisi* is a synonym of *Protesilaus xenaides* (Hewitson) (Fig. 2D) (Johnson, Rozycki & Matusik 1986, J. N.Y. Entomol. Soc. above:fig. 4F).

W. J. Holland (1927, Ann. Carnegie Mus. 17:299–365) noted that Ehrmann, in describing many (often synonymic) taxa, sometimes made clerical errors. Holland, in his entry concerning *P. morrisi,* repeats Ehrmann's citation of "Peru" as the type locality, but in text cites Ehrmann's "notebook" as stating "Laja, Peru" [sic]. Holland questioned this as possibly "Loja" [Ecuador]. The holotype's labels, not figured by Holland (but shown here in Fig. 1B) appear to say "Loja" [Ecuador], compatible with data on two paratype males (CMNH) labelled "Rio Bamba, Ecuador".

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REPEATED COPULATION IN AN ORANGE HAIRSTREAK, *SHIROZUA JANASI*: A CASE OF MATE GUARDING?

Additional key words: Lycaenidae, mating, behavior.

In butterflies, multiple copulations are common not only in males (Svärd, L. & C. Wilkund 1986, Behav. Ecol. Sociobiol. 18:325–330) but also in females (Burns, J. M. 1968, Proc. Nat. Acad. Sci. U.S.A. 61:852–859; Ehrlich, A. H. & P. R. Ehrlich 1978, J. Kans. Entomol. Soc. 51:666–697; Thornhill, R. & J. Alcock 1983, The evolution of insect mating systems, Harvard Univ. Press, Cambridge, Massachusetts, 547 pp.; Drummond, B. A. 1984, pp. 291–370 *in* Smith, R. L. (ed.), Sperm competition and the evolution of animal mating systems, Academic Press, Orlando, Florida, 687 pp.). However, within-a-day repeated copulations are very rare in both sexes (Svärd & Wilkund, above; Fujii, H. unpubl. data).

Recently, Tanaka and Unno (*in* Fukuda, H., E. Hama, K. Kuzuya, A. Takahashi, M. Takahashi, B. Tanaka, H. Tanaka, M. Wakabayshi & Y. Watanabe 1984, The life histories of butterflies in Japan, Vol. 3, Hoikusha, Osaka, 373 pp., Japanese, English summary) observed that females of an orange hairstreak, *Shirozua janasi* (Janson) soon copulated with other males after preceding copulations. Such immediate remating seems to be exceptional in butterflies.

In the summer of 1986, I observed repeated within-pair copulations in *S. janasi*. This paper describes mating behavior in *S. janasi* and suggests that mate guarding is a possible consequence of remating.

Shirozua janasi is the only omnivorous species in the tribe Theclini. Like other Theclini, it has one generation per year, and imagines are on the wing from late July to September (Fukuda et al., above).

Field observations were made in secondary forest including *Quercus serrata* Murray (Fagaceae), *Pinus densiflora* Sieb. et Zucc. and *Larix Kaempferi* (Lamb.) (both Pinaceae), at Sakai village, Nagano, Japan in August 1986.

The male of *S. janasi* flies 3–10 m above the ground and alights just behind the female. This has been called a patrolling-type mate-locating strategy (Scott, J. A. 1973, J. Res. Lepid. 11:99–127; Fujii, H. 1982, Yadoriga (107/108):1–37, Japanese). Then the male's wings are held open about 30° apart and fluttered. The male moves slowly to the side of the female, bends its abdomen towards the tip of the female's abdomen, and copulates (Fig. 1). This courtship sequence usually ends in successful copulation within 5 sec.

During the survey, five courting pairs were found, and all copulated thereafter. At intervals after copulation began, I disturbed these pairs by approaching or touching them with my fingers until they separated or flew away *in copula*. As shown in Table 1, most

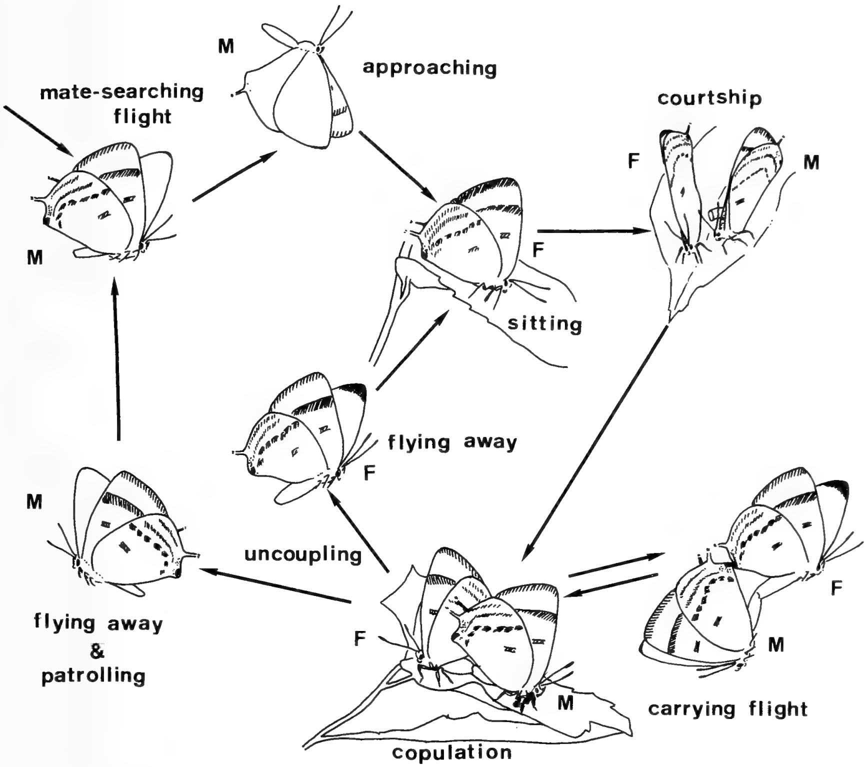

FIG. 1. Sequence of repeated copulations in *S. janasi*. M: male, F: female. Further details in text.

pairs (No. 1; No. 2, 1st & 2nd copulations; No. 3, 1st & 2nd; No. 4, 1st; No. 5, 2nd) were separated easily when disturbed within 10 min after they initiated copulation. In contrast, the pair (No. 5, 1st copulation) that had been copulating more than 30 min was not easily separated. Instead, it usually flew away *in copula*, during which the female always carried the male. Possible mate guarding was observed when the pair was separated as a result of my disturbance: an uncoupled male flew away but returned immediately to where the male had copulated just before. An uncoupled female from a disturbed pair also flew away from the place where it had copulated (usually a leaf), but the female rarely moved so far. Therefore, a returned male could usually find its previous partner, and then the male courted and mated the same partner again (Fig. 1). Such behavior was observed in four of the seven separated pairs, including not only pairs that had copulated for less than 10 min but one pair that had copulated more than 150 min and then remated twice (Table 1).

According to Tanaka and Unno (Fukuda et al., above), copulation in *S. janasi* usually starts within about 10 sec and ends within 10 min of first contact. In this study, most pairs ended copulations within 10 min as a result of my disturbances. It should be noted, however, that the 1st copulation of pair No. 5 lasted about 2.5 h in spite of my intensive disturbances (Table 1). Further observations are needed to determine how long a bout of copulation lasts under undisturbed conditions.

Although my data are insufficient to say how long a time is necessary for the male to inseminate the female, it seems that 10 min is too short for successful insemination because

TABLE 1. Effects of artificial disturbances on *in copula* pairs. Asterisk indicates occurrence of remating. C: first copulation. R: remating. U: uncoupling. F: flight (flying female always carried male). L: uncoupled male lost previous partner even though he seemed to search for her. X: I could not follow uncoupled individuals because of rapid flights. S: I stopped observing.

Pair no.	Distance from previous copulation (m)	Time after copulation began (min)						
		0	1	3	5	10	30	150
1	—	C	UX					
2	—	C	FF	FU				
2*	1	R	F		UL			
3	—	C			FU			
3*	1	R	UL					
4	—	C	F			U		
4*	0	R	F	FX				
5	—	C	FF	F		FF	FF	FFFU
5*	0	R	FF	U				
5**	2	R			S			

duration of copulation in almost all butterflies is known to last over 30 min (Scott, above; Shields, O. & J. F. Emmel 1973, J. Res. Lepid. 12:25–64; Fukuda et al. 1982–1986, The life histories of butterflies in Japan, Vol. 1, Hoikusha, Osaka, 277 pp., Vol. 2, 325 pp., Vol. 3, above, Vol. 4, 373 pp., Japanese, English summary). If so, any male that uncouples within 30 min after copulation begins should remate with the previous partner to insure successful insemination. If this male does not find the previous partner, she will be inseminated by another male. In fact, Unno and Tanaka observed that such a female copulated again with another male.

Pair No. 5 remated twice after the 1st copulation, which lasted about 2.5 h. The male of this pair is likely to have transferred its sperm to the female's bursa copulatrix during the 1st copulation, because in butterflies most successful copulations are known to finish within 1–2 h (Scott, above; Shields & Emmel, above). If insemination did occur, the 2nd and 3rd copulations of pair No. 5 may be copulatory mate guarding behavior by the male. Copulatory mate guarding has not been reported in Lepidoptera previously (Thornhill & Alcock, above; Drummond, above), but Drummond considered that lepidopteran males might also guard their mates from the advances of other males while still *in copula*. However, in some cases where the male successfully copulates several times within 1 or 2 days, a bout of copulation may last several hours after the 2nd copulation (Svärd & Wilkund, above; Fujii unpubl.). Additional studies are needed to know whether or not repeated copulations in *S. janasi* are truly copulatory mate guarding.

Although *in copula* pairs of *S. janasi* were separated very easily by my disturbances, this is not true in other butterflies (Fujii, H. 1975, Gekkan-Mushi [52]:14–19, Japanese). Why do *in copula* pairs of *S. janasi* separate so easily? Longer copulations are probably more dangerous than shorter copulations, because *in copula* pairs are more conspicuous and less mobile and should therefore suffer higher predation. Moreover, both sexes of *S. janasi* are reddish orange in color, so they are very conspicuous on green leaves. Therefore, the easy-to-separate copulation behavior of *S. janasi* may have evolved in response to predation pressure. In favor of the hypothesis is the fact that two other orange hairstreaks, *Japonica lutea* (Hewitson) and *J. saepestriata* (Hewitson), copulate at dusk (Fujii, above; Fukuda et al., above), while *S. janasi* copulates during the day when bird predation seems much heavier (Fujii, above; Saigusa, T. 1983, 30th annual meeting of the Lepidopterological Society of Japan).

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AN EMENDED SPECIFIC NAME IN *EUPITHECIA* (GEOMETRIDAE)

Additional key words: Chile, *Eupithecia taracapa, E. tarapaca.*

Prof. Raúl Cortés, of the Instituto de Entomologia, Universidad Metrolitan de Ciencas et la Educacion, Santiago, Chile, called my attention to an incorrect geographical name and a resulting incorrect species-group name in my 1987 paper "The *Eupithecia* (Lepidoptera, Geometridae) of Chile," Bull. Am. Mus. Nat. Hist. 186:269–363. On p. 325 I gave the type locality of the new species as being in "Taracapá" Province and Region, and proposed for it the specific name *Eupithecia taracapa,* a noun in apposition taken from the type locality. The correct geographic term is Tarapacá, and so I am emending the name of the species to *Eupithecia tarapaca,* thus replacing the incorrect *E. taracapa* Rindge 1987; both names have the same holotype. This emendation is in conformity with Articles 32(d) and 33(b)(ii) of the International Code of Zoological Nomenclature.

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THE VALID GENERIC PLACEMENT FOR "*CALOTHYSANIS*" *AMATURARIA* (WALKER) (GEOMETRIDAE, STERRHINAE)

Additional key words: taxonomy, *Timandra amaturaria*.

The common eastern North American sterrhine geometrid moth described by Walker in 1866 as *Timandra amaturaria* has often been placed in the genus *Calothysanis* Hübner 1823. Examples are A. S. Packard (1876, Monograph of the geometrid moths or Phalaenidae of the United States, *in* Hayden, F. V., Report of the United States Geological Survey of the Territories 10:317), L. B. Prout (1934, Lepidopterorum catalogus, Part 61: 51), Prout *in* A. Seitz (1936, Macrolepidoptera of the world, Vol. 8:94), and W. T. M. Forbes (1948, Lepidoptera of New York and neighboring states, Part 2:119).

Timandra, on the other hand, was used in the 1917 check list of Barnes and McDunnough and the 1938 one of McDunnough (numbers 3913 and 4205, respectively), as well as in earlier works by A. Guenée, C. F. Gumppenberg, and Prout himself (1913, *in* Seitz, A., Macrolepidoptera of the world, Vol. 4:47). Both combinations have appeared in other literature, and on the head labels of collections, creating considerable confusion.

Since *Calothysanis* Hübner 1823 predated *Timandra* Duponchel 1829, and had been applied by Forbes and by Prout in his most recent works, I used *Calothysanis* in my Sterrhinae section of the R. W. Hodges (ed.) (1983) Check list of the Lepidoptera of America north of Mexico (p. 100) and my *Field Guide to Moths of Eastern North America* (Covell 1985, p. 377; pl. 46, fig. 14).

Prout (1913) chose *Timandra* over *Calothysanis* on the basis of Butler's selection of *Acidalia imitaria* Hübner as the type of *Calothysanis* (Butler, A. G. 1881, Trans. Entomol. Soc. London 1881:342). D. S. Fletcher (1979, *in* Nye, I. W. B., Generic names of the moths of the world, Vol. 3:34) verified that selection.

The type of *Timandra* was originally designated as *Phalaena amataria* Linnaeus 1761. Fletcher, in his treatment of *Timandra* (p. 206), pointed out that *Phalaena amataria* Linnaeus is an unjustified emendation of *P. amata* Linnaeus, and therefore an objective synonym of *amata*. The original description of *amata* was based not on specimens but on two figures in another work, which turn out to be two other species. An unnamed series of moths left by Linnaeus were misidentified by later workers as *P. amataria.* Fletcher concluded that *Timandra griseata* Petersen 1902 is the earliest available name for those moths which Linnaeus had misidentified as *P. amataria,* and is therefore the type of *Timandra.*

Since *imitaria* Hübner is in the genus *Scopula* Schrank 1802, *Calothysanis* must be considered a junior synonym of *Scopula* as it was thus first published by Prout (1934: 169).

The generic and species treatments in Hodges (above) should therefore read as follows:

TIMANDRA Dup., 1829
BRADYEPETES Steph., 1831
7147 amaturaria Wlk., 1866
effusaria (Prout, 1936)

The other 14 species of *Timandra,* including *griseata,* occur in Eurasia (Prout 1934).
The author thanks an anonymous reviewer for helpful criticism.

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BOOK REVIEWS

THE MOTHS OF AMERICA NORTH OF MEXICO. The Wedge Entomological Research Foundation, Washington, D.C. (Distributed by the Wedge Entomological Research Foundation, % National Museum of Natural History, MCR-127, Washington, D.C. 20560; E. W. Classey Ltd., P.O. Box 93, Faringdon, Oxfordshire SN7 7DR, England; Bioquip Products, 17803 LaSalle Ave., Gardena, California 90248; Entomological Reprint Specialists, P.O. Box 77224, Dockweiler Station, Los Angeles, California 90007.)

Fascicle 18.1. Geometroidea, Geometridae (Part), by Douglas C. Ferguson. 1985. 131 pp., 4 color pls. Soft cover. $55.

The appearance of this fascicle of "MONA," as Richard B. Dominick affectionately dubbed it, is unique. It is a memorial fascicle in which intimate details of Dick's life, personality, and contributions to lepidopterology as founder of this series are presented most touchingly by his widow, Tatiana. This, with a full-page portrait of Dick, precedes the paginated body of the work.

Also, this fascicle is the first covering "macros" since the Lymantriidae volume in 1978, and is also the first to treat a subfamily of Geometridae.

Ferguson's treatment consists of nomenclatural and descriptive introduction to the subfamily Geometrinae, leaving superfamily and family material as headings followed by "(continued)," thus anticipating placement of Archearinae, Oenochrominae, and Ennominae ahead of the greens in phylogenetic order. We can expect superfamily and family treatments in a later fascicle.

Tribal and generic descriptions follow, each with a key to the next lower category. Species, and where appropriate, subspecies, are painstakingly described, with illustrations of wing venation and genitalia adding greatly to the usefulness of descriptions. In addition to the bibliography, there are appended abbreviations for contributing collections and individuals, an animal-name index, and a plant-name index.

This work is based primarily on Ferguson (1969, A revision of the moths of the subfamily Geometrinae of America north of Mexico [Insecta, Lepidoptera], Bull. 29, Peabody Museum, Yale University)—a publication based on his doctoral dissertation. Since publishing that work, Ferguson has made some changes, most of them introduced in R. W. Hodges, ed. (1983, Checklist of the Lepidoptera of America north of Mexico, The Wedge Entomological Research Foundation, Washington, D.C., 284 pp.). These include *Synchlora albolineata* and *S. liquoraria* treated as subspecies of *S. aerata*; three new synonyms for *S. frondaria*; *S. frondaria denticularia* reduced to synonymy of *S. frondaria frondaria*; *S. xysteraria* (Hulst) applied to the Florida moths treated as *S. gerularia*, a similar species reaching North America only in southern Texas; *S. herbaria hulstiana* reduced to synonymy of *S. herbaria*; *Merochlora* synonymized to *Chetoscelis* (not indicated as new synonymy in the Checklist); exchange of position of *Xerochlora* and *Chloropteryx* (the 1969 work had *Xerochlora* first); addition of *Hemithia aestivaria* (Hbn.), a European introduction discovered in Canada in 1979; and elevation of *Hethemia pistasciaria insecutata* from synonym to subspecies status, with *auranticolorata* as its synonym. In addition, the 1985 fascicle elevates former synonym *remotaria* (Wlk.) to replace the name *latipennis* Hulst—a correction from the 1969 treatment in which *remotaria* was attributed to Grossbeck.

The text abounds in small refinements and improvements over the revision, and reduction in details that a formal revision normally includes. Ranges and other information are improved for some species. I found partial life history information available for 8 species of the 76 in our fauna for which none appeared in the earlier work. An example of range extension is that of *Nemoria tuscarora* Ferguson (1969:61), once known only from Appalachian North Carolina, Virginia, and West Virginia, now known from north-central Kentucky with flight date extending into August from the 27 July limit stated earlier. Likewise, the ranges of *N. saturiba* Ferguson and *N. elfa* Ferguson are extended northward by addition of Kentucky records in the fascicle.

Genitalia and other line drawings are copious and well rendered, and the delicate patterns and pastel colors of the moths on the four plates are appealing. Several years elapsed between photography of the plates and their production for the book, however; some moths appear more grayish green or duller than specimens with which I compared their published likenesses. Having had similar disappointments with color registry, I am sure Ferguson must be equally disappointed that the lovely green colors did not come out as well in production as one would wish.

This is a well written and illustrated book which enables one to identify usually by superficial features the North American Geometrinae. It also contains considerable information additional to that in Ferguson's earlier revision, plus variation represented in the color plates by multiple illustrations of some species (six of *N. elfa*, for example). It is a worthy addition to the MONA series, and a fitting fascicle to commemorate the life and contributions of Dick Dominick.

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Fascicle 7.1. Gelechioidea, Gelechiidae (Part), Dichomeridinae, by Ronald W. Hodges. 1986. 195 pp., 4 color & 34 monochrome pls. Soft cover. $70.

This volume presents the first revision of any large group of North American Gelechiidae in contemporary times, and as such, it brings welcome order to part of a family of small moths whose classification is chaotic at best. The fauna covered is small, however, in relation to the size of the family: 84 species out of possibly 1500+ on this continent. Three genera are recognized (one is monobasic), with most species (74) placed in *Dichomeris*. How confused the group was previously is reflected in the 81 generic synonyms under *Dichomeris*, 60 of which are new or revised. The generic synonymy will prove especially useful because it is worldwide in scope. Also noteworthy in the treatment of one genus, *Helcystogramma*, is a list of extralimital (non-North American) species. Unfortunately, a similar list is not included for the larger genus *Dichomeris*, presumably for reasons of length (it includes several hundred species worldwide). The number of new species, 42 or 50% of taxa treated, is a fair reflection of how poorly North American gelechiids are known.

Because this is the first MONA fascicle to treat gelechiids, family and subfamilies are defined. Only three subfamilies are recognized, with Gelechiinae being vastly enlarged to include the majority of our gelechiids. It is quite probable that this assemblage of taxa comprising several thousand species worldwide is defined by primitive character states, and that it will eventually be broken up into monophyletic units. Nevertheless, Hodges must be praised for attempting to delineate precisely the notoriously ill-defined higher categories of gelechiids.

Keys based on external features are given for *Dichomeris* and *Helcystogramma* species. They do not permit the separation of all species, however, because several species are distinguished with certainty by genitalia only. This is an unavoidable fact of many microlepidoptera groups, at least until distributions and natural histories become better known. For *Dichomeris* species, there are also keys based on male and female genitalia.

Species descriptions are lengthy and detailed. They could have been shortened to conserve space and improve readability by deleting unnecessary details of color. For many species, genitalia receive only a brief reference to a figure. It would have been more useful to give distinctive, comparative features because of their importance for species separation. Perhaps this was omitted on account of lepidopterists who dislike or are unable to make genitalia preparations. However, it is likely that whoever is interested in these small moths will also get involved in the techniques required for their study. This notwithstanding, omission of genitalia comparisons partly defeats the purpose of including plates showing genitalia of all species treated because the reader is often left trying to figure out what detectable differences in the figures have taxonomic value. Systematists with a phylogenetic bent will be pleased to find a table of character states that covers 38 characters, albeit nonpolarized, for the 20 species groups of *Dichomeris*.

The four color plates are stunningly sharp—an improvement over previous fascicles on oecophorids and cosmopterigids in which the pictures were slightly fuzzy. The line drawings are of fine quality, although several genitalia illustrations lack contrast between membranous and sclerotized parts, giving the impression that these structures are somewhat uniformly sclerotized. The 34 monochrome plates illustrating male and female genitalia are generally of excellent quality. Hodges is to be praised for doing such a fine job at the very difficult task of microphotography. However, the shortcomings of using photographs to illustrate genitalia are apparent in discrepancies in slide quality, mostly brought out by different staining intensities. Some genitalia are too dark, and their details obscured. In the aedeagus illustrations, one wonders whether visible differences in the photos represent taxonomic differences or artifacts of preparation. Differences are even more tenuous in female genitalia where one can only guess at the important characters. Loss of resolution has been minimized by using contact prints, which accounts for the large format of photographs and the fact that many are composites of two prints.

As in previous "micro" fascicles, the style resembles more that of a taxonomic revision than a general manual, but this seems to be an unavoidable aspect of treating groups where lack of previous revisionary work and large numbers of undescribed taxa preclude more popular-style treatment.

The author is to be commended for this fine treatment of little known, small moths. Like previous fascicles on microlepidoptera, this one should be on the shelf of any serious student of moths, but given its price, it is hardly a manual for the general lepidopterist.

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Fascicle 15.2. Pyralidae (Part), Phycitinae (Part—*Acrobasis* and Allies), by H. H. Neunzig. 1986. 114 pp., 5 monochrome & 6 color pls. Softcover. $45.

This is the sixth fascicle on Pyralidae and the first to be written by H. H. Neunzig. In this fascicle, Neunzig does an exhaustive study of the large and complex genus *Acrobasis*, and allied genera *Cryptoblabes*, *Trachycera*, *Anabasis*, and *Hypargyria*. There has been much difficulty with the identification of species in this group, in particular those of *Acrobasis*. Using primarily C. Heinrich (1965, U.S. Natl. Mus. Bull. 207:1–581) as a basis, Neunzig incorporated his own studies on biology and immature stages. In his more comprehensive approach, he examined all available type specimens, studied in detail male antennae, shape of male forewings, color pattern of the undersurface of wings and thorax of males, ventral scale tufts of the eighth abdominal segment of males and females, and male and female genitalia.

Neunzig made significant taxonomic changes, including description of three new species, and placement of 16 new synonyms and 2 new combinations. The 38 species of *Acrobasis* are divided into 10 species-groups based on adult and immature morphology and biology. A convenient table is provided which gives host plant relations and geographic distributions of the species-groups. Future taxonomic work will be facilitated also by the designation of 18 lectotypes in this fascicle.

Accurate identification is aided by detailed species descriptions, excellent illustrations, and keys to genera, to adults and larvae of *Acrobasis*, and to adults of *Trachycera*. Many characters of larvae and adults are nicely shown with 61 line drawings. Included also are drawings of larval frass tubes and pupal chambers for 17 *Acrobasis* species. Four monochrome plates have very good scanning electron micrographs of male antennal characters. In addition, another monochrome plate shows the black scaling of the undersurface of the wings of six species. As with preceding fascicles of MONA, the fine color plates are a strong contribution to this work. Neunzig shows the variation within species by using 6 color plates and 258 specimens to show 44 species photographed at twice natural size. The specimens are in good to excellent condition (few have missing abdomens). A minor inconvenience is the carryover of the same species to subsequent plates, probably to economize on space and reduce costs.

I noticed one error in the text on page 11: "ZMHB" was used for the Museum Alexander

Humboldt, Berlin, instead of "HUMB," the standard found in "Notes" on page vii. I did not find "ZMHB" in type specimen data or elsewhere in text.

This fascicle will be a valuable addition to the library of those who curate collections, and especially those who are interested in Pyralidae. Those concerned with economic species such as the cranberry fruitworm, leaf crumpler, pecan nut casebearer, pecan leaf casebearer, walnut shoot moth, and the birch tubemaker will find it especially useful to have the known biological information, keys for identification, and color photographs in one publication. Neunzig has made a significant contribution to the knowledge of *Acrobasis* and its allies through a more comprehensive approach, and is to be congratulated on his work.

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Journal of the Lepidopterists' Society
43(1), 1989, 76

A TAXONOMIC REVISION OF THE NEW WORLD MOTH GENUS *PERO* (LEPIDOPTERA: GEOMETRIDAE), by Robert W. Poole. 1987. U.S. Dept. Agric., Agric. Res. Serv., Tech. Bull. 1698. 257 pp., 1116 figs. No price given.

This work is but one of a small handful of major revisionary papers on the New World Geometridae—in fact, for any large family of New World moths. As such, it is an invaluable aid for determining the members of this genus, which have been in utter taxonomic chaos. That this genus has proven to be a problem over the years is indicated by the list of 10 generic synonyms given, with 6 being placed in synonymy in this paper.

Pero is one of the largest genera in Ennominae; it makes up, by far, the largest portion of the Azelini. Members are restricted to the New World, and occur almost everywhere except in the far northern and southern regions. *Pero* includes 294 species, of which Poole described 119 as new, and there are 74 junior synonyms for the genus. (One omission is the four subspecific names I proposed in my 1955 paper on this genus in western North America, even though my paper is cited in the text.) With this many species, it is not surprising that there are some that exhibit sexual dimorphism, polymorphism, extreme geographic variation, and a high degree of individual variation. This means that genitalic dissections are often necessary to place the correct name on a species; in fact, I prefer to base determinations on study of genitalia rather than pattern and color of an individual specimen.

This work is a condensation of Poole's doctoral thesis. Descriptions have been reduced to diagnoses, as the author uses them to supplement illustrations of the adults (photographs) and genitalia (drawings). One item I believe should have been included is length of forewings, as specimens range from about 10 to nearly 30 mm; there is no indication in text or photographs, as to specimen size. Each species has a listing of localities for the specimens examined.

For anyone interested in New World moths, especially the Geometridae, this paper is a necessary addition to his or her library.

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Journal of the Lepidopterists' Society
43(1), 1989, 77–78

IMMATURE INSECTS, Volume 1, Frederick W. Stehr (ed.). 1987. Kendall-Hunt, Dubuque, Iowa. 754 pp. Quarto. Hard cover. $69.95.

Had the finger of zoological fate pointed to larvae as the "perfect" insect stage instead of adults, entomology and lepidopterology might be different today. The applied branch, so concerned with larvae, might include systematics; the *Code* might outlaw adults for naming purposes; dermestids might matter less; and visionaries like Alvah Peterson, and now Fred Stehr, might be drawing our attention to the neglected adult stage instead of to the neglected larval stage.

A decade in the making, *Immature Insects* doubtless had its origin in the summer of 1957 when Stehr took a field course in immatures from Alvah Peterson at the Itasca Biological Station of the University of Minnesota. Stehr and a generation of Ohio State University students taking Peterson's immature insects course (including me) duly keyed the collected or prescribed material, but sometimes without relish. The main tool then was Peterson's *Larvae of Insects*, a plesiomorphic ancestor; Stehr and company's *Immature Insects* is an apomorphic, streamlined descendant.

Volume 1 of *Immature Insects* deals with 24 orders, but is dominated by Lepidoptera, to which more than 300 pages are devoted; when supporting sections are considered, easily half of this big book concerns Lepidoptera. The Lepidoptera section, coordinated by general editor Stehr, contains contributions by 19 specialists, a number large enough to greatly thin the ranks of candidates to review the book. Volume 2 of *Immature Insects*, covering the 10 remaining orders, including worldwide coverage of Coleoptera, should appear in 1989.

The book's focus is larvae rather than eggs or pupae. Additional sections of integral interest to lepidopterists include Introduction (6 pages), Techniques for Collecting, Rearing, Preserving, and Studying Immature Insects (12 pages), Key to Orders of Immature Insects and Selected Arthropods (28 pages), Glossary (11 pages), Host Plant and Substrate Index (6 pages), and the overall Index (26 pages). The key to orders includes immature, brachypterous, and wingless adult insects as well as other terrestrial and freshwater invertebrates that might be confused with immature insects.

The Lepidoptera section provides coverage basically to family level. Treated families number 75 whose larvae occur north of Mexico. Classification largely follows the 1983 Check List. Backbone of the section is the dichotomous key to families developed by Stehr and P. J. Martinat. With a whopping 225 couplets, the key is essentially in two parts; it may be entered at couplet 39 for larvae with normal numbers of thoracic legs and prolegs. By comparison, Peterson's three-part key had 99 couplets. The authors did not attempt to make the key reflect phylogeny or reveal all family characters.

Refreshingly, the key was designed with uncommon consideration for the user. It is sprinkled with helpful hints, reminders, cautions ("may be very small, look carefully"), as well as italic and boldface type for extra emphasis (". . . *distinctly* closer."). It successfully decreases conditional statements, the bane of many a key user: there is 1 such statement per 9 couplets compared with Peterson's 1 per 6, and the ones left are not very convoluted.

The new and larger key resulted from use of more characters as well as decomposition of complex couplets. The authors rightly claim that key paths are not necessarily longer: I found the ratio of number of key-out points to number of couplets to be high, 227/225 or 1.00 compared to Peterson's 100/99 or 1.01. The authors say it is possible to make wrong choices in the key and still arrive at the correct family. Such robustness is likewise supported by my checking: there are more key-out points for five diverse moth and butterfly families than in Peterson's key: 8 vs. 2 for Noctuidae; 4 vs. 1 for Pyralidae; 3 vs. 1 for Geometridae; 7 vs. 5 for Nymphalidae (broad sense); and 6 vs. 1 for Lycaenidae. Most key characters are illustrated with serviceable line drawings which occupy part of every page of the key for ready accessibility. The ratio of such illustrations to number of key couplets exceeds 0.80. When introductory illustrations are added, the ratio becomes 0.95; the introductory illustrations are part of some 15 pages of larval description preceding the key that thoroughly review external anatomy, and include setal maps as well as chaetotaxic tables.

Following the key, every family is individually discussed. These discussions are uniformly presented under the headings Relationships and Diagnosis, Biology and Ecology, Description, Comments, and Selected Bibliography. Most are accompanied by instructive line drawings and photographs ranging from structural details to whole larvae. The Selected Bibliographies provide easy entry to pertinent literature for each family. The family information is up to date and insightful, a result of the specialist expertise of the various authors. I found the family discussions an unexpected highlight of the book; they form an encyclopedic source of current information on North American Lepidoptera.

There are no keys to genera of Lepidoptera. However, for Noctuidae, Pyralidae, and Tortricidae, three of the five most speciose families, there are keys to selected species. The pyralid keys treat stored product and corn-sugarcane pests; the tortricid keys treat pine feeders, soybean-alfalfa-cultivated legume feeders, and pome-fruit feeders; and the noctuid key, representative last instars. The value of such keys seems equivocal to me. At worst, they mislead the unwary; at best, they provide a starting point from which comprehensive keys can be built. Fortunately, the keyed species of Pyralidae and Noctuidae are illustrated or described to help confirm key results.

Physically, the big green book is sturdily manufactured and attractively designed. An eye-catching color photograph of a limacodid caterpillar adorns the front cover.

Immature Insects delivers a solid background for an interest in lepidopterous and other larvae; I venture it will also inspire much new interest in larvae. It will surely build a following among a new and more demanding generation of students and devotees. Hardly anyone could fail to get a good lepidopterological return on its purchase price.

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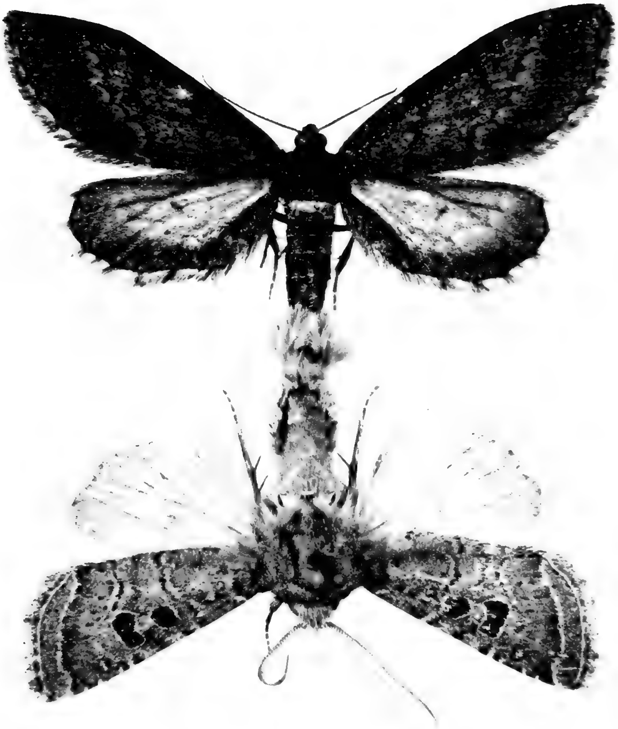
Journal of the Lepidopterists' Society
43(1), 1989, 79

FEATURE PHOTOGRAPH



A rare and perhaps unique interfamily mating between a female *Glaucina erroraria* Dyar (Geometridae) (upper) and a male *Protorthodes melanopis* (Hampson) (Noctuidae) (lower) shown 2.8× natural size. Taken in copulo at 5131 Bannock St., Pueblo del Sol, Huachuca Mts., Cochise Co., Arizona, at UV light, 25 March 1988. Collected and mounted, still attached as shown, by Ronald S. Wielgus of the above address. Specimens deposited in the National Museum collection under *G. erroraria*. Identified and photographed by Douglas C. Ferguson, Systematic Entomology Laboratory, U.S. Dept. Agric., % U.S. National Museum of Natural History, Washington, D.C. 20560.

Date of Issue (Vol. 43, No. 1): 3 March 1989

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Contributions to the *Journal* may deal with any aspect of Lepidoptera study. Categories are Articles, General Notes, Technical Comments, Book Reviews, Obituaries, Feature Photographs, and Cover Illustrations. *Journal* submissions should be sent to the editor at the above address. Short manuscripts concerning new state records, current events, and notices should be sent to the *News*, June Preston, Editor, 832 Sunset Drive, Lawrence, Kansas 66044 U.S.A. *Journal* contributors should prepare manuscripts according to the following instructions, and submit them flat, not folded.

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SHEPPARD, P. M. 1959. Natural selection and heredity. 2nd ed. Hutchinson, London. 209 pp.
——— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10:165–216.

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Cover illustration: Larvae of the small-eyed sphinx, *Paonias myops* (J. E. Smith) (Sphingidae), resting "leaf-like" on a shoot of black cherry, *Prunus serotina* Ehrh. (Rosaceae). Submitted by Gerald P. Wykes, 2569 Reinhardt Road, Monroe, Michigan, 48161.

JOURNAL OF
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43(2), 1989, 81–92

ELECTROPHORETIC COMPARISONS OF VICARIANT *VANESSA*: GENETIC DIFFERENTIATION BETWEEN *V. ANNABELLA* AND *V. CARYE* (NYMPHALIDAE) SINCE THE GREAT AMERICAN INTERCHANGE

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ABSTRACT. *Vanessa carye* and *V. annabella* are very similar species found in South America and North + Central America, respectively; they probably differentiated in the three million years since the Great American Interchange. Electrophoretically they are differentiated at a level typical of animal morphospecies (Nei's I = 0.855, D = 0.157) and are much more unlike than small samples of *V. cardui* from California vs. France. Using the Sarich method of estimating time of divergence, we date their speciation at roughly 2.97 million years ago, suggesting that *Vanessa* was an early crosser of the Panama land bridge. Our results support continued recognition of *V. carye* and *V. annabella* at the species, rather than the subspecies, level.

Additional key words: systematics, biogeography.

Since the emergence of protein electrophoresis as a technique in population genetics, it has been applied widely in systematics as well (Burns 1975, Ayala 1983). Several attempts have been made to compare levels of electrophoretic differentiation to conventional (morphologically-based) taxonomic judgment (Avise 1974, Ayala 1983, Ayala & Powell 1972, Ayala et al. 1974, Nevo et al. 1974, Mickevich & Johnson 1976, Thorpe 1982). Burns and Johnson (1967) first suggested that enzyme variation might offer a powerful tool for recognizing sibling species; Webster and Burns (1973) demonstrated its value in a pioneering study with lizards. Despite the widespread use of electrophoresis in systematic investigations of other taxonomic groups, it has seldom been brought to bear on butterflies (Geiger & Scholl 1985). The present study attempts to resolve the status of two putative vicariant mor-

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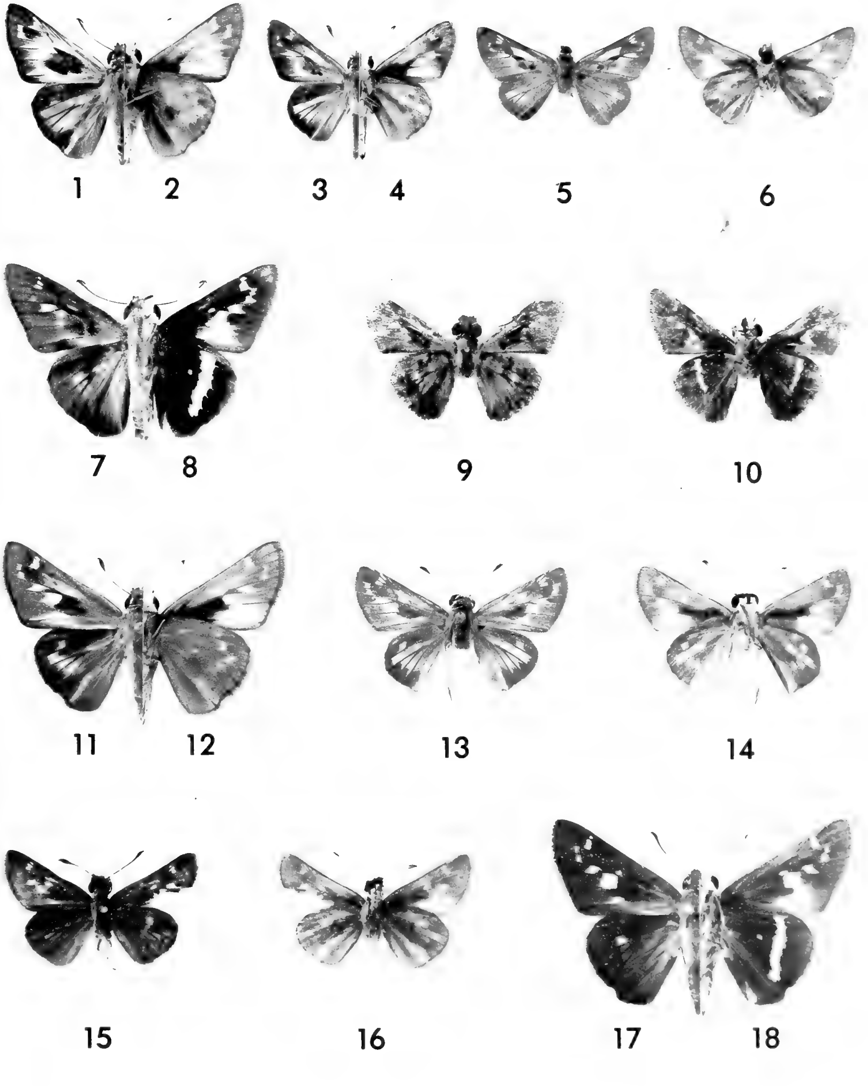
phospecies of the genus *Vanessa* Fabricius (Nymphalidae) by electrophoretic means, and interprets the data in historical-biogeographical terms to estimate the antiquity of their speciation event.

Hamadryas carye was described by Hübner in 1812 with no specific type locality. The name was subsequently applied to both North and South American, superficially similar populations later placed in the genus *Vanessa*. As early as 1951, W. D. Field had noted color and pattern differences between North and South American specimens, which he communicated personally to his Chilean collaborator J. Herrera. Herrera et al. (1958) then asserted that "after studying the genitalia of the examples which we possess from the United States (Oregon and California), Mexico, Argentina and Chile we are able to affirm that we are dealing with two quite different species." Once Field was able to establish from Hübner's figure that his (lost) type must have been South American, it was now possible to fix that usage; Field (1971) named the (newly-nameless) North American entity *Cynthia annabella*. Although his generic judgment has not been generally accepted, the specific epithet *annabella* continues in use for material from Central America northward.

Vanessa carye, sens. str., and *V. annabella* have sufficient phenotypic differences (in both habitus and genitalia) that if they co-occurred without intergrading there would be no hesitation in calling them different, though very closely related, species. However, they are apparently completely allopatric; *carye* ranges from southern Patagonia to Colombia, *annabella* from British Columbia to Guatemala. Neither species is recorded from montane or lowland Costa Rica (DeVries 1986). Such allopatric sister-species were called "vicars" by Udvardy (1969) and are commonly known as "vicariants" or "vicariant species" in the literature; they are often considered to be relatively recently-differentiated. In the absence of genetic data, and sometimes in the *presence* of such data, taxonomists' judgments as to how to rank such entities are often controversial. Thus, the suggestion by Higgins and Riley (1970) that several Palearctic-Nearctic pairs of pierid taxa were conspecific has remained unresolved despite laboratory hybridizations and electrophoretic studies (Shapiro 1980, Shapiro 1983, Shapiro & Geiger 1986 for *Pontia*, in which compatibility studies were done between populations far-removed from one another on the alleged Holarctic cline). In *Vanessa carye* and *annabella* there is near-unanimity in usage; doubts as to the validity of a species-level distinction have remained largely unpublished, appearing only in one major work (Scott 1986:283–284 treats them as subspecies). Such doubts are sure, however, to be exacerbated by the recent demonstration by Herrera (1987) of wing-pattern overlap between the taxa, and his forthcoming publication of laboratory

ERRATUM

A printing error resulted in the omission of the numbers on Figures 1–18 in John M. Burns' article, "Phylogeny and zoogeography of the bigger and better genus *Atalopedes* (Hesperiidae)," which appeared in Volume 43, Number 1 of the *Journal of the Lepidopterists' Society*, pp. 11–32. The original version of this figure is reprinted here. To correct this error in your copy, cut around the figure below, peel off the back, and affix it above the caption on page 14 of Volume 43, Number 1.



hybridization data (Herrera pers. comm.). Although we had only limited local samples available, we considered it worthwhile to attempt to assess the level of electrophoretic differentiation between the taxa. Since there are no published taxic comparisons within the Nymphalini, we attempted to place the data in context by comparing these two entities to members of different species-groups in *Vanessa*, to European vs. American *V. cardui* L., and to a few other nymphalines to which we had access at the time the study was done. Once in hand, the data permit a very crude estimate of the time since gene flow was interrupted, that is, the time of speciation—an estimate which is particularly interesting in cases such as this one, in which very different models of the history and biogeography of the situation may be advanced.

MATERIALS AND METHODS

The sources of our samples are listed in Table 1. All animals were collected from the field, transported alive and immediately stored at −70°C until electrophoresis. Only autumn 1985 through 1986 catches were used, except for European *V. cardui*; we had only a handful of old frozen specimens (1979) of these, but they had conserved most of their activity such that the zymograms were completely satisfactory for comparison with recent American material. All wings were retained by HJG. The head and thorax of each butterfly were homogenized in four volumes of Tris-HCl buffer (0.05 M, pH 8.0). We used horizontal starch gel electrophoresis procedures slightly modified from Ayala et al. (1972) (Geiger 1981). Twenty-two enzymes were scored:

adenylate kinase (AK-1, AK-2)
aldolase (ALD)
arginine kinase (APK)
fumarase (FUM)
glutamate-oxaloacetate transaminase (GOT-1, GOT-2)
glutamate-pyruvate transaminase (GPT)
glyceraldehyde-phosphate dehydrogenase (GAPDH)
α-glycerophosphate dehydrogenase (α-GPDH)
hexokinase (HK)
indophenol oxidase (IPO)
isocitrate dehydrogenase (IDH-1, IDH-2)
malate dehydrogenase (MDH-1, MDH-2)
malic enzyme (ME-1, ME-2)
phosphoglucomutase (PGM)
6-phospho-gluconate dehydrogenase (6-PGD)
phosphoglucose isomerase (PGI)
pyruvate kinase (PK)

There are no studies known to us of the heredity of any of these loci in Nymphalini, and we made the usual assumption by treating electromorphs as alleles. "Allelic" distributions were generally in good accord with Hardy-Weinberg expectations in samples large enough to warrant such a test. The most frequent "allele" in *carye* was arbitrarily given the standard index 100 in all cases; electromorphs with different mobilities are designated with relation to it, such as an "allele 105" for an enzyme that migrates 5 mm faster than the commonest *carye* allelic product.

TABLE 1. Localities and dates of samples. Altitudes are given only for mountain samples.

Vanessa carye, sens. str.

ARGENTINA: Prov. Salta: Abra Molina, 4000 m, i.2.86 (n = 3); Valle Encantado, 2700 m, i.22.86 (n = 2); Salta, i.22.86 (n = 2). Prov. Tucumán: San Javier, i.18.86 (n = 3); Abra Infiernillo, 3300 m, i.20.86 (n = 1); Tafí del Valle, 2100 m, i.23–27.86 (n = 7); San Miguel de Tucumán, i.29–iii.9.86 (n = 5 + 1 reared ex *Sida*).

V. annabella

CALIFORNIA, USA: Siskiyou Co.: Ball Mt., 2200 m, viii.23.86 (n = 7); Yolo Co.: Davis, ix.7.86 (n = 10); Solano Co.: Suisun City, ii.6.86 (n = 1), Fairfield, ii.6.86 (n = 2); Nevada Co.: Donner Pass, 2100 m, ix.25.85 (n = 9), Lang Crossing, South Yuba River, 1750 m, ix.25.85 (n = 1).

V. cardui

CALIFORNIA, USA: Nevada Co.: Donner Pass, ix.4.86 (n = 5). FRANCE: Dept. Vaucluse: Bollène, vi.4.79 (n = 1); Dept. Bouches du Rhône: Le Grau du Roi, vi.4.79 (n = 1); Dept. Herault: Oppidium d'Enserune, vi.2.79 (n = 1).

V. virginiensis

CALIFORNIA, USA: Nevada Co.: Donner Pass, ix.4.86 (n = 3).

Polygonia zephyrus W. H. Edwards

CALIFORNIA, USA: Nevada Co.: Donner Pass, ix.25.85 (n = 2).

Nymphalis milberti Godart

CALIFORNIA, USA: Nevada Co.: Donner Pass, ix.25.85 (n = 2).

The statistic $\bar{I}$ (Nei 1972) was used to estimate genetic similarity between samples over all loci. Calculated $\bar{I}$ values were then used to construct a dendrogram (Fig. 1) by cluster analysis (UPGMA method, Ferguson 1980). Because the set of loci is very similar and the same statistic has been used, direct comparisons may be made to earlier studies from our laboratories (Geiger & Scholl 1985 for example), while comparisons to others must be made with more caution. For estimating time of divergence of the taxa, a different statistic (D or I, not $\bar{I}$) was employed, as explained below.

RESULTS

There are genetic differences at several loci between *Vanessa carye* and *V. annabella* (Tables 2, 3). At most loci they consist of moderately to strongly divergent allelic frequencies; at only one locus (HK) is there an apparent fixed difference. In sympatry these data would be unequivocal evidence for speciation. In allopatry they must be compared to similar data for entities in other groups, using the same statistic and more or less similar procedures, to determine what constitutes a "species-level" difference. It is now well-established that some groups are much more conservative electrophoretically than others, and that the relation

TABLE 2. Common alleles for all taxa investigated.[a]

	APK	AK-1	AK-2	IDH1	IDH2	PGI	PGM	MDH1	MDH2	GOT1	GOT2	ALD	ME-1	ME-2	GPT	6PGD	GPDH	FUM	GAPD	PK-1	HK	IPO
annabella	100	100	100	100	100	100	103	100	100	100	100	100	100	100	104	107	100	100	100	100	96	100
carye	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
cardui France	100	100	100	101	110	100	112	100	100	94	90	100	102	100	93	103	100	100	120	110	95	100
cardui USA	100	100	100	101	110	100	105	100	100	94	90	100	102	100	93	103	100	100	120	110	95	100
virginiensis	100	100	100	96	110	100	109	100	100	94	98	100	103	100	90	107	100	100	120	110	100	100
zephyrus	100	100	100	88	100	100	102	89	100	94	90	100	95	96	85	105	100	100	120	110	104	110
milberti	100	100	100	84	90	100	102	89	100	105	90	100	107	92	102	105	100	100	100	110	110	110

[a] Common allele of *carye* always designated "100."

TABLE 3. Allelic frequencies at loci with high variability between *Vanessa annabella* and *V. carye*.

	N	PGM				GPT			6PGD			HK	
Sample		95	100	103	107	60	100	104	100	107	110	96	100
Davis	10			1.0				1.0		1.0		1.0	
Donner Pass	9			1.0				1.0	0.06	0.94		1.0	
Ball Mt.	7			1.0				1.0		0.86	0.14	1.0	
Σ *annabella*	30	0.02		0.98				1.0	0.02	0.95	0.03	1.0	
Tucumán	5		0.70		0.30	0.10	0.70	0.20	1.0				1.0
Tafí	7	0.17	0.50		0.33		0.21	0.79	1.0				1.0
Σ *carye*	24	0.04	0.65		0.30	0.02	0.70	0.28	0.96	0.04			1.0

between rates of morphological and electrophoretic differentiation can be extrapolated among taxa only with great caution. The classic study of the *Drosophila willistoni* (Diptera: Drosophilidae) complex by Ayala et al. (1974) established $\bar{I}$ values of 0.970 for conspecific, geographic populations; 0.795 for subspecies; 0.873 for semispecies; 0.517 for sibling species and 0.352 for morphospecies (recalculated from the original figures, which were given for Nei's I). The corresponding values for the same taxonomic levels are considerably higher in pierid butterflies, a very conservative group at the level of electrophoretic genetics (Geiger 1981, Geiger & Scholl 1985, Shapiro & Geiger in prep.). Thus, within the genus *Pieris, sens. lat.*, the European and Japanese subspecies of *Pieris rapae* L. cluster at 0.989; these with the morphospecies *P. mannii* Mayer at 0.902; these three with *P. canidia* L. at 0.874; the European and North American groups of "*napi*"-taxa with each other at 0.748 and the *napi* and *rapae* species-groups *in toto* at 0.546 (23 loci). The $\bar{I}$ value for *V. carye* and *V. annabella,* being in the mid-0.8 range, would indicate very well-differentiated species in *Pieris* and in Pieridae generally, but only infraspecific status in the *D. willistoni* group.

By Field's (1971) classification, the other two *Vanessa* used in this study (*cardui* and *virginiensis* Drury) belong to different species-groups (or splitter's genera). Thus the degree of differentiation in the dendrogram (Fig. 1) is not surprising. The lack of differentiation between Californian and French *V. cardui* mirrors their phenotypic similarity but is still somewhat surprising, especially given the small samples which would tend to amplify any differences purely probabilistically. *Vanessa cardui* is migratory in both Europe and America, with a huge summer breeding range (whence come our samples from both continents) but a much smaller overwintering one. This situation would tend to swamp out any tendency to local population differentiation, as in the Monarch, *Danaus plexippus* L. (Danaidae) (Eanes & Koehn 1979, Kitching 1985). But migration between Europe and America is neither known nor suspected for *Vanessa cardui*; nor is it a recent introduction in North America—at least Boisduval (1868) and Scudder (1889) treat it as native on the Pacific and Atlantic coasts, respectively. The possible stability of gene frequencies over its vast range deserves further study.

Both *Vanessa carye* and *V. annabella* are highly vagile, though neither is documented as a seasonal mass-migrant as is *V. cardui.* Our samples are drawn in both cases from more or less contiguous lowland and montane sites. There are hints in both species (Shapiro unpubl.) of a disorganized, individual altitudinal migration in mountainous terrain, tracking the seasonal availability of hosts. The virtual identity between nearby high- and low-elevation populations is not surprising. The biology of *V. carye* in Argentina is largely unpublished, but like *V.*

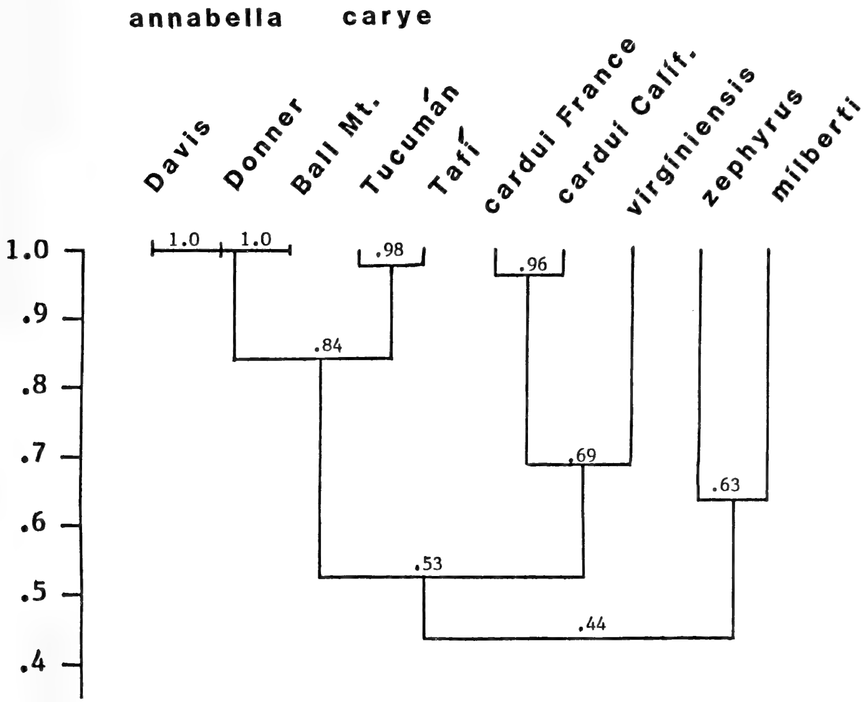


FIG. 1. Dendrogram illustrating clustering among three populations of *Vanessa annabella,* two of *V. carye,* and small samples of *V. cardui, V. virginiensis, Polygonia zephyrus* and *Nymphalis milberti,* using Nei's statistic Ī.

annabella it is a "weedy," often urban species, and its behavior is nearly identical to *V. annabella*. There is very pronounced rainfall seasonality at Tafí del Valle, while hosts are available all year at San Miguel de Tucumán. Other butterflies—several Pierini and Coliadini at least—appear to undergo regular seasonal up- and downslope movements in the Province of Tucumán (Shapiro & R. Eisele pers. obs.).

DISCUSSION

Instances in which speciation can be associated with a specific geohistorical event afford the opportunity to time-calibrate rates of biochemical evolution in particular groups, which is intrinsically superior to existing procedures for estimating time of divergence from genetic similarity or distance data (Nei 1971, Sarich 1977, Carlson et al. 1978, Thorpe 1982, Menken 1982). When biogeography suggests a specific time of speciation, this can be cross-checked using these procedures; agreement does not necessarily validate the scenario, nor disagreement falsify it, but such results are always suggestive.

The ranges of *V. carye* and *V. annabella* can be viewed as products of strict vicariance (a formerly continuous range divided by the appearance of a barrier) or of dispersal followed by differentiation (the classic geographic-speciation model). Herrera (1987) takes a vicariance position and attributes this case to continental drift, the "vicariance event" leading to speciation being the breakup of Pangaea. Such a scenario makes the last common ancestor of *carye* and *annabella* as old as the Triassic (some 200 million years ago), which seems unlikely for many reasons. However, the geography of this case strongly suggests dispersal across the Isthmus of Panama during the Great American Interchange which commenced roughly three million years ago when that corridor emerged, and which is very thoroughly documented for mammals (Marshall 1988, Stehli & Webb 1985). It resulted in colonization of each continent by faunal elements from the other, with a higher percentage of successful colonizations from North into South America than the reverse. Until fairly recently there was a tendency to attribute virtually all High Andean occurrences of otherwise Holarctic groups to this event (compare Mani 1968), regardless of the amount of evolutionary differentiation observed in the Andean biota (which by this view must have occurred since the Interchange). A consensus is now emerging to the effect that insects have evolved more slowly than mammals, at least in the Quaternary (Brown 1982, Coope 1978, 1979; D. W. Jenkins & L. D. Miller pers. comm.)—such that evolutionary origin of taxa above the species level in the Quaternary seems unlikely in Lepidoptera. Indeed, most butterfly evolution in the Quaternary seems to have been at the subspecies level, despite great geoclimatic dynamism. We suspect that the level of differentiation shown by *V. carye* and *V. annabella*, if fairly represented here, lies near the high end of the range to be expected once many candidates for Quaternary trans-Isthmian differentiation have been investigated.

The Panama land bridge was not only a corridor for migration and colonization by terrestrial organisms; it also formed a barrier to marine ones at the same time (Woodring 1966), and several speciation events have been attributed to it as a result. The genetic differentiation of sister species of marine organisms in the tropical eastern Pacific vs. the Caribbean has been quantified and cross-checked using dating estimates from electrophoretic data (Lessios 1979, 1981, Vawter et al. 1980). There is no reason in principle why the same should not be possible for terrestrial species. Like Vawter et al., we used Sarich's (1977) procedure, as modified by Carlson et al. (1978), to convert Nei's distance measure for *V. carye* and *V. annabella* ($I = 0.855$, $D = 0.157$) to an estimate of time of divergence, which is 2.97 million years (discussion of significant figures below). Such estimates entail many assumptions and should not be taken unduly seriously, even when they give remarkably close agreement to estimates derived from biogeography. [Sarich's method was developed using vertebrate data, and we are aware of the dangers in extrapolating among taxonomic groups—as were Vawter et al. (1978)]. But this number is in fact very consistent with speciation consequent on the Great American Interchange and with an early dispersal across Panama, perhaps even before a continuous land corridor was available. What is most important is that it is wildly inconsistent with Herrera's (1987) invocation of the breakup of Pangaea, 250 to 100 million years ago depending on how far the animals could still disperse over water.

It is premature to state the direction of dispersal before a careful phylogenetic analysis of *Vanessa* is completed. There are more species-groups represented in North than South America, but more species on the latter continent. Herrera (1987) provides no explicit rationale for his claim that "The origin of *carye* is indubitably in Gondwanaland."

We have successfully resisted the temptation to generate scenarios for the history of *V. carye* and *annabella,* such as the proximate cause of the interruption of gene flow after invasion of one continent from the other, or for their failure to re-establish contact in montane Central America. Such exercises of the imagination are not in any sense testable with the tools used in this investigation.

Summing over many studies, Thorpe (1982) concludes that in general, "If allopatric populations of dubious status have genetic identities below about 0.85 it is improbable that they should be considered conspecific, while nominate species with I values above 0.85 should be considered doubtful if there is no other evidence of their specific status." He goes on to chide geneticists for violating common sense and the rules of significant figures by treating three-digit decimal I values as givens. Thorpe's rule of thumb for species status is inappropriate for Pierini but may be appropriate in Nymphalini and various other butterflies; time (and more studies) will tell. Nymphalini seem to undergo very slow morphological differentiation: Nearctic and Palearctic populations of *Nymphalis* and *Vanessa* species do not differ phenotypically; the genera are so uniform morphologically that generic splitting and lumping are a chronic problem in the group; even different genera show homologous responses to temperature shock during development (Shapiro 1984); and an Oligocene fossil attributed to *Vanessa* by Miller and Brown (1988) demonstrates morphological near-stasis over geologic time. On the other hand, Nymphalini seem to be more normal animals electrophoretically than Pierini are, that is, more labile, at least to judge by our work.

We agree with Thorpe's comments on significant figures; slight differences in electrophoretic data must be interpreted reasonably in the context of overall patterns of variation in the group, and calculations such as Sarich's estimator—one more manipulation removed from reality—must be used with still more caution. When one is primarily interested in orders of magnitude, as we are here, they are still quite valuable. Although our findings are very preliminary and we are cognizant of the limitations of our study, including small sample sizes and the use of samples from arbitrary locations within very large ranges, we are pleased with the outcome—and still comfortable with Field's decision to treat *Vanessa annabella* as a species distinct from *V. carye*.

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EVALUATION OF SPERMATOPHORE COUNTS IN STUDYING MATING SYSTEMS OF LEPIDOPTERA

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ABSTRACT. Counts of spermatophores contained by field-collected females have been widely used to investigate mating behavior of Lepidoptera. We present new counts for *Papilio glaucus* L. females and reanalyze published data for this species to evaluate the often implicit assumptions of this technique. In addition, we relate spermatophore size and sequence to mating history of tiger swallowtail females captured in Wisconsin. Number of spermatophores per female increased with both wear class and capture date. Females that received small first spermatophores were significantly more likely to contain one or more additional spermatophores than those that received large first spermatophores. This suggests that more spermatophores per female result from inferior initial matings and not necessarily from male mating preference.

Additional key words: spermatophore size, multiple-mating probability, *Papilio glaucus*, Papilionidae.

Because one spermatophore is passed during each copulation in most Lepidoptera, and generally persists in recognizable form, counts of spermatophores contained in females have been used to infer aspects of mating systems in this taxon (Burns 1966, 1968, Taylor 1967, Pliske 1973, Ehrlich & Ehrlich 1978, Smith 1984). Burns (1968) documented the validity of these two assumptions and warned of potential biases from different aged samples. However, interpretations of spermatophore data are limited in additional ways that frequently have been ignored.

Mating histories of female tiger swallowtails, *Papilio glaucus* L., as revealed by spermatophore counts, probably are documented better than any other species of butterfly (Drummond 1984). Over much of its geographic range, *P. glaucus* females may be tiger-striped yellow like males, or dark mimics of the distasteful *Battus philenor* (L.) (Brower 1958). Spermatophore counts were analyzed to evaluate the role of sexual selection in maintaining this sex-limited color dimorphism in female adults (Burns 1966, Makielski 1972, Pliske 1972, Platt et al. 1984). Drawing on this literature and additional studies in our laboratory, we illustrate the strengths and limitations of using spermatophore count data.

Materials and Methods

Samples of *Papilio glaucus canadensis* females were collected from five adjacent counties in north-central Wisconsin during the flight period of the single generation in 1985. Of the 282 females collected, 152 were set up for oviposition; the other 130 were frozen until dissected.

Females were assigned to a condition class either when set up or dissected. We classified 78% of the females for wing wear within a four-day period, which reduced potential bias due to changing standards by the classifier during the flight season as discussed below. Females were carefully dissected so that both number of spermatophores and their relative position in the bursa copulatrix were determined (Drummond 1984). Since the spermatophore of an additional mating forces the previous spermatophore forward in the saclike, posteriorly opening bursa copulatrix, and since spermatophores change from creamy white to yellow and collapse with time, accurate sequences of spermatophore deposition were determined for 98% of collected females. Volumes of the nearly spherical *P. g. canadensis* spermatophores were estimated by averaging the longest and shortest diameters and calculating the volume of such a sphere. Spermatophore dimensions were not measured for 52 females.

RESULTS AND DISCUSSION

Reliability. Spermatophore counts are generally reliable as a measure of female mating history (Burns 1968, Lederhouse 1981, Drummond 1984). Deviations from the one copulation-one spermatophore assumption are rare. Only occasionally will *Papilio* males not pass a spermatophore during coupling, and we have detected only one case of two spermatophores being passed during a single copulation ($n = 226$ hand-pairings of *Papilio*). This exceptional case occurred during a prolonged coupling lasting over 24 h. The same sample also contained one female that laid viable eggs but contained no detectable spermatophore. She did have seminal material in her bursa. Spermatophores are persistent in swallowtail females; even females that have been maintained for 20–30 days in the laboratory have obvious spermatophores. However, spermatophores may disintegrate rapidly in the lower Lepidoptera (Taylor 1967) where the spermatophore lacks chitin. Also, spermatophores are gradually absorbed in females of a variety of higher Lepidoptera (Burns 1968, Ehrlich & Ehrlich 1978). This is particularly true for species where females use nutrients contributed by males at copulation for egg production (Boggs & Gilbert 1979, Boggs 1981). Therefore, it seems prudent to verify the one copulation-one spermatophore relation for each species for which spermatophore counts are used.

Ageing females. Even when spermatophore counts reliably indicate number of copulations, there remain a variety of factors that must be considered in evaluating such data in the context of mating behavior and sexual selection. The difficulties chiefly involve controlling for female age and spermatophore quality.

It is logical to assume that older females should carry more sper-

TABLE 1. Mean number of spermatophores contained by *Papilio glaucus canadensis* females from Wisconsin in relation to wing condition and date of capture.

Condition	June 1985			
	6	13	20	27
Fresh	1.00	1.00	1.50	1.63
Slightly worn	1.20	1.13	1.55	1.85
Intermediate	1.56	1.61	1.84	2.33
Very worn	2.00	2.10	2.12	2.62
Mean	1.48	1.53	1.89	2.30
Sample size	25	108	79	70

matophores than younger females. However, it is difficult to age field-collected females accurately. Recapture rates of marked females are usually too low to provide known age samples (Lederhouse 1982). Wing wear is an estimate of age, but may reflect the quality of life (encounters with predators, inclement weather, or other factors; Lederhouse et al. 1987) as much as its quantity. By their nature, estimates of age are subjective and may vary from investigator to investigator. Since representatives of all age classes are not present throughout a flight season, our experience suggests a tendency to overestimate age early in a generation when very worn individuals are scarce and underestimate it late in a generation when very fresh individuals are rare. Nevertheless, spermatophore numbers carried by females of a variety of species have been shown to increase with estimates of age such as wing wear (Burns 1968, Lederhouse 1981, Drummond 1984, Lederhouse & Scriber 1987). This is illustrated within and across four sampling days for *P. g. canadensis* females (Table 1).

Accurate comparisons of samples rely on similar age structures or the ability to control for age structure in analysis. However, female age structures of natural butterfly populations are largely unknown. Spermatophore counts necessarily underestimate lifetime mating frequency. Sampling removes females at an artificial point. Once sampled, a female that would have remated the next day, and perhaps again the following week, becomes equivalent to a female that would never have remated. Since females may be singly-mated as a result of their mating system or their young age, studies indicating female monogamy (Wiklund 1977, 1982, Wiklund & Forsberg 1985) must give age estimates for their samples.

Comparisons of mating histories for different female morphs within a population must control for female age. Pliske (1972) questioned the importance of sexual selection in maintaining the frequency of the yellow female phenotype in a Florida population of *P. glaucus* because he found no difference in number of spermatophores carried by yellow or dark females. Our reanalysis of Pliske's data indicates that his sample of *P. glaucus* females cannot address effects of sexual selection on differential remating of the two female morphs because females of both morphs had mated too few times for a differential to be detectable. Either females in his sample were too fresh (young) for many to have mated more than once, or multiple-mating was rarer in central Florida *P. glaucus* populations (Pliske 1972, 1973) than elsewhere (Burns 1966, Makielski 1972, Platt et al. 1984, Lederhouse & Scriber 1987).

Spermatophore quality. Spermatophore quality may influence the frequency with which a female mates. A common assumption is that more spermatophores indicate superior mating, which is based on the supposition that all spermatophores are equal. Yet young or frequently-mating males produce smaller than average spermatophores (Sims 1979, Svard & Wiklund 1986). Spermatophore volumes in early season *P. g. canadensis* females suggest a bimodal distribution (Fig. 1). Hand-pairing in our laboratory indicates that the larger spermatophores (about 7 mm^3) result from males' first matings and the smaller ones (about 4 mm^3) from subsequent matings (Lederhouse, Ayres & Scriber in prep.). Spermatophore size distribution from a late-season sample shows a significant increase in frequency of smaller spermatophores compared with the early-season sample (Fig. 1; Kolmogorov-Smirnov test, $P < 0.005$). Small spermatophores may result in lower egg fertility or more rapid fertility declines (Lederhouse & Scriber 1987). Size of spermatophores is therefore an important aspect of quality that should be considered.

Since stretch receptors in the female's bursa copulatrix may determine female receptivity (Sugawara 1979), smaller than average spermatophores might produce a shorter mating refractory period or none at all. Indeed, a multiway contingency analysis of the probability of *P. g. canadensis* females carrying multiple spermatophores demonstrates a significant effect of spermatophore size, in addition to date of capture and female condition class (Fig. 2, Table 2). Only 45% of 160 females that received a large first spermatophore (>4 mm^3) carried more than one spermatophore compared with 63% of 70 females that had a small first spermatophore (≤ 4 mm^3). This difference is significant (χ^2, $P = 0.002$, Table 2) although both samples had similar age distributions as indicated by wing-wear classes (χ^2, $P > 0.25$). This suggests that females mated again to replace a small spermatophore. We observed a similar relation for *P. g. glaucus* from an Ohio population (Lederhouse & Scriber 1987). Of 164 females that received a large first spermatophore, 45% had mated more than once compared with 67% of 165 females

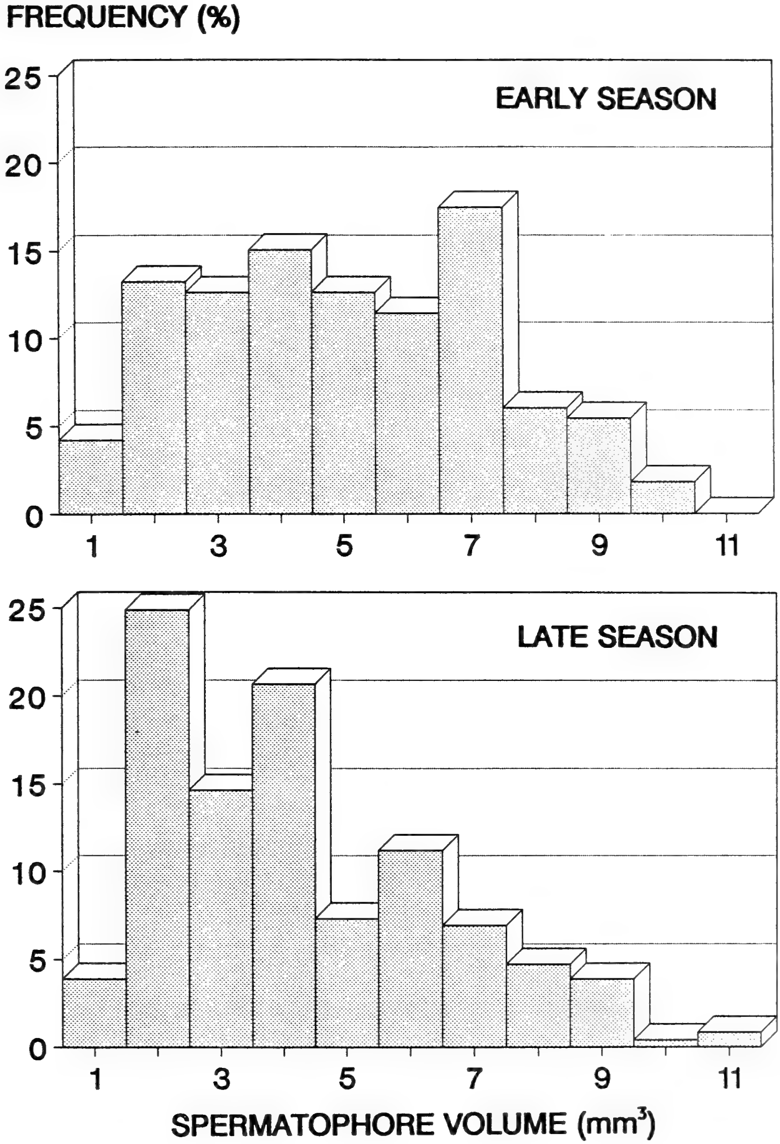

FIG. 1. Size distribution of Wisconsin *Papilio glaucus canadensis* spermatophores found in early-season females (captured 6–13 June 1985) and in late-season females (captured 20–27 June 1985). N = 166 and 232 spermatophores, respectively.

TABLE 2. Results of multiway contingency analysis (SAS CATMOD) of the probability of multiple-mating in *P. g. canadensis*. The null hypothesis tested for each source effect was that proportion of remated females (carrying 2 or more spermatophores) did not differ between categories of the independent variable. A graphical representation of the analysis is in Fig. 2.

Source	df	Chi-square	P
Condition	2	32.4	0.0001
Spermatophore size	1	10.2	0.002
Date of collection	1	5.6	0.018
Condition × date	2	4.7	0.10
Other interactions	1–2	<3.0	>0.22

that had a small first spermatophore ($\chi^2 = 15.1$, $P < 0.0001$, where condition class and year were other sources of variation in the model).

Male *P. glaucus* generally emerge before females (Berger 1986), which provides time for them to reach full sexual maturity before copulation. Nevertheless, some small spermatophores carried by early females could come from immature males because emergence curves of the sexes do overlap (Berger 1986). The significant relation between date of capture and probability of remating (Tables 1, 2) may result from an increased proportion of females mating with previously mated males later in the generation. Since size of spermatophore passed by a male decreases with additional matings in *P. g. canadensis* (Lederhouse, Ayres & Scriber in prep.) and proportion of males that had mated at least once appears to increase later in the generation (Fig. 1), later mating females were more likely to receive an insufficient spermatophore and mate again after a short refractory period. Late in the generation, it was not uncommon for even fresh females to carry three or four smaller than average spermatophores.

Even the size of a spermatophore may be a poor indicator of its quality (Greenfield 1983, Jones et al. 1986). In our study of 1985 *P. g. canadensis* females, we could detect no significant relation between spermatophore size and percent egg hatch, despite wide variation in egg hatch (range 0.0–97.5%, $\bar{x} = 58.5$, $n = 23$). Similar-sized spermatophores may vary in relative proportions of different constituents (Marshall 1982, Alcock & Hadley 1987, Marshall & McNeil in press). This may be particularly important for those species where the spermatophore and associated secretions contribute to the nutrient pool available to females for reproduction. Selection could favor male sperm delivery strategies that treat females of different reproductive value differently (Boggs 1981), or that fool a female with large but inexpensive, low quality spermatophores.

Persistence of courtship is related to mating history in some lepi-

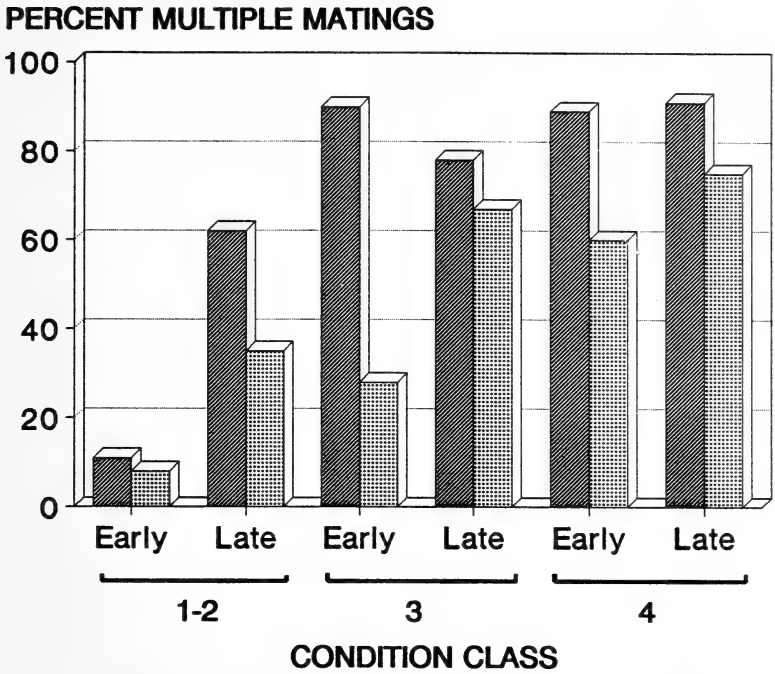

FIG. 2. Probability of remating in Wisconsin *Papilio glaucus canadensis* females as influenced by first spermatophore size, date of collection, and condition class. In 6 of 6 comparisons females receiving a small 1st spermatophore (hatched bars) were more likely to remate than females receiving a large 1st spermatophore (stippled bars). Associated contingency tests are in Table 2. Early-season females were captured 6–13 June and late-season females 20–27 June 1985.

dopteran species (Rutowski 1979, 1980). High selectivity by either a male or a female could lead to passing of a larger than average spermatophore followed by a longer than average mating refractory period. Thus, preferred females might carry fewer but larger spermatophores on average. Larger *Dryas julia* Fabr. females received larger spermatophores (Boggs 1981). Less selective males might mate more frequently but pass smaller than average spermatophores. Less selective females might receive smaller spermatophores, remate at shorter intervals, and as a result carry more spermatophores on average. Such potential results run counter to the logic of Burns (1966) and others.

These various factors do not invalidate spermatophore counts but suggest that more care must be taken in interpreting count data. Counting spermatophores remains a valuable tool, but count data must be integrated with that of other techniques to yield an accurate appraisal of mating behavior in Lepidoptera.

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BEHAVIOR OF THE TERRITORIAL SPECIES *LIMENITIS WEIDEMEYERII* (NYMPHALIDAE) WITHIN TEMPORARY FEEDING AREAS

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ABSTRACT. Behavior of a population of *Limenitis weidemeyerii* Edwards (Nymphalidae) was studied in central Colorado using mark-recapture and observations. In 1984, individuals of both sexes fed on sap excreted from a willow via holes made by sapsuckers. The following season, *L. weidemeyerii* of both sexes fed on honeydew excreted by aphids. In addition, in both years, individuals fed at artificial high-quality food sources experimentally placed within the habitat. Territorial behaviors (patrols, chases, and investigations) were not observed within the temporary feeding areas, possibly because high intruder pressures affected the defendability of these sites. It is suggested that some studies citing a lack of territoriality in lepidopterans may have been conducted within temporary feeding areas.

Additional key words: admiral butterfly, territoriality, sap feeding.

Resource defense territoriality involves defense of resources that are patchy, predictable, and economically defendable (Davies 1978a). In lepidopteran territoriality, males generally defend locations where females reliably can be found: oviposition sites (Baker 1972), landmark sites (Shields 1967, Davies 1978b, Lederhouse 1982), or routes used by females for feeding or oviposition (Fitzpatrick & Wellington 1983, Baker 1972). While food resources are commonly defended in other taxonomic groups (Wittenberger 1981), reports of butterflies defending areas around adult feeding sites are rare. This may stem from the economic defendability of adult lepidopteran feeding sites. Because nectar resources used by butterflies often are widely scattered (Rutowski 1984; but see Murphy 1983, Murphy et al. 1984), it might prove difficult for a butterfly to maintain exclusive use of a patch of flowers, even though other insects (especially bees) do defend floral resources. Male mason bees (*Hoplitis anthocopoides* (Schenck): Megachilidae) for instance, have been found defending patches of flowers (Eickwort & Ginsberg 1980). In addition to floral resources, Lepidoptera often use temporary food sources such as sap holes, puddles, animal excreta, and carrion (Wilson & Hort 1926, Norris 1936, Downes 1973, Adler & Pearson 1982) which might prove to be more economically defendable.

I describe here the behavior of individuals of a territorial species, *Limenitis weidemeyerii* Edwards (Nymphalidae) during two flight seasons when the population had access to an unpredictable, patchy food supply in addition to its normally undefended floral foraging sites. During one season (1984), individuals of both sexes were found feeding

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at holes on a willow made by yellow-bellied sapsuckers (*Sphyrapicus varius* L.: Picidae). The following year this site was not used, presumably because sap no longer flowed freely. Individuals of both sexes were found feeding at another temporary food supply: honeydew on willow leaves in a stand where there were abundant aphids (*Chaitophorus viminalis* Koch: Aphididae). Neither location was used by this species during the previous three years as territorial, feeding, or oviposition sites. Artificial food sources also were placed in similar sites at random locations and times, and presence or absence of territorial behavior was recorded.

METHODS

A population of *Limenitis weidemeyerii* was studied during July and August 1984 and 1985 along Cement Creek in Gunnison Co., Colorado, as part of a larger study of social and genetic organization of populations of this species (Rosenberg 1987). All individuals seen were marked and color-coded using the 1-2-4-7 system of Ehrlich and Davidson (1960), so individuals could be easily identified on the wing. Territorial behavior of this species is reported in greater detail elsewhere (Rosenberg 1987). Briefly, territorial behavior consists of a perched male flying out to investigate any passing object, resulting in either a spiral flight (individuals fly around one another), or a chase (flight directly towards an intruder leading away from the perch site). Territorial behavior also includes patrols: smooth flights from and back to the perch without obvious stimulus. Feeding behavior also was recorded.

During the 1984 flight season individuals of both sexes were found aggregating at a series of holes made by yellow-bellied sapsuckers on a 1.5 m tall willow bush (*Salix* sp., hereafter called sapwillow) located approximately 23 m from the nearest territorial site. Behavior of individuals at this location was recorded at various times through the day (0900–1800 h), over the season (12 July–27 August), and observations also were concentrated for a full day only on activities at this site. Weather conditions (sun, cloud, rain), time of day, sex, identity and behavior as described above were recorded. Ages were estimated by wing-wear in increments of 0.5 from scores of 1 (newly emerged) to 4 (many scales missing), following the conventions of Watt et al. (1977). For unmarked individuals sighted, weather, time of day, and behaviors were recorded; ages were unknown, and sex of only a sample of individuals could be ascertained by noting approximate wing lengths. As with most nymphalids (Howe 1975), females of this species are larger than males.

During the 1985 flight season the sapwillow was no longer used by the butterflies. Instead, they frequented a willow stand of 10 m^2 area ca. 100 m away (and 90 m from the nearest territorial site) where approximately 60% of leaves contained aphids on their undersides. Behavior and identity of individuals visiting this site, weather conditions, time of day, sex, and ages of a sample of individuals were recorded during the 1985 season (25 July–27 August). Observers could approach within 0.25 m of individual butterflies at both sites.

Four times each season artificial food sources were placed for a minimum of two days in arbitrary locations in the habitat, and identity, sex and age of individuals feeding there were recorded. Artificial sources contained fermented fruit, beer or wine, and were placed in cages styled after Platt (1969).

RESULTS

In the 1984 season there were 70 sightings of *L. weidemeyerii* feeding at the sapwillow: 20 marked males, 4 marked females, and 21 unmarked individuals. The marked butterflies fed there 49 different times on 13 separate days, many of these individuals (42%) feeding there repeatedly on different days. It is possible that unmarked butterflies also were resighted on different days. Individuals of various ages were found at this site feeding at all times of the day and in all weather conditions. The majority of the marked butterflies (84%) were not newly emerged; the average age-class was approximately 2. In more than 30 h of observation, only feeding was observed at the sapwillow; no territorial behaviors (patrols, chases, investigations) were observed. Other taxa also fed there, including unidentified species of Diptera and Hymenoptera, and other Lepidoptera such as *Vanessa atalanta* L., *Nymphalis antiopa* L., and birds such as yellow-bellied sapsucker, and broad-tailed hummingbird.

In the 1985 season there were 62 sightings of *L. weidemeyerii* of both sexes feeding at the willow stand containing aphids: 1 marked female, 16 marked males, and 34 unmarked individuals (at least 4 of the last were females). Marked butterflies were sighted there 28 times; 8 of the marked males fed there on multiple days. Some of the unmarked butterflies also may have fed there on different days. The only marked female sighted had previously mated (as evidenced by a sperm plug). No newly emerged individuals were found there. On average, the marked individuals were of age-class 3 (out of a maximum wing-wear score of 4). Weather conditions were noted for 23 observations: only 4 sightings occurred during a cloudy period, the other 19 when there was sunshine. Feeding was observed at all times of day. Individuals within the site spent most of their time probing with their proboscides on sticky spots on leaf surfaces. The butterflies apparently were feeding on the honeydew flicked onto the top surfaces by the aphids on leaves above (as in Wilson 1971). In the laboratory after feeding, I observed *L.*

weidemeyerii regurgitate and probe repeatedly at the regurgitant. Because in the field this species was observed to probe repeatedly on the leaves, it is reasonable to assume they were imbibing fresh (or possibly dissolved) honeydew. In more than 10 h of intensive observation, patrol flights never were seen in this area. Interactions between individuals were extremely brief and slow moving, and rather than involving chases away from the site, always resulted in the individuals landing on leaves there and feeding. Other taxa also were observed feeding on the honeydew including Diptera (Sarcophagidae, Muscidae) and Hymenoptera (*Dolichovespula arenaria* (Fabricius): Vespidae, and *Dialictus* sp.: Halictidae).

Five individuals were found at artificial food sources placed in the field: four males and one female. These individuals on average were scored as age 2 (out of a total wing-wear score of 4). In more than 6 h of observation, no territorial behavior was observed at or near these sources.

DISCUSSION

Patchy and predictable resources in nature often are defended via territoriality (Davies 1978a). Unpredictable sources, even if high quality often are not defended. Male territorial behavior (perching, patrolling, investigating, chasing) was not observed at three temporary feeding sites of a population of *Limenitis weidemeyerii* in central Colorado. These feeding sites, at sapsucker sap holes, leaves with aphid honeydew, and artificial sources, were high-quality sources rich in sugars and free amino acids. Four other willow stands with evidence of previous sapsucker damage were found within the boundaries of this population, suggesting that although this food source is unpredictable in time and space, it had been encountered by this population of *L. weidemeyerii* previously. *Limenitis* butterflies have been reported feeding at sap holes (Flemwell 1914, Wilson & Hort 1926) and Platt (1969) successfully traps *Limenitis* using baits. To date there have been only a few reports of adult butterflies other than lycaenids feeding on aphid honeydew (Kershaw 1907, Bingham 1907, Johnson & Stafford 1986).

Limenitis weidemeyerii males defend sites where they have good vantage points of approaching conspecifics, generally either at locations of emerging females or along flyways with an open central area bounded on other sides by vegetation (Rosenberg 1987). Although feeding locations described here proved to be good rendezvous sites for a single season, they were within wide open areas, and there is no guarantee of their utility in the following generation. Males appear to mate with females emerging within their territorial sites (Rosenberg 1987); thus, ovipositing within a previously unused territorial site might lead to offspring being unmated longer. Also, larvae in these sites might be harmed because sap can attract adults of predatory and parasitic groups (Stary 1970), and also can breed bacteria. Finally, females visiting these sites were older ones, hence probably not receptive anyway (Rosenberg 1987), so defense of these locations may have been a waste of a territorial male's time and energy.

Butterflies were observed feeding at these sites under all weather conditions. Finding males feeding there on sunny days is particularly interesting because in most butterfly species territorial defense occurs on sunny days (Baker 1972, Davies 1978b, Lederhouse 1982, Wickman & Wiklund 1983, Rosenberg 1987). It is probable that individuals come to the temporary sites to quickly stoke up with a high energy food source to support other activities such as territorial defense, mating, and oviposition.

Alternatively, these high energy sources may not be defended territorially because it would be uneconomical on account of high intruder pressures. A breakdown of territorial behavior at feeding sites also has been noted for other butterfly species (Baker 1972, Fukuda 1974), as well as for birds (Gill & Wolf 1975).

Before the recent acceptance of lepidopteran territoriality, there were a number of reports on a "lack of territoriality" in butterflies (Ross 1963, Suzuki 1976, Scott 1974). One such report, on two species of *Hamadryas*, seems to have been undertaken at a temporary feeding area; Ross (1963) described tree sapholes within the study site. The "lack of territoriality" hence may only refer to this feeding location. More detailed study of these species away from a potential high-quality temporary feeding area may indicate these to be territorial species. If so, it is unfortunate that Ross's study has been so widely cited as negative evidence for lepidopteran territoriality. Further studies of the behavior of individuals with and without unpredictable high quality food sources can help us to better understand territoriality in Lepidoptera.

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A NEW NEOTROPICAL *ANONCIA* SPECIES (COSMOPTERIGIDAE)

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ABSTRACT. *Anoncia crossi* is described from 1 male and 15 females collected in Guerrero, Mexico. *Anoncia crossi* is differentiated from *A. diveni*, the only other congener to occur in the Neotropics, by structural differences in male and female genitalia, and shape of the eighth tergum. A photograph of the imago and illustrations of wing venation, modified eighth tergum and sternum of the male, and male and female genitalia are included.

Additional key words: Gelechioidea, Cosmopteriginae, Mexico, *Anoncia crossi*, *A. diveni*.

Anoncia is a New World genus with 31 species known from the SW United States, Mexico, and Honduras (Hodges 1978, 1983). Larvae feed on Labiatae, Loasaceae, and Verbenaceae as leaftiers and leafminers, or in immature ovaries of developing fruit (Hodges 1978).

Clarke (1941a) proposed *Anoncia* to include seven previously described species. After the description of a new *Anoncia* and two species transferrals into *Anoncia* (Clarke 1942), the genus was ignored in taxonomic treatments until the studies of Hodges (1962, 1978, 1983). Hodges (1962) described 9 *Anoncia* and made 2 synonymies, and in a review of the genus (Hodges 1978) synonymized 2 species and added 16 species including 3 new combinations. Hodges (1978) provided adequate descriptions, and a generic key that places the species described here in *Anoncia* on the basis of the following characters: hindwing with M_3 and Cu_1 connate or stalked, rarely separate; forewing with Cu_1 and Cu_2 slightly downcurved from cell then parallel with M_3, ocelli absent; aedeagus without dorsal projection from midregion.

Discovery of the species described here resulted from examination of unidentified specimens during systematics study of North American Blastobasidae (Gelechioidea). The new species is described here because it is only one of two species of *Anoncia* known from the Neotropics, and will undoubtedly contribute to future understanding of the evolution of the genus.

Pinned specimens and genitalic preparations were examined using a stereomicroscope and a phase-contrast microscope. Colors of vestiture were described using Kornerup and Wanscher (1978) as a standard. Genitalia were dissected as described by Clarke (1941b), except that mercurochrome and chlorazol black were used as stains.

1

FIG. 1. *Anoncia crossi*, holotype female.

Anoncia crossi Adamski, new species
(Figs. 1–6)

Head. Scales on frontoclypeus and vertex basally and apically white with subapical brown band, or white with brown apex; scape, pedicel, flagellomeres mostly brown intermixed with white scales, antennal pecten concolorous with vertex scales; 2nd segment of labial palpus with basal and dorsomedial scales brown, medial and subapical scales white, terminal segment with basal and dorsomedial scales white, medial and subapical scales brown, or with mostly brown scales on outer surface, and mostly white scales on inner surface. **Thorax.** Tegulae and mesoscutum concolorous with vertex scales, or brown intermixed with light-brown, or mostly brown scales, tegulae occasionally with white marginal scales. **Legs.** Mostly brown intermixed with white scales, each segment and tarsomere with white apical band, each tibia with median band (sometimes not expressed on tibia 1), coxa 1 and femora 2–3 occasionally mostly white intermixed with brown scales. **Forewing** (Figs. 1, 2). Length 6.7–8.4 mm (n = 16); ground color gray; basal wing scales white with brown, light-brown, or brownish gray apex; submedial fascia with mostly semierect brown scales, delimiting a subcircular patch of light-brown scales near middle of discal cell, posterior portion of submedial fascia pale; scales on wing adjacent to inner margin of submedial fascia mostly white, intermixed with white scales tipped with light-brown; scales on distal portion of wing mostly white, tipped with light-brown, intermixed with white scales tipped with brown; ventral surface uniform grayish brown; venation as in Fig. 2 (n = 3). **Hindwing** (Figs. 1, 2). Dorsal and ventral surfaces uniformly light grayish brown; venation as in Fig. 2 (n = 3). **Abdomen.** Anterior portion of segments with grayish brown scales, posterior portion with light grayish brown scales; eighth tergum and sternum modified as in Figs. 3–4, seventh segment unmodified (n = 1). **Male genitalia** (Fig. 5) (n = 1). Uncus absent, gnathos with two highly sclerotized asymmetrical projections, apical setae absent, larger projection serpentine-shaped and apically blunt, smaller projection apically pointed posteriorly, posterior margin deeply arched; tegumen and aedeagus heavily sclerotized, aedeagus ankylosed with heavily sclerotized diaphragma, partially setose on apical rim, cornuti absent; vinculum broad throughout; valvae asymmetrical, right valva reduced laterally, with large basal lobe, broad at base, left valva laterally broadened, modified basally into a long, thin, apically setose projection, slightly expanded basilaterally. **Female genitalia** (Fig. 6) (n = 3). Ostium bursae asymmetrically

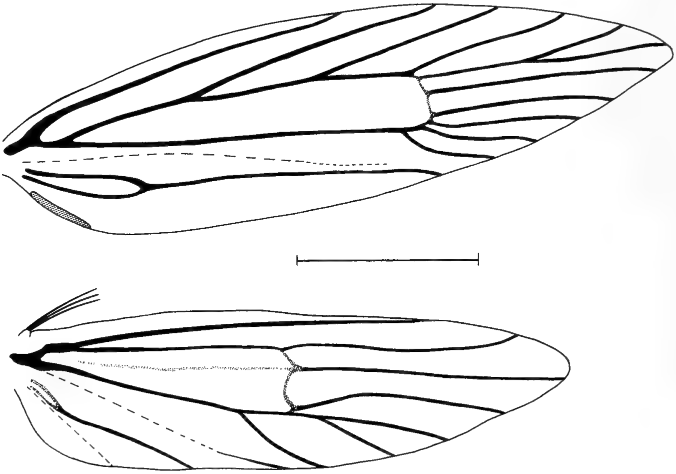

FIG. 2. Wing venation of *Anoncia crossi*. Scale line = 2.0 mm.

situated on eighth tergum; ductus bursae membranous throughout; corpus bursae membranous with spinules on walls, with accessory bursae at base; ductus seminalis arising from accessory bursa, signum absent; apophyses anteriores widely separated basally, arising from lateral margin of eighth tergum; eighth tergum with pair of short submedial

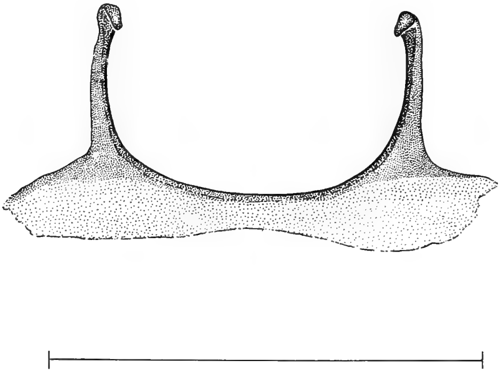

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FIG. 3. Eighth tergum of male *Anoncia crossi* (dorsal view). Scale line = 0.5 mm.
FIG. 4. Eighth sternum of male *Anoncia crossi* (dorsal view). Scale line = 0.5 mm.

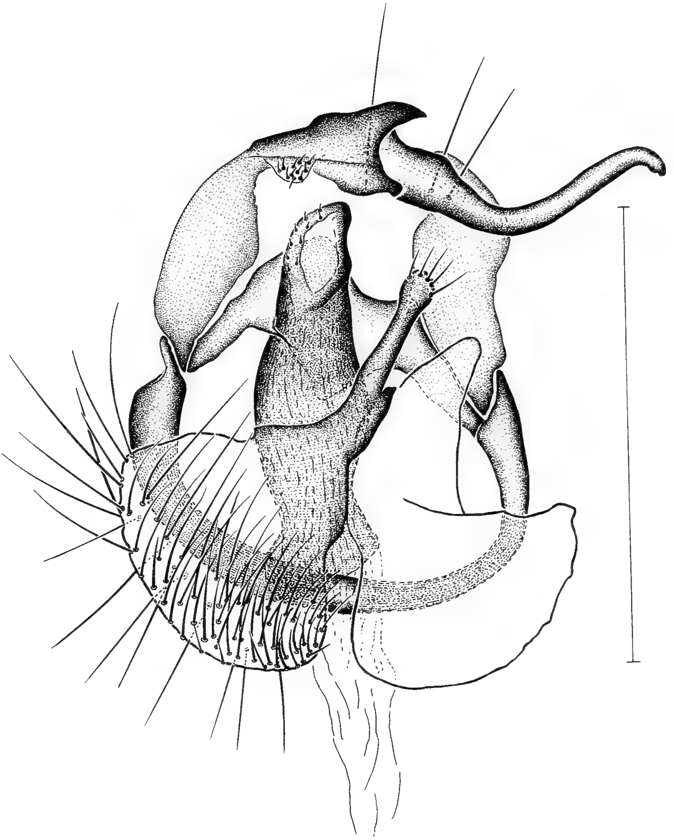

FIG. 5. Male genitalia of *Anoncia crossi* (posterior view). Scale line = 0.5 mm.

projections, posterior margin slightly emarginate medially; seventh abdominal segment unmodified.

Types. Holotype (Fig. 1) female: Mex[ico], Guerrero, Zapilote C[an]y[o]n, 8 km S[outh] Mezcala, IX-10-82, 550 m; [Collectors] J. A. Powell and J. A. Chemsak, at light. Holotype not dissected, deposited in Essig Entomology Museum, University of California, Berkeley, California. Paratypes (1 male, 14 females): 1 female same data as holotype; 4 females Mex. Guerrero, 32 km W Eguala, IX-11-82, elev. 1350 m; J. A. Powell and J. A. Chemsak, D. Adamski wing slide nos. 3029, 3129, 3130 and gen. slide nos. 3127 and 3128; 2 females same as previous data except IX-15-87; 1 male, 5 females same except IX-15-82, D. Adamski male gen. slide no. 3027; 2 females 10 km E Tixtla; IX-18/22-82; elev. 1770 m, D. Adamski female gen. slide no. 3028. Two female paratypes in U.S. National Museum, other paratypes in same depository as holotype.

Remarks. *Anoncia crossi* appears closely allied to *A. diveni* (Heinrich), and these are the only *Anoncia* congeners known in the Neotropics. Each possess a light-brown patch of scales within the submedial fascia of the forewing. Males of both species possess an unmodified seventh abdominal segment, valvae are short and broad, and size and shape of aedeagus are similar. Females of both species have a membranous ductus bursae, an accessory bursae that arises from base of the corpus bursae, lack signa, and have apophyses anteriores that arise from lateral margins of the eighth sternum.

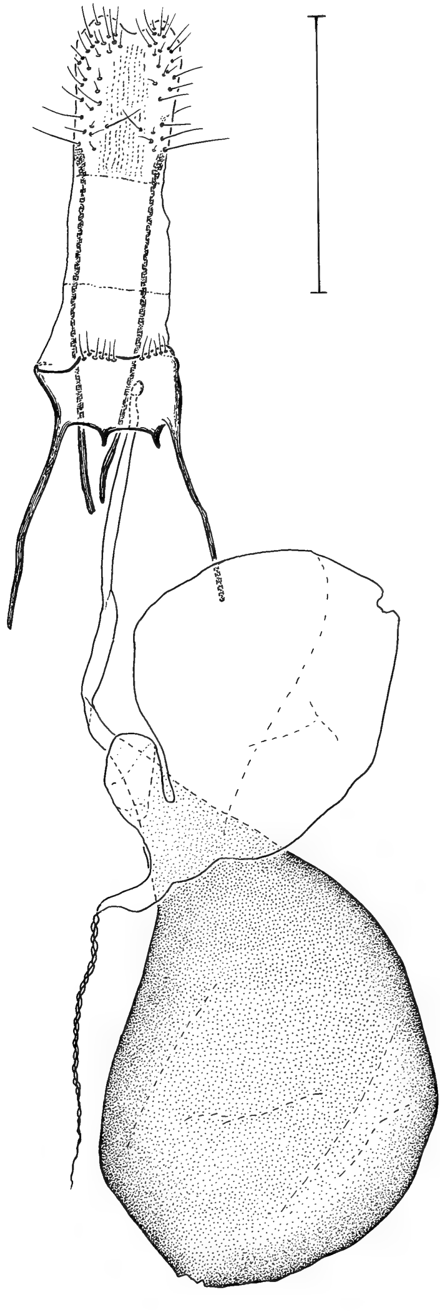

FIG. 6. Female genitalia of *Anoncia crossi* (dorsal view). Scale line = 1.0 mm.

Males of *crossi* can be separated from those of *diveni* by the acute angle and broader lobe on the right valva, presence of apical setae on basal projection of the left valva, presence of expanded base of the basal projection of the left valva, broad vinculum throughout, pointed apex of the left brachium, absence of a dorsal projection on base of right brachium, presence of setae on apical rim of the aedeagus, and linear shape of the eighth abdominal tergum. Females of *crossi* can be separated from those of *diveni* by presence of a pair of small projections on the anterior margin of the eighth tergum between apophyses anteriores.

Hodges's (1978) key to species of *Anoncia* is modified below to include *A. crossi*. In the part treating males, couplet 23 is modified, and couplet 23′ added; in the part treating females, couplet 39 is modified and couplet 39′ added. The modifications read as follows:

23. Valvae short, broadly joined basally (text fig. 17b) .... 23′
– Valvae longer, narrowly joined basally (text fig. 18d) 24
23′. Left valva with basal lobe setose apically .... *diveni*
– Left valva with basal lobe without setae .... *crossi*
39. Eighth abdominal tergum concavely excavated, genital plate at least ½ width of 8th abdominal tergum (text fig. 28a) .... 39′
– Eighth abdominal tergum concavely excavated, genital plate less than ⅓ width of 8th abdominal tergum (text fig. 26f) .... *diveni*
39′. Anterior margin of 8th abdominal tergum with two short lobes .... *crossi*
– Anterior margin of 8th abdominal tergum without such lobes .... *smogops*

Etymology. The new species is named in honor and memory of Dr. William H. Cross, naturalist, ecologist, taxonomist, and founder of the Mississippi Entomological Museum at Mississippi State University, who died in Mexico in 1984 on a collecting expedition.

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I thank J. A. Powell, University of California, Berkeley, for loan of the specimens examined, R. W. Hodges, U.S. Dept. of Agriculture, Systematic Entomology Laboratory, Washington, D.C., for confirming the identity of the species, and Larry Corpus, Dept. of Entomology, Mississippi State University, for preparation of Fig. 1. Research supported in part by National Science Foundation Grant no. BSR-8501212 and Mississippi Agricultural and Forestry Experiment Station Projection no. J-6933.

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A NEW SUBSPECIES OF *NEONYMPHA MITCHELLII* (FRENCH) (SATYRIDAE) FROM NORTH CAROLINA

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ABSTRACT. In 1983, a colony of *Neonympha mitchellii* was discovered in south central North Carolina. Before 1983, *mitchellii* was known only from Michigan, Indiana, Ohio, and New Jersey. The newly discovered population co-occurs with *Neonympha areolatus* (J. B. Smith). Comparison of 60 male genitalia of *mitchellii* from Michigan and New Jersey and 20 from North Carolina with 60 of *areolatus* showed that the two have distinct valvae and are separate species. Comparison of 200 Michigan and New Jersey *mitchellii* with 47 North Carolina *mitchellii* revealed several population differences. The North Carolina population is here named *N. m. francisci.* Both nominate and new subspecies are in need of conservation.

Additional key words: *Neonympha mitchellii francisci,* systematics, biology, endangered, habitat.

Neonympha mitchellii French (1889) is one of the most restricted butterflies in the eastern U.S. Its known range before 1983 was Michigan, Indiana, Ohio, and New Jersey (Opler & Krizek 1984). On 2 June 1983, Kral discovered a small colony of *mitchellii* on Fort Bragg Military Reservation, Fort Bragg, North Carolina. This discovery was both a new State record and a significant extension of known range.

There has been confusion as to whether *Neonympha mitchellii* and *N. areolatus* are distinct species (Scott 1986, Mather 1965). Wing maculation characters are not always reliable. There are several populations in North Carolina where some *N. areolatus* have round hindwing ocelli much like typical *N. mitchellii.* Such a population is adjacent to the habitat of the North Carolina *N. mitchellii* population, and there are similar phenotypes in other *N. areolatus* populations such as in Gates Co., North Carolina. The problem of identification is obviously greatest where the ranges of the two species overlap. This confusion is resolved here by genitalic structure. Male genitalia of 60 nominate *mitchellii* from Michigan and New Jersey and 20 from North Carolina were compared with 60 of *areolatus,* with results as follows. The distal process of the *areolatus* valva has a distal toothlike process that projects sharply dorsad, while that of *mitchellii* has a distal process that projects laterad and is denticulate (Fig. 1).

Comparison of North Carolina *mitchellii* with Michigan and New Jersey *mitchellii* revealed several population differences (Table 1). Be-

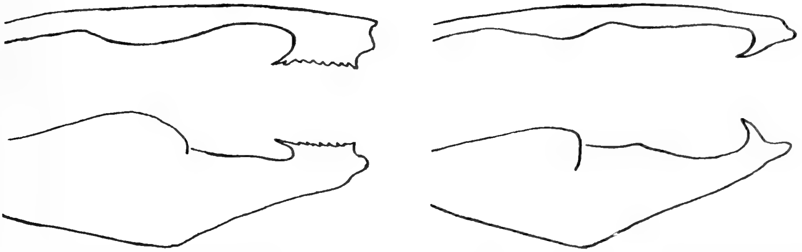

FIG. 1. Top left and right lateral views of *Neonympha* male valvae. Left, *N. mitchellii*, Jackson Co., Michigan; right, *N. areolatus*, Fort Bragg, North Carolina.

low we describe and name the North Carolina population. Parenthetical color names are based on Ridgeway (1886).

Neonympha mitchellii francisci Parshall & Kral, new subspecies
(Fig. 2, Table 1)

Description (male holotype). Left forewing length 17.0 mm (for all males, mean 16.7 mm, range 15.0–18.0 mm, N = 35). Dorsal wing surfaces uniform chocolate-brown (vandyke brown) except for apex and outer margins. Outer margins and forewing apex have modified hairlike scales slightly lighter brown than rest of dorsal surfaces, resulting in lighter brown fringe along outer margins, and much wider (1 mm) band of light-brown buff scales (drab brown) forming a second submarginal band which follows contour of forewing margin. Second submarginal band lighter brown than fringe scales or rest of ground scales of dorsal wing surfaces. A line of dark brown scales identical to first completes submarginal bands. Dorsal submarginal bands viewed together are widest on hindwing surfaces, forming uniform width of nearly 2 mm. Hindwing inner margin covered with light brown scales from inner margin vein 2A to submarginal band at anal angle. It then flows basally, completing the triangular light brown area. Rest of dorsal surface uniformly unmarked.

Ventral surfaces of both wings light brown, lighter than dorsal surfaces but not as light as ventral surfaces in nominate *N. mitchellii*. Fringes of apex and outer margin much darker than dorsal surfaces, slightly contrasting to lighter ground color of these surfaces. Outer marginal fringe followed by a rufous (ochraceous-rufous) submarginal band. This band, 0.75 mm wide, begins along costal margin, closely following contour of outer margin, ending at inner margin. Proximad to this band is a very thin submarginal line of dark brown scales which follows entire length of much wider rufous band. A second less rufous band follows lighter band. Second proximad rufous band is thinner than first and follows outer margin contour beginning subapically at vein R_5 and ending at inner margin. Three submarginal bands together are ca. 1.5 mm wide.

Forewing postmedial area has row of 4 ocelli in cells M_1, M_2, M_3, and Cu_1. Ocelli in M_2 and M_3 largest and most developed. Ocellus of cell M_1 only faintly present. All 4 ocelli have silvered pupils which are a series of flat, clear scales with silver sheen. Each 3 fully developed ocelli have a thin ring of yellow buff scales with interior ground of black with silver pupils. Ocellus in cell M_3 is largest.

Forewing with 2 medial transverse bands, 1 barely extracellular, the other transcellular, both darker brown than rufous. Extracellular transverse band begins subapically at vein R_4 and meets 2nd submarginal band to form continuous band. Extracellular band then flows diagonally to vein M_1 ca. 2 mm from junction of M_1 and discal cell, ending vertically at inner margin at vein 2A. This medial line forms closure around postmedial row of ocelli open at inner margin. Second or transcellular line parallels path of first, ending

TABLE 1. Comparison of *Neonympha mitchellii* subspecies.

Character	*m. francisci* (North Carolina)		*m. mitchellii* (Michigan & New Jersey)	
	Male	Female	Male	Female
Left forewing length				
Mean ± SD	16.7 ± 0.8	18.8 ± 0.8	16.4 ± 0.75	18.3 ± 0.5
Range	15.0–18.0	17.5–20.1	16.0–19.0	18.0–24.0
N	35	12	44	31
No. forewing ocelli				
Mean ± SD	3.3 ± 0.7	4.0 ± 0.65	3.7 ± 0.5	5.9 ± 0.7
Range	2–5	3–5	2–4	5–6
N	35	12	44	31
No. hindwing ocelli				
Mean ± SD	5.5 ± 0.6	5.75 ± 0.4	5.5 ± 0.55	5.9 ± 0.45
Range	4–6	5–6	5–6	5–6
N	35	12	44	31
3rd & 4th hindwing ocelli bifid				
%	2			
N	47		200	
3rd & 4th ocelli set at oblique angle*				
%	74	100	18	20
N	35	12	100	100
Ocelli ring	Thin, not very contrasting with ground color		Thick, contrasting with ground color	
Ventral wing color	Not brightly contrasting with dorsal surface		Brightly contrasting with dorsal surface	
Medial transverse bands	More rufous than brown, thin, and contrasting with ground color (98% of sample)		Dark brown, contrasting less with ground color (90% of sample)	
N	200		47	
Voltinism	Bivoltine		Univoltine	
Habitat	Treed fen		Tamarack bog	

* Frequencies underlying percentages differ between subspecies for both males and females ($P < 0.01$, 2 × 2 contingency tables, adjusted *G*-test).

near inner margin. Distance between the two parallel bands is visually uniform width of 3.75 mm. Ventral forewing outer margin fringed as dorsally. Two submarginal rufous bands separated by light band of ground scales. Rufous bands of hindwing larger and more rufous than forewing.

Six postmedial hindwing ocelli arranged in curved pattern mirror contour of outer margin. Cells R_5, M_1, M_2, M_3, Cu_1, Cu_2 have ocelli. Ocelli of cells R_5, M_1 greatly reduced but retain silvered pupils. Ocelli in cells M_2, M_3 largest, best developed. All ocelli ovoid and pointed distally. Third and 5th ocelli of cells M_2, Cu_1 nearly bifid with double silvered pupils. Fourth ocelli in cell M_3 double-pupiled but not bifid. Each ocellus with a thin yellow buff circulus as in forewing. Ocelli of cells M_2, M_3 set at oblique angle, pointing distally away from each other at 60°; ocellus of M_2 pointing in anterior direction, ocellus of cell M_3 pointing in posterior direction.

Types. Holotype male, Fort Bragg, North Carolina, 21 August 1984, in U.S. National Museum, Washington, D.C.; 46 male and 13 female paratypes in collections of American

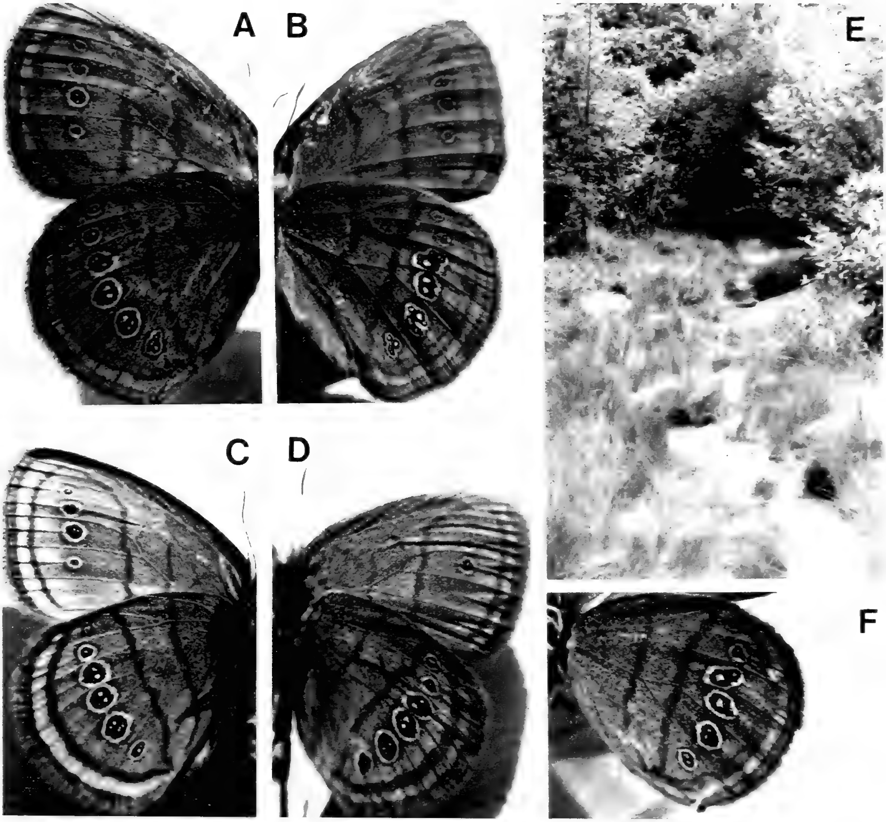

FIG. 2. *Neonympha mitchellii.* A, *N. m. francisci* female paratype, Fort Bragg, North Carolina, 31 August 1984. B, *N. m. francisci* holotype male. C, *N. m. mitchellii* female, Jackson Co., Michigan, 5 July 1984 leg. D. K. Parshall. D, *N. m. mitchellii* male, Springdale, New Jersey, 12 July 1970 leg. W. B. Wright Jr. E, *N. m. francisci* type locality. F, *N. m. francisci* paratype showing hindwing with oblique ocelli.

Museum of Natural History, New York; private collections of Thomas W. Kral, Richard Anderson of Gainesville, Florida, and David Parshall.

Etymology. We name the new subspecies in honor of Saint Francis of Assisi, known for kindness to animals and a love of natural beauty.

DISCUSSION

Paratype males differ little from the holotype male. Female paratypes are larger and more variable than male paratypes, with ventral ground color lighter in females (Table 1).

Subspecies *francisci* differs from the nominate in several ways (Table 1). Dorsal surfaces contrast less with ventral in *francisci* males and females; sexual dimorphism in number of forewing ocelli is less pronounced in *francisci*; *francisci* females are darker ventrally, with less round ocelli distally more pointed; the yellow ring of ocelli is thinner and contrasts less with ground color; third and fourth ventral hindwing ocelli are occasionally (2%) bifid; and ventral forewing and hindwing transverse bands are more rufous and contrast more with ground color.

The habitat of *N. m. francisci* is quite different from that of nominate *mitchellii* (Fig. 2). McAlpine (1936) described the nominate type locality in Cass Co., Michigan, as grassy glades along streams running through a tamarack bog. Pallister (1927) and Rutkowski (1966) gave much the same description for Ohio and New Jersey habitats.

The North Carolina habitat is a treed fenlike area surrounded on three sides by thickly forested sandhills. The colony occurs along an apparently spring-fed stream where succulent growth of sedges and grasses has developed in openings of a few meters. The surrounding sandhill forest is composed mainly of *Magnolia grandiflora* L., *M. virginiana* L., *Sassafras albidum* (Nutt.) Nees, *Carya cordiformis* (Wangenh.) K. Koch, and *Pinus taeda* L., with an understory of fern and *Arundinaria tecta* (Walkt.) Muhl., *Vaccinium coymbosum* L., and with thick alder often choking the water course.

Only a few butterfly species are on the wing in this habitat at the same time as *Neonympha m. francisci*. The most notable is *N. areolatus* which begins flight at the end of the flight of *N. m. francisci* and, like the latter, is bivoltine. Flight dates for *N. m. francisci* are 5 May to 6 June, and 26 July to 21 August. Flight dates for *N. areolatus* at Fort Bragg are 30 May to 28 June, and 15 August to 8 September (1983–86).

Subspecies *francisci* is isolated from all known nominate *mitchellii* populations. The North Carolina population is bivoltine; all nominate populations are univoltine, peaking around the first week in July. Isolation of the North Carolina population may represent a preglacial distribution and adaptation, or a post-Wisconsin isolation and adaptation. Other colonies may exist south of North Carolina, and might yield evidence to support a southern preglacial origin of *mitchellii*.

The North Carolina population of *mitchellii* is small, with less than 100 adults produced per season, but seems secure for the short term because of its isolation on Fort Bragg away from the public. The Ohio population is likely extinct (Shuey et al. 1987), and the small New Jersey population's status is unclear. In Indiana, the known range is greatly restricted but may be somewhat protected because it still occurs in a few State parks and preserves (Shull 1987). In 1987, Michigan placed *N. mitchellii* on the State list of threatened and endangered species, making the collection of *mitchellii* unlawful without a permit (Michigan Public Act 203 of 1974 rules as amended effective 4 Sept. 1987). While this gives the species some protection in Michigan for the short term, it limits study of the insect to those who seek a permit, and does not protect its habitat for the long term.

There is not a more endangered butterfly population in the eastern U.S. than *N. m. francisci*. Because of its small population and uncertain future over the long term on military lands, this butterfly will need conservation. We hope in naming this unique population that more field research will be generated, and that this attention will lead to real protection of not only the colony at Fort Bragg but colonies elsewhere as well.

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We thank R. A. Anderson for sharing his knowledge and help in acquiring material for study; L. D. Miller for the original determination of the North Carolina *mitchellii* specimen; the late Leland Martin for his much valued companionship in the tick-infested swamps of North Carolina; D. C. Ferguson of the U.S. National Museum for allowing us to examine material; J. A. Scott, D. C. Iftner and E. H. Metzler for critically reviewing the manuscript; M. C. Nielsen for much interesting discussion and help; and Leni Wilsmann of the Michigan Department of Natural Resources for help.

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REVISION OF *CHLOROSTRYMON* CLENCH AND DESCRIPTION OF TWO NEW AUSTRAL NEOTROPICAL SPECIES (LYCAENIDAE)

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ABSTRACT. Neotropical *Chlorostrymon* Clench is revised to comprise six species, including the austral *C. patagonia,* new species (Patagonian Steppe biotic province, Argentina); *C. chileana,* new species (Central Valley biotic province, Chile); and *C. kuscheli* (Ureta), new combination (N Andean Cordillera-High Andean Plateau biotic provinces, Chile). Three additional congeners are *C. simaethis* (Drury) (*Thecla simaethis jago* Comstock & Huntington, new synonym, Antilles; *C. s. sarita* (Skinner), *C. s. rosario* Nicolay, new synonym, mainland Neotropics), *C. telea* (Hewitson) (Central and South America), and *C. maesites* (Herrich-Schaeffer) (Antilles). Differentiating characters include female genitalia. The Andes have produced three distinctive species isolated in high montane and austral regions.

Additional key words: Eumaeini, systematics, biogeography.

Chlorostrymon was erected by Clench (1961) to include three familiar and widely distributed New World hairstreaks: *C. simaethis* (Drury), *C. telea* (Hewitson), and *C. maesites* (Herrich-Schaeffer). Subsequently, Nicolay (1980) elucidated the original generic description, and Clench (1963) further distinguished the Antillean species. *Chlorostrymon* species are distinctly marked, and aside from the naming of some subspecies (Skinner 1898, Stallings & Turner 1947, Comstock & Huntington 1943, Nicolay 1980), the genus has appeared to be one of the best known and taxonomically stable in Eumaeini (Nicolay 1980).

I have assembled and studied eumaeine samples from the austral Neotropics (Johnson et al. 1986, 1988, Johnson 1987, 1989, Johnson in press). These specimens derived from unsorted and unincorporated material principally at the British Museum (Natural History) (BMNH), and Museum National d'Histoire Naturelle, Paris (MNHN). Specimens were also provided by the Central Entomological Collection, University of Chile, Santiago (CECUC), and the Museo Nacional de Historia Natural, Chile, Santiago (MNHNC).

Three distinctive austral South American members of *Chlorostrymon* are apparent: *Thecla kuscheli* Ureta (1949), hitherto not examined by northern workers, and two new species. Unique characters in these austral populations require expansion of Nicolay's (1980) redescription of the genus. I revise *Chlorostrymon* to comprise six species, including these newly discovered austral ones.

Because of peculiar intraspecific variation, there is little utility in pursuing extensive subspecific division of the three familiar *Chlorostrymon* species (Nicolay 1980). Accordingly, I synonymize some subspecies. I reduce subspecies in *C. simaethis* to two (Antillean and mainland, consistent with the distribution of *C. maesites* and *C. telea*), and reduce subspecies in *C. maesites* to the nominate. I treat *C. maesites* and *C. telea* as species based on their traditionally cited features (Comstock & Huntington 1943, Klots 1951, Clench 1961, 1964, Riley 1975, Thorne 1975, Pyle 1981, Opler & Krizek 1986, Scott 1986) as well as a statistically significant difference in their female genitalia.

METHODS AND MATERIALS

I follow Clench (1961) in abbreviating dorsal hind- and forewing to DHW and DFW, respectively, and ventral hind- and forewing to VHW and VFW, respectively. I also use TL for type locality.

Distribution data derive from specimens at the Allyn Museum of Entomology–Florida State Museum (AME), American Museum of Natural History (AMNH), BMNH, Carnegie Museum of Natural History (CMNH), CECUC, Instituto Miguel Lillo (Tucumán, Argentina) (IML), Milwaukee Public Museum (MPM), MNHN, and MNHNC. To study consistency of morphological characters, I dissected genitalia of males and females from localities spanning distribution of each taxon, as well as more extensive series available from particular sites. Such material is listed for each taxonomic entry.

Chlorostrymon Clench
(Figs. 1–6)

Chlorostrymon Clench (1961:189). Clench (1963:248; 1976:269; 1977:186), dos Passos (1970:27), Brown & Heineman (1971:4; 1972:230), Emmel & Emmel (1973:51), Ferris (1974:278), Riley (1975:100), Thorne (1975:277), Ross (1976:188), Nicolay (1980:253), Miller & Brown (1981:99; 1983:54); Pyle (1981:464), Schwartz & Jimenez (1982:8), Garth & Tilden (1986:189), Opler & Krizek (1986:88), Scott (1986:359), Llorente-Bousquets et al. (1986:25), Schwartz (1989).

Diagnosis. In wings (Figs. 1–3), DFW and DHW are variously iridescent blue to violet like many Eumaeini (though lacking DFW male androconia as in some Eumaeini), but *Chlorostrymon* is distinctive in its brilliant green (often chartreuse) ventral ground color; VHW with brilliant white to silver bands (usually across entire wing) and lavish reddish brown or gray suffusion across limbal area; and VFW postmedian silver-white or blackish bands. These markings are distinctive in overall pattern regardless of occasional reduction, and can be confused only with *Cyanophrys crethona* (Kaye), as discussed later under *Chlorostrymon simaethis*. *Chlorostrymon* genitalia (Figs. 5, 6) differ from other Eumaeini by the male aedeagus having its terminus separated from the rest of the shaft by a transparent juncture, but conjoined internally by the elongate, pointed cornutus, as discussed further on.

Type species. *Papilio simaethis* Drury (1773) by original description.

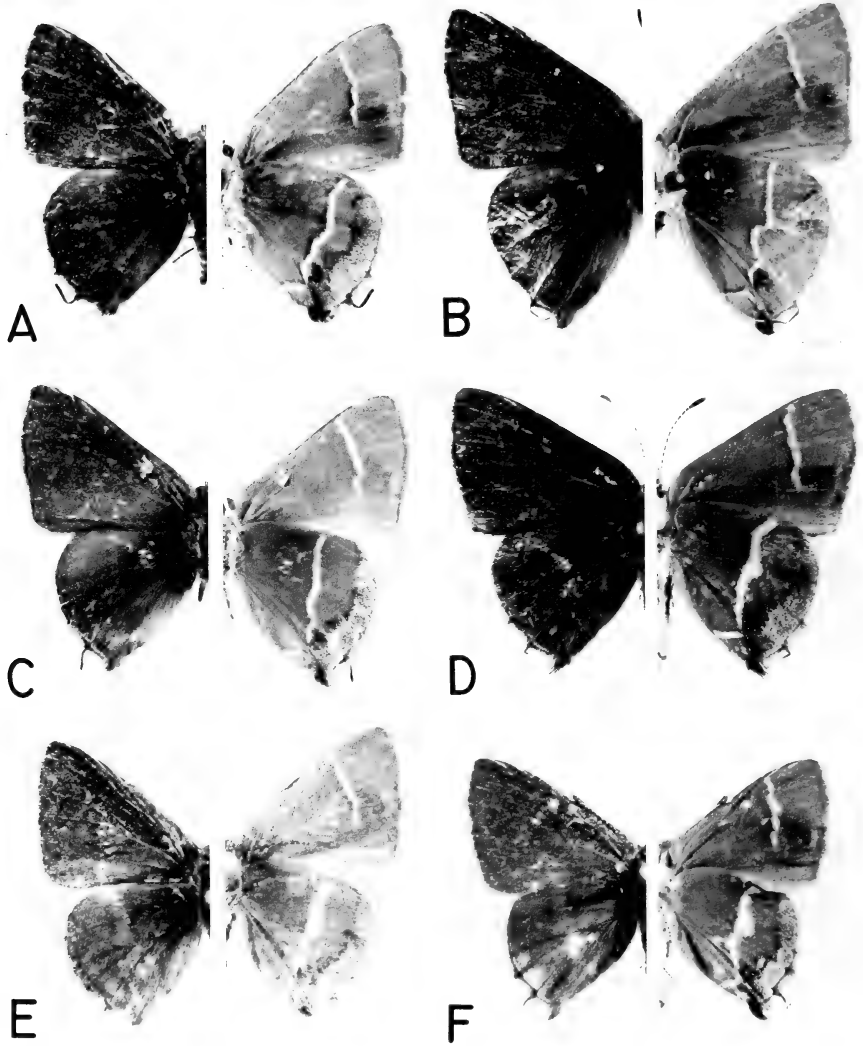

FIG. 1. Adult male *Chlorostrymon simaethis* (left, upper surface; right, under surface) (AMNH except as noted). A, *C. s. simaethis,* proximate topotype (TL given as generalized locality), Basseterre, St. Kitts. B, *Thecla s. jago,* holotype. C, *C. s. sarita,* proximate topotype, San Antonio, Texas, 29 October 1933. D, *C. s. sarita,* Caripito, Venezuela, 1 July 1913. E, *C. s. sarita,* Callao, Lima Department, Peru (BMNH). F, *C. s. sarita,* Arroyo San Pedro, Jujuy Province, Argentina, 17 July 1978.

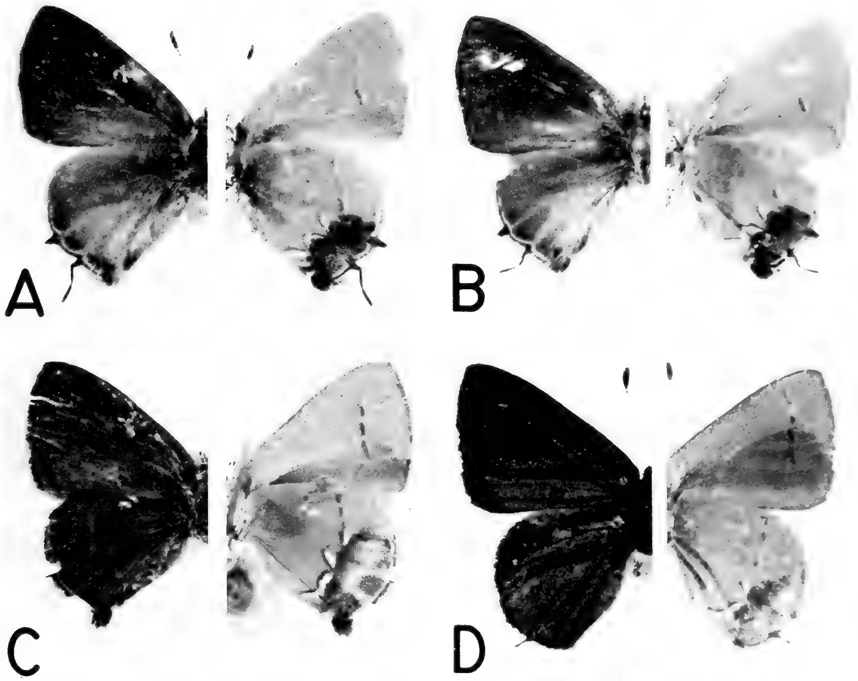

FIG. 2. Adult female *Chlorostrymon telea* and *C. maesites* (left, upper surface; right, under surface) (AMNH except as noted). A, *C. telea*, proximate topotype, Obidos, Amazonas State, Brazil. B, *C. telea*, Villa Ana, Santa Fe Province, Argentina, 26 February 1927 (BMNH). C, *C. maesites*, proximate topotype, Guantanamo Bay, Cuba. D, *Thecla m. clenchi*, allotype.

Diversity. Previously comprising the species *simaethis*, *telea*, and *maesites*; hereafter, these species, *kuscheli*, and the two new species. All are distinguished in the following key. A key character is not considered "distinctive" if obscure.

Wing Character Key to Species

1 VHW postdiscal band distinctive across entire wing 2
VHW postdiscal band distinctive only costad vein M_3 or caudad vein M_3 3
2 VFW postmedian line white or silver 5
VFW postmedian line black (without white) or faint to absent 4
3 VHW postdiscal band distinctive only costad vein M_3 .... *chileana*, new species
VHW postdiscal band distinctive only caudad vein M_3 and with the costal fold of forewing extremely wide (≥ 1 mm) and rufous colored .... *patagonia*, new species
4 VHW limbal patch extending costad to M_1; postmedian line forming a distinct "W"; VFW postmedian line very faint to absent .... *telea*
VHW limbal patch extending costad to M_3; postmedian line not forming a "W"; VFW postmedian line black .... *maesites*

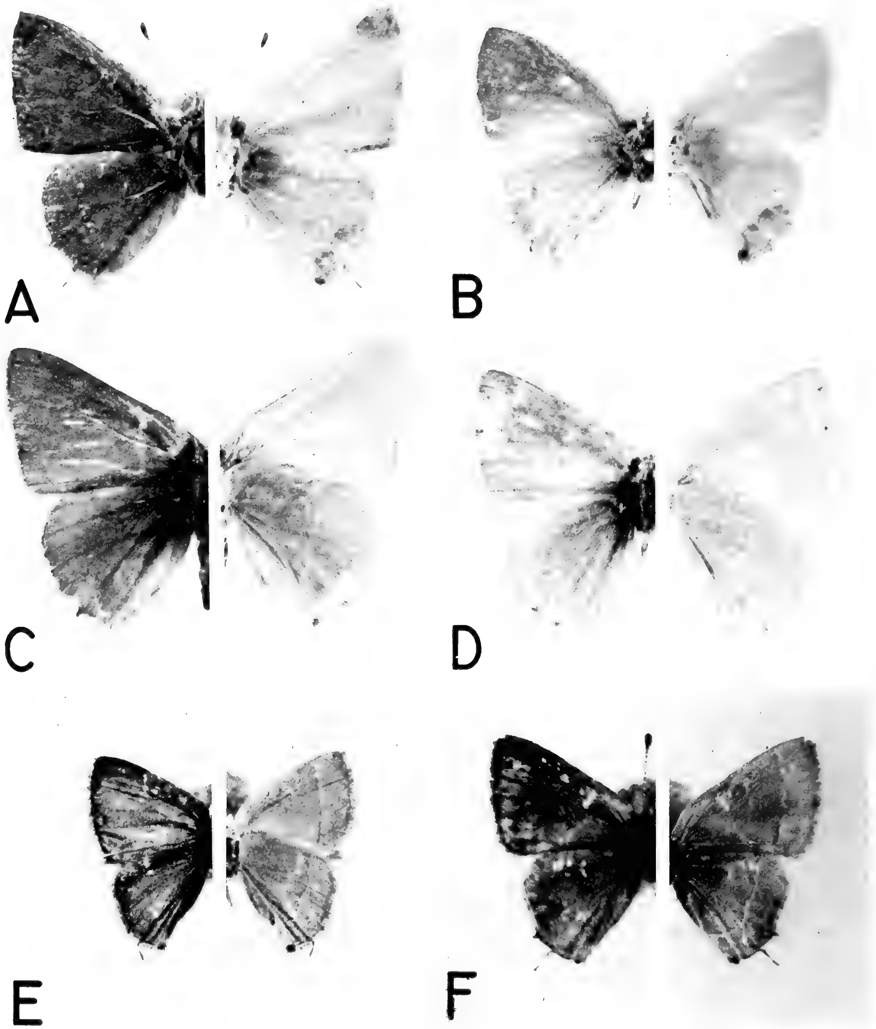

FIG. 3. Adults of austral South American *Chlorostrymon* (left, upper surface; right, under surface). A, *C. patagonia*, allotype male. B, *C. patagonia*, holotype female. C, *C. chileana*, allotype male. D, *C. chileana*, holotype female. E, *C. kuscheli*, paratype male. F, *C. kuscheli*, female, data in text.

5 VFW, VHW band wide, silver-white; DHW with uniformly colored ground .... *simaethis*

VFW, VHW band extremely thin, white; DHW with bright rufous limbal patch .... *kuscheli*, new combination

Wing characters are correlated with characters of the female genitalia. Since the latter have not been previously treated, the following key uses features of the ductus bursae and cervix bursae.

Female Genitalic Key to Species

1 Ductus bursae cephalically inclined 60–90°; cervix bursae with two dorsal sclerotized pads (Fig. 6A–F) .... *simaethis*
  Ductus bursae inclined <60° or not at all; cervix bursae without sclerotized pads (Fig. 6G–O) 2
2 Ductus bursae with cephalic tubular ductus and caudally flared antrum (Fig. 6G–I) 3
  Ductus bursae with caudally flared antrum only, antrum connected directly to corpus bursae (Fig. 6N, O) 4
3 Ductus bursae inclined 30–60° 5
  Ductus bursae not inclined or inclined <20°; length of antrum less than length of ductus bursae (Fig. 6H, I) .... *maesites*
4 Terminus of antrum only slightly flared; lamella postvaginalis parabolic (Fig. 6O) .... *chileana,* new species
  Terminus of antrum greatly flared; lamella postvaginalis distally lobate (Fig. 6N) .... *patagonia,* new species
5 Length of antrum (Fig. 6A) equalling or exceeding length of ductus bursae (Fig. 6G) .... *telea*
  Length of antrum less than length of ductus bursae (Fig. 6M) .... *kuscheli,* new combination

Distribution (Fig. 4). Extreme southern United States (S Florida, S Texas to Baja California and neighboring areas), Greater and Lesser Antilles and Mexico, S through South America to northern and central Chile and northern Patagonia.

Characters. Along with the distinctive wing pattern, Nicolay (1980) proposed several diagnostic genitalic characters for *Chlorostrymon.* From my analysis of 121 male and 138 female genitalia, one character of male genitalia appears common to all *Chlorostrymon* taxa: separation of aedeagal terminus and shaft by a stripe of transparent sclerotization conjoined internally by the single elongate cornutus (Nicolay 1980:225) (Fig. 5). Because of great structural divergence of male genitalia in Eumaeini, other male genitalic characters of *Chlorostrymon* appear less diagnostic.

In the female genitalia, Nicolay distinguished *Chlorostrymon* from other Eumaeini by the cephalic one-quarter of the ductus bursae dorsally inclining ca. 90°, and by two sclerotized pads occurring on the dorsum of the cervix bursae (Fig. 6A–F). However, my samples indicate that only *C. simaethis,* the type species, has these characters.

Phylogenetic position. Search for the sister group of *Chlorostrymon* (Hennig 1966) appears difficult and will probably be resolved only by further study of the many undescribed Eumaeini. Considering *Chlorostrymon's* distinctive wing characters, and the wide geographic range of its two sympatric congeners, the genus is probably very old. The distinctive *Chlorostrymon* aedeagus may occur in other as yet undescribed or unstudied Eumaeini, and be a key to recognizing the outgroup. In other respects, male and female *Chlorostrymon* genitalia resemble taxa of *Electrostrymon* Clench (type species *Papilio endym-*

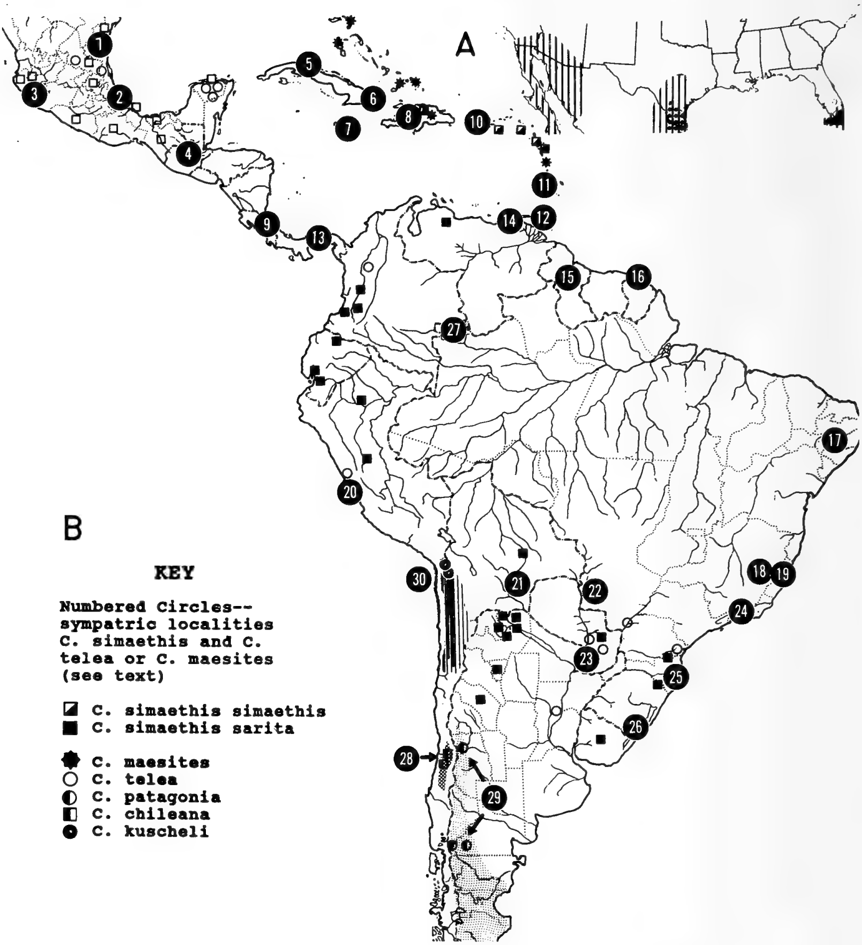

FIG. 4. Geographic ranges of *Chlorostrymon* species. A, United States and northern Mexico distributions of *C. simaethis* (vertical hatches), *C. telea* (stippled), and *C. maesites* (black), from localities assembled by Scott (1986) and Opler and Krizek (1986). B, Neotropical and austral distributions (specimens in AMNH except as noted). Numbers 1–27: sympatric Neotropical localities of *C. simaethis* and *C. telea* (mainland) or *C. maesites* (Antilles). Only localities not mentioned in text are given here. 1, San Francisco, Tamaulipas State, Mexico. 4, Guatemala City, Guatemala. 5, Havana, Cuba. 6, Guantanamo, Cuba. 9, Turrialba, Costa Rica. 10, Coamo Springs, Puerto Rico. 11, St. Vincent, Lesser Antilles. 12, Port-of-Spain, Trinidad. 15, Barta District, Guyana. 17, Pernambuco, Brazil (AMNH, BMNH). 19, Espirito Santo, Brazil (MPM, BMNH). 20, Callao, Lima Department, Peru (BMNH). 22, Campo Grande, Mato Grosso State, Brazil (BMNH). 27, Óbidos, Amazonas State, Brazil. Numbers 28–30: austral species distributions and biotic provinces (BP): 28 & cross hatches, *C. chileana*, Cental Valley BP. 29 & stippling, *C. patagonia*, Patagonian Steppe BP. 30 & vertical hatches, *C. kuscheli* (dark hatches, Northern Andean Cordillera BP; light, High Plateau BP).

ion Fabricius). However, *Electrostrymon* has not been revised and, since Clench (1961, 1963) never listed the taxa it included, the genus has been subject to various interpretations (Barcant 1970, Riley 1975, Johnson & Matusik 1988). Johnson and Matusik (1988) suggested the Barcant and Riley treatments of *Electrostrymon* were, at least, diphyletic. To complicate matters, the short, non-inclined female genitalia of *Chlorostrymon maesites* and the new austral *Chlorostrymon* species (Fig. 6H, I, M–O) resemble those of at least two groups of Eumaeini whose wing patterns differ greatly: the taxa-rich "*Thecla celmus*" and "*Thecla phrutus*" groups (Johnson 1986, Johnson & Matusik 1988), and *Parrhasius* Hübner and *Michaelus* Nicolay (Nicolay 1979). Without a designated outgroup, or a basis for describing outstate characters, phylogenetic inference concerning *Chlorostrymon* taxa is too speculative.

Conspecificity of *Chlorostrymon telea* and *C. maesites*. This has been much debated (Riley 1975, Clench 1961, Opler & Krizek 1986, Scott 1986). Some early workers, and recently Scott (1986), proposed the synonymy of the two taxa. Genitalic study indicates that, along with traditionally cited pattern differences, female genitalia of the two taxa differ consistently and distinctly (Female Genitalic Key, Fig. 6, and discussion under *C. telea*). Accordingly, these taxa are treated as distinct species here.

Temporal and spatial distribution. Rarity of *Chlorostrymon* taxa, compared to many other hairstreak butterflies (Opler & Krizek 1986), is reflected in museum samples. There is a correlation between *Chlorostrymon* occurrence (particularly sympatry of *C. simaethis* with *C. telea* or *C. maesites*) and location of major collectors. Study of such samples indicates *Chlorostrymon* taxa are local, but sometimes locally common. Major historical sources of *Chlorostrymon* specimens warrant mention because they explain the origin of most data on the genus, and have allowed study of *C. simaethis* and *C. telea* or *C. maesites* from numerous areas of sympatry (Fig. 4). Such collectors, common collecting localities, and depositories are listed with Fig. 4 locality numbers as follows:

(2, 3) Mexico: Presidio, Cordoba, Vera Cruz State, Colima, Colima State; N. Hoffman (AMNH). (7) Jamaica: B. Heineman (AMNH). (8) Hispaniola: A. Schwartz (private, AME), D. Matusik (private, FMNH, AMNH, CMNH), K. Johnson (AMNH, AME). (12) Trinidad-Tobago: R. Rozycki (AMNH). (13) Panama: collections of AMNH Research Station (AMNH). (15) Venezuela: Caripito; collections of New York Zoological Society (AMNH). (16) French Guiana: northern localities; expedition collections of MNHN (MNHN). (18) Brazil: Minas Gerais; collections of J. F. & W. Zikán (Instituto Oswaldo Cruz, Guanabara). (21) Bolivia: eastern localities; J. Steinbach (CMNH, BMNH). (23) Paraguay: Santissia-Trinidad; B. Podtiaguin (AMNH). (24) Brazil: Rio de Janeiro vicinity; P. Gagarin (MPM). (25, 26) Brazil: Curitiba, Paraná State, Pelotas, Rio Grande del Sol State; C. Biezanko (BMNH, AMNH). (29) Argentina: northwestern localities; R. Eisele (AME, AMNH), B. MacPherson (AMNH), K. Hayward and N. Giocomelli (BMNH, IML). Austral South America: Patagonia; C. Larsen (MNHN). (28) Chile (Valparaíso, Santiago); R. Martin (MNHN). General: collections of CECUC, MNHNC.

Chlorostrymon simaethis (Drury)
(Figs. 1, 5A–D, 6A–F)

Papilio simaethis Drury (1773:3; 1770:pl. 1, fig. 3) (name given in index published in 1773).

Mitoura simaethis: Dyar (1903:38).

Tmolus simaethis: Kaye (1914:567).

Chalybs simaethis: Kaye (1921:103), Barcant (1970:251).

Thecla simaethis: Kirby (1871:398), Dewitz (1877:233, pl. 1), Godman & Salvin (1879–1901:720, pl. 81), Moeschler (1889:301), Ståhl (1882:93), Gundlach (1887:622), Draudt (1919:798, pl. 158,f), Barnes & Benjamin (1923:17), Hall (1925:188; 1936:276), Kaye (1926:462), Holland (1931:232), Wolcott (1936:403), Hoffman (1941:716), Schweizer & Webster Kay (1941:19), Comstock & Huntington (1943:58, 73; 1961:54; 1963:190), Beatty (1944:157), Comstock (1944:488), Avinoff & Shoumatoff (1946:284), Zikán & Zikán (1968:57), Hayward (1973:157).

Thecla lycus Skinner (1898:48) (takes authorship of "*lycus* Hübner" Skinner 1898:48) (misspelling, misattribution of author, not *licus* Hübner 1807:pl. 150, not *lydus* Hübner 1818:75, no. 753), Dyar (1903:36), Draudt (1931:798), Barnes & McDunnough (1917:13) (all follow Skinner, in error), Barnes & Benjamin (1923:17), Comstock & Huntington (1958–64 [1963]:190) (both cite Skinner 1898 as an error).

Thecla sarita Skinner (1895:112; 1898:48), Barnes & McDunnough (1917:3), Barnes & Benjamin (1923:17), McDunnough (1938:24), Stallings & Turner (1947:40) (the last make *sarita* a subspecies of *simaethis*).

Strymon simaethis: Barnes & McDunnough (1917:13), Bates (1935:194), McDunnough (1938:24), Stallings & Turner (1947:40), Klots (1951:139), Ziegler 1961:22 (as "*Strymon*"), Lipes (1961:56), dos Passos (1964:56), Lewis (1974:67).

Chlorostrymon simaethis: Clench (1961:189; 1964:248; 1976:269; 1977:192), dos Passos (1970:27), Brown & Heineman (1971:230), Emmel & Emmel (1973:51), Riley (1975:100), Thorne (1975:277), Ross (1976:188), Nicolay (1980:253), Miller & Brown (1981:99; 1983:54), Pyle (1981:465), Schwartz & Jimenez (1982:8), Garth & Tilden (1986:189), Opler & Krizek (1986:89), Scott (1986:359), Llorente-Bousquets et al. (1986:25), Schwartz (1989).

Diagnosis. DFW, DHW brown, strongly suffused with iridescent purple (much duller on females); VFW, VHW ground chartreuse, VHW postdiscal band white to pearly white, distinctive across entire wing; VFW postmedian line, thick, white or pearly white (Fig. 1). Male genitalia with vincular arc, valvae, saccus and aedeagus all more elongate than congeners (and aedeagus not ventroterminally declined) (Fig. 5A–D); brush organs moderately dense, articulated to small basal membrane along each ventrocephalic edge of vincular arc (Fig. 5J); female genitalia with ductus bursae cephalically inclined 90°, cervix bursae with two dorsal sclerotized pads, papillae anales terminally lobate, apophyses of papillae anales short (not extending entire length of ductus bursae) (Fig. 6A–F).

Types. *Papilio simaethis* type reported lost (Miller & Brown 1981); TL "St. Christopher's" (=St. Kitts, Riley 1975). *Chlorostrymon simaethis* is unambiguous in facies; there is no need for a neotype. *Thecla lycus* type and TL unknown (Comstock & Huntington 1961).

Distribution. In United States, extreme S California, Arizona, Texas, and Florida; Baja California, throughout Mexico and Central America, most of Greater and Lesser Antilles; in South America, SW to central Peru, E over entire continent except Amazon basin, SE along Brazilian coast, and W from SE Brazil to Paraguay and E Bolivia, S to NW Argentina (Fig. 4). Scott (1986) portrays the Baja California distribution as transient. However, since Opler and Krizek (1986) document recent establishment of the species in Florida, the large series of specimens from numerous Baja California locales (AMNH, CMNH) may also represent resident populations. John Brown (San Diego Museum, pers. comm.) suspects that marked genitalic variation between Baja California populations may reflect a flux of resident and transient populations.

Superficially similar noncongeners. As noted in Diagnosis, *Cyanophrys crethona* (Kaye) somewhat resembles *C. simaethis* because both have lavish VHW limbal suffusion. The former is much larger (forewing base to apex in the male 15 mm, in the female 17 mm, compared with 12 and 14 mm for *simaethis*; Riley 1975); its DFW and DHW are deep iridescent blue with wide black borders; and its VHW and VFW are deep lime green, with VHW postdiscal band continuous basad discal cell, disjunct costad.

Variability. Klots (1951) and Nicolay (1980) noted that wing pattern variability in *Chlorostrymon simaethis* caused most of its subspecies to be ill-defined geographically. Except for two major allopatric segregations, subspecies are dropped here by placement in appropriate synonymies. Below, I summarize these synonymies and the character variation on which they are based.

1. Nominate *C. s. simaethis* (Fig. 1A) and Jamaican *C. s. jago* (*Thecla s. jago* Comstock & Huntington, 1943:74, pl. 1, fig. 7; holotype male, Fig. 1B, allotype female, both AMNH, TL Dunrobin District, Mandeville, Manchester, Jamaica), **NEW SYNONYMY.**

By virtue of its type locality, nominate *Chlorostrymon s. simaethis* has historically been considered restricted to the Antilles. However, while *C. simaethis* was still poorly known from the Antilles, Comstock and Huntington (1943) described subspecies *jago* from Jamaica. Later, Riley (1975) noted that wing characters of *jago* duplicated those of *C. simaethis* occurring on Hispaniola.

Compared to mainland populations, Antillean *C. simaethis* display some homogenous wing characters (Fig. 7A), but Jamaican specimens are no more distinct than other Antillean populations. Female genitalia of Jamaican specimens have a widely flared, elongate antrum (Fig. 6A). However, equally distinctive innovations appear in other Antillean *C. simaethis*: Virgin Islands specimens show a distinctively narrow and elongate ductus and antrum; Hispaniola specimens have a markedly constricted genital plate. Male genitalia also have numerous localized innovations, including a cephalically elongated vinculum in Jamaica (Fig. 5A), an elongate, narrow, valve in Puerto Rico, and a wide, blunt-ended valve in Hispaniola. Genitalia of Hispaniolan females most resemble Cuban females; genitalia of Hispaniolan males most resemble St. Vincent males. Such genitalic variation in Antillean *C. simaethis* makes *jago* appear no more distinct than other Antillean populations. Further, there is no distinctive character correlation between *C. simaethis* of Jamaica and that of southern Hispaniola, which, if present, would have biogeographic significance (Schwartz 1989, Schwartz et al. 1984, 1986a, 1986b, Johnson

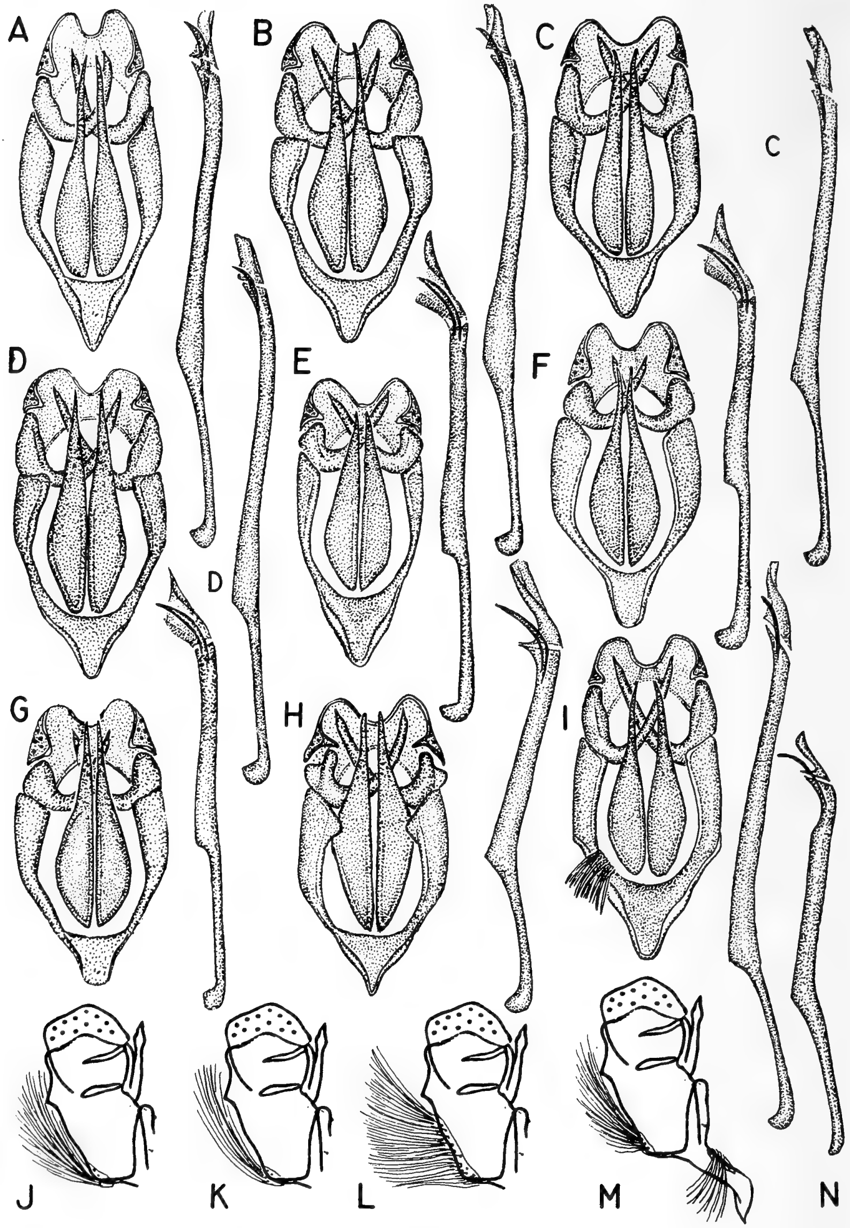

FIG. 5. Male genitalia (A–I, N) and brush organs (J–M) of *Chlorostrymon*. Genitalia shown in ventral view at left without aedeagus, aedeagus in lateral view at right (specimens in AMNH unless otherwise noted here or in text). A, *Thecla simaethis jago,* holotype. B, *C. simaethis sarita,* proximate topotype, San Antonio, Texas, 29 October 1933. C, *C. s. simaethis,* proximate topotype, Basseterre, St. Kitts. D, *C. s. sarita,* Caripito, Venezuela.

& Matusik 1988). Description of subspecies from Antillean populations would invite an inflated trinomial nomenclature on the mainland. **Dissections examined** (all AMNH). *C. s. simaethis*: CUBA: Santiago (♀), Havana (♂), Guantanomo Bay (♂, ♀). DOMINICAN REPUBLIC: El Numero, Barahona Province, 3 July 1986 (3 ♂, 2 ♀). HAITI: Petionville, 9 May 1930 (♀), 24–29 January 1922 (♂). LESSER ANTILLES: St. Vincent (♂, ♀); Dominica, Canefields, 1–8 December 1933 (4 ♂, 16 ♀), October 1919 (♀); St. Kitts, Basseterre (♂, ♀). UNITED STATES: Puerto Rico, Cuamo Springs, 26 December 1914 (♂); Virgin Islands, St. Croix, 14 March 1951 (5 ♂, 6 ♀). *C. s. jago*: JAMAICA: primary types, paratypes with same data except 23 December 1919 (♂), 28 January 1919 (♀), 4, 22, 28 December 1919 (3 ♀), 4 November 1919 (♀), Mt. Diablo, 5 March 1951 (♂), Constant Springs, 4 January 1924 (3 ♀).

2. *C. s. sarita* (Skinner 1895:112; holotype male, CMNH, TL Comal Co., Texas) (Figs. 1C, 5B, 6B) and *C. s. rosario* (Nicolay 1980:254; holotype male and 10 paratypes in AME, TL La Kenedy, Pichincha, Ecuador; 1 paratype, S. Nicolay Collection, same locality; allotype female, San Bartolo, Ecuador, AME), **NEW SYNONYMY.**

Subspecies *sarita* has usually been characterized by generally straight VHW band (poised perpendicular or slightly slanted costad FW inner margin), and with discal area of band sometimes distally produced (Fig. 1). Stallings and Turner (1947) presented data recommending use of *C. s. sarita* for populations extending from the SW United States into Mexico. Subsequently, *C. s. sarita* was applied southward into Central America (Llorente-Bousquets et al. 1986) and South America (Nicolay 1980). Nicolay (1980) also described a new subspecies (*C. s. rosario*) from then unique Ecuadorian specimens. Subsequently, however, numerous variable series of *C. simaethis* have been accumulated from Ecuador (Banõs: AMNH, CMNH; Aguarico, Duran, Latas, Mishahualli: AMNH) and the species taken southward in Peru (AMNH, BMNH).

Mainland *C. simaethis* are generally distinct from Antillean populations (Fig. 7A), and notably high frequencies of wing characters occur in some regional mainland populations (Fig. 7A). Though northern populations usually have a more uniform hindwing band, a few (notably S Texas and insular montane Vera Cruz and Guerrero in Mexico) show extreme swelling of the discal area of the VHW band. This trait becomes much more common in South America (Figs. 1D–F, 7A) but the distinction is obviated by blending in the Panamanian isthmus region.

In contrast to haphazard local genitalic variation in Antillean *C. simaethis*, genitalic characteristics in both sexes of mainland *C. s. sarita* are often regional. Homogeneity is most common in contiguous lowland regions and appears more varied in disjunct or high montane areas. Male and female genitalia are most uniform from S Texas S across Mexico (Figs. 5B, 6B) with variation increasing in specimens from S California-Baja California, and Guatemala S through Panama. Males from S California-Baja California exhibit an elongate vinculum, and females an unusually wide ductus (width ½ that of lamella; normally about ⅓). From Guatemala S through Panama, females are more locally variable in antrumal width and ductus length, and males more variable in valval width, terminal recurvature and saccus length. In South America, males have more distally shouldered valvae which are less terminally elongate or recurved. The last trait is strongest in populations from Colombia E across the Guyana shield (Fig. 5D). Populations S of the Amazon basin, SE Brazil to NW Argentina, show more elongation in the valve but not increased recurvation. In South American females the antrum is usually outstanding and greatly flared (most often from about half the distance between the lamellal termini and the

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E, *Thecla telea*, holotype. F, *C. maesites*, Nicoll's Town, North Andros Island, Bahamas. G, *Thecla maesites clenchi*, holotype. H, *C. patagonia*, allotype (MNHN). I, *P. chileana*, allotype (MNHN), with saccal brush organ. Brush organs shown in diagrammatic lateral view from vinculum to labides including abuttment of anchoring membrane. J, *C. simaethis*. K, *C. telea* and *C. maesites*. L, *C. patagonia*. M, *C. chileana* (including saccus and saccal brush organ). N, Aedeagus of *C. kuscheli* paratype male (CECUC).

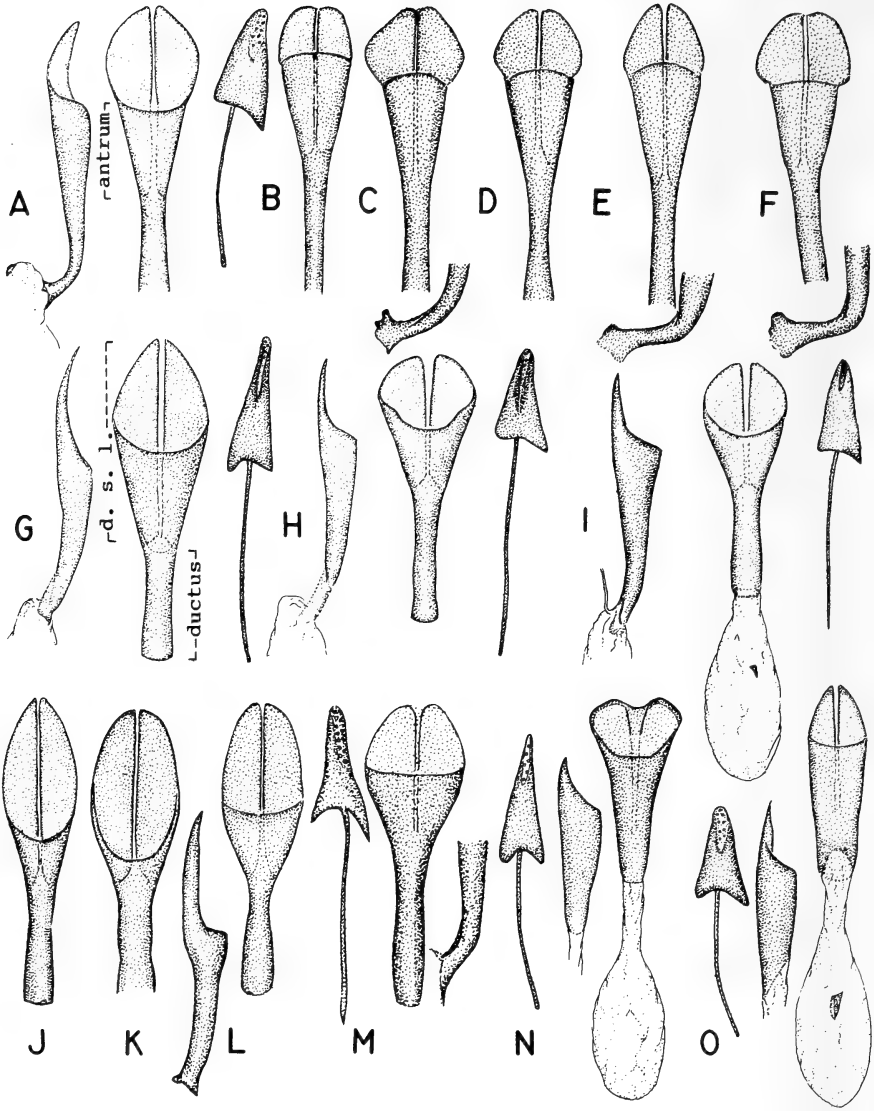

FIG. 6. Female genitalia of *Chlorostrymon*. Unless otherwise indicated, lateral view at left; ventral view at center (antrum indicated in A; dorsal suture line, d.s.l., and ductus indicated in G); lateral view of papillae anales and their apophyses at right (specimens in AMNH unless indicated otherwise here or in text). A, *Thecla simaethis jago*, allotype. B–F, *Chlorostrymon simaethis sarita*, proximate topotype, San Antonio, Texas, 29 October 1933 (ventral only, with lateral view of cephalic inclination in C, E, F). C, *C. s. simaethis*, proximate topotype, Basseterre, St. Kitts. D, *C. s. sarita*, Caripito, Venezuela. E, *C. s. sarita*, Balsapuerto, Huanuco Department, Peru. F, *C. s. sarita*, La Rioja, La Rioja Province, Argentina. G, *C. telea*, proximate topotype, Óbidos, Amazonas State, Brazil. H, *C. maesites*, proximate topotype, Guantanamo, Cuba. I, *Thecla maesites clenchi*, allotype

cephalic area where the ductus is dorsally inclined) (Fig. 6D–F). Variation from this ground plan is usually limited to difference in ductal length before and after the dorsal inclination. Most notably, isolated montane Peruvian populations have the ductus more elongate on both sides of the dorsal inclination (Fig. 6E), and Colombian specimens have a decreased dorsal inclination. The numerous high montane populations in Ecuador show extreme local variation.

In conclusion, some mainland regions evidence certain distinctive characters, but overall contiguity suggests validity of a single name: *C. s. sarita.* Unless numerous subspecies are recognized in South America, *C. s. rosario* is best considered a synonym of *C. s. sarita.* **Dissections examined** (all AMNH). *C. s. sarita*: ARGENTINA: La Rioja Province, La Rioja (2 ♂, 1 ♀); Salta Province, Yariquarenda (1 ♂, 2 ♀), Agua Blanca (2 ♂, 1 ♀), Mosconi (2 ♂, 2 ♀), Tartagal (1 ♂, 1 ♀), La Merced (1 ♂, 1 ♀); Jujuy Province, San Pedro (2 ♂, 2 ♀), Rio Lazares (1 ♂, 1 ♀). BOLIVIA: Rio Surutu, 350 m, E Bolivia (1 ♂, 1 ♀). BRAZIL: highlands nr. Massaranduba Blumenau (♂); Annaburg, St. Catarina (♂). COLOMBIA: Cauca Valley, 3200 ft (975 m), 25 January 1935 (3 ♀). COSTA RICA: Turrialba, 29 May 1946 (♂, ♀). ECUADOR: Banõs, February 1939 (6 ♂, 2 ♀); Duran, 400 ft (122 m), 24 June 1914 (1 ♂, 1 ♀); Aguarico, November 1979 (8 ♂, 6 ♀), Mishahualli (♂); Latas, Oriente (♀). GUATEMALA: Guatemala City (♂, ♀). GUYANA: "British Guiana" (♂); Bartica District, Bartica (♂). MEXICO: Baja California, Arroyo del Refugio, 5 May 1935 (2 ♂, 3 ♀); Arroyo del Rosario, 21 March 1935 (3 ♀); Cape San Lucas, 24, 26 December 1938, 13 November 1938 (3 ♀); North End, San Jose Island, 12 December 1938 (2 ♂, 2 ♀); Vera Cruz State, Presidio (♂, ♀), Jalapa (4 ♂, 2 ♀); Colima State, Colima, April 1918 (1 ♂, 3 ♀); Tamaulipas State, San Francisco, August 1964 (♂, ♀). PANAMA: La Boca, Canal Zone, 25 January 1908 (♂, ♀). PARAGUAY: Santissima Trinidad, Cordillera Province, June–July (2 ♂, 2 ♀). PERU: Balsapuerto, Paranapura River, Loreto, June 1933 (♂); Callao (BMNH) (♂, ♀); Chanchamayo, Huanuco (BMNH) (♂); Chosica, 850 m, January 1900 (BMNH) (♀). TRINIDAD-TOBAGO: Port-of-Spain, 1–9 April 1929 (2 ♂). UNITED STATES: Texas, Brownsville, 30 October 1965 (4 ♂, 5 ♀), Pharr (4 ♀), San Antonio (Comal Co.; TL), 29 October 1933 (♂, ♀); Arizona, Portal, 10 June 1958 (♂); California, San Diego Co., 193- [sic] (2 ♂, 4 ♀). VENEZUELA: Caripito (3 ♂, 3 ♀); San Felipe Venezuela, 6 May 1938 (♂). *C. s. rosario*: I saw *C. s. rosario* type series but did not dissect specimens; I rely on illustrations of Nicolay (1980) and specimens variously identified as *rosario* listed above under ECUADOR (AMNH).

Chlorostrymon telea (Hewitson)
(Figs. 2A, B, 5E, K, 6G, J–L)

Thecla telea Hewitson (1868:4) (cited by Comstock & Huntington 1958–64 [1964]:123, as "1868, Specimen of a Catalogue of Lycaenidae in the British Museum, p. 4", probably referring to text later published by Classey with preface by L. Higgins; see Higgins 1972). Kirby (1871:398), Hewitson (1862–78 [1873, February], vol. 1:143, vol. 2:pl. 57, figs. 350, 351), Dewitz (1877:233, pl. 1), Godman & Salvin (1879–1901: 720), Moeschler (1889:301), Ståhl (1882:93), Gundlach (1887:622), Draudt (1919:798, pl. 158,f), Kaye (1926:462), Barnes & Benjamin (1923:17), Holland (1931:232), Bates (1935:190), Wolcott (1936:402), Hoffman (1941:462), Beatty (1944:157), Comstock (1944:488), Comstock & Huntington (1943:73; 1958–64 [1964]:123) (last two citations place *telea* as subspecies of *maesites*; Comstock 1944, however, makes *telea* a species), Avinoff & Shoumatoff (1946:284), Hayward (1973:158).

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(including entire corpus bursae). J–L, *Chlorostrymon telea* (ventral only, with lateral view of cephalic inclination in L); J, Port-of-Spain, Trinidad; K, Villa Ana, Santa Fe Province, Argentina (BMNH); L, Callao, Lima Department, Peru (BMNH). M, *C. kuscheli,* data in text (ventral view, cephalic inclination). N, *C. patagonia,* holotype (including entire corpus bursae). O, *C. chileana,* holotype (including entire corpus bursae).

Thecla maesites telea: Comstock & Huntington (1943:73; 1958–64 [1964]:123), Zikán & Zikán (1968:57).

Eupsyche telea: Dyar (1902:36), Wolcott (1936:402), Grossbeck (1917:23).

Chalybs telea: Kaye (1921:103), Barcant (1970:85).

Strymon telea: Barnes & McDunnough (1917:13), McDunnough (1938:24), Rindge (1952:11), Ziegler (1960:22) (as "*Strymon*"), Lipes (1961:56), dos Passos (1964:55).

Strymon maesites telea: Young (1937:47), Klots (1951:139), Kimball (1965:47).

Chlorostrymon telea: Clench (1961:190; 1976:269; 1977:186), dos Passos (1970:27), Riley (1975:100), Thorne (1975:278), Ross (1975:189), Miller & Brown (1981:99; 1983:54), Pyle (1981:464), Opler & Krizek (1986:89).

Chlorostrymon maesites telea: Brown & Heineman (1972:229) (Brown, in Miller & Brown 1981, 1983 considers *telea* a species), Scott (1986:360).

Diagnosis. DFW, DHW brilliant iridescent azure blue; VFW postmedian line black (with only faint white borders, if any); VHW limbal suffusion extending costad to M_1; postdiscal band thin ("line"), often broken costad discal cell; line forming distinct "W" basad limbal area (Fig. 2A, B). Male genitalia with vincular arc, valvae, saccus, and aedeagus less elongate than *C. simaethis* (Fig. 5E), brush organs attached as in *C. simaethis* but less dense (Fig. 5K). Female genitalia less elongate and not cephalically inclined as in *C. simaethis*, papillae anales terminally constricted, papillae anales apophyses long (usually extending entire length of ductus bursae) (Fig. 6G, J–L). For genitalic comparison to *C. maesites*, see below.

Types. Holotype male in BMNH (Fig. 5E); TL "Amazon".

Distribution (Fig. 4). From S Texas S across Mexico and Central America; in South America from SW Colombia SE (except for Amazon basin) along SE coast of Brazil, W across Uruguay and Paraguay to E Bolivia and E Argentina. W from SW Colombia but only a few specimens from coastal Peru, none from Ecuador. Reports of *C. telea* from Florida are usually considered to be *C. maesites* (Klots 1951, Opler & Krizek 1986, Scott 1986, and as discussed below).

Conspecificity of *C. telea* and *C. maesites*. Possible conspecificity of *C. telea* and *C. maesites* has been often discussed, and favored by several early authors, more recently by Scott (1986). The taxa have well defined morphological characters (Figs. 5–7) which are homogeneous in their respective ranges. For this reason I retain them as species.

The major difference occurs in female genitalia: *C. maesites* (Fig. 6H, I) has a much smaller antrum and lamellal configuration than *C. telea* (Fig. 6G, J–L). As Nicolay (1980) noted, the lamellal area of *Chlorostrymon* has a membranous ventral covering. This occurs in various Eumaeini (Brown 1982), but is artifactual since the covering strips away easily to expose underlying structures (Johnson 1976, 1978). In *Chlorostrymon*, when this membrane is stripped away, the lamella antevaginalis may be damaged. Thus, the best measure of visual difference between *C. telea* and *C. maesites* is the ratio of the "dorsal suture line" (Fig. 6G, extending from terminus of lamellae to base of "antrum", Fig. 6A) to the remaining length of ductus bursae. Samples of *C. telea* and *C. maesites* (each spanning distributions characterized in respective Dissections Examined sections) produced frequency distributions (Fig. 7B), whose means differ by *t*-test ($P < 0.05$). To be sure that extreme morphology in *C. m. clenchi* (Fig. 7B, intervals 1.2–1.4) did not prejudice the distribution of *C. maesites*, *t* was recomputed without these specimens, and also proved significant ($P < 0.05$). Conversion of the data to "meaningful pairs" lacking intracorrelation reduced *t*-values, but they are still significant ($P < 0.05$). This difference in female genitalia along with the long cited differences in characters of the wing make these allopatric taxa distinctive. As discussed under *C. maesites*, lesser differences are apparent in male genitalia. *Chlorostrymon simaethis* shows no comparable major difference between mainland and Antillean populations.

As with my treatment of *C. simaethis*, I did not subdivide *C. telea* into subspecies.

Dissections examined (AMNH except as indicated). VENEZUELA: Caripito (♂, ♀). TRINIDAD-TOBAGO: Port-of-Spain (♀). BRAZIL: Paraná State, Caviuna (♀); Santa Catarina State, highlands above Massaranduba, Blumenau (♂); Amazonas State, Óbidos, January 1936 (♀). COLOMBIA: Caldaz, 14 May 1914 (♂, ♀). MEXICO: Vera Cruz State, Presidio (♂, ♀); Colima State, Colima (♂, ♀); Tamaulipas State, San Francisco (♂, ♀). UNITED STATES: Texas, Loredo (♀). COSTA RICA: Turrialba (2 ♂, ♀). GUATEMALA: Guatemala City (♀) (BMNH). PANAMA: La Boca, Canal Zone (♂, ♀).

Chlorostrymon maesites (Herrich-Schaeffer)
(Figs. 2C, D, 5F, G, 6H, I)

Thecla maesites Herrich-Schaeffer 1864:165. Dewitz (1877:233, pl. 1), Moeschler (1889: 301), Ståhl (1882:93), Gundlach (1887:623), Wolcott (1936:402), Comstock & Huntington (1943:72; 1958–64 [1961]:158), Comstock (1944:487), Zikán & Zikán (1968: 57).

Thecla maesites clenchi Comstock & Huntington (1943:72) (holotype male, allotype female [Fig. 2D], AMNH, Roseau Valley, Dominica, British West Indies, April). **NEW STATUS.**

Thecla moesites [sic]: Kirby (1871:398), Draudt (1919:798) (misspelling; Comstock & Huntington 1958–64 [1961]:158 incorrectly attribute error to Draudt).

Thecla moesites Draudt (1919:798). Comstock & Huntington (1958–64 [1961]:158, 171) (incorrect *nomen nudum* attributed to Draudt).

Strymon maesites: Barnes & McDunnough (1917:13), Bates (1935:194), Young (1937:47), McDunnough (1938:24), Klots (1951:140), Kimball (1965:47), Rindge (1952:11), Ziegler (1960:22) (as "*Strymon*"), dos Passos (1964:55).

Chlorostrymon maesites: Clench (1961:189; 1963:248; 1976:269; 1977:186), dos Passos (1970:27), Riley (1975:100), Thorne (1975:277), Miller & Brown (1981:99; 1983:54), Pyle (1981:464), Opler & Krizek (1986:88), Scott (1986:360), Schwartz (1988).

Diagnosis. DFW, DHW brilliant iridescent azure blue; VHW terminal patch extending costad to M_3, postmedian line not making a "W"; VFW postmedian line black (Fig. 2C, D). Genitalia differing

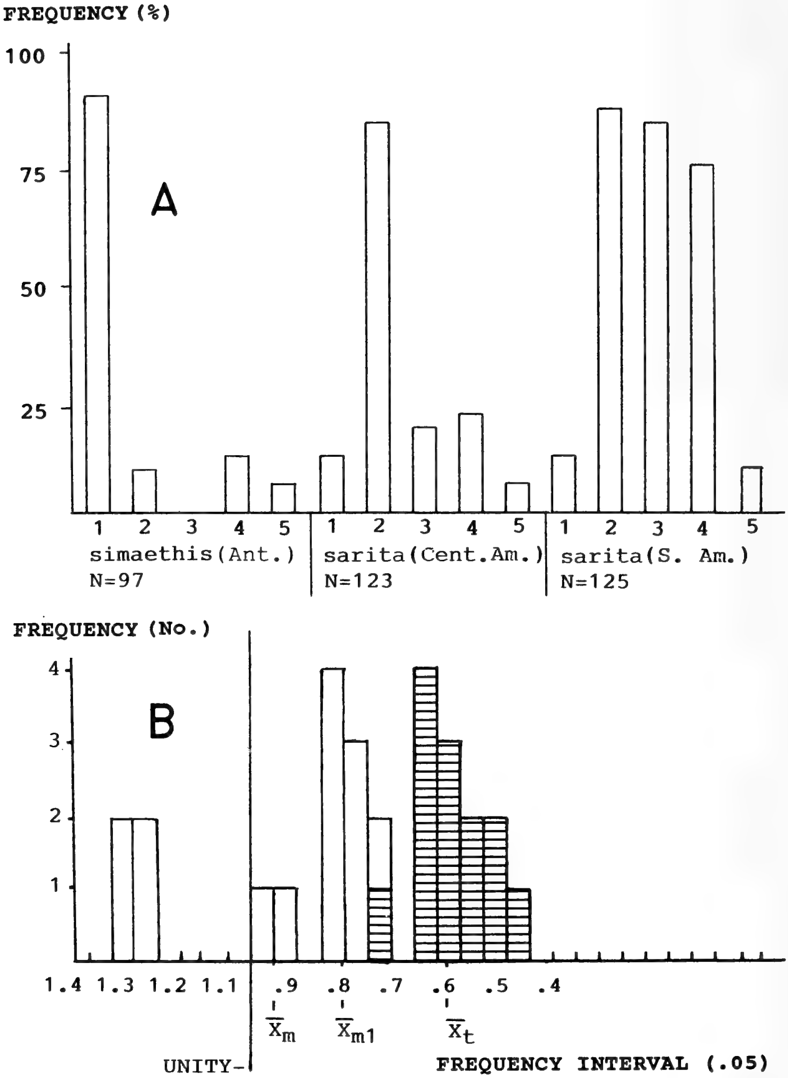

FIG. 7. Frequencies of characters in certain *Chlorostrymon* populations. A, Wing characters in *C. simaethis simaethis* (Antilles) and *C. s. sarita* (Central America, South America). Characters: 1, VHW postdiscal band undulate (angles of band, along inner surface at consecutive veins, changing at least 6 times costad of vein 2A). 2, band generally straight (not as in 1, and in at least 3 of 5 cells costad of vein 2A, generally in same plane). 3, band swollen distad in area adjacent to discal cell. 4, VFW with marginal and submarginal areas, cells CuA_1 and M_3, suffused red-brown and gray. 5, FW with basal area of costa folded and colored orange. B, Female genitalic shape in *C. telea* (hatched) and *C. maesites* (white). Shape expressed as ratio of length of dorsal suture line (d.s.l.) to length of ductus (d) (d.s.l./d). $\bar{x}$m is mean of *C. maesites* sample including *C. m. clenchi* (0.95, N = 14); $\bar{x}$ml is mean of *C. maesites* excluding *C. m. clenchi* (0.81, N = 10); $\bar{x}$t is mean of *C. telea* sample (0.58, N = 14).

from *C. simaethis* as in *C. telea*. For genitalic comparison to *C. telea* see *C. telea* and below.

Types. Location of *T. maesites* type not known (cited as possibly Havana, Cuba, by Miller & Brown 1981:note 357); TL Cuba. Comstock & Huntington (1958–64 [1961]:171) cite a "species" "*moesites* Draudt", taking Draudt's (1919) treatment of this name as a description. They cite no type or type locality as Draudt gave none. Draudt's treatment of "*moesites*" was an incorrect repetition of an earlier misspelling by Kirby (1871:398). Clearly, Kirby, and consequently Draudt, were treating *T. maesites.*

Distribution (Fig. 4). S Florida, Bahamas, Greater and Lesser Antilles S to St. Vincent.

Specificity of *C. maesites* and *C. telea*. Considering *C. telea* and *C. maesites* separate species, Clench (1961) stated, without elaboration, "the two . . . are different in many traits". Such observations probably resulted from Clench's experience with *Chlorostrymon* species in the field (Clench 1976, 1977).

Variability of *C. maesites*. As noted under *C. telea,* male genitalia of *C. telea* and *C. maesites* are similar (Fig. 5E–G). They differ from *C. simaethis* (Fig. 5A–D) by a generally reduced vincular arc, shorter valval configuration, and aedeagus (a) short, its length usually not exceeding 3× maximum width of vincular arc (in *C. simaethis,* 3.5–4.0×), and (b) with terminal ¼ greatly flared and ventrally inclined about 60°. Female genitalia of *C. telea* (Fig. 6G, J–L) and *C. maesites* (Fig. 6H, I) differ consistently in structure of ductus and antrum (Fig. 7B). In addition, papillae anales of *C. maesites* are not as terminally constricted as in *C. telea* (Fig. 6G–I). In Antillean *C. maesites,* as with Antillean *C. simaethis,* infraspecific variation is more extreme than in mainland populations. For example, male genitalia from the Bahamas and Puerto Rico show notable cephalic sculpturing along outer valval margins. These do not occur in any other *Chlorostrymon* and are probably a parallelism. Female genitalia vary most in ratio of lengths of antrum and ductus bursae (Fig. 7B), and in degree of dorsal inclination, if any, at the cephalic terminus of ductus bursae (Fig. 6G–L). Dominican endemic *C. m. clenchi* (Fig. 6I) and some specimens from Jamaica have a somewhat reduced cephalic terminus on the ductus bursae. In the two new austral species described here, this tendency is so extreme that only the area of the antrum remains.

Subspecies of *C. maesites*. Comstock and Huntington (1943) noted that *C. m. clenchi* lacked a tail at vein CuA_1, and that both sexes had a dull DFW, DHW ground color, and pronounced black apical borders (noticable in male; emphatic in female, obscuring almost any DFW blue). The wing pattern in *C. m. clenchi* is distinctive, more so than degree of local differentiation in other Antillean *C. m. maesites.* However, certain genitalic features of *C. m. clenchi* are duplicated in other Antillean *C. maesites* (female discussed under species treatment; in male, elongation of valval terminus in *C. m. clenchi* [Fig. 5G] duplicated in males from Puerto Rico and the Bahamas). As in *C. simaethis*, there appear to be Antillean populations of *C. maesites* that might equally be considered worthy of subspecific status. Nevertheless, I recommend that no further subspecies of *C. maesites* be recognized, although the name *clenchi* might still be useful historically to note the pattern morph typifying Dominica.

Dissections examined (all AMNH). *C. m. maesites*: BAHAMAS: Nicoll's Town, Andros Island (♂, ♀), North Caicos, 17–18 May 1983 (2 ♂, 1 ♀). CUBA: Guantanamo Bay. JAMAICA: Port Antonio, 10 March 1954 (♂), Baron Hill, Trelawny, 16 February 1931 (♂), Montego Bay, 3 January 1965 (♂), Reading, St. James, 27 March 1939 (♀), Sandy Gully, St. Andrews, 20 June 1951, 3 December 1951 (2 ♂), 8 July 1951 (♀). UNITED STATES: Miami, Florida, various dates (7 ♂, 7 ♀), Brickell Hammock, Florida, 6 August 1914 (♂, ♀), Coamo Springs, Puerto Rico, 26–29 December 1914 (2 ♂, ♀). *C. m. clenchi*: types. DOMINICA: Roseau, 11 April 1929 (2 ♂, 3 ♀).

Chlorostrymon kuscheli (Ureta), new combination
(Figs. 3E, F, 5N, 6M)

Thecla kuscheli Ureta (1949:98, pl. 1, fig. 4), Comstock & Huntington (1958–64 [1961]: 58), Rojas (1964:103).

Diagnosis. FW small, base to apex 8.0–9.5 mm (N = 2); DFW, DHW iridescent lavender in male, dull brown in female, and DHW of both sexes with bright rufous suffusion across limbal area. VFW, VHW with white bands limited to thin lines, VHW limbal suffusion only barely perceptible as silverish streaks. Female genitalia with cephalic end of ductus dorsally inclined as in *C. telea*, but with ductus length far exceeding that of lamellae, as in *C. maesites*; papillae anales with apophyses elongate, extending entire length of ductus bursae.

Description. Male. DFW, DHW iridescent lavender. VFW, VHW ground dull chartreuse; each wing with complete postmedial band, but constricted as thin white lines. VFW with red-brown suffused discal slash; VHW with limbal area vaguely suffused silverish. Length of forewing: 8.0 mm (N = 1). **Female.** Similar to male but slightly larger, with DFW, DHW duller brown. Length of forewing: 9.5 mm (N = 1). **Male genitalia** (Fig. 5N). Only aedeagus remains of paratype genitalic preparation; aedeagus typical of genus but angled at junction of shaft and caecum, latter rather elongate for genus. **Female genitalia** (Fig. 6M). Cephalic ductal terminus inclined dorsally about 45°, ductus elongate compared to length of dorsal suture line (ratio 0.99). Papillae anales with apophyses extremely elongate, extending entire length of ductus.

Types. Holotype male, MNHNC, Larancagua, Tarapaca, Chile, 2800 m, 9 December 1946. Allotype female, MNHNC, same data except 25 February 1948. Paratype (Fig. 3E), CECUC, labelled "*Thecla kuscheli*; Larancagua, 2700 m, Kuschel, 8 xii 1946; Paratypus; donada par E. Ureta."

Distribution (Fig. 4). Tarapaca State, Chile, near border with Bolivia and Argentina.

Remarks. Ureta's description, in Spanish, was not widely distributed, and specimens of *C. kuscheli* have only recently been available to northern workers. Though uniquely marked, the species clearly belongs in *Chlorostrymon* by wing, male aedeagal, and female genitalic characters. The DHW rufous coloration is unique for the genus; reduced VFW, VHW bands, and limbal suffusions are common to all austral *Chlorostrymon* (but differ in each species). Female genitalia do not show marked reduction of ductus bursae as in the new austral species described further on. Though wing pattern in *C. kuscheli* is extreme, and somewhat reminiscent of *C. simaethis*, genitalia are more like *C. maesites* and *C. telea*.

Biogeography. The species is apparently a high montane (2700–3650 m) isolate of the genus. Specimens are known only from the cusp of the Northern Andean Cordillera and Andean High Plateau biotic provinces (Irwin & Schlinger 1986, Davis 1986) in northern Chile, but may also occur in adjacent high montane Bolivia and Argentina.

Dissections examined (all CECUC). Paratype ♂. CHILE: Putre, Arica region, 3650 m, 25 February 1940, leg. Ureta (♀).

Chlorostrymon patagonia, new species

(Figs. 3A, B, 5H, 6N)

Diagnosis. Male DFW, DHW iridescent red-violet; fuscous, basally overlaid with dull blue-gray in female. Both sexes with FW costa basally folded, colored bright rufous; VFW, VHW without bands, patterned as short silver cellular streaks across VHW discal cell and cells CuA_2 to caudal M_3 (limbal suffusion, dull rusty-red to grayish, generally restricted to latter cells). Larger than *C. telea* and *C. maesites*: forewing base to apex averaging 12.2 mm, range 10.0–13.0 mm (N = 8); in *C. telea* 8.8 mm, range 7.5–10.0 mm (N = 19); in *C. maesites* 8.6 mm, range 6.0–11.0 mm (N = 18). Female genitalia sclerotized only in the terminal antrumal configuration (as only in *C. chileana*), corpus bursae uniquely lacking signa (Fig. 6N); male resembling *C. telea* and *C. maesites* except bilobed valval configuration wider, more shouldered, saccus reduced to small terminal point, aedeagus with unique cephalic inclination and marked terminal declination, and brush organs attached to long membrane spanning ventral surface of vincular arc (Fig. 5H, L).

Description. Male. DFW, DHW bright iridescent red-violet, basal area of costa widely folded and colored bright rufous. VFW chartreuse, patterned only with occasional, hardly visible, light streaks in various cells from costa to cell M_3; VHW chartreuse, patterned only by light slash through discal cell, and silvery zig-zag markings, basad dull rusty-red to slightly gray suffusion from cells CuA_2 to caudal M_3. Stubby tail, terminus of vein CuA_2. FW length 12.0 mm (allotype). **Female.** Similar to male, but DFW, DHW fuscous and suffused dull blue-gray on base of FW and basal half of HW. FW length 12.0 mm (holotype). **Male genitalia** (Fig. 5H). Similar to *C. telea* and *C. maesites* but differing by wider, more shouldered bilobed valval configuration; reduced, funnel-shaped saccus; aedeagus markedly inclined at caecum, declined at terminus; and brush organs attached along entire ventral surface of vincular arc. **Female genitalia** (Fig. 6N). Resembling only *C. chileana*, with sclerotized components including only the antrumal structure. Lamellae distally lobated as in *C. telea* and *C. maesites*; corpus bursae lacking signa; papillae anales constricted terminad as in *C. telea*, but apophyses of papillae anales short (about equal to length of antrumal sclerotization).

Types. Holotype female, allotype male, Nahuel Huapí, Mendoza Province, Argentina, 15 March 1911 (♀), 3 December 1908 (♂) (C. S. Larsen Collection in MNHN). Paratypes: MNHN—same data as allotype (♂), Mendoza, Argentina, 8 April 1907 (♂), 14 March 1907 (♂), 13 December 1906 (♂), all C. S. Larsen Collection; AMNH—same data as allotype (♂); MPM—Patagonia, August 1939, P. Gagarin Collection (♀).

Distribution (Fig. 4). Known only from N to central Patagonian Steppe biotic province (Davis 1986) of Argentina.

Remarks. In facies, *C. patagonia* might be considered a *C. telea* population of extremely reduced wing pattern if it were not for its larger size, unique wing characters, and female genitalia resembling only *C. chileana*. The southernmost record of *C. telea* is Villa Ana, Santa Fe Province, Argentina (BMNH); the southwesternmost, Callao, Peru (BMNH) (Fig. 4). These specimens are females and typical of *C. telea* (Figs. 2B, 6L, M).

It should be noted that Clench (1961) called the upper surface iridescent color of *C. telea* "red-violet". This is unfortunate since this surface in *C. patagonia* is truly red-violet and distinctive from *C. telea*, generally characterized by other authors as brilliant blue. The widely folded, rufous colored DFW costal fold is also obvious on all specimens of *C. patagonia*. A survey of 38 *C. telea* from across its range shows no such costal character. An orangish costal fold occurs in occasional specimens of *C. simaethis* (Fig. 7A). In genitalia, the sclerotized structures in female *C. patagonia* (and *C. chileana*) duplicate only the antrumal structure of other *Chlorostrymon* species. The ductal area of *C. patagonia* (and *C. chileana*) is wholely membranous. Male genitalia of *C. patagonia* resemble those of *C. telea* and *C. maesites* most, but differ as summarized in Diagnosis.

I speculate that such unusual characters in *C. patagonia* and *C. chileana* are autapomorphic, as discussed under *C. chileana.*

Biogeography. *Chlorostrymon patagonia* is found within the Patagonian Steppe biotic province of Davis (1986). From 30°S latitude, this province extends S in a thin strip E of the Andean Cordillera to encompass all of Patagonia S and E of 44°S latitude. Vegetation is xeric grassland, compatible with known habitats of *Chlorostrymon* taxa. Several other butterfly species have insular distributions like *C. patagonia.* One is the distinctly marked *Thecla thargelia* Burmeister, found only occasionally northward to Tucumán (IML, MNHN). Five others are *T. larseni* Lathy, *T. restricta* Lathy (both described from MNHN C. S. Larsen material), and three species of *Eiseliana* Ajmat de Toledo located recently in Patagonian material at AMNH, BMNH, and MNHN.

Chlorostrymon chileana, new species

(Figs. 3C, D, 5I, 6O)

Diagnosis. DFW, DHW of both sexes, dull brown, male slightly suffused purplish. VFW, VHW lacking bands, VHW patterned only with vague postdiscal line from discal cell costad to margin. Limbal area suffused only vaguely gray-brown and dusted basad with silver from cells CuA_1 and CuA_2. Female genitalia sclerotized only in terminal antrumal configuration (as in *C. patagonia*); male genitalia resembling *C. simaethis* most but with an enlarged, broad saccus, and an additional brush organ occurring distally at each juncture of saccus and vinculum.

Description. Male. DFW, DHW dull fuscous slightly hued with purplish blue. VFW, VHW ground dull chartreuse, VFW without pattern, VHW with obsolescent postdiscal line, discal cell costad to costal margin; limbal area, cells CuA_1 and CuA_2 slightly suffused reddish to grey distad, silver basad; stubby tail at terminus of HW vein CuA_2. FW length 11.5 mm (allotype). **Female.** Similar to male except DFW, DHW dull brown. FW length 11.0 mm (holotype). **Male genitalia** (Fig. 5I). Similar to *C. simaethis* but with saccus enlarged and broad (length & width nearly equal and each equally about ⅔ length of vincular arc), a second brush organ distally at juncture of saccus and vinculum, aedeagus short, its shaft only slightly exceeding length of entire genitalia, and with caecum somewhat laterally displaced. **Female genitalia** (Fig. 6O). Resembling *C. patagonia,* with sclerotization limited to antrum; lamellae parabolic as in *C. simaethis*; signa reduced as small blunt spines; papillae anales lobate; apophyses of papillae anales short (length barely exceeding that of antrumal sclerotization).

Types. Holotype male, allotype female, Santiago, Chile, R. Martin, deposited in MNHN. Paratypes: MNHN—same data as primary types

(4 ♂, 1 ♀); BMNH—"Chili", Walker, J. J. Joicey Collection, "*Thecla* sp. not in collection, S.G" (♂); AMNH—same data as primary types (♂).

Distribution (Fig. 4). Known only from TL and "Chili".

Remarks. *Chlorostrymon chileana* differs greatly from *C. simaethis* in its nearly immaculate undersurface and unusual male and female genitalia. Female genitalia superficially resemble *C. patagonia* while male genitalia have a number of unique characters as summarized in *C. patagonia* and *C. chileana* Diagnosis sections.

Biogeography. MNHN has substantial series of butterflies bearing the labels "Santiago, Chile, R. Martin" and "Valpariso, Chile, R. Martin". *Chlorostrymon chileana* occurs only in the Santiago samples. This locality, if taken literally, is within the Central Valley biotic province (Davis 1986, Irwin & Schlinger 1986)—relatively xeric, former thorn forest now extensively replaced by cultivation. This province is quite small, extending inland from the Central Coastal Cordillera from about 32–38°S latitude. Its ecology is typical of that associated with *Chlorostrymon* taxa. These circumstances, along with unusual characters, suggest that *C. chileana* is an insular species. Its present-day occurrence may be severely restricted by land use, as noted for several central Argentinean plains butterflies (Johnson et al. 1988). The Central Valley biotic province lies directly opposite the distribution of *C. patagonia* on E slopes of the Andes in Argentina. MNHN "R. Martin" samples include a number of butterflies previously unrecorded for Chile which have congeners occurring directly eastward in Argentina's Coquena biotic province (Davis 1986). Examples include *Calycopis* Scudder (Johnson et al. 1988), *Femniterga* Johnson (1987), the little known hairstreaks *Thecla americensis* Blanchard and *T. wagenknechti* Ureta, and others. From such diversity, and comparison with information from more recent Chilean collections (such as J. Herrera's, on loan to AME), I suspect that MNHN "Santiago" and "Valpariso" labels include diverse Chilean habitats.

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GENERAL NOTES

PAPILIO TROILUS L. ON A NEW AND RARE LARVAL FOOD PLANT

Additional key words: Papilionidae, endangered, *Lindera melissifolia.*

Papilio troilus L. is a common swallowtail found over a broad geographic range. It is known from southern Canada to Florida and W to Manitoba and Texas, becoming less common W of the Mississippi River (Klots, A. B. 1951, Field guide to the butterflies, Houghton-Mifflin, Boston, 349 pp.). At least 15 species have been reported as larval food plants; these are mainly in the families Lauraceae, Rosaceae, and Rutaceae (Teitz, H. M. 1972, An index to the described life histories, early stages, and hosts of Macrolepidoptera of the continental United States and Canada, Allyn Mus. Entomol., Sarasota, Florida, 1041 pp.; Opler, P. A. & G. O. Krizek 1984, Butterflies east of the Great Plains, Johns Hopkins Univ. Press, Baltimore, 294 pp.). Species for which there is direct evidence of complete larval development are *Cinnamomum camphora* Nees & Eberm., *Lindera benzoin* (L.) Blume, *Persea borbonia* (L.) Spreng., and *Sassafras albidum* (Nutt.) Nees (R. C. Lederhouse pers. comm.).

In Mississippi, *Lindera benzoin* is the most common and widely distributed spicebush. The related pondberry or swamp spicebush, *L. melissifolia* (Walter) Blume, is an endangered species throughout its range in the SE United States (Kral, R. 1983, U.S. Dep. Agr. Forest Service Tech. Publ. R8-TP2, 1305 pp.; Currie, R. 1985, Federal Register 50: 32581–32585). Pondberry is known in Mississippi only from the Delta Region in Bolivar, Sharkey, and Sunflower counties.

On 18 June 1988, when the latest Mississippi population of *L. melissifolia* was discovered in Sunflower Co., a larva of *Papilio troilus* was noticed in its weblike, longitudinally rolled nest on a leaf of *L. melissifolia.* The preserved larva was given to the Mississippi Entomological Museum at Mississippi State University, Mississippi State, Mississippi, and voucher specimens of *L. melissifolia* are deposited in university herbaria at Florida, Michigan, Vanderbilt, and other herbaria.

In Mississippi, *Papilio troilus* larvae are commonly found on *Sassafras albidum* and *Lindera benzoin,* both in Lauraceae. *Sassafras albidum* is common in the Delta Region of Mississippi, but *Lindera benzoin* is relatively rare there, being more frequent eastward in the Loess Bluff Region. It is therefore logical that *P. troilus* utilizes another species in this family and in the genus *Lindera.* This observation is unique because a common butterfly seems to accept a rare food plant in the natural environment when other sources are much more common. However, no individuals of sassafras were located in the immediate area, and populations of the more common spicebush are kilometers away from the collection site.

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SPENCER COLLECTION GIVEN TO SMITHSONIAN

The National Museum of Natural History (Smithsonian Institution) has received the Spencer Collection of Western Butterflies. The Collection consists of over 4000 specimens, primarily of the genus *Speyeria,* and represents eight western states, Mexico, and Canada.

Among the species are fine series of *Speyeria nokomis nitocris* (Edwards), a topotypical series of *S. n. coerulescens* (Holland), and a series of *S. cybele pugetensis* F. Chermock and Frechin. Two important butterflies were rediscovered by Spencer: *S. nokomis nigrocaerulea* (W. and T. Cockerell), near Taos, New Mexico, and *Clossiana selene nebraskensis* (Holland), near Valley, Nebraska. The Collection is rich in Nebraska material, including the only known Nebraska specimen of *Colias alexandra krauthii* Klots, from Sow Belly Canyon, Sioux County, and the only recent eastern Nebraska specimen of *Speyeria aphrodite alcestis* (Edwards). Nearly all of the *Speyeria* specimens were reared, and each species series displays rich coloration and individual variation.

Mr. Orville D. Spencer and his wife Eunice of Lincoln, Nebraska spent 40 years amassing their collection of Lepidoptera. Spencer's interest in butterflies began when he was a boy in Lincoln. Later he developed a highly successful technique for collecting eggs from butterflies and rearing them at home. Mr. Spencer's background is engineering, having retired in 1980 from the Lincoln Telephone Company. From the collector-made drawers to the carefully placed antennae, the time spent and the love shown in preparing this collection is evident to the viewer.

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EVIDENCE FOR GENETIC DETERMINATION OF VARIATION IN ADULT SIZE AND WING MELANISM OF *PARNASSIUS PHOEBUS* F.

Additional key words: phenotype, geographic variation, Papilionidae.

Parnassius phoebus F. (Papilionidae) ranges from Europe across Asia, and throughout much of montane western North America. The species is highly variable in wing coloration and size throughout its range, both within and between populations. C. D. Ferris (1975, J. Res. Lepid. 15:1–22) described the taxonomic variation of non-Arctic North American populations. I described some of the variation in wing color and size from an ecological viewpoint (Guppy, C. S. 1986a, Can. J. Zool. 64:956–962; 1986b, Oecologia 70:205–213).

To arrive at an understanding of the systematic and ecological significance of phenotypic variation of *P. phoebus*, it is necessary to know if the variation is due to genetic differences between populations. Ferris (above) believed that variation in wing melanism is environmentally controlled, and J. A. Scott (pers. comm.) believes it is genetically determined. In this paper I provide evidence for the genetic basis of some geographic variation in wing melanism and size (wing length) of *P. phoebus*.

Parnassius phoebus is a medium-sized to large butterfly with wings that are white with various black markings and usually red ocelli. There is a predominantly black region at the base of the hindwings which varies considerably in width, in proportion of black to white scaling within the black region, and in density of scaling (transparency) of the black region. This black region has a thermoregulatory significance (Guppy 1986b, above). The forewing distal region has marginal and submarginal black markings which vary greatly in development, especially in females. This region may be very transparent, especially in females, but it apparently lacks thermoregulatory significance (Guppy 1986b, above). Body size is highly variable, with a general trend of decreased size with increased elevation (Guppy 1986a, above).

I reared offspring concurrently from one or two arbitrarily selected females from each of five *P. phoebus* populations (Table 1) under uncontrolled (outdoor) conditions in 1980. Arbitrary samples from parent populations and all reared offspring were scored for six

TABLE 1. *Parnassius phoebus* sample origins and sizes. Eggs were obtained in 1979.

Locality no.	Description	Sample size*			
		Mw	Mr	Fw	Fr
1	Montana, Missoula, elev. 1525 m	12	2	11	2
2	Alberta, Kananaskis Rd., Regal Ck., elev. 1525 m	2	6	2	8
3	British Columbia, Manning Park, Gibson Pass, elev. 1370 m	7	13	5	14
4	British Columbia, Big Bar Creek, Poison Mt., elev. 2135–2195 m	9	5	9	4
5	British Columbia, Penticton, Mt. Apex, elev. 2190–2247 m	24	8	4	6

* Number of males (M) and females (F) in wild (w) and reared (r) samples.

phenotypic characters by methods described and illustrated previously (Guppy 1986a, above). Briefly, characters were defined as follows: "basal patch width"—proportion of the centerline of the dorsal hindwing discal cell covered by the predominantly black region. "Basal blackness"—proportion of scales in the basal black patch which were black (the rest were white). "Basal transparency"—proportion of the basal black patch which was without scales (in the absence of scale erosion). "Distal blackness"—proportion of 100 quadrats in a microscope's optical grid (oriented so outer corners at the points where veins M_3 and Cu_2 met the forewing margin) in which >25% (males) or >50% (females) of scales were black. "Distal transparency"—proportion of distal forewing area not covered by scales (in the absence of scale erosion). Forewing length was measured with a metric ruler from thoracic attachment point to wing apex. All phenotypic measurements except forewing length were arcsine (square root) transformed before analysis to normalize distributions.

Data were analyzed by nested analysis of variance (ANOVA), with PHENOTYPE a function of LOCALITY, and ENVIRONMENT (reared vs. wild) nested within LOCALITY (Zar, J. H. 1974, Biostatistical analysis, Prentice-Hall, Englewood Cliffs, New Jersey, 620 pp.). In the ANOVA's, if LOCALITY is significant, then there are significant differences between reared samples, and those differences are correlated with differences in the wild populations. Therefore, such differences must be genetically controlled. The ENVIRONMENT term could not be interpreted unambiguously because it included both effect of developmental environments (six wild and one reared) and genetic effects due to each reared sample having originated from eggs of 1–2 females instead of from a random sample of eggs from all females in a population. However, if all reared samples deviate in the same direction from corresponding wild sample phenotypes, it can be concluded that developmental environment is important in determining phenotype. Absence of such consistent deviations does not necessarily mean that environmental effects are absent, because the rearing environment may not have deviated in a consistent direction relative to wild environments.

Basal patch width of males, distal transparency of both sexes, and wing length of males (Fig. 1) differed significantly among reared samples, and those differences are correlated with differences between wild populations (LOCALITY terms $P < 0.05$). Therefore, genetic differences among populations cause at least some of the interpopulation variation in these characters.

LOCALITY terms were nonsignificant ($P > 0.05$) for female basal patch width, female basal blackness, and distal blackness for both sexes. ANOVA's were not done for male basal blackness, basal transparency for both sexes, and female forewing length because of nonhomogeneous variances.

Basal blackness and basal transparency are apparently affected by developmental environment. Nine of the 10 reared samples (both sexes) were darker and less transparent

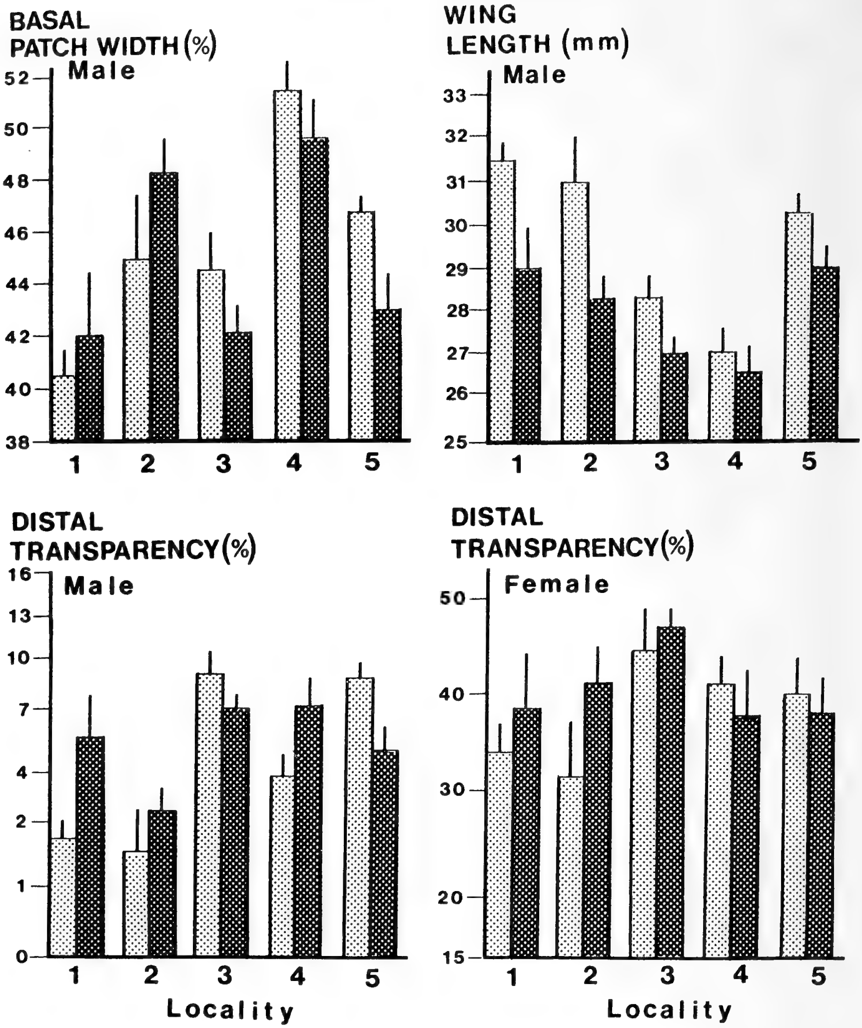

FIG. 1. Characters of *Parnassius phoebus* for which a genetic basis was detected. Dark bars, reared samples; light bars, wild samples. Vertical lines represent 1 SE. Sample origins and sizes are given in Table 1.

than the corresponding wild samples. Locality No. 4 males showed no difference between reared and wild samples in basal darkness and transparency. In addition, 9 of the 10 reared samples have shorter forewing lengths than the corresponding wild samples (Locality No. 5 reared sample averaged 1 mm longer than the wild sample). Therefore, size as indicated by forewing length (Miller, W. E. 1977, Ann. Entomol. Soc. Am. 70:253–256) is also affected by developmental environment.

Significant ENVIRONMENT terms ($P < 0.05$) occurred for female basal patch width, female basal blackness, male distal blackness, male distal transparency, and male forewing length, but, as mentioned above, interpretation of ENVIRONMENT is ambiguous.

This study provides evidence of a genetic basis for interpopulation variation in three of six phenotypic characters examined for *P. phoebus*. There is also evidence for developmental environment affecting phenotype for three characters. In light of the small sample sizes, failure to detect either a genetic or an environmental component to variation in a character does not mean that these components are unimportant, merely that they were not detected.

This research was partly supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) operating grant to Judith H. Myers at the University of British Columbia.

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EFFECT OF REFRIGERATION ON EGG INCUBATION PERIOD OF THE TASAR SILK INSECT *ANTHERAEA MYLITTA* DRURY (SATURNIIDAE)

Additional key words: sericulture, India.

Antheraea mylitta Drury is a semidomesticated tasar silk insect reared thrice in a year during July–August, September–October and November–December. January to middle of June is the diapause period. In recent years, 40–60 percent of fertile egg production from May to mid-June has gone unutilized for rearing due to lack of quality leaves in tasar food plants and excessive outdoor temperatures (39 ± 4°C). This situation causes loss and scarcity of eggs for subsequent commercial tasar crops. It would be desirable to prolong egg incubation by some suitable means to enable utilization of those eggs at the onset of the favorable rearing period, and to synchronize hatching of all egg batches for simultaneous rearing.

The egg of *A. mylitta* normally requires seven days of incubation at room temperature, and hatches on the eighth day after oviposition. Refrigeration is a common means to delay hatching of other silkworm eggs. Information is available on the effect of low temperature on the incubation periods of the mulberry silkworm, *Bombyx mori* L. (Tayade, D. S., M. D. Jawale & P. K. Unchegaonkar 1987, Sericologia 27:297–299) and the Eri silkworm, *Philosamia ricini* H. (Choudhury, S. N. 1982, Eri silk industry, Directorate of Sericulture and Weaving, Govt. of Assam, Gauhati, 177 pp.; Viswakarma, S. R. 1982–83, Indian J. Seric. 21–22:36–39). Since no information was available on the effect of refrigeration of eggs of *A. mylitta,* this investigation was made.

In the Mayurbhanj district of Orissa, India, 29,000 freshly oviposited eggs were collected from 290 DFl's (disease free layings from 290 healthy mated females) of the Sukinda trivoltine race of *A. mylitta* on 22 May 1987 at 0900 h, and were kept at room temperature (31 ± 2°C) as a common stock. Every day at 0900 h from the first to seventh day after oviposition, 4000 eggs (40 DFl's) were taken from the common stock and divided into four equal groups for 1, 2, 3, and 4 days of refrigeration treatment at 10 ± 1°C, after which they were again allowed to incubate at room temperature until hatching. The remaining 1000 eggs (10DFl's) served as the control. The incubation period of the treated groups was then compared with the control. The experiment was repeated five times during the same period and under the same conditions.

The incubation period of control eggs was seven days. One and two days of refrigeration of 1st- (fresh or 0-day-old) and 2nd-day (1-day-old) eggs increased the incubation period to 12 days (Table 1), 5 days more than the control. Three and four days of treatment to such eggs increased the incubation period to 13 days (Table 1), 6 days more than the control.

One and two days of refrigeration increased the incubation period by two days beyond the control in 3rd- (2-day-old), 4th- (3-day-old), and 5th-day (4-day-old) eggs, and by

TABLE 1. Incubation period of *Antheraea mylitta* eggs refrigerated at different ages for different periods.

Day after oviposition	Age of eggs (days)	Incubation period when refrigerated for:			
		1 day	2 days	3 days	4 days
1st	0 (fresh eggs)	12	12	13	13
2nd	1	12	12	13	13
3rd	2	9	9	11	11
4th	3	9	9	10	10
5th	4	9	9	11	11
6th	5	8	8	10	10
7th	6	8	8	9	9

TABLE 2. Analysis of variance.

Source of variation	df	SS	MS	F
Between refrigeration periods	3	61.71	10.28	108.27*
Between ages	6	14.28	4.76	50.12*
Error	18	1.71	0.09	—
Total	27	77.71	—	—
Critical difference ($P < 0.05$) for refrigeration period = 0.35				

* Significant ($P < 0.05$).

one day in 6th- (5-day-old) and 7th-day (6-day-old) eggs. Similarly three and four days of refrigeration increased the incubation period by four days in 3rd- and 5th-day eggs, by three days in 4th- and 6th-day eggs, and by two days in 7th-day eggs.

The data were analyzed as two-way classified. There is significant variation ($P < 0.05$) among different refrigeration treatments as well as among different ages of eggs; further, the critical difference indicates that the two-day refrigeration treatment differed significantly from the three-day (Table 2).

Thus the fresh and one-day-old eggs of *A. mylitta* refrigerated for three and four days showed maximum increase of the incubation period amounting to six days. Viswakarma (above) observed that the incubation period of *P. ricini* eggs when refrigerated at 7 ± 2°C for five days increased by four to five days. Choudhury (above) reported prolongation of the incubation period of *P. ricini* eggs by four days of refrigeration at 15°C. Tayade et al. (above) observed one or two days extension of the incubation period in *B. mori* eggs with increase of refrigeration at 5°C to 55 days. Studies on the effect of different degrees of temperature on incubation and embryonic development of *A. mylitta* eggs should be carried out.

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BOOK REVIEW

THE SATURNIIDAE OF AMERICA. CERATOCAMPINAE, by Claude Lemaire. 1988. 480 pp., 64 pls., 379 text figs. Mus. Nac. Costa Rica. Soft cover. $80.00.

This is the third volume by Lemaire in his series of monographs of the New World Saturniidae; its predecessors concerned Attacinae (=Saturniinae) (1978) and Arsenurinae (1980). All three follow the same format; the two earlier volumes were illustrated in black and white, but the present one shows the moths in color.

The use of Ceratocampinae may come as a surprise to some, rather than Citheroniinae, which has been used by recent workers. Fourteen subfamily names are listed as being available for this group of moths; the oldest, by 25 years, is Ceratocampinae. Two additional available family-group names also have priority over Citheroniinae.

This subfamily is second only to Hemileucinae in numbers of species; 170 are covered in this volume, and they are placed in 27 genera. The group is restricted to the New World, with the taxa being distributed from southern Canada to southern South America. The highest percentage of endemic species is found in Mexico and Central America, the next largest group in the general area of southeastern Brazil.

The introductory section of the book gives morphological characters for the subfamily, geographic distribution, a summary of knowledge of the early stages (with six color plates showing caterpillars of 24 species), a discussion of taxonomy and name usage, and phylogeny, followed by a key to genera. Each genus has its bibliography, followed by most of the subjects listed above. Following keys to included species, each taxon is treated in a similar fashion. Drawings of male and female genitalia, plus distribution maps, are always present; antennae, venation, and legs are illustrated for most genera. Each species (and subspecies when present) is illustrated in color, usually with several examples being shown.

While the text is in French, each taxon, from subfamily to subspecies, has a diagnostic summary in English; in addition, there is a Spanish summary for the subfamily and for each genus. This makes the book readily understandable to those who do not read French; Lemaire is to be highly commended for including these extremely useful additions.

The taxonomic approach is based on study of specimens from the entire New World. This method, rather than defining genera by use of species from a restricted geographic area, has led to some name changes. On the generic level, the only change for the North American fauna is that *Syssphinx* is used instead of *Sphingicampa*. Lemaire takes a conservative approach to nomenclature; his treatment of some species and subspecies differs from some recently published papers. It is a pleasure to see how he handles these problems, utilizing his knowledge and perspective, and shedding new light on some areas that need this type of analysis.

This volume, like the two before it, is handsomely done; the color plates are a great improvement over the earlier black and white illustrations. In a work of this size it is not surprising that a few errors have inadvertently been made; an included erratum sheet covers most of these. Lemaire is to be congratulated; we look forward to each additional volume in this series by the leading specialist of New World Saturniidae.

This and the two previous volumes will be the standard by which identifications and curating will be followed for decades to come. They will be of interest to anyone curious about this family of moths. Now that the basic taxonomy has been done, the invitation is there for much needed work on ecology, life histories, food plants, and behavior of these interesting moths, to mention a few possible fields of study.

Copies may be obtained by sending a check for $80.00 (U.S.), made to Fundacion Neotropica, Museo Nacional de Costa Rica, Aptdo. 749-1000, San Jose, Costa Rica; for airmail delivery, add $5.00 to the price. To obtain Vols. 1 (Attacinae) and 2 (Arsenurinae), I suggest contacting the author directly, as he had these volumes privately printed. The address of this Lepidopterists' Society member is La Croix des Baux, F-84220 Gordes, France.

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FEATURE PHOTO

Unusual moth pupa, *Gonionota* sp. (Oecophoridae), from Ecuador. It is covered with blunt projections and two lateral flanges, and is shown in dorsal view. It measures 10 mm high by 6 mm maximum width and was found upright and exposed on a leaf surface. It probably mimics an inedible object. Other *Gonionota* spp. (J. A. Powell 1973, Smith. Contr. Zool. 120, 302 pp.) and *Hypertropha* (I. F. B. Common 1980, Entomol. Scand. 11:17–31) share a similar mode of pupation. Photo taken with a Minolta X-570 and 80 PX ring flash on a 50 mm macrolens. Pupa collected in Ecuador, Pichincha Prov., Hotel Tinalandia, during the period 5–15 May 1988 by S. Passoa, on an undetermined shrub; adult emerged 19 May 1988.

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MANUSCRIPT REVIEWERS, 1988

The merit of a scientific journal depends on the quality of its reviewers as well as of its authors, but the former are usually unknown to readers. The *Journal* acknowledges with gratitude the services of the people listed below from whom manuscript reviews were received in 1988.

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Cover illustration: Female of *Gastropacha populifolia* (Esper) (Lasiocampidae) in natural resting position on a dead branch, Beijing, China. Submitted by Yu Xiangming, No. 31, Qian Men Wai Zhu Bao Shi, Beijing, China.

JOURNAL OF
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Journal of the Lepidopterists' Society
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PRESIDENTIAL ADDRESS, 1988: LEPIDOPTERISTS—COLLECTORS *AND* BIOLOGISTS?[1]

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Additional key words: food plants, diapause, behavior, longevity, seasonal abundance.

Traditionally this Society has invited the president to expose ideas and opinions in an address, even though they may reflect little hard data. Today is no exception. This discussion will try to encourage collectors, especially amateurs, to devote part of their seemingly limitless energy to the study of Lepidoptera biology.

For purposes of this discussion, an amateur is someone who has to pay money to study Lepidoptera; a professional is someone who gets paid to study Lepidoptera. We all know amateurs who do excellent work and accomplish an astonishing amount, and some professionals who don't get much done. There may even be a few examples of the reverse. Similarly, by this definition there are amateurs with Ph.D.-level training in biology and professionals without it. Hence, there is no inferior connotation in my use of the term amateur.

I thought it might be fun to begin by looking at a subject that is of interest to spouses and other people who get dragged to these meetings or into other embarrassing situations, that is: Why do we collect Lepidoptera?

The urge to accumulate collections is, of course, not restricted to Lepidoptera—the affliction is widely expressed in non-biological artifacts, and it seems unrelated to genetic or environmental inheritance.

My earliest recollections of collecting, when I was 7 or 8 years old, are of bottlecaps. (This was long before twist-top caps were invented, and it was a challenge to get specimens in perfect condition, because

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[1] Delivered to the Annual Meeting of The Lepidopterists' Society in Pittsburgh, Pennsylvania, on 16 July 1988

people would bend the caps when popping them off with openers called "church keys"; these were given out free with beer purchases and had beverage company names imprinted, so some people collected church keys, although I never found that particularly fascinating.) My parents, who never had the slightest interest in collections (which is also true of my brother, wives, and kids), watched, presumably bemused, as I progressed through matchbook covers, military implements, fossils, seashells, and moths, assuming I suppose, that I would mature, get over the penchant, and settle down to dentistry or some other respectable career. They were, of course, wrong on all counts.

Recently I heard a M.D. who collects art and antiques, express it on TV: "Collecting is an affliction that is intractable as any virus, one for which there is no immunity nor cure." We simply have it. I understand that psychologists term it a "personality disorder"; but, quite frankly, I find people who don't have the addiction kind of deprived.

Gary Larsen's cartoon depicting the guys returning triumphantly from the hunt with a huge swallowtail tied to the hood of their car probably gives a better perception of our feelings than most of us could verbalize; nonetheless, I will try to analyze why collectors collect Lepidoptera. I divide the phenomenon into four components: 1) Lure of Collectibles, 2) Hunter Instinct, 3) Acclaim from Peers, and 4) Satisfaction in Discovery.

Probably any lepidopterist would think of other ways to dissect the reasons why collecting is compelling, but most will recognize two or three elements here that contribute to the urge to collect. Any one of these might be the main source of pleasure for any given collector, but probably most of us have never tried to explain it and don't feel a need to. It is only our incredulous friends and relatives that ask, or don't ask but just sigh and look the other way.

Lure of collectibles. It is unfathomable what constitutes collectibles. Apparently, like a queue in England, it only takes two or three. A few of anything that can be conceived of as constituting a set or series will suffice to start a collection. I find it imponderable that someone recently paid $650 for a copy of the high school yearbook of Don Mattingly's graduating class. In fact I don't understand the urge to collect where it depends mainly upon purchases, such as art, yet it must be incredibly compelling. Every conceivable series of objects (or even non-series in the case of Andy Warhol) can be and is collected. The urge has nothing to do with biology, necessarily, as can be attested by the number of lepidopterists who also collect postage stamps—one even collects monogrammed golf balls!

Pleasure from the collection itself is the primary goal in some instances, as epitomized by European collectors who buy specimens from

Tropical Regions at auction for large sums. (Others of us buy them discretely from Welling or Plaumann.) Many collectors seem to derive a lot of their satisfaction and pleasure from the appearance of a neatly curated collection. They actually like spreading and preparing specimens, I guess. This aspect of the affliction provides continuing challenges in time and effort of preparation of specimens, in attempting to obtain perfect specimens to replace less aesthetically pleasing ones (if this is the main goal), and in keeping up with costs of equipment and space for storage (less a challenge with micros than with saturniids, of course).

Hunter instinct. Quite aside from the resultant collection, there is considerable satisfaction derived from the challenge of the hunt—planning the quest, searching for the appropriate habitats, predicting the timing of visits and so on. The anticipation is half the fun (often more). Also satisfying is the skill required in stalking and catching the prey, particularly for rare species and especially for those not seen before. As we all know, those are the hardest ones to catch. This seems to be the leading source of satisfaction for some collectors, to hear them boast. It certainly must be more important than preparation and curating for many collectors, to judge from the amount of papered material that accumulates.

For many of us, I think, it is the lure of adventure that is a strong factor. To see the open road ahead, leading to new and potentially exciting areas (particularly if other lepidopterists have not visited them), is the seduction, coupled with the anticipation that something new may be discovered. The adventure: to collect in exotic areas is the need—the specimens are secondary. Most lepidopterists, if given the choice, obey Powell's Law (Munroe, E. G. 1969, Proc. Entomol. Soc. Ontario 99:43), which can be paraphrased as, "No biologist willingly collects within 1,000 miles of his home base." Thus, lepidopterists living in California go to Mexico to collect, or to Costa Rica if we have a grant; our host at the Carnegie leaves Pennsylvania to collect in Ecuador and Taiwan; people in Kentucky and northward all go to Florida every spring, while those in Florida are gone to Trinidad or Hispaniola (that is not 1000 miles unless you are from Gainesville, but that's OK because it's an island); people in Washington spend summers in Colorado and Utah, except for Don Davis who collects everywhere else in the world; everybody collects in southern Arizona except Arizonans, who go to Mexico.

Doug Ferguson is the exception; they say he collects in his yard in Maryland. Incidentally, Ferguson, our immediate past president, wrote me and said he would not be able to attend the Executive Council meeting here—he is collecting in British Columbia.

Simply the enjoyment of getting out to natural areas, away from phones, freeways, smog, commuting, demands of the job and responsibilities at home has to be a big factor, for amateurs and professionals alike. After all, collecting is a lot more fun than committee meetings, preparing lectures or budget reports, etc.

Acclaim from peers. For some, there is pride in exhibiting accomplishments; presumably these often are the same people who get the most satisfaction out of the collection itself. Competitiveness is a factor, certainly more so for some people than others.

Most lepidopterists would not believe that fame is much of a factor in why we collect (notoriety is a better descriptor), yet I wonder how many of us would maintain enthusiasm if we thought *absolutely* nobody else cared (as opposed to hardly anybody else)? Even though we go collecting mainly for the enjoyment, challenge, and satisfaction in obtaining the specimens, can you really say that often you don't think "wait till so and so hears about *this*!"?

I know one of the things I really enjoy is discovering things for other researchers, and I think this is a prevalent feeling among many collectors, amateur or professional (of course it is particularly enjoyable if it is a species I think they have overlooked in areas they have or could have worked).

The lure of patronyms should be mentioned. Some collectors are unabashed in their admitted desire for this form of immortality; others do not admit it, yet they look coyly away, suppressing a smile of delight, if you mention it. Possibly some hardened professionals don't care at all, but you would be tempted to question their honesty. The indignant condemnation of the increasing use of patronyms voiced by Dimock (1984, J. Res. Lepid. 23:94–101) was misguided and pathetic—misguided because he did not list the two most useful roles patronyms fulfill, to acknowledge collectors' efforts and to avoid secondary homonymy, and pathetic because it will be ignored.

Satisfactory in discovery. Beyond the fun of collecting and the pleasure in curating the collection, for biologists there is the added feeling of accomplishment in discovering new information, finding out things that nobody has known before. I see this as a bonus to the lure of collecting, one that you would not derive from collecting stamps or baseball cards.

For sheer joy of accomplishment, I don't think the discovery of facts "new to science" is surpassed by any other aspect of collecting. Who among us is not pleased by finding a new population or state record of even a well-known species?

For specialists in microlepidoptera, finding a new species in a museum collection is not very exciting; it means more dissections and descriptive work—Ron Hodges has how many new *Chionodes,* 150? But finding a new species that you recognize in the field—ah! that is another matter. Then you feel you are the discoverer, not just a processor filling in another space in the stamp album.

For me, there are two kinds of discoveries from which I derive the most satisfaction. First, there is the finding of a "lost" species, one collected and described long ago and perhaps known only from one or a few specimens. For example, the rediscovery in Chihuahua of *Apodemia phyciodoides* a few years ago must have been a great thrill to Richard Holland (although no doubt he showed no outward display of excitement). Second, even more enjoyable to me, is the discovery of the key to an insect's biology, particularly a species that has been known for a long time to lots of collectors.

It is this last, of course, that I wish to emphasize today—a satisfaction that is available to everybody without obeying Powell's Law, if you spend some time watching the animals instead of taking the pinch-first-and-ask-questions-later approach. I can share a couple of experiences of these kinds of discoveries:

1) Rediscovery of *Ethmia minuta.* I began a study of *Ethmia* while still a student. One day on a visit to the San Diego Natural History Museum, I found specimens of this elegant little species—at the time the smallest known member of the genus and the only one with marked sexual dimorphism in wing color—the kind of thing that, as a specialist, you say immediately: "that's new." But these had been collected by W. S. Wright in 1916 and labelled "San Diego." During the interim, San Diego had grown from a village of several thousand people to a city with a population of ¾ million and huge urban sprawl, so there seemed little hope of recovering the species. I will never forget the thrill then, when a couple of years later in the foothills back of the city I found adults of this "lost" (for 45 years) species at flowers of *Cryptantha,* which proved to be the key to its interesting biology, with the female ovipositor greatly modified to penetrate the densely hirsute floral buds.

2) The surprising biology of *Ethmia scylla.* I collected the first specimen of this nondescript species at Mt. Diablo near my home in 1959. John Burns and I went out the following spring and collected a nice series, which was gratifying; but 10 years were to pass before I discovered its biology. This involved repeated trips early each spring, misguided in the belief that some borage or hydrophyll must be the host plant because most ethmiids depend upon those plants. Finally I caged females with unlikely (to me) plants from the habitat, and in one day the females chose what they wanted for oviposition. The larvae feed

in the flowers of *Collinsia*; *Ethmia scylla* is the only species in this worldwide genus known to use Scrophulariaceae. It was a satisfying find but also taught me a lesson about making assumptions.

WHAT KINDS OF BIOLOGICAL STUDIES ARE NEEDED?

In the remaining time, I will briefly summarize some examples of biological studies of the kinds any of you can carry out with minimal equipment in your local area.

Larval Foods and Habits

The most obvious biological characters to most lepidopterists are the food plants. You might think that this aspect is pretty well documented, but even for North American butterflies much remains to be discovered. One of the most famous for his untiring efforts in this field is Roy Kendall in Texas. In response to my inquiry he estimates that he has reared more than 750 species of Lepidoptera, including about 330 species of butterflies. About 40% of these are thought to have been previously unknown. He has more than 2000 vials of preserved larvae. I would like to quote from a letter:

"I can't recall anytime during the past 30+ years when there was no livestock in my lab, and there is no end in sight [at age 76]. Although many lepidopterists consider certain species 'trash,' I find them very interesting and often rear these as well as 'goodies' numerous times from different localities." He also says, "Incidentally, I am an amateur in every sense of the word. The only formal training received was a 3-hour high school course in zoology." Yet Kendall probably has contributed more to our knowledge of larval biology of North American Lepidoptera than any other single person. Publications by Kendall or others with whom he readily shares unpublished data have recorded host plants or other information on about 500 species.

While it often is a lot of work, compared to merely collecting and killing adult Lepidoptera, I cannot overemphasize the need for this kind of work: the repeated study of biologies of different populations of the same species, in order to confirm existing records and to discover and document geographical and seasonal variation in biological characteristics. Just because a butterfly book states that a certain plant is the host of a species does not mean that its biology is known. You should question all such statements; errors are perpetuated by repeating from such books, and, even if correct, the statement may be based on a single record or apply only to a portion of the insect's range. Moreover, when one of the beautiful adults emerges, it is a lot more satisfying than going to some locality listed in the Season Summary to recollect adults.

Important kinds of rearing studies that need to be carried out include emphasizing diverse larval niches, not just external foliage feeding caterpillars. Many species feed in leaf litter or as borers within roots or stems, in seeds, galls, or leaf mines. Backyard studies, such as that reported here yesterday by Bill Miller on sibling species of gall moths, await the attention of lepidopterists in every part of North America. Few places have been well surveyed for leaf mining species, yet the various genera have highly characteristic forms of mines by which you can learn to identify them, and they often live for long periods in this stage, so that the precise timing of search needed for the adults is not so critical. Wagonloads of food plant and a pitchfork are not needed as when you rear saturniids; just hold the leaf in a vial for a few days and often a beautiful (and frequently undescribed) moth comes out.

Such studies are best carried out on a local basis, where you can repeatedly visit a habitat. Any place in the Western Hemisphere will have literally hundreds of species that have never been reared before, or have only been studied in another region. John De Benedictis has carried out a several-year survey at San Bruno Mountain near San Francisco and to date has reared about 150 species of microlepidoptera; still, each visit recovers larvae that he, and often anyone else, has never seen before. Patience and painstaking search of the different ecological horizons (roots, stems, flowers, fruit, mines, etc.) of all available potential host plants are the requisites.

Before leaving this topic, I'll make a pitch for preserving larvae. It is easy to obtain good specimens by simply immersing in boiling water for a few seconds or minutes and then preserving in drugstore rubbing alcohol. Far more species have been reared than the number for which we have material useful for larval studies, even in butterflies. Much of the emphasis in the past has been to obtain perfect specimens of the adults. Photographs of the larvae are not adequate for identification of most moths, and our knowledge of larval taxonomy lags far behind that of the adults for nearly all families.

Adult Behavior, Longevity

Mark-release-recapture studies of individuals, while time-consuming, are fun to do. They yield information on dispersal, differential movements of males and females, lifespan, feeding habits and so on, and they have been carried out for rather few North American Lepidoptera. These studies do not have to be very sophisticated to produce new information. All you really need is a felt-tipped pen with permanent ink, a notebook, and a net. For example, Smith (1982, J. Lepid. Soc. 35:172) marked and released common butterflies in his backyard in Sacramento and learned from recaptures that individuals of *Pieris rapae* and *Papilio rutulus* live up to 39 days, *Battus philenor* up to 44 days.

We lack this kind of information for almost all Nearctic butterflies and moths.

My backyard was the exotic locality where I studied mating behavior of *Incisalia iroides* (1968, J. N.Y. Entomol. Soc. 76:47). The whole study, which I think still records the most data on mating of any North American thecline, took place at a small lemon tree that the males liked to use as a perch. Mating occurred in late afternoon and extended into evening, so I could easily handle the mated pairs, mark individuals, and return them undisturbed to their perch. I suspect that mating habits of theclines generally have been overlooked because the butterfly people tend to keep bankers' hours.

Waldbauer and Sternberg (1982, J. Lepid. Soc. 36:154–155) released marked *Hyalophora* in Illinois and recorded recaptures of 18 males 6.8 miles away, using virgin females as bait; and, in a similar study, Toliver and Jeffords (1981, J. Lepid. Soc. 35:76) recorded *Callosamia* movements 14 and 36.5 miles from their release points. But for the vast majority of Lepidoptera we have no data on dispersal capabilities.

Mark-release-recapture studies of skippers have been few and not wholly successful. Handling most species evidently disturbs the individuals more so than is true of other butterflies. After releasing about 50 marked *Paratrytone* and never seeing one return, I developed a method of marking them without capture. Using a brush made from a feather, I found that males could be marked as they perched, with a mixture of ink and paint. Residency and competition for perches could then be monitored.

Studies of adult feeding also are needed. Paul Opler recorded floral visitations of butterflies in Virginia and found their choices to be a correlation of tongue length and corolla depth (Opler, P. A. & G. O. Krizek, 1984, Butterflies east of the Great Plains, Johns Hopkins Univ. Press, Baltimore, Maryland, 294 pp.), rather than just by color, or by plant taxon, as butterfly enthusiasts often assume.

One of the most remarkable studies on feeding is that of Bill Miller, who carried all his equipment to the stage when he reported the study to us at Berkeley last year: a dixie cup, a water vial, and a wick. He demonstrated increased fecundity in the spruce budworm when females imbibe nutrients (1987, Environ. Entomol. 16:1291–1295). This may not seem profound to you, but a recent bibliography recorded more than 4000 references to this insect, easily the most intensively studied species of Nearctic Lepidoptera, yet nobody had done this kind of study previously.

"Mud puddling" has received some attention, but there are many unanswered questions. Only one extensive study, that of Adler, has been carried out (1982, J. Lepid. Soc. 36:161–173). He recorded 93 species of moths at mud in New York; 99% were males. However, 80% of one geomtrid visited flowers instead. Why don't females do this, and why is it so rare in California? Why do some species have this habit while others do not?

Predation is another phase of biology that everybody seems to take for granted but nobody does much about documenting. The observations by Paul and Anne Ehrlich on lizard predation of tropical butterflies a few years ago is an example of how data can be recorded with a little patience (1982, J. Lepid. Soc. 36:148–152).

Seasonal Abundance

This is another field wide open for investigation. The classic study is Ehrlich's team research on *Euphydryas editha* over a 25-year period (1975, Science 188:221–228, *et seq.*). But such sophistication and funding are not necessary. The counts by Sidney Hessel of *Catocala* attracted to mercury vapor lamps at one site in Connecticut during a 12-year span, summarized in Sargent's book (1975, Legion of night, Univ. Massachusetts Press, Amherst, 222 pp.), are almost without parallel. Indications of increase or decline seen during a five- or six-year period were misleading when longer term fluctuations were observed. Smith (1984, J. Lepid. Soc. 37:275–280) also did this by counting butterflies for two-hour periods in his backyard for 12 years. There were large year-to-year fluctuations but no general trends, such as are often alleged.

This is a reason that the annual counts of butterflies sponsored by the Xerces Society are useful. We had 87 counts reported in 1987 [99 in 1988]; if we can obtain 150 or 200 that are reported on a continuing basis, general trends in abundance, as well as migrations and other comparative data, will be enhanced. A 15-mile diameter circle is selected and all the butterflies seen in one day counted. The object is to compare abundances from year to year at about the same date at each site. Obviously a place like Berkeley is not going to have the species richness of a site in southern Arizona or the Rocky Mountains, but after 14 years we have a good basis for predicting and explaining increases and decreases in abundance from one year to another in our circle.

Diapause

For most species we have little information on diapause development. The study by Sims of *Papilio zelicaon* (1983, J. Lepid. Soc. 37:29–37) is a good example of what can be done. He showed that populations on native umbells were univoltine, and modification of the diapause pattern enabled adventive populations to colonize urban areas on sweet fennel throughout the season. Incidentally, outdated terms such as "breaking" and "triggering" should be dropped from your vocabulary;

the process is a dynamic one that takes place over many weeks or months. Treatments such as constant temperature chilling that results in development in one instance may not do so for all populations of a species or even all individuals of a population.

A special interest of mine has been prolonged diapause, the maintenance of dormancy for more than one year. I published a summary of knowledge for Lepidoptera last year (1987, J. Res. Lepid. 25:83–109). In yucca moths under optimum winter environments, all or nearly all larvae complete development, while in adverse conditions, all or nearly all maintain diapause. Adults emerge over several years, even though neighbors in the same plant have completed development in a prior season. I have emergences now up to 19 years [20 years in 1989] after collection of the fully fed, prepupal larvae, so they are prepared to wait out the adversity and the lepidopterists' patience. One advantage of such studies is that they are not very labor intensive.

In conclusion, the take-home message is that I think the anticipation and realization of discovering something new is a major factor in the attraction of collecting Lepidoptera. This part of the enjoyment and satisfaction can be fulfilled in your local area if part of your effort is devoted to study of biological or behavioral aspects of butterfly and moth populations, rather than continuing an emphasis on subspecies and county records.

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REPRODUCTIVE ENHANCEMENT BY ADULT FEEDING: EFFECTS OF HONEYDEW IN IMBIBED WATER ON SPRUCE BUDWORM

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ABSTRACT. Captive budworm adults obtained as wild pupae were divided into two groups, and each group was offered liquids to imbibe once daily. One group received plain water, the other water containing honeydew of hemispherical scale, *Saissetia coffeae* (Walker), at concentrations averaging 6.5%. Two such experiments were conducted, a preliminary one with 28 fertile pairs, and the main one with 34 fertile pairs. In both experiments, honeydew prolonged female lifespan, egg maturation, and oviposition, the latter two causing redistributions within apparently fixed oocyte complements. Honeydew effects interacted with female body size, large females laying relatively more eggs than small females. In the main experiment, imbibing did not begin until the third day of adulthood. Thereafter, fertile females imbibed more often than infertile ones, the frequency among the former peaking at 97% of their number during the seventh and eighth days of adulthood. Amount imbibed per individual per day averaged 4.5 mg as determined by weighing females before and after imbibing. In fertile females of average lifespan, expected lifetime honeydew-water intake was 31.6 mg of liquid containing 2.05 mg dry weight of honeydew, the latter corresponding to 3.5% of female average initial live weight. Enhanced reproductive effects did not appear until late in adulthood.

Additional key words: *Choristoneura fumiferana*, Tortricidae, Tortricinae, fecundity, *Saissetia coffeae*.

That tortricine adults are capable of imbibing has long been known (Powell 1965:26), but only recently was reproduction in a tortricine rigorously shown to be enhanced by imbibing. Thus, the spruce budworm, *Choristoneura fumiferana* (Clemens) (Tortricidae), matured more oocytes and laid more eggs when females received water containing 15% bee honey than when they received plain water (Miller 1987). Imbibing habits of the adults are still obscure, however.

Honeydews might be available to spruce budworm adults in nature. Precipitated water is often present, and such water is doubtless sweetened at times by honeydews of co-occurring insects such as the balsam twig aphid, *Mindarus abietinus* Koch (Aphididae). While bee honey consists mostly of fructose and glucose (White 1975), honeydews may contain these sugars as well as sucrose, other sugars, and nitrogenous compounds (Auclair 1963).

Here, for captive budworm females given plain water or water containing honeydew, I report several aspects of reproduction as well as imbibing frequencies and amounts imbibed. Reproductive attributes measured were lifespan, oviposition period, number of eggs laid daily, egg viability, number of mature and immature oocytes in ovaries after death, and attributes derived from these. The honeydew source was hemispherical scale, *Saissetia coffeae* (Walker) (Coccidae).

MATERIALS AND METHODS

Two experiments were conducted, a preliminary one followed by the main one. In both experiments, one group of moths received honeydew solution for imbibing, and a second group received plain water. The main experiment differed from the preliminary one chiefly in that pupae and emergent adults were not cold-stored before use, female imbibing was recorded, the different imbibing liquids were dispensed in exactly the same way, and reproductive attributes were measured in greater detail.

For both experiments, wild pupae reachable from the ground were collected from 25 or more large trees of balsam fir, *Abies balsamea* (L.) Mill. (Pinaceae), growing in one area of 0.1 ha or less. Pupal collections were timed to coincide with incipient adult emergence. In the preliminary experiment, pupae came from 12 km E of Meadowlands, St. Louis Co., Minnesota, and in the main experiment, from 8 km W of Grand Marais, Cook Co., Minnesota. In the preliminary experiment, pupae and emergent moths were stored within 36 h of collection at 8°C and held for two weeks during a start-up delay. In the main experiment, pupae and emergent moths were in use within 36 h of collection.

The first step in both experiments was to sex pupae (Jennings & Houseweart 1978) and emergent adults. Some females were freeze-killed within 2 h of eclosion for ovarial study. Male-female pairs for imbibing experiments were placed in 1-pint (0.48 l) cardboard ice cream containers capped with Petri dish lids, one pair per container. A shoot of balsam fir ca. 8 cm long was placed in each container as a substrate for oviposition; in the preliminary experiment, the shoot also served as an imbibing substrate for plain water. Containers were numbered and assigned by equal and odd numbers to the two imbibing treatments.

Moth containers in both experiments were held in a temperature-controlled room maintained at 23°C during the preliminary experiment, and at 25°C during the main experiment. In the former, moths received natural July light through a large N-facing window; in the latter, they received fluorescent light on a 12L:12D schedule. Containers were examined daily near mid-day, at which time imbibing liquids were introduced and reproductive data were gathered.

The honeydew-providing colony of hemispherical scale infested a 2-m tall indoor-growing spineless yucca, *Yucca elephantipes* Regel (Liliaceae). Upper surfaces of the plant's leaves were nearly completely coated with honeydew. In both experiments, segments ca. 6 cm^2 were cut from the honeydew-laden leaves, misted with water just short of runoff to form honeydew-water solution, and placed in moth containers for imbibing. Segments were misted every day and replaced every second or third day. Plain water for imbibing was provided in the preliminary experiment by misting the balsam fir shoot, and in the main experiment by misting yucca leaf segments also ca. 6 cm^2 from which honeydew had been washed. All misting was done outside containers with a hand-powered household sprayer containing distilled water.

Misted yucca leaf segments remained wet in moth containers for 1.2–1.5 h before drying naturally. Whether or not females imbibed was determined by monitoring main-experiment individuals during this interval on arbitrarily chosen days. Imbibing moths were spotted by their characteristic preimbibing head movements, and by proboscises extending to the wet yucca leaf segments.

Liquid intake was measured as the difference between pre- and postimbibing weights of individual females preweighed just before they were routinely offered liquids. Sample females were selected arbitrarily for this purpose, and weights were recorded to the nearest 0.1 mg. Imbibing occurred rapidly enough so that pre- and postimbibing weighings were seldom separated by more than 25 min. To verify that weight differences truly represented intake, two females that walked and rested on misted yucca leaf segments for 5 min without imbibing were weighed in the same manner as imbibing females. These nonimbibers underwent no weight gain, thus indicating that imbibing liquids were not absorbed by body parts coming in contact with wet surfaces.

Eggs were spotted by examining shoots and container walls under a 2× reading magnifier. Shoots were removed from containers for this examination. Deposited eggs were counted under stereomicroscope magnifications up to 25×. In the preliminary experiment, female fertility and egg viability were determined by observing 21–112 deposited eggs per female for a week or until larval heads showed through chorions. In the main experiment, fertility and viability were determined by observing all deposited eggs until hatching or imminent hatching.

Oocytes in excised ovaries were identified as mature or immature by size and stainability after 2–4 min exposure to ca. 0.2% aqueous methylene blue. Chorionated (mature) eggs take up such stains less readily than nonchorionated (immature) ones (Jennings 1974). Immature oocytes were counted at stereomicroscope magnifications up to 45×. Length of one forewing measured to the nearest 0.5 or 0.2 mm in the preliminary and main experiments, respectively, was used as a female body size index (Thomas et al. 1980, Results section of present paper).

For chemical analyses of hemispherical scale honeydew, several honeydew-laden yucca leaves were sprayed with distilled water, and 75

TABLE 1. Performance of spruce budworm females imbibing plain water and honeydew-water in the preliminary experiment. SD preceded by ±, range in parentheses.

Attribute	Mean		Departure from plain-water group (%)
	Plain water [19 pairs]	Honeydew-water [9 pairs]	
Oviposition span, days[1]	8.8 ± 1.8 (6–12)	10.3 ± 4.1 (5—17)	17[a]
No. eggs and oocytes			
Total	326 ± 46 (243–395)	339 ± 75 (204–446)	4
Matured	200 ± 46 (134–291)	245 ± 71 (109–350)	22[b]
Laid	197 ± 46 (130–289)	235 ± 76 (98–348)	19
Change in no. laid (L) as function of forewing length (W)	28.2	102.8	264[c]
Unlaid immature	127 ± 28 (88–176)	94 ± 58 (0–184)	−26[a]
Egg viability, %	75 ± 20 (28–97)	81 ± 15 (50–94)	8

[1] Defined as time from first oviposition to death, usually one day longer than oviposition period.

[a] $P < 0.01$, 1-tailed Wilcoxon 2-sample test.

[b] $P < 0.05$, 1-tailed Student *t*-test.

[c] $P < 0.01$, *F*-test. Values are slope coefficients from the regressions $L = 28.2W - 126$ ($r = 0.40$) and $L = 102.8W - 930$ ($r = 0.75$).

ml of runoff were collected. One aliquot was analyzed for sugars by high-pressure liquid chromatography, one for total nitrogen by a high-sensitivity Kjeldahl method, and one was oven-dried at 70°C to nominally constant weight for dry-weight conversions.

Honeydew concentration of imbibed honeydew-water was determined from weighings as follows. Honeydew-laden 25–50 cm^2 yucca leaf segments were weighed (weight x), misted as for imbibing, reweighed (weight y), thoroughly washed, towel-dried, and again reweighed (weight z). These weightings were completed within 15 min, and were to the nearest 0.1 mg. Honeydew concentration (c) was computed as $c = (x - z)/[(y - x) + (x - z)]$.

In both experiments, attribute variances often differed significantly between imbibing treatments (variance-ratio test). Treatment differences in such cases were analyzed nonparametrically by the Wilcoxon two-sample test. Otherwise, treatment differences were analyzed parametrically by *F*- and Student *t*-tests. Because honeydew-water was expected to have positive effects, most testing was one-tailed.

"Infertile" here refers to females not producing viable eggs whether mated or not. Standard deviation is abbreviated SD.

RESULTS

Preliminary experiment. Of 28 pupal and adult containers set up for the honeydew-water imbibing treatment, and 29 set up for the plain-water imbibing treatment, 9 and 19, respectively, produced viable eggs and complete reproductive attribute records. Shortfalls were caused

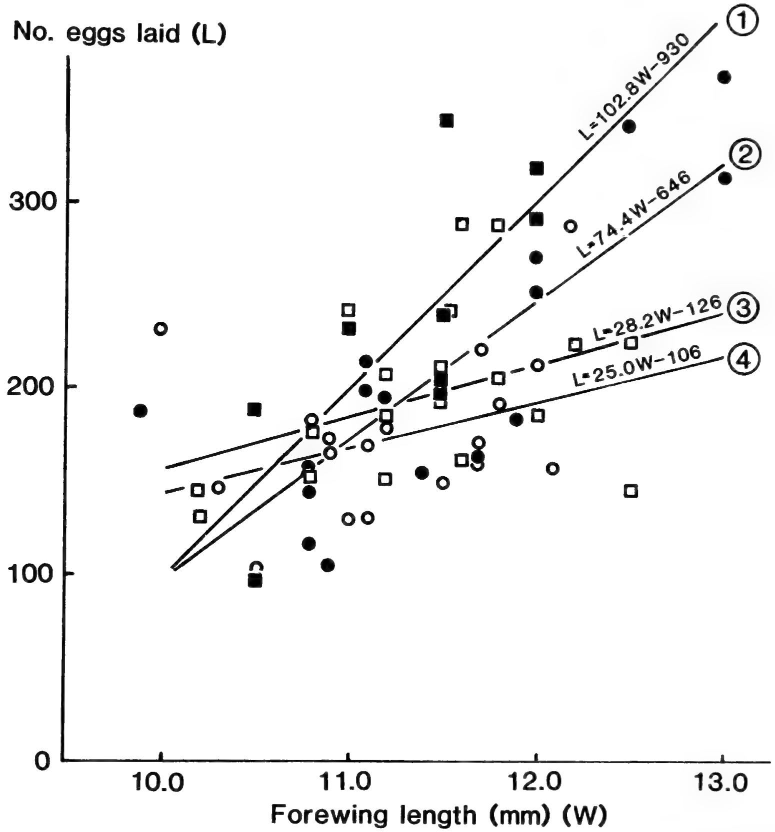

FIG. 1. Role of spruce budworm female body size in determining number of eggs laid in response to honeydew- and plain-water imbibing treatments. Each symbol represents one female. Line ① (closed squares) and line ② (closed circles) depict honeydew-water imbibers in the preliminary and main experiments, respectively; line ③ (open squares) and line ④ (open circles), plain-water imbibers.

by sexing errors, asynchronous eclosions, moth escapes, and unexplained infertility.

Females given honeydew-water outperformed those given plain water in four of seven reproductive attributes tabulated (Table 1). On average, honeydew-water imbibers had a 1.5-day (17%) longer oviposition span, matured 45 (22%) more oocytes, and contained 33 (26%) fewer immature oocytes at death. Some tests were not robust enough to detect biologically relevant attribute differences. The prime example concerns number of eggs laid (Table 1, Fig. 1). In this and all attributes except total oocyte number and egg viability, the effect of honeydew interacted with body size. Thus an 11.0-mm female on honeydew-water laid 201 eggs (11.0 × 102.8 − 930 = 200.8) while one on plain water laid 184 (11.0 × 28.2 − 126 = 184.2) (9% difference); but a 12.5-mm female on honeydew-water laid 355 eggs (12.5 × 102.8 − 930 = 355.0) while one on plain water laid 226 (12.5 × 28.2 − 126 = 226.5) (57% difference). Forewing length of females in the honeydew- and plain-water treatments averaged 11.3 mm (SD = 0.6, range 10.5–12.0) and 11.2 mm (SD = 0.7, range 10.2–12.5), respectively. For attributes with variances shown in Table 1 (in SD, or square-root form), variances for the honeydew-water treatment are usually greater numerically, two of them greater statistically ($P < 0.05$, variance-ratio test), than for the plain-water treatment.

In 2-h-old freeze-killed females, egg maturity averaged 7% ($n = 8$). On average, these females contained 266 oocytes (SD = 40, range 228–333), 60–73 fewer than the 326 and 339 totals shown in Table 1 for imbibing females. The differences arose not because of inherently different oocyte numbers, but because freeze-killed females were smaller. Their forewing lengths, averaging 10.5 mm (SD = 0.7, range 9.5–11.6 mm), were 0.7–0.8 mm less than for imbibing females. Regressions of oocyte counts on forewing lengths among freeze-killed and imbibing females did not differ significantly ($P > 0.75$, F-test of slope-coefficient differences).

Dry-weight constituents of hemispherical scale honeydew (including other water-soluble substances that also may have been on yucca leaf surfaces) were fructose, 23.7%; glucose, 19.8%; sucrose, 12.8%; total nitrogen, 0.6%; nonsugar and non-nitrogenous matter, 43.1%. These amounts are similar to those previously reported for scale and aphid honeydews (Auclair 1963).

Main experiment. Of 26 pupal and adult containers set up for the honeydew-water imbibing treatment, and an equal number for the plain-water imbibing treatment, 16 and 18, respectively, produced viable eggs and complete reproductive attribute records. Shortfalls were caused by the same factors as in the preliminary experiment.

Pairs given honeydew-water outperformed those given plain water in 4 of 11 reproductive attributes tabulated (Table 2). On average, honeydew-water imbibers had a 0.7-day (6%) longer female lifespan, a 1.8-day (23%) longer oviposition period, and contained 41 (68%) fewer immature oocytes at death. As in the preliminary experiment, some tests were not robust enough to detect attribute differences, and number of eggs laid is again the prime example (Table 2, Fig. 1). In this and all attributes except total oocyte numbers and egg viability, the effect of honeydew interacted with body size. Thus an 11.0-mm female on honeydew-water laid 172 eggs (11.0 × 74.4 − 646 = 172.4) while one on plain water laid 169 (11.0 × 25.0 − 106 = 169.0) (2% difference);

TABLE 2. Performance of spruce budworm pairs imbibing plain water and honeydew-water in the main experiment. SD preceded by ±, range in parentheses.

Attribute	Mean or other value		Departure from plain-water group (%)
	Plain water [18 pairs]	Honeydew-water [16 pairs]	
Preoviposition period, days	2.2 ± 0.7 (1–3)	2.3 ± 0.8 (1–4)	
Lifespan, days			
Female	10.7 ± 2.0 (7–14)	11.4 ± 3.4 (6–17)	6[a]
Male	9.4 ± 2.8 (5–14)	8.7 ± 3.8 (4–17)	−7
Oviposition period, days	7.7 ± 2.2 (4–11)	9.5 ± 3.6 (4–15)	23[b]
No. eggs and oocytes			
Total	238 ± 60 (104–332)	233 ± 80 (126–404)	−2
Matured	177 ± 43 (104–288)	214 ± 78 (111–372)	21
Laid	175 ± 43 (102–288)	210 ± 79 (104–370)	20
Change in no. laid (L) as function of forewing length (W)	25.0	74.4	198[c]
Viable	156 ± 36 (98–245)	181 ± 78 (59–325)	16
Unlaid immature	60 ± 41 (0–134)	19 ± 29 (0–104)	−68[d]

[a] $P < 0.01$, 1-tailed Wilcoxon 2-sample test.
[b] $P < 0.05$, 1-tailed Student *t*-test.
[c] $P < 0.01$, *F*-test. Values are slope coefficients from the regressions $L = 25.0W - 106$ ($r = 0.36$) and $L = 74.4W - 646$ ($r = 0.81$).
[d] $P < 0.01$, 1-tailed Student *t*-test.

but a 12.5-mm female on honeydew-water laid 284 eggs ($12.5 \times 74.4 - 646 = 284.0$) while one on plain water laid 206 ($12.5 \times 25.0 - 106 = 206.5$) (38% difference). For 9 of the 10 attributes with variances shown in Table 2 (in SD, or square-root form), variances for the honeydew-water treatment are greater numerically, four greater statistically ($P < 0.05$, variance-ratio test), than those for the plain-water treatment.

In 2-h-old freeze-killed females, egg maturity averaged 10% ($n = 13$). On average, these females contained 259 oocytes (SD = 83, range 132–424), a number not inherently different from the 238 and 233 totals shown in Table 2 for imbibing females ($P > 0.75$, *F*-test of differences in slope coefficients of oocyte number–forewing length regressions). Forewing length of freeze-killed females averaged 10.7 mm (SD = 1.2, range 10.1–12.7).

Daily oviposition records in both imbibing treatments were similar until the latter half of the oviposition period (Fig. 2). Beyond day 8 of adulthood, live female-days/female averaged 3.5 in the honeydew-water group and 1.7 in the plain-water group, and respective numbers of eggs laid/female were 35 and 10.

Individual females were monitored for imbibing more than 150 times

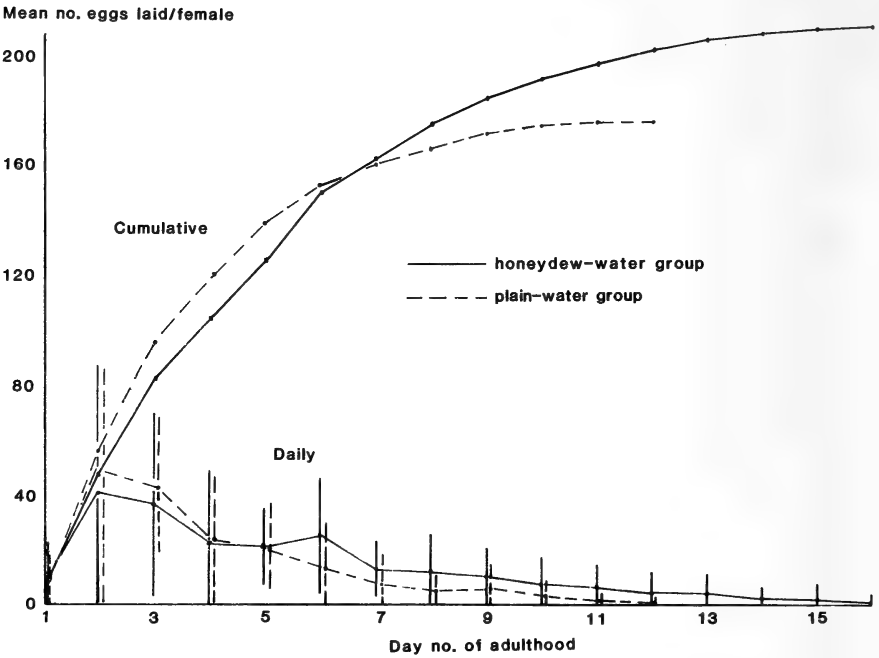

FIG. 2. Oviposition records for fertile spruce budworm females in the main experiment. Sixteen females in the honeydew-water group, 18 in the plain-water group. Vertical bars represent SD.

during the daily period of liquid availability. Imbibing started within 20 min after liquids were offered, usually much sooner, and individual imbibing episodes lasted as long as 5 min. No monitored female imbibed more than once daily, and none was seen excreting liquids anally. After drying, honeydew presumably was not consumed until the next misting.

Females did not imbibe on the first or second days of adulthood (n = 11 and 12, respectively). During days 3–12 of adulthood, fertile females imbibed more often than infertile ones, the former using 78% of their opportunities (62/79), the latter 50% (23/46). The difference is significant ($P < 0.01$, 2×2 contingency table, *G*-test).

Among fertile females, imbibing frequency was unrelated to presence or absence of honeydew. During days 3–12 of adulthood, sample females in the plain-water treatment imbibed essentially as often as those in the honeydew-water treatment, the former using 77% of their opportunities (33/43), the latter 80% (29/36). Imbibing frequency was affected by female age, however. Thus imbibing frequency rose from 60% on days 3–4 of adulthood to 97% on days 7–8, then fell to 54% on days 11–12 (Table 3). Pooling by two-day intervals in Table 3 increased the base and reliability of percentages.

TABLE 3. Imbibing frequencies by age of fertile spruce budworm females offered honeydew-water or plain water in the main experiment.

Day no. of adulthood	No. females observed	Percent of females imbibing[1]
3–4	5	60
5–6	15	80
7–8	30	97
9–10	16	69
11–12	13	54

[1] Underlying frequencies significantly dependent on female age ($P < 0.01$, 2 × 5 contingency table, G-test with Williams correction).

For 10 fertile females monitored for imbibing on two successive days, 30% imbibed both days (3/10), and 70% imbibed one day only (7/10). These females were in the 5th to 11th day of adulthood at the first observation, averaging day 8.

Regressing weights of fertile females determined just before daily imbibing episodes (M, range 13.8–86.0 mg) on forewing length (F, range 9.8–13.0 mm) and day number of adulthood (D, range 1–12) produced the equation $M = 11.7F - 4.6D - 70.8$ ($R = 0.91$, $n = 37$). Based on this equation, live weights of honeydew-water imbibing females of average forewing length on days 1, 4, 7, and 10 of adulthood were, respectively, 59.2, 45.4, 31.6, and 17.8 mg. Such weight decline during adulthood reflects egg laying and depletion of stored reserves. Forewing length of females in the honeydew- and plain-water treatments averaged, respectively, 11.5 mm (SD = 0.9, range 9.3–13.0) and 11.25 mm (SD = 0.6, range 10.0–12.2).

Intake per imbibing episode did not differ significantly between plain- and honeydew-water or fertile and infertile classifications in any partition of data in Table 4 ($P > 0.13$, one-tailed Student *t*-tests); it likewise varied independently of female size and age (*r*-range 0.03–0.57, none approaching $P = 0.05$). Intake per episode averaged 4.5 mg

TABLE 4. Intake per investigated imbibing episode by individual spruce budworm females offered liquids daily in the main experiment. SD preceded by ±, range in parentheses.

Fertility status	No. observed	Mean age (days)	Mean forewing length (mm)	Amount imbibed (mg)
		Plain-water imbibers		
Fertile	9	8.1 ± 2.4 (5–12)	11.1 ± 0.3 (10.5–11.7)	3.9 ± 2.3 (0.9–8.1)
Infertile	5	4.6 ± 1.8 (3–7)	10.7 ± 0.6 (9.8–11.2)	4.3 ± 1.5 (2.7–6.5)
		Honeydew-water imbibers		
Fertile	7	8.0 ± 1.0 (7–10)	11.7 ± 0.8 (10.8–13.0)	5.2 ± 2.5 (1.7–10.0)
Infertile	7	5.1 ± 1.3 (4–7)	10.8 ± 0.5 (9.8–11.2)	3.0 ± 1.8 (1.0–6.5)
		All imbibers		
Mixed	28	6.7 ± 2.3 (3–12)	11.1 ± 0.7 (9.8–13.0)	4.5 ± 2.4 (0.9–10.0)

of liquid (Table 4), or 8, 10, 14, or 25% of the live female weights computed above on days 1, 4, 7, and 10 of adulthood.

Honeydew concentration in honeydew-water on yucca leaf segments averaged 6.5% by weight (SD = 2.1, range 3.5–9.4, n = 5).

During and immediately after adult eclosions observed under a binocular microscope (4 females, 2 males), the paired galeae were separate for most of their length as reported for lepidopterans generally (Hepburn 1971). Within 15–30 min after pupal skin splitting, however, galeae had engaged along their full lengths to form proboscises. During much of the engagement process, which seemed assisted by the narrow corridor formed by palpi, galeae twitched and intertwined. In two cases, a droplet of clear fluid appeared near the base of galeae during the engagement period.

DISCUSSION

Honeydew in imbibed water clearly had positive reproductive effects. In both experiments, these effects were prolonged female lifespan, oocyte maturation, and oviposition, the latter two causing redistributions within apparently fixed total oocyte complements (Tables 1 & 2). Effects were strongest in the largest females (Fig. 1).

With only 7–10% of oocytes mature at female eclosion, a range consistent with observations by Outram (1971), much oocyte maturation necessarily takes place after eclosion. Thus an opportunity exists for adult imbibing to influence oocyte maturation. However, females were slow to begin imbibing under a regime that provided a once daily opportunity. There was no evidence that they imbibed on the first or second days of adulthood; even after four days, 40% of fertile females still had not imbibed (Table 3). This explains why preoviposition period was unaffected in this study, and perhaps also why positive reproductive effects appeared late in adulthood. Preoviposition period was affected in earlier work when the period lasted longer, and a stronger nutrient solution (15% bee honey) was available constantly (Miller 1987). Abstinence from imbibing in early adulthood did not appear to be morphological in origin; proboscises were formed and presumably functional within 0.5 h after eclosion.

In imbibing frequency and intake per imbibing episode, females showed no clear preference for honeydew-water over plain water. This result suggests that the moths merely respond to liquid.

Products (I) of age-specific imbibing frequencies (Table 3) and average intake per imbibing episode (4.5 mg, Table 4) plotted on female age (A) resulted in a nearly straight line. This line is closely described by the equation $I = 3.45A - 7.7$, and computed I-values differ by no more than 7% from actual ones. Based on this equation, lifetime expected honeydew-water intake for fertile females of average lifespan

(11.4 days, Table 2) is 31.6 mg. Since honeydew concentration in honeydew-water on yucca leaf segments averaged 6.5% by dry weight, corresponding honeydew intake is 2.05 mg (31.6 × 0.065 = 2.05). Attribute departures among honeydew-water imbibing females may therefore be ascribed to average consumption of ca. 2 mg of dry honeydew per individual, or ca. 3.5% of initial live weight of females of average forewing length in the main experiment (2.05/59.2 = 0.035).

The greater attribute variability (variances) noted among honeydew-water imbibers in both experiments probably results from the interaction between honeydew effect and female body size. However, in an experiment in which bee-honey concentration was a constant 15%, and honey-water was constantly available, no tendency to heterogeneous variability appeared (Miller 1987).

How much the positive reproductive effects of imbibed honeydew might influence the dynamics of natural populations would seem to hinge on how long females survive in nature, as well as on how readily available honeydew is to them.

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WORLD NUMBERS OF BUTTERFLIES

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ABSTRACT. World butterflies number about 17,280 species representing described taxa that have not been synonymized, and are currently grouped into 1855 genera, 35 subfamilies, and 7 families. Butterflies constitute only 9–12% of all lepidopteran species.

Additional key words: faunal realms, genera, subfamilies, families, conservation.

Published estimates of the total number of butterfly species in the world range from 7700 (Kirby 1872) to 20,000 (Fox & Fox 1964, Vane-Wright 1978, Landing 1984), although most authors do not cite specific sources used in forming their estimates. An exception is Robbins (1982), whose world total of 15,900–18,225 was compiled by faunal realms, although he largely estimated numbers for the Neotropics and Orient and did not adjust for the percentage of species that extend into two or more realms. Affinities between the west Palearctic and Ethiopian butterfly faunas are indeed minimal (De Jong 1976), but a modest amount of exchange (perhaps 5–10%) is to be expected across the Nearctic-Neotropical, east Palearctic-Oriental, and Oriental-Australian frontiers (cf. Schmidt 1954, Rapoport 1971). The total number of butterfly species, coupled with the land area they occupy, measures butterfly richness and density on a global scale, of interest to ecologists and conservationists. Here I present a current estimate of butterfly species numbers as part of the continuing effort to determine just how many species of living organisms there are on earth (cf. Jones 1951, May 1988, Wilson 1988).

METHODS

Species totals for most butterfly subfamilies (Table 1) were obtained from the recently published catalogs of Bridges (1988a, 1988b, 1988c, 1988d), which counts species that extend into two or more realms only once. Some of the Nymphalidae subfamilies, however, have not been recently cataloged. The number of Nymphalinae species was estimated by multiplying its number of genera (181) by 14 (the average number of species per genus in Danainae *s. str.*, its close relative) to yield ca. 2500 species. This figure compares well with the roughly 2700 species I estimate for Nymphalinae using faunal lists. Numbers of species for Satyrinae and Morphinae are also estimates (see footnotes 6 and 7, Table 1). For the Danainae and Brassolinae, species numbers are based on figures provided by researchers currently revising these groups (see footnotes 4 and 8, Table 1).

RESULTS AND DISCUSSION

The grand total of described butterfly species is about 17,280 (see Table 1). This total is higher than the 13,000 estimate of Owen (1971), the 14,750 estimate of Scott (1986), the 15,600 low estimate (when Hesperiidae are included) of Ehrlich and Raven (1964), and the 15,900 low estimate of Robbins (1982) and is lower than the world maximum estimates of 18,225 (Robbins 1982), 18,600 (Ehrlich & Raven 1964), and 20,000 (Fox & Fox 1964, Vane-Wright 1978, Landing 1984). The total is only 945–1320 species less than the maximum estimates of Ehrlich and Raven (1964) and Robbins (1982). Bridges (1988d) lists 1855 world genera, though, of course, generic limits are largely subjective. For example, Bridges' (1988d) figure of 1326 genera (excluding skippers) sharply contrasts with the estimates of 730–930 and 953 genera given by Ehrlich and Raven (1964) and Scott (1986), respectively. The number of described species of butterflies in the world constitutes 9–12% of all described Lepidoptera species, whose total numbers are estimated to be 150,000–200,000 (Kristensen 1984).

Subfamilies with the greatest numbers of species are (in descending order) Nymphalinae, Satyrinae, Theclinae, and Hesperiinae (greater than 2000), followed by Pyrginae, Polyommatinae, and Riodininae (greater than 1000). Baroniinae, Curetinae, Styginae, Pseudopontiinae, Libytheinae, and Calinaginae are morphologically archaic subfamilies each containing only one or two genera and fewer than two dozen species. Three families (Hesperiidae, Lycaenidae, and Nymphalidae) comprise 82% of all butterfly species and are the only families to use both dicots and monocots extensively as larval hostplants (cf. Ehrlich & Raven 1964). About 30% of all butterfly species feed only on monocots, especially the Trapezitinae, Hesperiinae, Megathyminae, Satyrinae, Morphinae (in part), and Brassolinae. The world species richness of butterflies, 17,280, when divided by 128,811,340 km^2, the total land area of the earth excluding Antarctica and inland waters, yields an average density of 0.000134 species per km^2. Roughly two-thirds of the species occur in the tropics.

The numbers of butterfly species presented here represent described taxa that have not been synonymized. Only in the best-known family, Papilionidae, is it possible to estimate closely the true number of species. Subfamilies like Theclinae, Polyommatinae, Riodininae, Nymphalinae, Calinaginae, and Satyrinae are so poorly known taxonomically that their counts probably inflate their actual species totals by including many unsynonymized names. Most other subfamilies fall somewhere between these two extremes. Cladistic analysis should aid in identifying monophyletic subfamilies in Nymphalidae but has not yet been per-

TABLE 1. Numbers of butterfly species by family and subfamily.

Family and subfamily	No. species	References
Hesperiidae	3592	
Pyrginae	1193	Bridges 1988a
Coeliadinae	80	Bridges 1988a
Pyrrhopyginae	155	Bridges 1988a
Trapezitinae	67	Bridges 1988a
Hesperiinae	2048	Bridges 1988a
Megathyminae	49	Bridges 1988a
Papilionidae	566	
Papilioninae	511	Bridges 1988b
Parnassiinae	54	Bridges 1988b
Baroniinae	1	Bridges 1988b
Lycaenidae[1]	4089	
Lipteninae	527	Bridges 1988c
Poritiinae	52	Bridges 1988c
Liphyrinae	20	Bridges 1988c
Miletinae	111	Bridges 1988c
Curetinae	22	Bridges 1988c
Theclinae	2128	Bridges 1988c
Lycaeninae	97	Bridges 1988c
Polyommatinae	1132	Bridges 1988c
Riodinidae	1366	
Hamearinae	97	Bridges 1988c, Robbins 1988a
Euselasiinae	154	Bridges 1988c, Robbins 1988a
Riodininae	1114	Bridges 1988c, Robbins 1988a
Styginae	1	Robbins 1988a, 1988b
Pieridae	1215	
Pseudopontiinae	1	Bridges 1988b
Dismorphiinae	95	Bridges 1988b
Pierinae	905	Bridges 1988b
Coliadinae	214	Bridges 1988b
Libytheidae	12	
Libytheinae	12	Shields 1985
Nymphalidae	6440	
Nymphalinae[2]	2500	Bridges 1988d, see text
Argynninae[3]	155	Warren 1944, 1955; dos Passos & Grey 1945; Grey *in litt.*; Common & Waterhouse 1972; Brown 1981
Acraeinae	240	Pierre 1987
Calinaginae	16	Oberthur 1919, 1922; Wu 1938
Danainae[4]	462	Ackery & Vane-Wright 1984; Drummond & Brown 1987
Apaturinae[5]	431	Stichel 1938, 1939; Le Moult 1950; Comstock 1961; van Someren 1975
Satyrinae[6]	2400	Gaede 1931; L. D. Miller, pers. comm.
Morphinae[7]	155	D'Abrera 1984; Parsons 1984
Brassolinae[8]	81	Stichel 1932
World total	17,280	present study

[1] Eliot (*in litt.*) estimates 44 species of Poritiinae and 15 species of Curetinae based upon his unpublished research, and he notes that the Neotropical Theclinae species listed by Bridges have many synonyms but also that hundreds of discovered but undescribed species of Theclinae exist.

[2] Includes the tribes Ageroniini (=Hamadryini), Biblidini (=Didonini, Ergolini, Eurytelini), Coeini (=Aganisthini,

formed; preliminary analysis indicates that some conventional nymphalid subfamilies are polyphyletic (DeVries et al. 1985).

The world number of species or "species richness" obscures much of the interesting ecological diversity of butterflies. Many polytypic species, e.g. in Heliconiini and Ithomiinae, have populations that differ markedly in behavior, food plant relationships, and color patterns.

It is instructive to compare butterflies with birds, taxonomically the best-known invertebrate and vertebrate groups. At the level of species, "The taxonomy of no other group of animals is as mature as that of birds" (Mayr 1982:292). Kirby (1872) estimated that the number of species of butterflies and birds was about the same. By the early twentieth century, Sharpe recognized 18,937 bird species (including fossil species and all subspecies as full species), a figure that dropped to 10,000–16,000 by the early 1930's (Mayr 1988). By 1935 careful zoogeographic and systematic research had reduced the estimated number of birds to 8500 (Mayr 1946). Today's best estimate of the number of bird species is ca. 7000 ± 200 (Mayr 1988), which is only 40% of the number of butterfly species reported in the present study. Since 1935 only about 140 valid new bird species have been described, with the reduction in the number of species names (by more than 60% over the past 80 years) primarily coming about by revisional downgrading of geographical isolates of polytypic species from the rank of species to subspecies (Mayr 1988). This same process is now occurring in butterflies, but so far it has progressed to a far lesser extent than it has in birds. Unlike birds, however, many new species of butterflies are still being discovered and described each year, particularly from the tropics.

←

Coloburini, Gynaeciini), Cyrestini (=Marpesiini), Epicaliini (=Callicorini, Catagrammini, Catonephelini, Dynamini, Epiphilini, Eunicini), Limenitidini (=Abrotini, Adelphini, Bebeariini, Chalingini, Euthaliini, Neptini, Neurosigmatini, Parthenini, Pseudacraeini), Nymphalini (=Araschniini, Cynthini, Diademini, Doleschallini, Euphydryini, Hypolimnini, Junoniini, Kallimini, Melitaeini, Phyciodini, Vanessini), Pseudergolini.

[3] Includes Heliconiinae, Cethosiini.

[4] Includes Ithomiinae (=Ithomiini, Tellervini). Drummond and Brown (1987) cite 305 species of Ithomiinae and include only one species of *Tellervo*, although Ackery (1987) claims there are 6. Other species estimates for Ithomiinae are extremely variable: ca. 300 (Drummond 1986), 318 (Mielke & Brown 1979), 349 (Fox 1953), ca. 400 (D'Abrera 1984), and 518 (Bryk 1937). Haensch (1909) in Seitz's *The Macrolepidoptera of the World* listed 883 named forms, most of which he treated as species. The best figure is 305 species, based largely on Brown's ongoing study of ithomiine phylogeny (*fide* Drummond). The Ithomiinae admirably show the gradual reduction in number of species as a group becomes better known (dropping by nearly two-thirds over the past 80 years), largely as a result of a growing recognition of the many widespread polytypic species in this group. There are 157 species of Danainae (*s. str.*) (Ackery & Vane-Wright 1984).

[5] Includes Charaxinae.

[6] Miller (1968) estimated between 2500–3000 Satyrinae species (including Brassolinae), but he now feels this is too high. His new estimate (pers. comm.) is about half again as many as in Gaede (1931). As Gaede listed 1605 species, the new estimate is ca. 2400 species.

[7] Includes Amathusiinae. Parsons (1984) estimates there are ca. 100 species of Amathusiinae. Morphinae now includes the Neotropical genera *Morpho*, *Antirrhea*, and *Caerois* (DeVries et al. 1985). D'Abrera (1984) lists 31 species of *Morpho*, 21 *Antirrhea*, and 3 *Caerois*. Smart (1977) estimates about 80 species of *Morpho*, probably too many (cf. D'Abrera 1984).

[8] Smart (1977) lists 75 species. Preliminarily there are 86 species according to Casagrande (*in litt.*) who is currently revising the subfamily.

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THE SPHINGIDAE (LEPIDOPTERA) OF BAJA CALIFORNIA, MEXICO

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ABSTRACT. Baja California is a rugged, mostly xeric peninsula situated along the northwestern coast of Mexico. With the exception of butterflies, the lepidopterous fauna of this region is poorly studied. Twenty-six species of Sphingidae are known from the peninsula, including one endemic species, *Sphinx xantus* Cary, and three endemic subspecies, *Manduca rustica cortesi* (Cary), *Pachysphinx occidentalis peninsularis* Cary [revised identification], and *Callionima falcifera guaycura* (Cary) [revised identification]. For each of the 26 species, information is presented on peninsular distribution, flight period, and possible larval host plants.

Additional key words: peninsular effect, host plants, distributions.

The peninsula of Baja California (or Lower California; here termed simply "Baja California") is situated along the northwestern coast of México, extending southeasterly approximately 1300 km from the international border to its tip at Cabo San Lucas. It is bordered by the state of California (Alta California) on the north, the Pacific Ocean on the west, and the Sea of Cortés (Gulf of California) on the east (Fig. 1). The mainland Mexican states of Sonora and Sinaloa lie to the east of the gulf. Much of the peninsula is a low lying desert. However, in the north are two major mountain ranges, the Sierra Juárez and the Sierra San Pedro Mártir, which represent extensions of the Peninsular Ranges of southern California. Two significant ranges occur in the southern third of the peninsula: the Sierra de la Giganta, running parallel to the eastern coast, and the Sierra de la Laguna in the center of the southern tip. Politically the peninsula is divided at the 28th parallel into a northern state, Estado de Baja California (here termed Baja California Norte to avoid confusion), and a southern state, Estado de Baja California Sur (Baja California Sur).

Although comparatively depauperate, the lepidopterous fauna of Baja California is nonetheless unique and diverse, primarily as a consequence of the nearly 10° range in latitude the peninsula embraces, and its relative isolation from mainland México. Except for butterflies,

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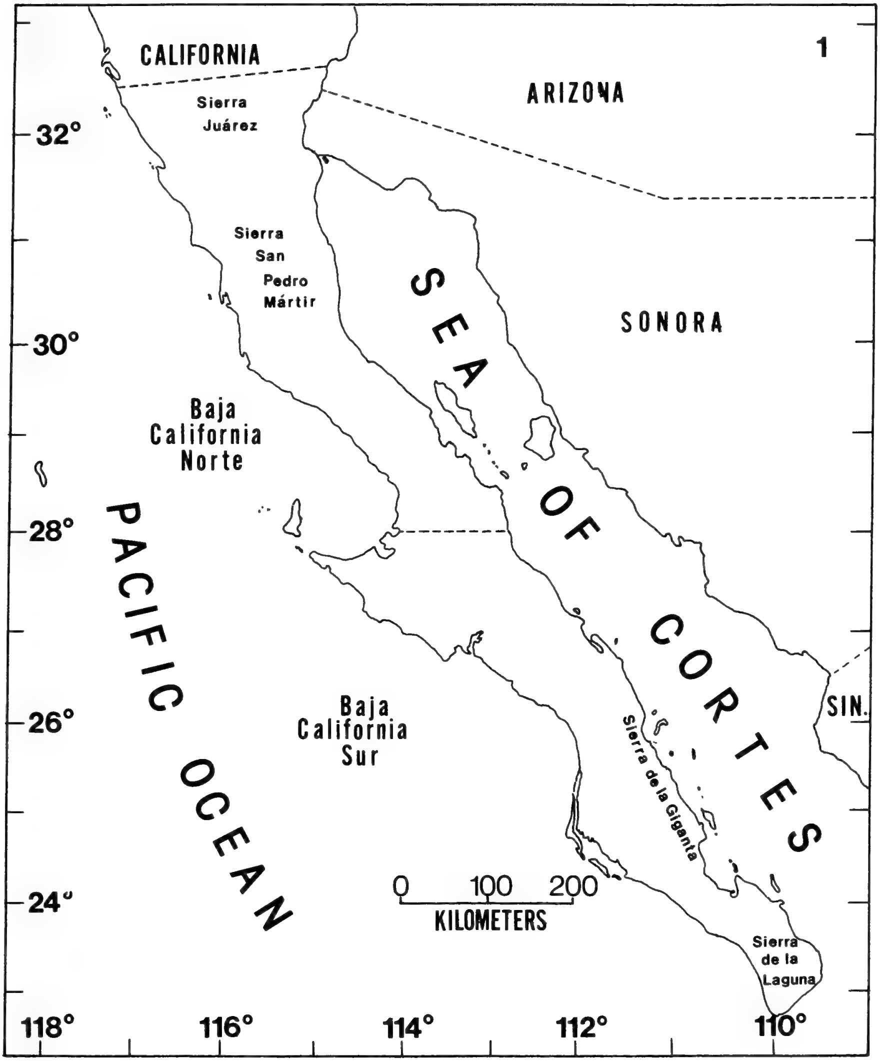


FIG. 1. The peninsula of Baja California and adjacent areas.

however, few lepidopterous families have been studied intensively. Prior to our study, a total of 20 species of Sphingidae had been credited to the Baja California fauna. Mooser (1940) treated 145 species of Sphingidae from the Republic of México, and specifically cited records of 5 species from Baja California, mostly in the collection of Carlos C. Hoffmann. Hoffmann (1942) cited 8 species, primarily Californian elements, as occurring specifically in Baja California, but provided no locality data. Cary (1963) presented records of 244 specimens representing 14 species taken in the Cape Region at the southern tip of the peninsula. Only two of these had been listed previously by Hoffmann (1942), the majority being widely ranging neotropical species cited by Hoffmann as occurring throughout México without specific reference to Baja California. In addition, Cary (1963) described four endemic taxa. Her paper laid the groundwork for biogeographic comparisons between the mainland and peninsular sphingid faunas. Schreiber (1978) cited Baja California as within the range of 7 species in his work on dispersal centers of neotropical Sphingidae; all of these had been listed previously either by Hoffmann (1942) or by Cary (1963). Recent collecting efforts have raised the number of sphingids known to occur in Baja California to 26.

SPHINGID DISTRIBUTIONS

Although large and highly vagile insects, Schreiber (1978) has shown that sphingids exhibit biogeographic patterns comparable to animals of much lesser mobility. The species present in Baja California conform reasonably well to the biotic provinces or phytogeographic regions presented by Shreve (1951) and Wiggins (1980). Four general patterns of distribution are exhibited. 1) The Californian Province in the northwestern portion of the peninsula has a distinctive fauna composed primarily of temperate species including several montane and oak woodland associated elements (Figs. 8 and 15). 2) The Cape Region at the southern end of the peninsula supports a limited fauna of tropical elements similar to that of adjacent mainland Mexico, but with many fewer species (Figs. 17 and 18). 3) A number of common, widespread species range the length of the peninsula (Figs. 4, 5, and 20). 4) Two species exhibit disjunct patterns shown by several butterfly species; they are restricted primarily to the Californian Province but are represented by isolated populations in the Cape Region (Figs. 9 and 10). Apparent conformity to the phytogeographic regions probably has been enhanced by lack of intensive collecting and by biases toward specific areas (e.g., the Cape Region has received far more attention than any other area).

Simpson (1964) first recognized that North American peninsulas had fewer species present at their distal tips than at their mainland bases. He suggested that this pattern was neither coincidental nor transient, but was the result of an equilibrium between species colonization and extinction. Subsequent studies on various North American vertebrates (Cook 1969, Kiester 1971, Taylor & Regal 1978) corroborated Simpson's observation, and this pattern became known as the "peninsular effect." Simply defined, the peninsular effect states that species density or richness decreases as a function of distance from the mainland base of a peninsula.

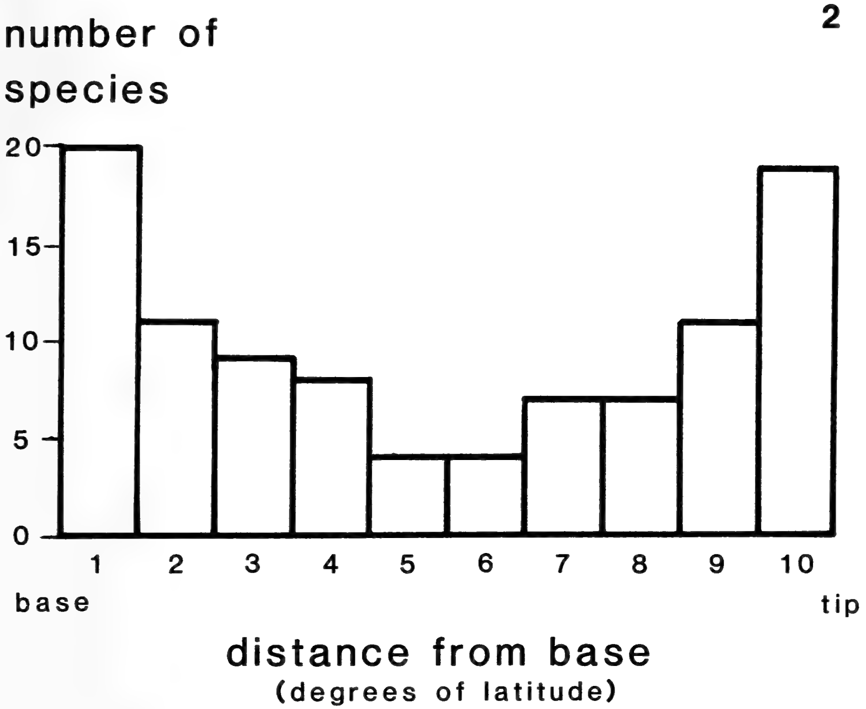


FIG. 2. Species density histogram for Baja California Sphingidae (base = north end of peninsula; tip = southern extremity).

Seib (1980) first questioned the general applicability of the peninsular effect when he demonstrated that the reptiles of Baja California did not conform to this pattern. Recently it has been shown that the butterflies of Baja California also do not conform to this biogeographic principle (Brown 1987). Likewise, sphingids illustrate a pattern of species richness contrary to that predicted by the peninsular effect (Fig. 2). High species density occurs not only at the northern base but at the distal tip as well. Species density appears to be a function of floral diversity (community complexity) and proximity to mainland species pools rather than distance from the mainland base of the peninsula.

SPECIES ACCOUNTS

Unless indicated otherwise, nomenclature follows that of Hodges (1971). All capture records are listed for species represented by fewer than 25 specimens. Locality data were transcribed from specimen labels, thus there is a mixture of metric and English systems for distance and elevation. The distribution maps include localities for all specimens personally examined by us as well as all additional records cited (i.e., personal communication, etc.). Disposition of examined specimens is indicated by abbreviations (e.g., AMNH) listed in the Acknowledgments. Original descriptions are cited in full in the text; additional references are in abbreviated style but are cited in full in the Literature Cited section.

1. *Agrius cingulatus* (Fabricius) (Figs. 3, 21)
   Sphinx cingulata Fabricius, 1775, Systema Entomologiae, 545.
   Agrius cingulatus; Hodges, 1971:22.

This widespread Neotropical species occurs throughout much of Mexico, ranging into the southern parts of the United States. Strays are known from as far north as Nova Scotia (Hodges 1971). Although most Baja California records are from the Cape Region, *A. cingulatus* probably occurs over most of the peninsula. It has been taken in coastal as well as montane areas, and there is a single record from the northern desert. *A. cingulatus* is probably multiple-brooded; adults fly from July through April in the southern portion of the peninsula. Possible host plants in Baja California include *Datura* (Solanaceae) and several species of *Ipomoea* (Convolvulaceae).

Specimens examined: BAJA CALIFORNIA NORTE: Rancho Santa Inez, 540 m, 1M, 27-VII-82, W. Clark and P. Blom (CI); SW end Isla San Estebán, 1M, 28-VII-86, D. Faulkner (SDNHM). BAJA CALIFORNIA SUR: Ramal de Naranjas, 6 mi W Highway near Santa Anita, 1M, 11-X-83, F. Andrews and D. Faulkner (SDNHM); 36.3 mi SE Todos Santos, 1M, 10-X-83, F. Andrews and D. Faulkner (SDNHM); El Salto, 8 mi E Todos Santos, 1F, 9-X-83, F. Andrews and D. Faulkner (SDNHM); Ricardo's RV Park, 2 mi N Cabo San Lucas, 1M, 6-I-84, R. Wells (RW); 2 mi E El Triunfo, 1F, 12-VIII-66, J. Chemsak, J. Doyen and J. Powell (UCB); Sierra de la Laguna, Rancho La Burrera, 1.9 rd mi S and 12.6 mi E Todos Santos, 1600′, 1F, 15-IX-85, J. and K. Donahue (LACM).

Additional records: BAJA CALIFORNIA SUR: San Bartolo microwave tower, 2000′, 24-VII-81, R. Holland (pers. comm.); Playa San Cristobal, 15 mi N Cabo San Lucas, 100′, 18-IV-84, J. Brown (sight record).

2. *Manduca sexta sexta* (Linnaeus) (Figs. 4, 22)
   Sphinx sexta Linnaeus, 1763, Centuria Insectorum Rariorum, 27.
   Phlegethontius sextus sextus; Cary, 1963:193.
   Manduca sexta; Hodges, 1971:29.

M. sexta is abundant throughout the peninsula, ranging north well into California; it is absent only at the highest elevations. Cary (1963) also records it from Sonora and Sinaloa. In Baja California adults have been taken from March through December. It is most common in the late summer and fall. Larvae feed on a wide variety of Solanaceae including potato, tomato, and tobacco.

3. *Manduca quinquemaculata* (Haworth) (Figs. 5, 23)
   Sphinx quinquemaculata Haworth, 1803, Lepidoptera Britannica 1:59.
   Phlegethontius quinquemaculatus; Cary, 1963:194.
   Manduca quinquemaculata; Hodges, 1971:31.

This species is very similar to *M. sexta,* from which it can be distinguished by the presence of an almost continuous, straight, black subterminal line on the forewing. The two are broadly sympatric throughout Baja California, however, *M. quinquemaculata* is considerably less abundant. It is equally common in both the northern and southern halves of the peninsula. Captures extend from March through October. Larval hosts are the same as those given above for *M. sexta.*

4. *Manduca rustica cortesi* (Cary) (Figs. 6, 24)
   Phlegethontius rusticus cortesi Cary, 1963, Ann. Carnegie Mus. 36:194.
   Manduca rustica cortesi; Schreiber, 1978:41, 62.

Although capture records do not illustrate an extensive peninsular distribution, *M. rustica* probably occurs throughout Baja California. It is frequent to the north in adjacent southern California where it is probably resident. The subspecies *cortesi* was described from specimens taken in the Cape Region, and the name is applicable to southern California material as well. *M. rustica cortesi* averages smaller than the nominate subspecies; its white over-scaling and black and white maculation are in strong contrast to the typical brown and white markings of *M. rustica rustica* (Fabricius). Adults fly in the summer and fall, with captures ranging from July to November. Hosts available in Baja California include *Bignonia* (Bignoniaceae) and *Verbena* (Verbeneaceae), and probably other members of these two families, such as the widespread *Chilopsis linearis* (Cav.) Sweet and the more southern *Tecoma stans* (L.) Juss. (both Bignoniaceae).

5. *Sphinx xantus* Cary (Figs. 7, 25)

Sphinx xantus Cary, 1963, Ann. Carnegie Mus. 36:196; Schreiber 1978:45.

This endemic species has been found over a wide range of elevations in the Cape Region, and ranges north along the eastern side of the peninsula to Bahía de las Animas in Baja California Norte. Captures extend from August to November. *S. xantus* is the peninsular counterpart of the mainland *S. istar* (Rothschild and Jordan). Cary (1963) presents several morphological characters distinguishing the two: *xantus* is smaller in forewing length and more somber brown than the lighter and variegated *S. istar*; the male genitalia are also distinct. The differences between *S. xantus* and *S. istar* are not as great as those between many species in the genus. However, until biological data to the contrary become available, we will treat them as separate species. The larval host plant is unknown.

Specimens examined: BAJA CALIFORNIA NORTE: Bahía de las Animas, sea level, 1M, 1F, 5-IX-85, J. and K. Donahue (#96,431, LACM). BAJA CALIFORNIA SUR: 7 mi S San Pedro, 3M, 10-VIII-66, Chemsak, Doyen and Powell (UCB); Highway 19, 14.5 rd mi NW Cabo San Lucas, 250′, 5M, 11-IX-83, J. and K. Donahue (LACM); Sierra de la Giganta, Ligui microwave tower, 32 mi S Loreto, 1500′, 1M, 4-IX-84, J. and K. Donahue (#88,114, LACM); Sierra de la Laguna, Rancho San Antonio de la Sierra, 11.6 rd mi SE KP 147.6, 3000′, 2M, 11/12-IX-85, J. and K. Donahue (#97,169, LACM); San José del Cabo, 1M (holotype), 26-XI-61, 1M (paratype), 27-XI-61, Cary-Carnegie Expedition (CMNH).

6. *Sphinx chersis* (Hübner) (Figs. 7, 28)

Lethia chersis Hübner, 1823, Sammlung exotischer Schmetterlinge, 2.
Sphinx chersis; Hodges, 1971:58.

This widespread western U.S. species ranges into the northern portion of the peninsula. Adults have been taken from May to September in adjacent southern California. Potential larval hosts available in Baja California include *Fraxinus* (Oleaceae), *Prunus* (Rosaceae), and *Populus* (Salicaceae) (Essig 1926, Hodges 1971).

Specimens examined: BAJA CALIFORNIA NORTE: 4 mi N Santo Tomás, 800′, 2M, 28-V-70, R. Holland (AMNH); Sierra San Pedro Mártir, Meling Ranch [2200′], 1M, 13-V-66 (LACM); 4 mi SW La Zapopita, Valle de Trinidad, 1M, 1F, 16-IV-61, F. Truxal (LACM).

7. *Sphinx libocedrus* Edwards (Figs. 8, 27)

Sphinx libocedrus Henry Edwards, 1881, Papilio 1:115; Hodges, 1971:61.

There are two records of *S. libocedrus* from near the southern tip of the peninsula. It is uncertain whether the specimens represent a resident population or stray individuals. Hodges (1971) indicates that *S. libocedrus* flies from July through September in Texas and Arizona; both Baja California captures are from September. *Forestiera neomexicana* A. Gray (Oleaceae), the only documented larval host (Hodges 1971), occurs in the Cape Region (Wiggins 1980).

Specimens examined: BAJA CALIFORNIA SUR: 10 mi SW San José del Cabo, 1M, 1-IX-59, Radford and Werner (CAS); 6 mi E El Aguaje, summit Cañon Santo Tomás Rd, 3500′, 1M, 1-IX-87, R. Wells (RW).

8. *Sphinx perelegans* Edwards (Figs. 8, 26)

Sphinx perelegans Henry Edwards, 1874, Proc. Calif. Acad. Sci. 5:109; Hoffmann, 1942:221; Hodges, 1971:61.

S. perelegans is common in the Californian Province, particularly in montane and oak woodland areas, and ranges south along the west coast to San Quintín. Capture records extend from April to September, probably representing two broods. Hodges (1971) suggests *Symphoricarpos* (Caprifoliaceae) as the larval host; Essig (1926) mentions *Prunus* (Rosaceae) and *Arctostaphylos* (Ericaceae).

9. *Sphinx sequoiae engelhardti* Clark (Figs. 9, 29)
   Sphinx dolli engelhardti Clark, 1919, Proc. New England Zool. Club 6:104.
   Sphinx sequoiae engelhardti; Clark, 1920:66.

In Baja California, *S. sequoiae* Boisduval is known only from the pinyon-juniper woodland areas at the northern end of the Sierra Juárez and near Valle de la Trinidad. The subspecies *S. sequoiae engelhardti* is primarily a desert inhabitant occurring in the southern portion of the range of *S. sequoiae*; it is phenotypically very similar to *S. dollii* Neumoegen. In adjacent southern California *S. sequoiae* has been collected from April to August. The larval host is *Juniperus californica* Carr. (Cupressaceae).

Specimens examined: BAJA CALIFORNIA NORTE: 16 km S La Rumorosa, 2M, 27-V-78, E. Sleeper (CSULB); 4 mi SW La Zapopita, Valle de la Trinidad, 1M, 16-IV-61, F. Truxal (LACM); near Zapopita, Valle de Trinidad, 1M, 7/8-IV-61, F. Truxal (LACM).

10. *Smerinthus cerisyi* Kirby (Figs. 9, 30)
   Smerinthus cerisyi Kirby, 1837, Fauna Boreali-Americana 4:301.
   Smerinthus cerisyi cerisyi; Mooser, 1940:435.
   Smerinthus cerisyi saliceti Boisduval, 1875, Histoire Naturelle des Insectes, Species Général des Lépidoptères Hétérocères 1:35; Hoffmann, 1942:222.
   Smerinthus cerisyi ophthalmica Boisduval, 1855, Bull. Soc. Entomol. France 332; Cary, 1963:197.

S. cerisyi occurs commonly throughout much of the Californian Province, particularly at middle elevations and in riparian habitats, but it is also represented in the Cape Region by an isolated population. The Cape Region of Baja California marks the southern limit of this characteristically temperate species (Cary 1963); Mooser (1940) noted its presence in Baja California Norte, without further detail. *S. cerisyi* has been recorded from March through September in the north, and in November and January in the Cape Region. *Salix* and *Populus* (Salicaceae) serve as larval hosts elsewhere (Comstock and Dammers 1943, Hodges 1971).

Specimens examined: BAJA CALIFORNIA NORTE: Meling Ranch (San José), 1M, 30-VI-68, 1M, 2-VII-68, 1M, 1F, 29-VI-68, all D. Patterson (CAS), 1M, 5-IV-71, H. Real (CAS); 1 mi N Meling Ranch, 1M, 17-III-72, J. Doyen and J. Powell (UCB); trail Las Encinas to La Sanja, Sierra San Pedro Mártir, 1M, 27-V-58, D. Patterson (CAS); 4 mi S Las Encinas, 1M, 2-VI-58, D. Patterson (CAS); "Mexicali, Rubirosa," 1M, 11-IX-61, D. Patterson (CAS); Agua Caliente (San Carlos), 18.5 km E Maneadero, 1M, 1F, 6-VII-73, P. Arnaud (CAS); 8 mi E Tecate, 1M, 6-VII-84, J. Brown and P. Tocco (SDNHM); Arroyo Santo Domingo, 5.7 mi E Hamilton Ranch, 1M, 1F, 22-IV-63, H. Leech and P. Arnaud (CAS); 3 mi S San José del Castillo, 1F, 16-VI-63, E. Sleeper (CSULB). BAJA CALIFORNIA SUR: 4 mi W summit, El Aguaje-Miraflores, Sierra de la Laguna, 1F, 23-I-87, R. Wells (RW); Arroyo San Bartolo, 4F, 1-XI-61, 2F, 15-XI-61, Cary-Carnegie Expedition (CMNH); Arroyo San Bernardo, 3F, 17-XI-61, Cary-Carnegie Expedition (CMNH); Puerto Chileno, 1F, 26-XI-61, Cary-Carnegie Expedition (CMNH).

Additional records: BAJA CALIFORNIA NORTE: Mike's Sky Ranch, Sierra San Pedro Mártir, 3600', 18-VI-70, R. Holland (pers. comm.).

11a. *Pachysphinx occidentalis occidentalis* (Edwards) (Figs. 10, 31)
   Smerinthus modestus var. *occidentalis* Henry Edwards, 1875, Proc. Calif. Acad. Sci. 6:92.
   Smerinthus imperator Strecker, 1878, Lepidoptera, Rhopaloceres and Heteroceres, Indigenous and Exotic, 125.
   Pachysphinx modesta imperator form *kunzei* Rothschild and Jordan, 1903, Novit. Zool. 9(suppl.):343.
   Pachysphinx modesta occidentalis; Mooser, 1940:436.

Pachysphinx modesta imperator; Hoffmann, 1942:223.
Pachysphinx occidentalis; Hodges, 1971:91.

The nominate subspecies is found sporadically throughout the northern portion of the peninsula. It is most common at middle elevations and in riparian areas where *Populus* and *Salix* (Salicaceae), its larval hosts, grow.

Specimens examined: BAJA CALIFORNIA NORTE: Meling Ranch (San José), 1M, 30-VI-68, 1M, 1-VII-68, D. Patterson (CAS); Agua de Chale, 22 mi S San Felipe, 1M, 18-VI-68, D. Patterson (CAS); Low. Corona, Sierra San Pedro Mártir, 1M, 14-VI-61, E. Sleeper (CSULB); San José del Castillo, 4M, 3-IX-61, 1M, 1F, 15-VI-61, E. Sleeper (CSULB); 3 mi S San José del Castillo, 1M, 1F, 15-VI-63, E. Sleeper (CSULB); 10 mi S San Matias Peak, Sierra San Pedro Mártir, 1F, 28-VIII-60, E. Sleeper (CSULB).

Additional records: Rothschild and Jordan (1903) cite a pair of specimens from Lower California (in the Paris Museum) in their original description of *P. modesta imperator* form *kunzei*, hesitating to recognize the taxon as a distinct subspecies for lack of enough material. We have not examined these specimens, but they may refer to *P. occidentalis peninsularis* (see below).

11b. *Pachysphinx occidentalis peninsularis* Cary (Fig. 10)
Pachysphinx modesta peninsularis Cary, 1963, Ann. Carnegie Mus. 36:198; Schreiber 1978:48.

A unique population of *P. occidentalis* was discovered in the Cape Region by the Cary-Carnegie Expedition (Cary 1963). No additional specimens have been collected. The type series is from San José del Cabo near the coast, but the insect also may inhabit the Sierra de la Laguna where its probable larval hosts, *Populus* and *Salix* (Salicaceae), occur.

Specimens examined: BAJA CALIFORNIA SUR: San José del Cabo, 2F (holotype and paratype), 25-X-61, Cary-Carnegie Expedition (CMNH).

12. *Erinnyis ello* (Linnaeus) (Figs. 11, 32, 33)
Sphinx ello Linnaeus, 1758, Systema Naturae (10th ed.) 1:491.
Erinnyis ello; Cary, 1963:198; Hodges, 1971:99.

This widespread species of the American tropics ranges throughout the peninsula, uncommon only in the mountains. *E. ello* is most abundant in the Cape Region. In the northern portion of the peninsula *E. ello* flies from July through September; in the southern portion captures range from July through January. Larval hosts include a variety of plants in the Euphorbiaceae.

13. *Erinnyis crameri* (Schaus) (Figs. 12, 34)
Dilophonota crameri Schaus, 1898, Entomol. News 9:136.
Erinnyis crameri; Hodges, 1971:100.

E. crameri occurs throughout most of mainland Mexico (Hoffmann 1942). It has been collected only once in Baja California, and may not be a breeding resident. Hodges (1971) indicates that all documented larval host plants are in the Apocynaceae.

Specimens examined: BAJA CALIFORNIA NORTE: Hiway 1, ca. 10 mi NNW Cataviña, 2400′, 1M, 1/2-IX-83, J. and K. Donahue (LACM).

14. *Erinnyis obscura obscura* (Fabricius) (Figs. 12, 35)
Sphinx obscura Fabricius, 1775, Systema Entomologiae, 538.
Erinnyis obscura; Cary, 1963:200; Hodges, 1971:101.

This little sphingid occurs throughout the lowlands, but is common only in the southern third of the peninsula, where it has been taken from sea level to 3000 feet. It is widespread on the mainland, ranging north well into the southern United States. It is occasional in southern California where it may be resident. Captures range from August through March in the Cape Region. It is both sexually and seasonally polymorphic, and there is some confusion whether *E. obscura* and *E. domingonis* (Butler) represent separate species or merely color forms of the same species (Hodges 1971). The two are genitalically indistinguishable, and *domingonis*-like individuals may be taken sympatrically with *E. obscura*. Comstock and Dammers (1935) report *Philibertia* (Asclepidaceae) as the larval host.

15. *Pachylia syces syces* (Hübner) (Figs. 13, 36)
Enyo syces Hübner, 1822, Verzeichniss bekannter Schmettlinge, 132.
Pachylia syces; Cary, 1963:200.

This widespread Neotropical species ranges north at least to the state of Sinaloa on the Mexican mainland (Hoffmann 1942). It was first reported from Baja California by Cary (1963). On the peninsula, *P. syces* is uncommon, and is confined to the Cape Region. D'Almeida (1944) reports *Ficus* (Moraceae) as the larval host; several species are available in the Cape Region.

Specimens examined: BAJA CALIFORNIA SUR: Los Barriles, 1F, XI-67, V. Stuart (RW); Hotel Hacienda, Cabo San Lucas, 1F, 16-II-80, J. McBurney (LACM); Los Cabos airport, 30 mi NE Cabo San Lucas, 1F, 5-IX-83, E. Hawks (LACM); 6 mi W Los Barriles, El Coro Rd, 1F, 25-I-87, R. Wells (RW); Bahia de las Palmas, 1F, 12-XI-61, Cary-Carnegie Expedition (CMNH).

16. *Callionima falcifera guaycura* (Cary) (Figs. 14, 37)
Hemeroplanes parce guaycura Cary, 1963, Ann. Carnegie Mus. 36:200.
Callionima parce guaycura; Schreiber, 1978:51.

Although long treated as *C. parce* (Fabricius) (Hoffmann 1942, Cary 1963, Hodges 1971, Schreiber 1978), J. Cadiou (pers. comm.) has examined the type specimens of this and related species, and advises that *C. falcifera* (Gehlen) is the correct name for this western Mexican taxon. The weakly distinguished, endemic subspecies *C. falcifera guaycura* is widely distributed throughout nearly the entire southern third of the peninsula, including the southern portion of the Vizcaino Desert. It is most common in the lowlands of the Cape Region, at times abundant at beach localities, but has been collected up to about 1000 m in the Sierra de la Laguna near San Antonio and Miraflores. Captures range throughout the year with peaks in September and October and again in April and May. During peak flight periods, *C. falcifera* may be taken in abundance. Although the early stages are unknown, the larvae of other members of the genus are known to feed on plants in the Apocynaceae.

17. *Aellopos clavipes* (Rothschild and Jordan) (Figs. 15, 38)
Sesia tantalus clavipes Rothschild and Jordan, 1903, Novit. Zool. 9(suppl.):436.
Aellopos clavipes; Hodges, 1971:111.

A. clavipes is abundant in the Cape Region; there is a single record from the northern portion of the peninsula. It occurs from the immediate coast to about 1300 m in the Sierra de la Laguna. Adults are diurnal and avidly visit flowers. Captures range from August to February. Other members of the genus utilize Rubiaceae as larval hosts.

Specimens examined: BAJA CALIFORNIA NORTE: San Quintín, 1F, 12-VIII-54, alfalfa, Rohlf (SDHNM). BAJA CALIFORNIA SUR: 2 mi S La Paz, 2M, 6-VIII-66, J. Chemsak (UCB), 1F, 11-VIII-66, J. Powell (UCB); San José del Cabo, 1M, 11/16-IX-67, J. Chemsak and A. Michelbacher (UCB); 26 mi W La Paz, 1M, 10-VIII-66, J. Powell (UCB); 7 mi S San Pedro, 1M, 10-VIII-66, J. Doyen (UCB); 9 mi SW La Paz, 1M, 1F, 14-VIII-66, J. Powell (UCB); Hotel Finisterra, Cabo San Lucas, 1M, 28-XI-80, J. and P. Brown (SDNHM); 4.2 mi W Miraflores, 1F, 30-IX-80, F. Andrews and D. Faulkner (SDNHM); 27 km NE Todos Santos, 900′, on flowers of *Antigonon leptopus,* 1F, 8/9-X-75, R. Snelling (LACM); Cañon Santo Tomás Rd., 6 mi E El Aguaje, 3500′, 3M, 1-II-87, R. Wells (RW).

18. *Hemaris diffinis* (Boisduval) (Figs. 15, 39)
Macroglossa diffinis Boisduval, 1836, Histoire Naturelle des Insectes, Species Général des Lépidoptères, 1:pl. 15.
Hemaris diffinis; Hodges, 1971:117.

This Nearctic species is restricted to the middle elevations (1300–1700 m) of the Sierra Juárez and the Sierra San Pedro Mártir. Captures range from June through September; it is most common in July. Adults are diurnally active and strongly attracted to the flowers of low growing annuals, especially the purple flowers of *Monardella* (Lamiaceae). Although *H. senta* (Strecker) is reported as occurring in Baja California Norte by Mooser (1940), Hoffmann (1942), and Schreiber (1978), based on specimens in the Hoffmann collection, their citations probably refer to *H. diffinis*. Reported larval hosts include *Symphoricarpos* and *Lonicera* (Caprifoliaceae) (Hodges 1971).

Specimens examined: BAJA CALIFORNIA NORTE: 15 mi E Meling Ranch, Sierra San Pedro Mártir, 4M, 1F, 20-VI-79, J. Brown and D. Faulkner (SDNHM); Las Encinas, Sierra San Pedro Mártir, 4M, 14-VII-80, J. Brown and D. Faulkner (SDNHM); 6 mi N Laguna Hanson, Sierra Juárez, 1F, 21-VII-80, J. Brown and D. Faulkner (SDNHM); 2–5 km S El Condor, Sierra Juárez, 1F, 5-IX-83, D. Faulkner (SDNHM); 19 mi E Ojos Negros, 1M, 21-VII-1980, J. Brown and D. Faulkner (SDNHM).

19. *Eumorpha satellitia* (Linnaeus) (Figs. 16, 40)
Sphinx satellitia Linnaeus, 1771, Mantissa Plantarum Altera, 539.
Eumorpha satellitia; Hodges, 1971:123.

This widespread Neotropical species is uncommon in Baja California. The few specimens are from the Cape Region, and were collected from July through October. Moss (1920) reports the larval host as *Cissus* (Vitaceae).

Specimens examined: BAJA CALIFORNIA SUR: 2.3 mi SW San Bártolo, 1F, 1-X-81, F. Andrews and D. Faulkner (SDNHM); Punta Lobos, 1M, 20-VII-71, H. Real and R. Main (CAS); Miraflores, 1M, 1-VIII-71, H. Real and R. Main (CAS); Los Cabos airport, 30 mi NE Cabo San Lucas, 1F, 5-IX-83, E. Hawks (LACM); Sierra de la Laguna, Rancho La Burrera, 1.9 rd mi S and 12.6 mi E Todos Santos, 1600′, 1M, 15-IX-85, J. and K. Donahue (#97,345, LACM); Sierra de la Laguna, Rancho San Antonio de la Sierra, 11.6 rd mi SE KP 147.6, 3000′, 5M, 3F, 11/12-IX-85, J. and K. Donahue (#97,169, LACM).

20. *Eumorpha achemon* (Drury) (Figs. 16, 41)
Sphinx achemon Drury, 1773, Illustrations of Natural History 2:51.
Pholus achemon; Hoffmann, 1942:229.
Eumorpha achemon; Hodges, 1971:124.

E. achemon occurs throughout much of the eastern United States ranging west to Arizona and California (Hodges 1971), and south into the Mexican states of Sonora, Chihuahua, and Durango (Hoffmann 1942). In Baja California, *E. achemon* has been collected rarely. Commonly associated with *Vitis* species (Vitaceae) elsewhere, *E. achemon* may eventually be encountered in the northwestern portion of the peninsula where grapes are cultivated.

Specimens examined: BAJA CALIFORNIA SUR: La Presa de San Ysidro, near La Purisima, 1M, 21/29-V-84, N. Bloomfield (SDNHM); Highway 1, KP 20, 12 rd mi NE Villa Insurgentes, 250′, 1M, 7-IX-83, J. and K. Donahue (LACM).

Record: "Baja California" (no further data) (Hoffmann 1942:229).

21. *Eumorpha vitis* (Linnaeus) (Figs. 17, 42)
Sphinx vitis Linnaeus, 1758, Systema Naturae (10th ed.) 1:491.
Pholus vitis; Cary, 1963:202.
Eumorpha vitis; Hodges, 1971:126.

Although confined to the Cape Region, this tropical species is the most common sphingid in the southern portion of the peninsula. It may be encountered in almost every habitat from the coasts to the mountains. Captures range from July through November. Hodges (1971) lists *Vitis* (Vitaceae) as the larval host in the southern United States and mainland Mexico. Two males from Sierra de la Laguna (LACM) have orchid pollinia attached to the eyes, suggesting the use of orchids as a nectar source.

22. *Eumorpha fasciata* (Sulzer) (Figs. 17, 43)
Sphinx fasciatus Sulzer, 1776, Abgekurtze Gesch. der Insecten 1:151.
Pholus fasciatus; Cary, 1963:202.
Eumorpha fasciata; Hodges, 1971:126.

Although widely distributed from northern Argentina to Nova Scotia (Hodges 1971), *E. fasciata* is extremely rare in Baja California. The single specimen listed by Cary (1963) is the only Baja California record to date. Moss (1912) reports the food plant as a member of the Onagraceae.

Specimen examined: BAJA CALIFORNIA SUR: San José del Cabo, 1F, 25-X-61, Cary-Carnegie Expedition (CMNH).

23. *Euproserpinus phaeton* Grote and Robinson (Figs. 18, 44)

Euproserpinus phaeton Grote and Robinson, 1865, Proc. Entomol. Soc. Philadelphia 5:178; Hoffmann, 1942:231; Hodges, 1971:143.

This diminutive, diurnal sphingid is exceptionally inconspicuous as it flies rapidly within a few inches of the ground. It is most frequently found in dry washes and flat areas in the desert regions of southern California. It ranges south into Baja California at least as far as Valle de la Trinidad, a desert intrusion between the Sierra Juárez and the Sierra San Pedro Mártir. The single spring brood flies from late February to April in southern California. Comstock and Dammers (1935) report *Oenothera* (Onagraceae) as the larval host.

Specimens examined: BAJA CALIFORNIA NORTE: Aguajito Spring, Valle de la Trinidad, 1F, 20-III-36, C. Harbison (SDNHM).

Additional records: BAJA CALIFORNIA NORTE: Hiway 3, 4.7 mi N Valle de las Palmas, 2M, 3F, 20/23-II-72, J.-M. Cadiou (JC).

24. *Xylophanes tersa* (Linnaeus) (Figs. 18, 45)

Sphinx tersa Linnaeus, 1771, Mantissa Plantarum Altera, 538.

Xylophanes tersa; Cary, 1963:202; Hodges, 1971:150.

Although seldom encountered in numbers, *X. tersa* may be locally and seasonally common in Baja California, where it is confined to the southern tip of the peninsula. It occurs from the coastal lowlands to about 900 m in the Sierra de la Laguna. It is apparently single-brooded with adults having been taken from September to early December. Elsewhere the larvae feed on Rubiaceae; larval hosts in Baja California are unknown.

25. *Xylophanes pluto* (Fabricius) (Figs. 19, 46)

Sphinx pluto Fabricius, 1777, Genera Insectorum, 274.

Xylophanes pluto; Hodges, 1971:149.

Hoffmann (1942) indicated that *X. pluto* occurred throughout Mexico with the exception of the northwestern region. We have examined single specimens from both Sinaloa (UCB) and Baja California. The probable host in Baja California is *Chiococca* (Rubiaceae).

Specimen examined: BAJA CALIFORNIA SUR: Hwy 19, 14.5 rd mi NW Cabo San Lucas, 250′, 1M, 11-IX-83, J. and K. Donahue (LACM).

26. *Hyles lineata* (Fabricius) (Figs. 20, 47)

Sphinx lineata Fabricius, 1775, Systema Entomologiae, 541.

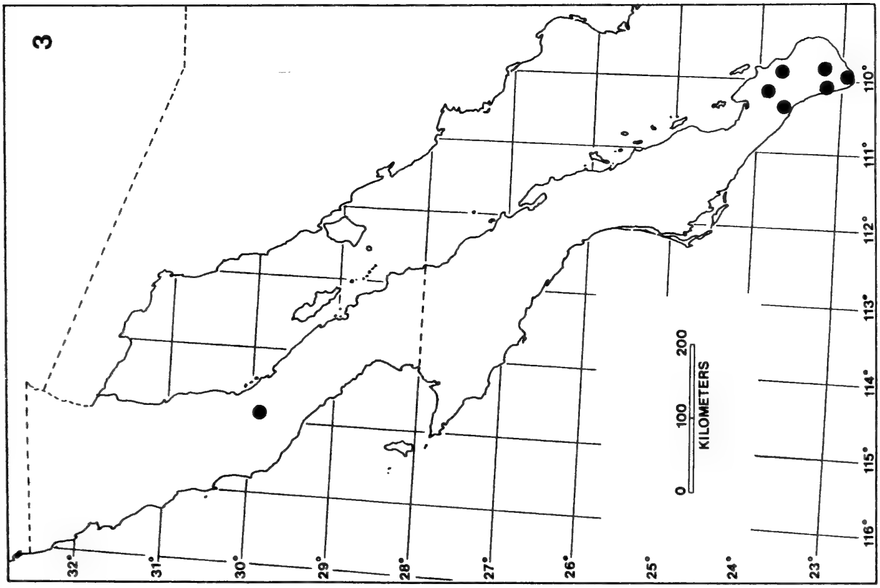
Celerio lineata; Cary, 1963:153.

Hyles lineata; Hodges, 1971:153.

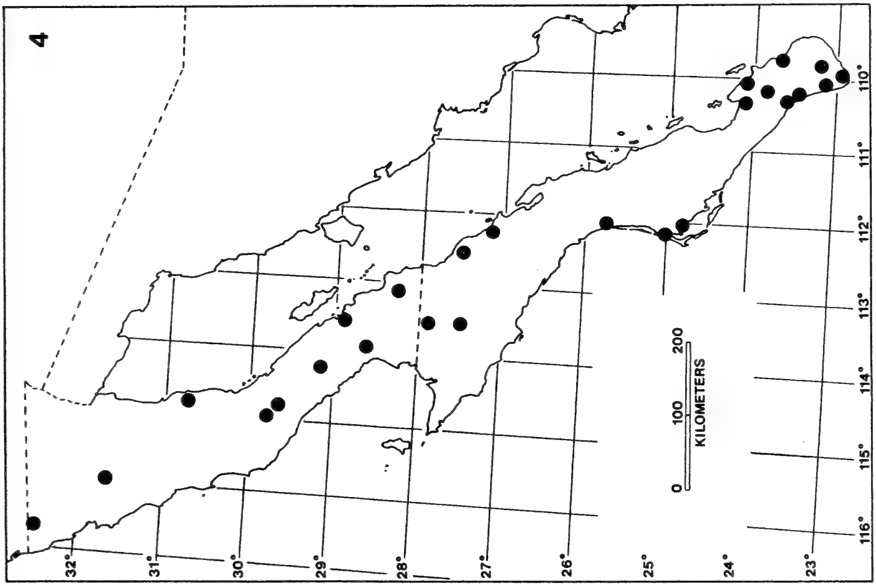
H. lineata is by far the most common and widespread sphingid in Baja California. It ranges from the coastal lowlands to the mountains; it is common in the desert areas; it is also known from several islands both in the Sea of Cortés (e.g., Isla Angel de la Guarda and Isla Mejia) and along the Pácific coast (e.g., Isla de Cedros and Isla Guadalupe). In the north it is on the wing from March through October; in the south captures range throughout the year with a peak in September through November. Larval hosts encompass many genera in several families including Rosaceae, Solanaceae, Onagraceae, Portulacaceae, and Nyctaginaceae.

Possible Species

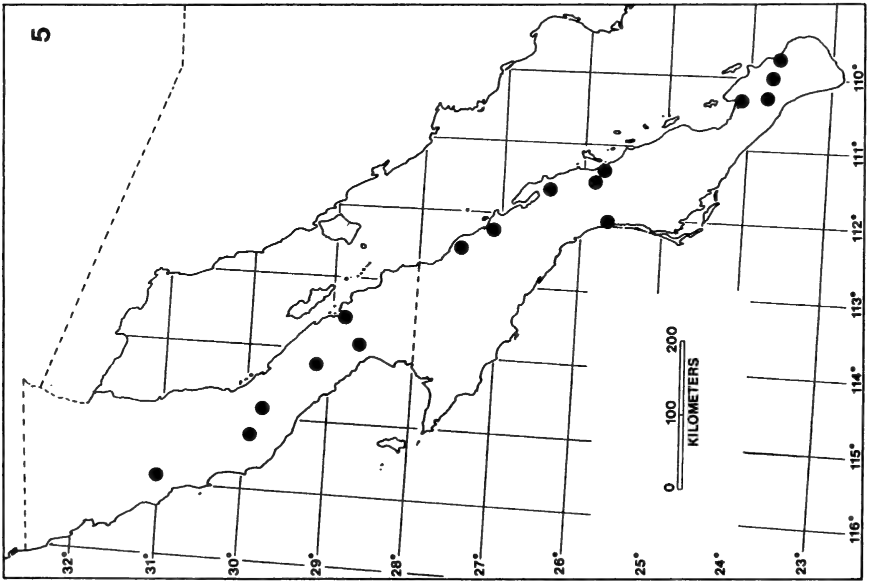
The Californian Province in the northwestern portion of the peninsula represents a significant southern intrusion of Nearctic elements, both floral and faunal. Physiographically, this region is an extension of the area to the immediate north. Most of the sphingids present in southern California occur here as well. Two Californian species for which recent Baja California records are conspicuously absent are *Proserpinus clarkiae* (Boisduval) and *Arctonotus lucidus* Boisduval. Mooser (1940) cites an unspecified number of each from Baja California Norte in the col-



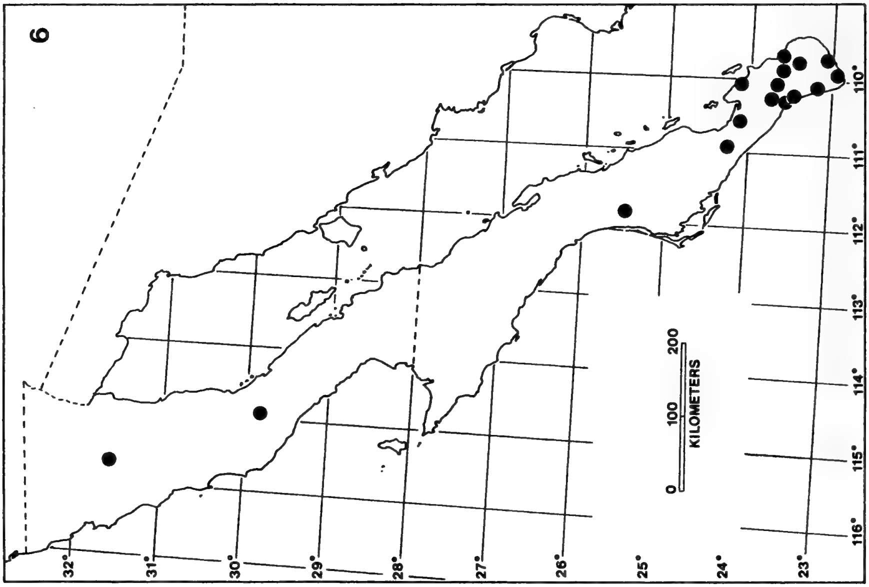
3. Distribution of *Agrius cingulatus.*



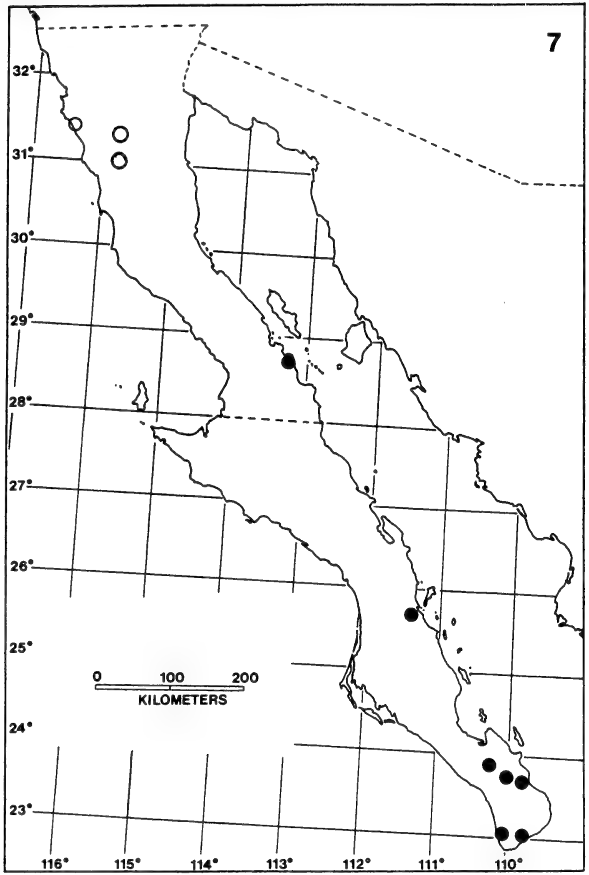
4. Distribution of *Manduca sexta.*



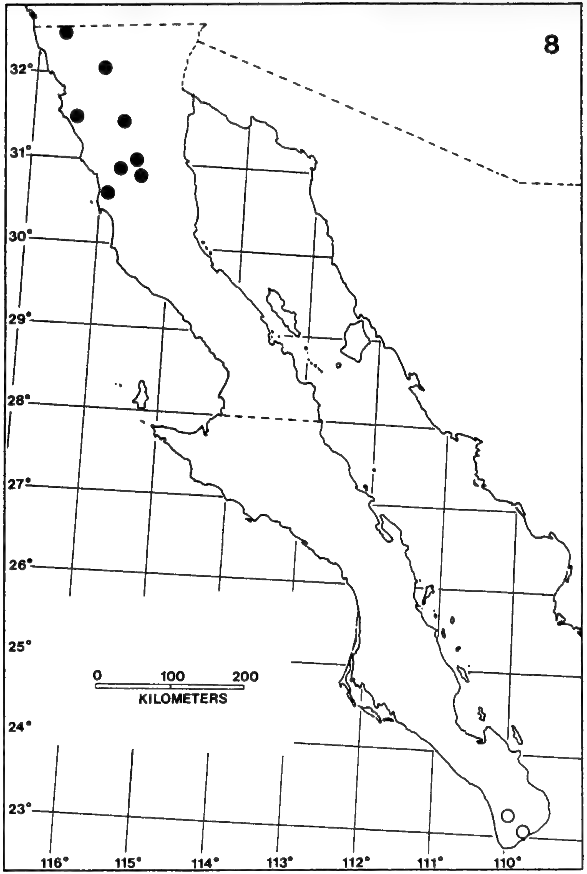
5. Distribution of *Manduca quinquemaculata*.



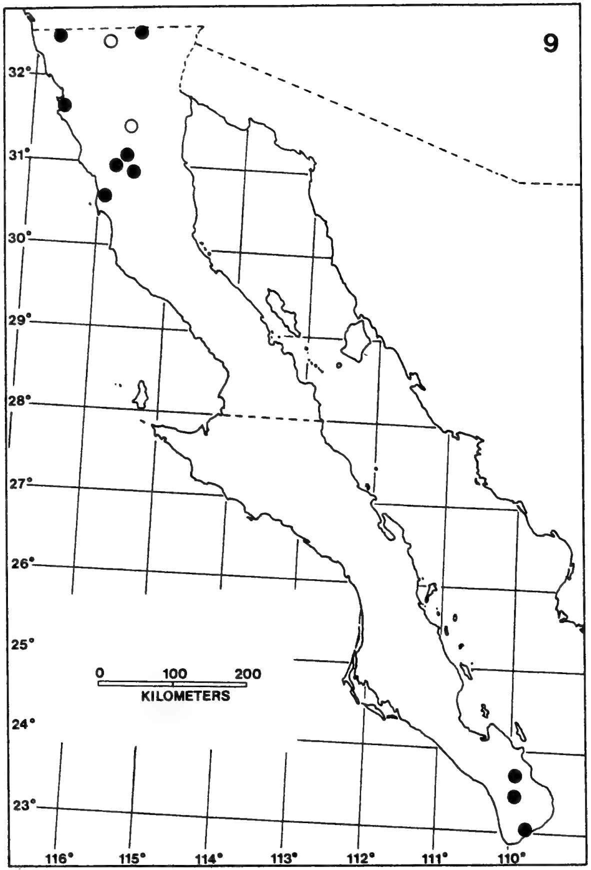
6. Distribution of *Manduca rustica*.



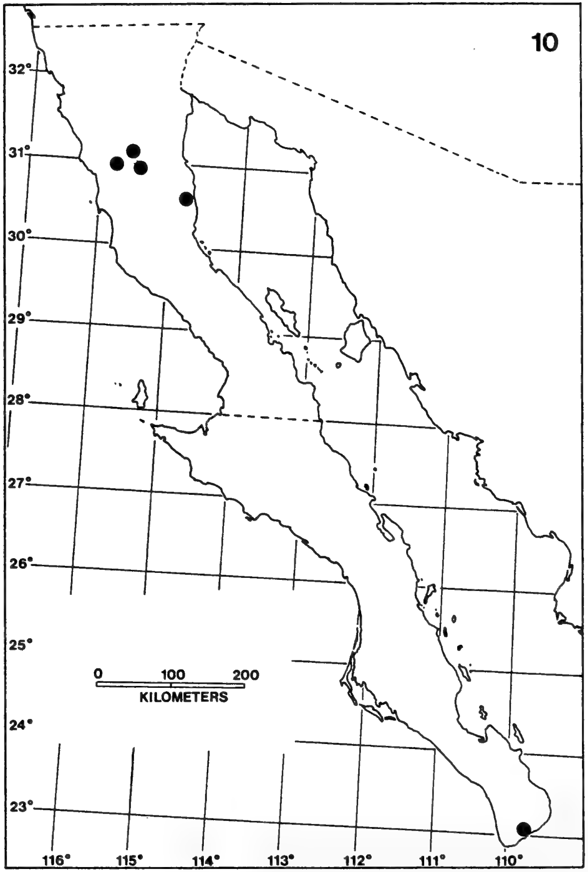
7. Distribution of *Sphinx xantus* (closed circles) and *S. chersis* (open circles).



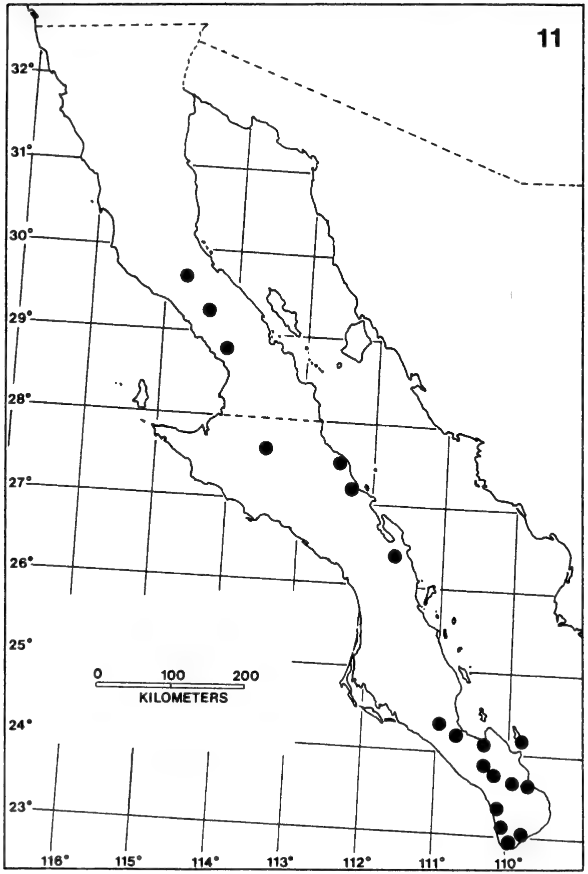
8. Distribution of *Sphinx libocedrus* (open circles) and *S. perelegans* (closed circles).



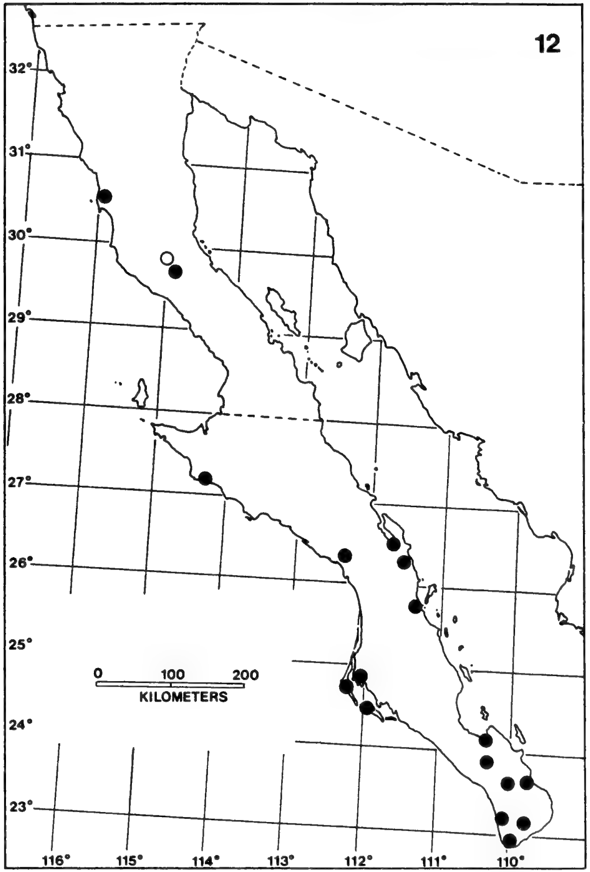
9. Distribution of *Sphinx sequoiae* (open circles) and *Smerinthus cerisyi* (closed circles).



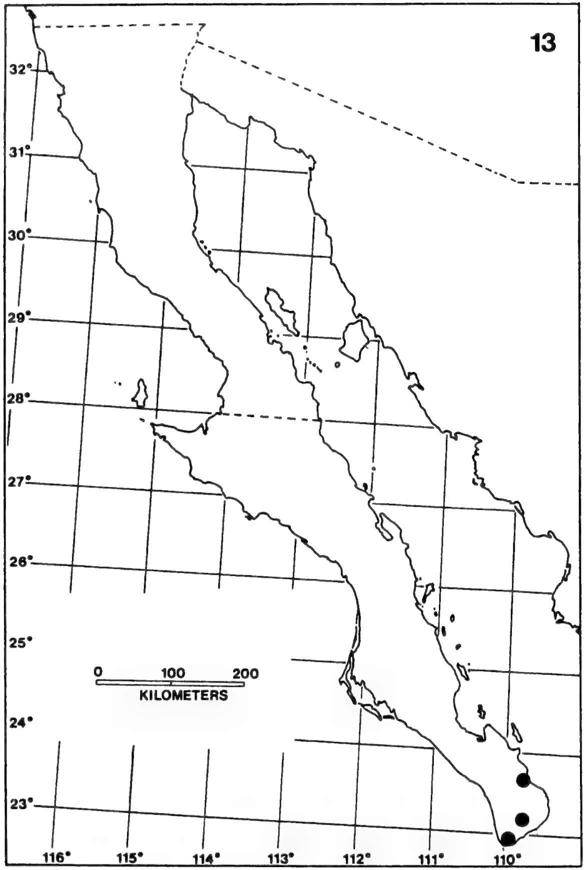
10. Distribution of *Pachysphinx occidentalis*.



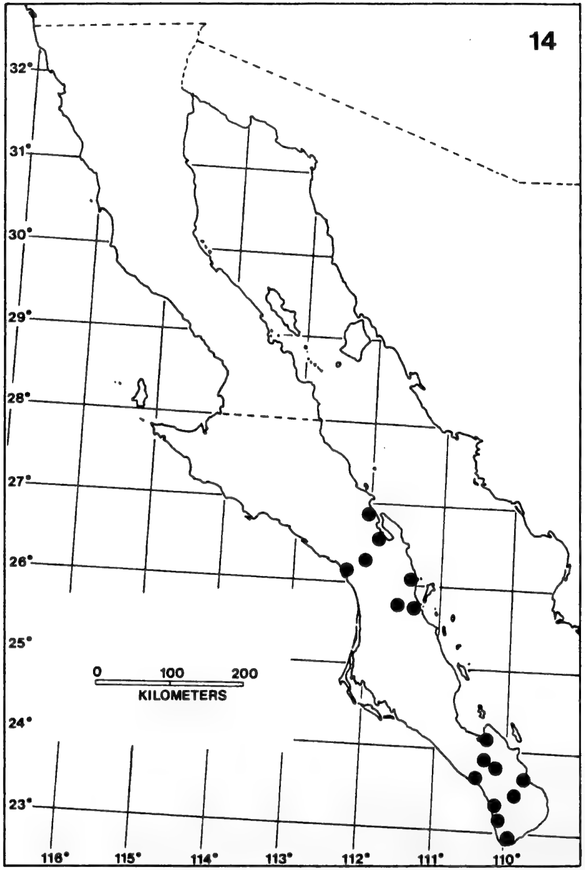
11. Distribution of *Erinnyis ello.*



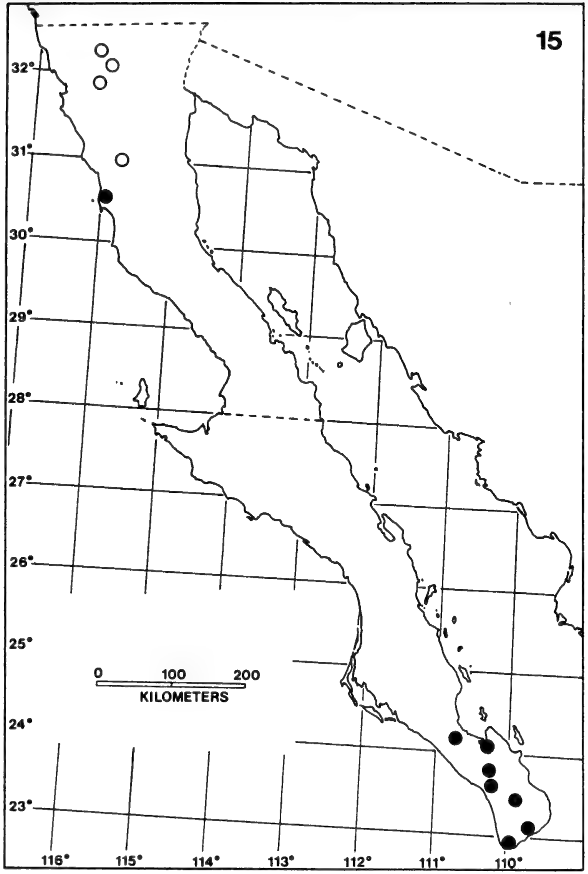
12. Distribution of *Erinnyis crameri* (open circles) and *E. obscura* (closed circles).



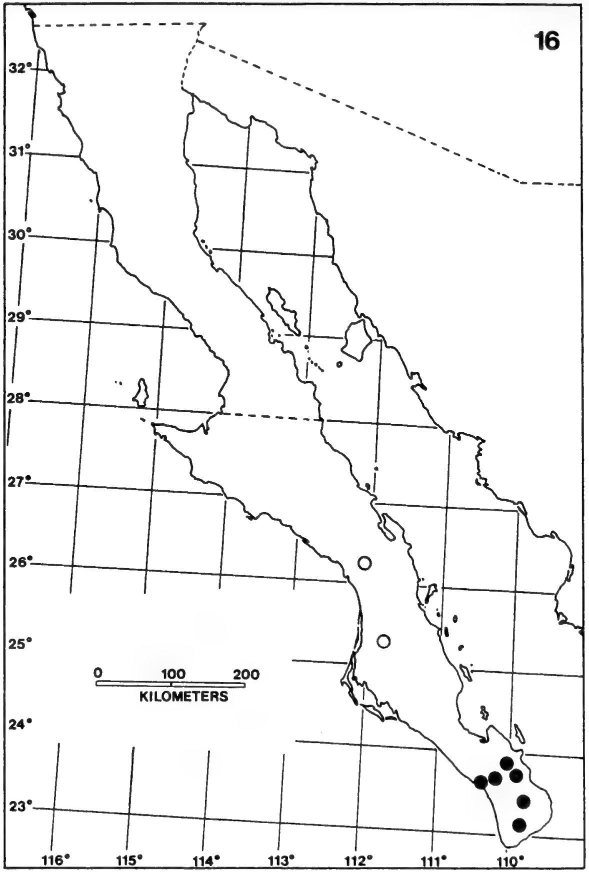
13. Distribution of *Pachylia syces*.



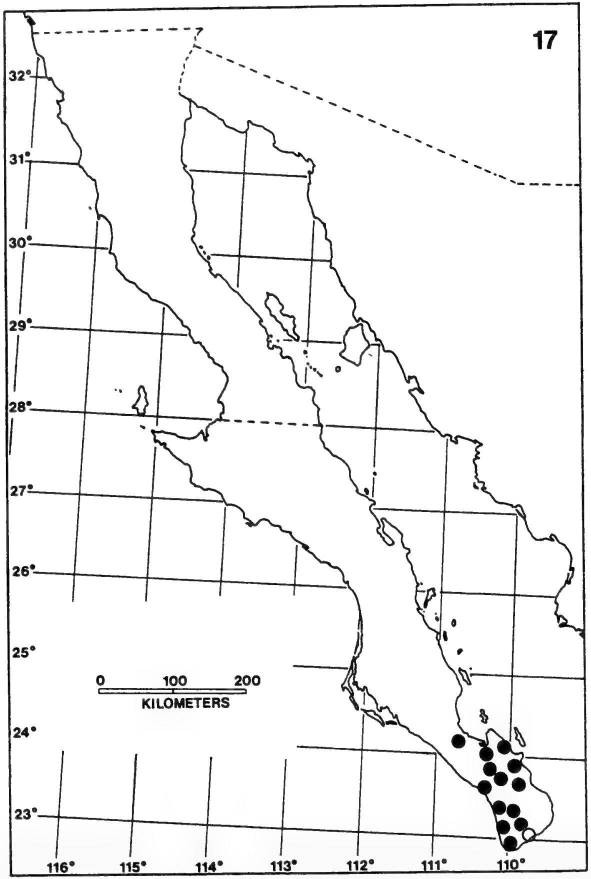
14. Distribution of *Callionima falcifera*.



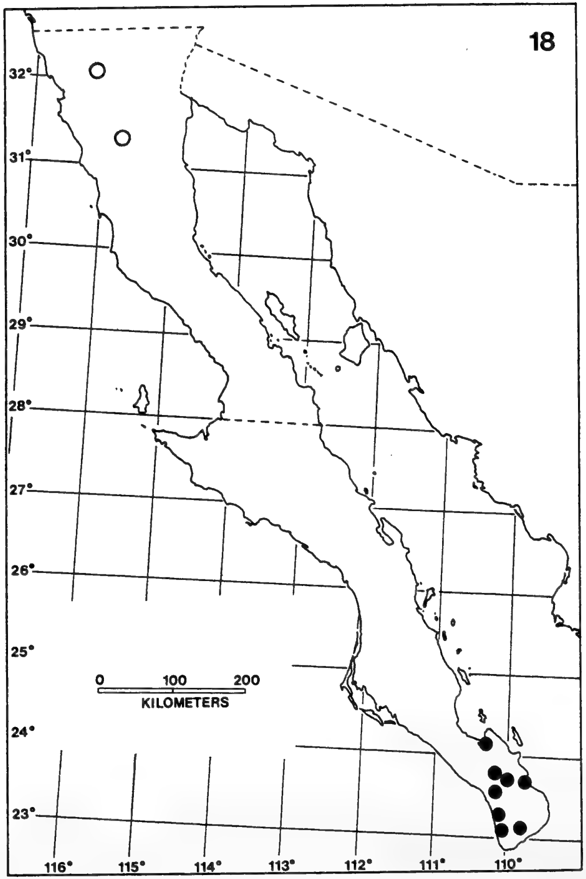
15. Distribution of *Aellopos clavipes* (closed circles) and *Hemaris diffinis* (open circles).



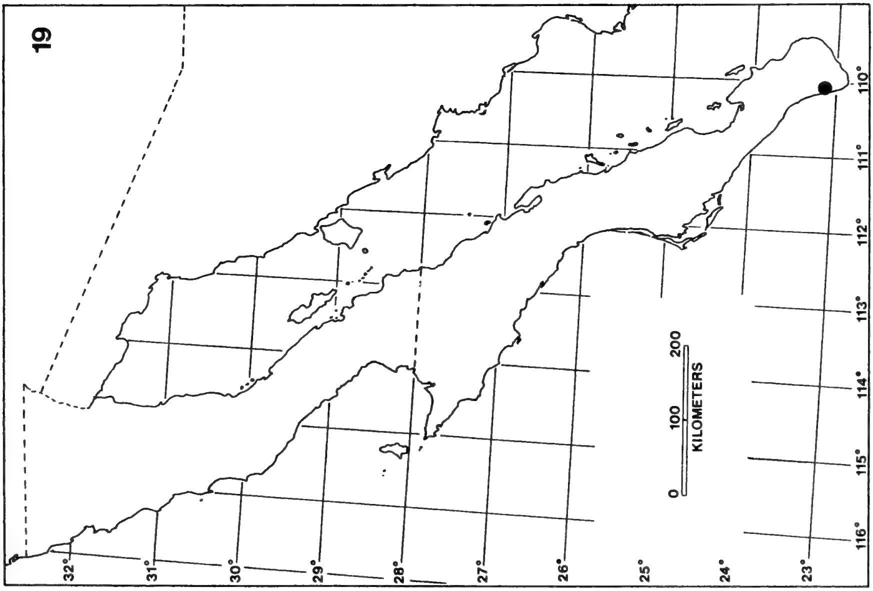
16. Distribution of *Eumorpha satellitia* (closed circles) and *E. achemon* (open circles).



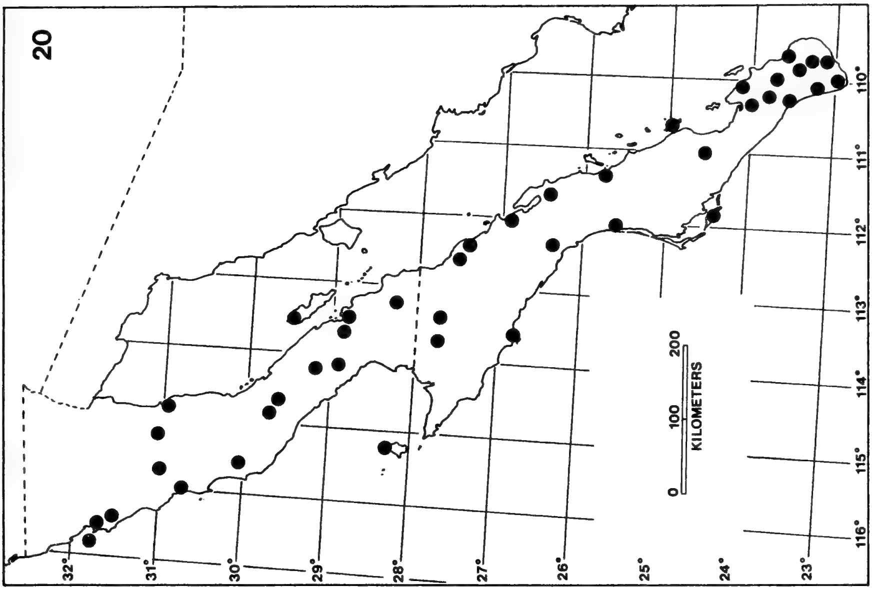
17. Distribution of *Eumorpha vitis* (closed circles) and *E. fasciata* (open circles).



18. Distribution of *Euproserpinus phaeton* (open circles) and *Xylophanes tersa* (closed circles).



19. Distribution of *Xylophanes pluto*.



20. Distribution of *Hyles lineata*.

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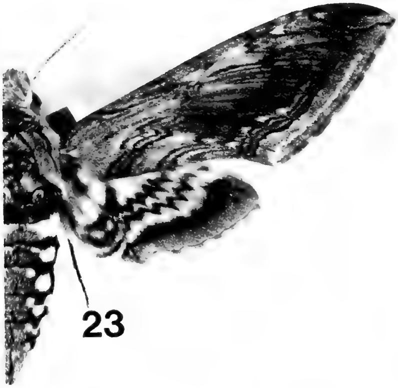

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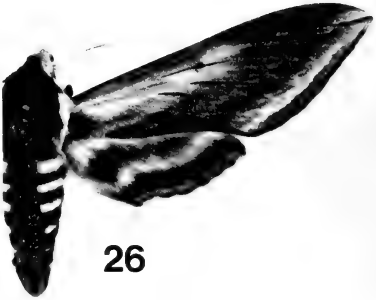

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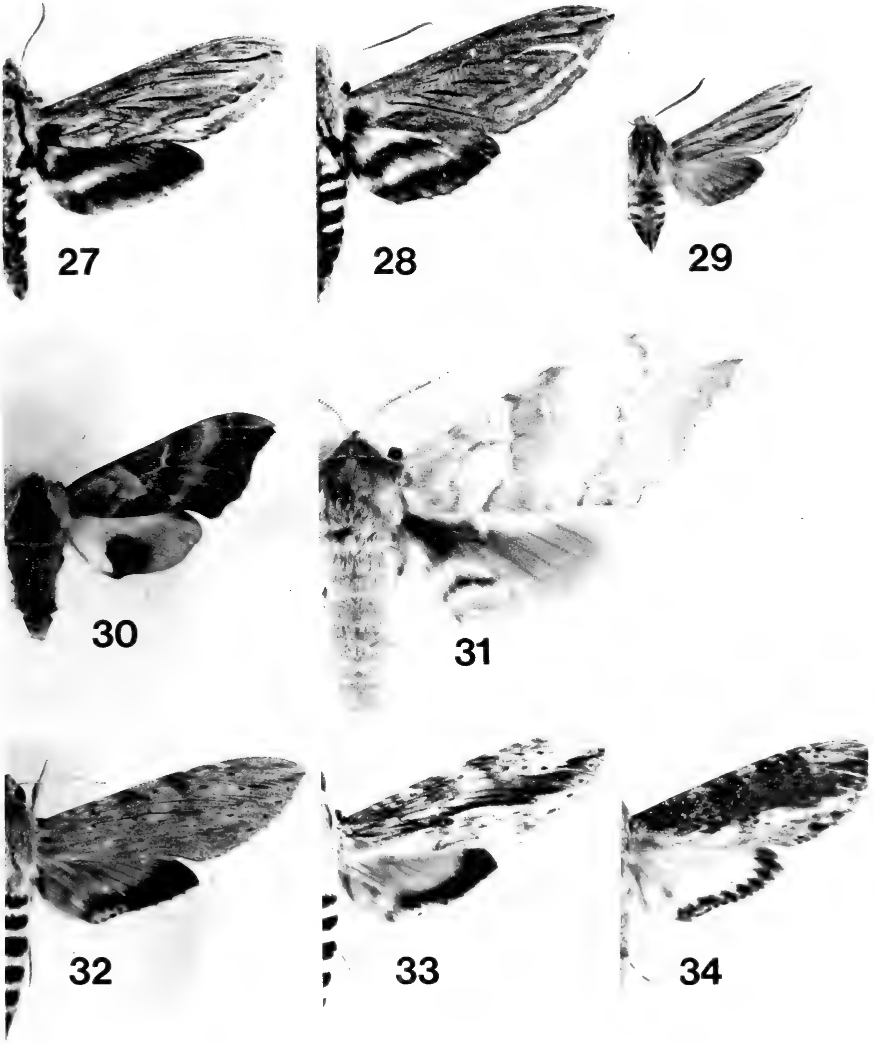
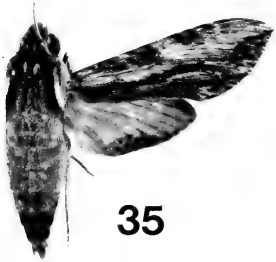
FIGS. 21–26. **21**, *Agrius cingulatus*. **22**, *Manduca sexta*. **23**, *Manduca quinquemaculata*. **24**, *Manduca rustica*. **25**, *Sphinx xantus*. **26**, *Sphinx perelegans*.



FIGS. 27–34. **27,** *Sphinx libocedrus.* **28,** *Sphinx chersis.* **29,** *Sphinx sequoiae.* **30,** *Smerinthus cerisyi.* **31,** *Pachysphinx occidentalis.* **32,** *Erinnyis ello* (male). **33,** *Erinnyis ello* (female). **34,** *Erinnyis crameri.*

lection of Carlos C. Hoffmann, a reference which subsequently has been repeated, without examination of the material, by Hoffmann (1942), Hodges (1971), and Schreiber (1978), for the former species, and by Hoffmann (1942) for the latter. Hodges (pers. comm.) indicates that he has not examined specimens from this area. Both Hodges' and



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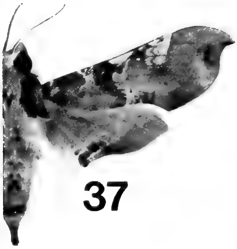

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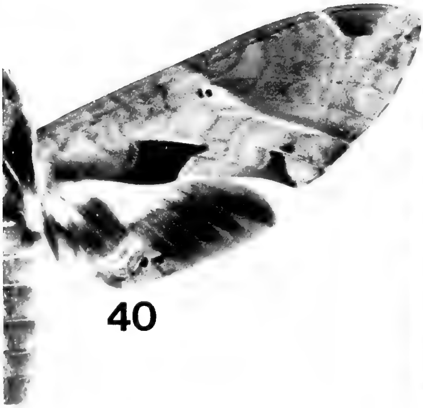

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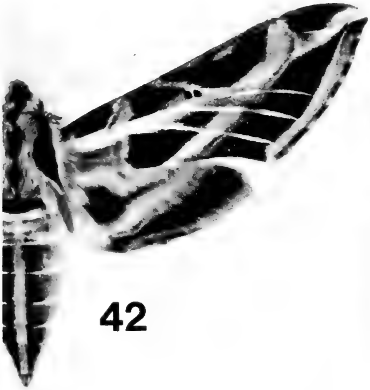
FIGS. 35–41. **35,** *Erinnyis obscura*. **36,** *Pachylia syces*. **37,** *Callionima falcifera* (female). **38,** *Aellopos clavipes*. **39,** *Hemaris diffinis*. **40,** *Eumorpha satellitia*. **41,** *Eumorpha achemon*.



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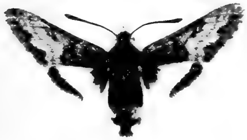

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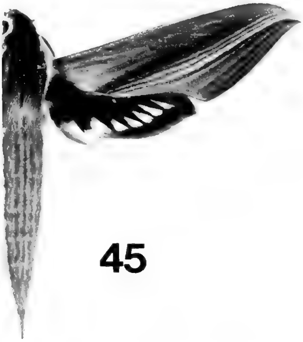

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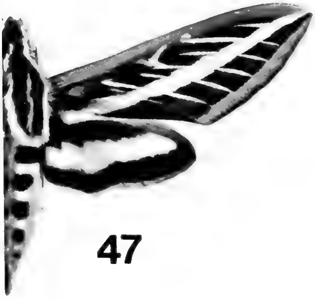

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FIGS. 42–47. **42,** *Eumorpha vitis.* **43,** *Eumorpha fasciata.* **44,** *Euproserpinus phaeton.* **45,** *Xylophanes tersa.* **46,** *Xylophanes pluto.* **47,** *Hyles lineata.*

Schreiber's citations presumably are based on Mooser's and/or Hoffmann's records. There is no apparent reason why either of these species should be absent from the northern chaparral or montane regions; both have been taken to the immediate north in San Diego County, California.

The Neotropical sphingid fauna of the Cape Region at the southern end of the peninsula is exceedingly depauperate compared with that of the Mexican mainland. Species recorded from Sinaloa and Sonora that eventually may be discovered in this region include *Sphinx merops* Boisduval, *Erinnyis yucatana* (Druce), *Pachylia ficus* (Linnaeus), *Cautethia spuria* (Boisduval), *Eumorpha labruscae* (Linnaeus), and *Xylophanes falco* (Walker). In addition, J. Cadiou (pers. comm.) has suggested that the following widely ranging Neotropical species may eventually be documented from the peninsula: *Erinnyis alope* (Drury), *E. domingonis*, *Enyo lugubris* (Linnaeus), and *Pseudosphinx tetrio* (Linnaeus).

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We acknowledge with thanks the assistance of the following individuals whose cooperation permitted the use of specimens in their care (the following abbreviations are used in the text to indicate disposition of specimens examined): F. Rindge, American Museum of Natural History (AMNH), New York; P. Arnaud, Jr., California Academy of Sciences (CAS), San Francisco; W. Clark, College of Idaho (CI), Caldwell; J. Rawlins, Carnegie Museum of Natural History (CMNH), Pittsburgh, Pennsylvania; E. Sleeper, California State University, Long Beach (CSULB); C. Hogue, Los Angeles County Museum of Natural History (LACM); E. and D. Hawks, San Diego, California (now LACM); J.-M. Cadiou (JC) personal collection, Saint Cloud, France; J. McBurney (JM) personal collection (now LACM), Anaheim, California; R. Wells (RW) personal collection, Jackson, California; D. Faulkner, San Diego Natural History Museum (SDNHM), San Diego, California; J. Powell, Essig Museum of Entomology (UCB), University of California, Berkeley; R. Schuster, Bohart Museum of Entomology (UCD), University of California, Davis. Duplicate specimens from the LACM collection are being deposited in the Instituto de Biología, Universidad Nacional Autónoma de México, D. F., México.

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BIOLOGY AND IMMATURE STAGES OF *SCHINIA MASONI* (NOCTUIDAE)

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ABSTRACT. *Schinia masoni* (Smith) was studied using field observations, laboratory rearing, and data from museum collections. Its larval host plant, not previously reported, is *Gaillardia aristata*. Adults also take nectar from this plant and are well camouflaged on its blossoms. The flight period of *S. masoni* is synchronized with the blooming of *Gaillardia aristata*, both peaking in late June. Eggs are deposited between disk-flowers of the host, there are five larval stages, and pupation occurs in the soil. Museum records suggest that this species occurs only in Colorado. *Schinia masoni* and forms with coloration almost identical to closely-related *S. volupia* occur sympatrically on *Gaillardia aristata* in east-central Colorado, and individuals with intermediate coloration are common in this area, raising a question about the systematic relationship of these two species.

Additional key words: *Schinia volupia, Gaillardia aristata,* Heliothinae.

Schinia masoni (Smith 1896), a heliothidine flower moth, feeds in the larval stage on flowers and developing seeds of blanketflower, *Gaillardia aristata* Pursh (Asteraceae). The burgundy wings and yellow head and thorax of adults make them extremely well camouflaged when feeding or resting on *G. aristata* blossoms (Cockerell 1910, Ferner & Rosenthal 1981, Owen 1980). Cockerell (1927) wrote that this species "was discovered by Mr. J. Mason, formerly of Denver, through the picking of a *Gaillardia* flower on which a moth happened to be resting." In his description of the species, Smith (1896) stated that it was collected on flowers of *Rudbeckia*. Several facts suggest that this may be an error: the flowers of *Gaillardia* and *Rudbeckia* are somewhat similar and are commonly confused by non-botanists; the colors of *Schinia masoni* do not match those of *Rudbeckia*; and it was never observed on *Rudbeckia* (n ≅ 400 blossoms) during this study even when these were interspersed with *Gaillardia aristata* on which *S. masoni* was observed. Cockerell (1910) observed it only on *Gaillardia aristata*.

Three photographs of *Schinia masoni* resting on *Gaillardia aristata* have been published (Brower & Brower 1956, Ferner 1980, Owen 1980), as well as one paper and two notes on how its behavior relates to camouflage (Brower & Brower 1956, Cockerell 1910, Ferner & Rosenthal 1981). The species was illustrated in Holland (1903) as *Rhododipsa masoni*; this generic name was later synonymized with *Schinia* (Hardwick 1958).

A combination of field observation, laboratory rearing, and data from museum collections was used in this study, which reports for the first time the larval host plant and immature stages of *Schinia masoni*, and considers the systematic relationship between *Schinia masoni* and closely-related *S. volupia*.

Biology

All but 6 of 90 specimens in several museums (American Museum of Natural History, Canadian National Collection, Denver Museum of Natural History, Los Angeles County Museum of Natural History, University of Colorado Museum, and the U.S. National Museum) come from Colorado, specifically the foothills of the Rocky Mountains between Denver and Ft. Collins. Six specimens from the U.S. National Museum are labelled from "Utah" or "U.T." These specimens have no dates of collection, and their locality data are incomplete and uncertain (R. W. Poole pers. comm.). *Schinia masoni* has been collected from only a very small part of the range of *Gaillardia aristata*, which occurs northward from Colorado into Canada and westward to Washington, Oregon, and British Columbia (Biddulph 1944).

Dates of collection of the 90 museum specimens of *Schinia masoni* range from 10 June–15 July, with a peak during the last week of June. Adults were observed in Boulder Co., Colorado, from 14 June–6 July, 1988, at elevations from 1820 to 2730 m. Adults appeared at the lowest elevations first.

During the day adults were usually observed resting on the disk of a flower ($n = 7$) or under the ray-flowers ($n = 2$). *Gaillardia aristata* has brick-red disk-flowers and yellow ray-flowers. Moths resting on the tops of flowers were often oriented with their yellow heads and thoraces outward over the bases of the yellow ray-flowers and their burgundy wings over the brick-red disk, the most advantageous position for camouflage, as noted by Cockerell (1910), Brower and Brower (1956), and Ferner and Rosenthal (1981). Adults were observed actively flying and seeking nectar at dusk ($n = 5$).

Captive adults ($n = 4$) were kept in the laboratory in 4-l glass jars with four or five blossoms of *G. aristata* in a small container of water. Blossoms were replaced daily; no other water or food was added. The laboratory room was open to free circulation of outdoor air, and temperatures were essentially the same as outdoors, ranging from 21° to 29°C. Captive moths were most active during the late afternoon and early evening, and rested on blossoms during the day. Captive adults lived up to 6 days.

Eggs oviposited by captive females were always laid between disk-flowers ($n = 27$), although in the field a few eggs were found on the surfaces of buds in which the disk-flowers were still very tightly packed. Three captive females oviposited in the laboratory. Oviposition was observed five times between 1200 and 2115 h, but most often (3/5 cases) at dusk. Captive females commonly laid more than one egg in each blossom; one laid seven eggs in one blossom. In the field it was not uncommon to find two or three eggs or small larvae in a flower. Unhatched eggs were found in the field on blossoms from the bud stage to those that were almost finished blooming (1½ weeks past the bud stage).

Newly-hatched larvae tunnelled into an adjacent disk-flower. Blossoms containing small larvae showed patches of brown and shrunken disk-flowers; larger larvae pushed up patches or ridges of disk-flowers in feeding on the developing seeds underneath.

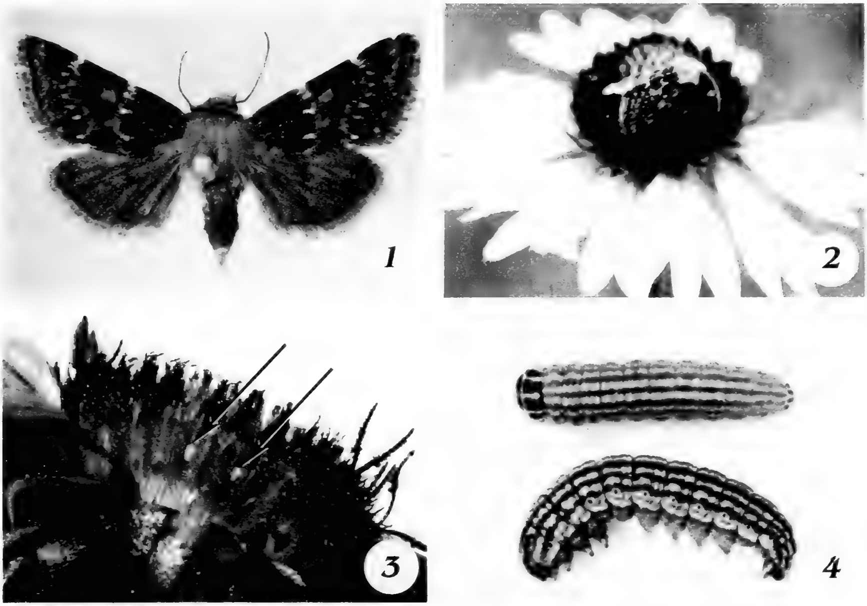
Larvae burrowed into the soil to pupate. Pupae removed from sandy soil in the laboratory had bound soil particles together with silk to a distance of approximately 5 mm in all directions to form a weak pupation chamber (n = 16). This species appears to be univoltine.

Description of Stages

Descriptions of immature stages are based on both field-collected and laboratory-reared larvae. Head widths and body lengths were measured on larvae collected in the field. Larvae were reared in the laboratory using techniques described by Hardwick (1958). They were examined every second day, and changes in body length, color pattern, and evidence of molting were noted. Duration of each larval stage was estimated from dated evidence of molts and body length measurements of laboratory-reared larvae, supplemented with head-width and body-length measurements from field-collected larvae. Unless otherwise noted, numerical data are means and standard deviations.

Adult. (Figs. 1, 2) (n = 19) Smith's (1896) original description seems generally accurate although the following differences or additions should be noted: **Abdomen:** dark grayish brown, rather than "blackish" as stated by Smith, often with row of yellow scales at posterior margin of each segment; some dark purplish pink scales ventrally and laterally. **Forewing:** burgundy or crimson due to mixture of dark purplish red and dark grayish brown scales (not "black" as stated by Smith). Lines and spots of very pale yellow; distinctness of lines variable. Antemedial (am) line with even outcurve and often with white teeth pointing basally. Postmedial (pm) line bisinuate, narrowing median space toward inner margin. Orbicular and claviform spots very pale yellow; claviform spot often appearing to connect am and pm lines. Subterminal line very pale yellow, often indistinct. Fringe grayish pink to pinkish fawn. Underside of forewing dark grayish brown (not "black" as stated by Smith) with carmine or burgundy around costal and outer margins. Fringe grayish pink to pinkish fawn. **Hindwing:** medium to dark grayish brown (not "black" as stated by Smith); outer margin and anal angle sometimes with burgundy tinge. Fringe grayish pink to pinkish fawn. Underside of hindwing mostly carmine or burgundy, often with dark grayish brown around inner margin and humeral and anal angles. Fringe pale pinkish yellow to pinkish fawn. Sexes same coloration. **Forewing length:** 10.8 ± 0.7 mm (n = 11).

Egg. (Fig. 3) (n = 10) White, sometimes with very pale yellow tint, iridescent. Elongate, 0.8–0.9 mm long and 0.3–0.4 mm wide, blunter and more rounded at micropylar end. Often deformed by compression between tightly-packed disk-flowers. Remains same color



FIGS. 1–4. *Schinia masoni* (Smith); adults and immature stages. **1,** Paralectotype *S. masoni,* male, Denver Museum of Natural History; **2,** adult feeding on its food plant *Gaillardia aristata* (not in head-out resting position most advantageous for camouflage); **3,** two eggs deposited between disk-flowers of *G. aristata*; **4,** fifth instar larvae, dorsal and lateral views.

until black head and thoracic shield become visible through chorion shortly before hatching. **Incubation period:** 3–4 days (n = 10).

First instar. (n = 16) Head, prothoracic, and suranal shields black. Body white. Spiracles with dark rims. **Head width:** 0.26 mm (n = 1). **Duration:** 4.5 days (n = 7).

Second instar. (n = 10) Head very dark brown. Prothoracic and suranal shields dark brown to black; sometimes solid color, sometimes with three longitudinal lines of cream or very pale yellow, lines usually less distinct than in later instars. Mid-dorsal line varying from medium brown, pale reddish brown and pale tan, to pale pink or yellowish pink. Subdorsal area cream or very pale yellow, usually with two subdorsal lines of same color as, or slightly paler than, mid-dorsal line. Supraspiracular line same color as mid-dorsal and subdorsal lines. Subdorsal and supraspiracular lines sometimes not well developed, pigmented only in middle of segments. Spiracular line and suprapodal area cream or very pale yellow. Spiracles with black rims. Thoracic legs varying from cream or very pale yellow to caramel. **Head width:** 0.56 ± 0.06 mm (n = 5). **Duration:** 4 days (n = 10).

Third instar. (n = 9) Head light to dark caramel, sometimes mottled with darker brown or black. Prothoracic and suranal shields black or very dark brown with three longitudinal stripes of ivory or very pale yellow. Mid-dorsal line varying from dark brown or dark purplish brown, through reddish brown and brick red, to pale pink or yellowish pink. Subdorsal area cream or very pale yellow with two subdorsal lines of same color as, or slightly paler than, mid-dorsal line. Supraspiracular line same color as mid-dorsal and two subdorsal lines. Spiracular line cream or very pale yellow. Spiracles with black rims. Suprapodal area usually cream or very pale yellow, sometimes with pale rose or brown color. Thoracic legs varying from cream or very pale yellow to caramel. **Head width:** 0.92 ± 0.06 mm (n = 19). **Duration:** 2.5 days (n = 9).

Fourth instar. (n = 9) Generally same as third instar. Pigmentation of suprapodal area often darkening; concolorous with, but paler than, mid-dorsal, subdorsal and supraspiracular lines. **Head width:** 1.45 ± 0.10 mm (n = 15). **Duration:** 3–3.5 days (n = 9).

Fifth instar. (Fig. 4) (n = 9) Head light to dark caramel, sometimes mottled with darker brown or black. Prothoracic and suranal shields black or very dark brown, divided into four bars by three longitudinal stripes of ivory or very pale yellow. Mid-dorsal line varying from dark brown or dark purplish brown, through reddish brown and brick red, to pale pink or yellowish pink. Subdorsal area ivory or very pale yellow with two subdorsal lines of same color as, or slightly paler than, mid-dorsal line. Supraspiracular line same color as mid-dorsal and two subdorsal lines. Spiracular line ivory or very pale yellow. Spiracles with black rims. Suprapodal area concolorous with, but usually paler than, mid-dorsal, subdorsal and supraspiracular lines, with a broken longitudinal line of ivory or very pale yellow. Thoracic legs varying from ivory or very pale yellow to caramel. Setal arrangement same as that of members of the elliptoid-eyed group of the genus (Hardwick 1958, fig. 87). On the first eight abdominal segments (A1 to A8), SD2 is minute and variably absent; on the first and second thoracic segments (T1 and T2), SD1 and SD2 are sometimes absent (Stehr 1987). **Head width:** 2.36 ± 0.06 mm (n = 11). **Duration:** 5.5–6 days (n = 9).

Total duration of larval life, laboratory rearing at 21–29°C: 19.9 ± 1.3 d (n = 9). At elevations between 2560 m and 2730 m collections of larvae made 18 days apart suggest that larval development may require up to twice as long as above, undoubtedly because of colder temperatures.

Pupa. (n = 16) Orange-brown. Spiracles on segments 2 and 3 borne on weak projections of cuticle; on segment 4 on a level with general surface of cuticle; on segments 5–7 in shallow depressions. Anterior margins of segments 5–7 with band of conspicuous pits. Proboscis terminating at apices of wings. Cremaster usually consisting of four setae borne on prolongation of 10th abdominal segment. Apical abdominal segments similar to those of *S. pallicinta* (Hardwick 1972a) or *S. jaegeri* (Hardwick 1972b) except for number of setae. Setae often slightly curved ventrally; inner pair (approx. 0.3–0.4 mm long) slightly longer than outer pair (approx. 0.2 mm long), which is directly lateral to inner pair. One or both outer setae occasionally much reduced or absent. **Length** from anterior end of pupa to posterior margin of fourth abdominal segment: 7.9 ± 0.5 mm (n = 16).

Larval Diagnosis

In the elliptoid-eyed members of the genus *Schinia*, Hardwick (1958) found that "chaetotaxy . . . has no significance on the specific level . . . . There is rather wide latitude in the setal arrangement of individual larvae but no interspecific variation is evident." In fact, throughout the genus *Schinia* setal patterns are of very little diagnostic use, whereas larval color patterns are very often diagnostic (D. F. Hardwick pers. comm.).

The color pattern of the fifth instar distinguishes *Schinia masoni* from other described species of *Schinia*. The four black or very dark brown bars on the prothoracic shield distinguish it from all but *S. pallicinta* (Hardwick 1972a), which was formerly placed in the genus *Rhododipsa* along with *S. masoni*. The prothoracic shield of *S. jaegeri* is similar, but the dark bars are not as well defined (Hardwick 1972b). The presence of a mid-dorsal band, two subdorsal bands, and a supraspiracular band, and the reddish pigmentation of these bands, distinguishes *S. masoni* from both *S. pallicinta* and *S. jaegeri*. These diagnostic pigmentation patterns may be seen in Fig. 4.

Larval Feeding Ecology

To compare the larval development of *S. masoni* with the rate of development of *Gaillardia aristata* blossoms, 10 blossoms were marked at the bud stage and photographed twice a week for three weeks. This record showed that it took 2½ weeks for a flower to go from the bud stage (ray-flowers absent or just emerging) to the early seed-head stage (ray-flowers dried and shriveled, or dropped; seeds beginning to dry and harden).

Nearly three weeks were required for *S. masoni* to complete its development from egg to pupa in the laboratory. In the field, it appeared that some larvae had completed development on a single blossom. However, captive fifth instar larvae ate the developing seeds of an entire blossom approximately every two days for about the last four days before pupation. Such a feeding rate makes it seem unlikely that a larva could complete development in the flower on which its egg was laid. Movement of larvae from flower to flower was observed in the field: several late third or early fourth instar larvae were seen crawling on uneaten blossoms near ones that had been eaten but that contained no larvae. On the other hand, many larvae were found on isolated blossoms many meters from any other, making it seem unlikely that they could locate and move to another blossom to complete their development. Clarification of this aspect of the larval feeding ecology of *S. masoni* will require further research.

Systematic Status

The original description of *Schinia masoni* (Smith 1896) recognized its close resemblance to *Schinia volupia* (Fitch), and these species are still considered to be closely related (D. F. Hardwick pers. comm.). The larval and adult food plant of *S. volupia* has not previously been reported; during this study it was found to be *Gaillardia pulchella* Fougeroux, at least in eastern Colorado. Specimens of *S. volupia* in the museums listed above were collected in Colorado, Kansas, Oklahoma, Texas, New Mexico, and Louisiana; this area overlaps most of the range of *Gaillardia pulchella* (Biddulph 1944).

During this study an area was found on the Palmer (Platte-Arkansas) Divide between Denver and Colorado Springs where typical *S. masoni* and individuals with coloration almost identical to *S. volupia* occur together on *Gaillardia aristata*. *Schinia volupia* has light pink to carmine-pink forewings and hindwings, and none of the specimens from eastern Colorado or New Mexico I examined (n = 12) had any grayish brown scales on either forewings or hindwings. The pale *volupia*-like forms from the Palmer Divide all had some grayish brown scales on the upper hindwings, giving them a visible brownish tinge not seen in typical *volupia*. Individuals with intermediate coloration were common in this area. If these intermediate forms are hybrids, it is possible that *S. masoni* and *S. volupia* are subspecies rather than full species.

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GENETIC DIFFERENTIATION AMONG CALIFORNIA POPULATIONS OF THE ANISE SWALLOWTAIL BUTTERFLY, *PAPILIO ZELICAON* LUCAS

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ABSTRACT. The anise swallowtail butterfly, *Papilio zelicaon* Lucas, is widely distributed in California. California *zelicaon* are composed of low- and high-elevation ecotypes defined by host-plant preference and diapause physiology. Electrophoretic-genetic surveys of 14 loci over 10 populations (157 samples total) demonstrate great similarity among these ecotypes, suggesting that their adaptive differences may be defined by a small number of loci rather than broad genomic differentiation.

Additional key words: ecotypes, electrophoresis, Papilionidae.

The anise swallowtail butterfly, *Papilio zelicaon* Lucas, is native to western North America, where it is widely distributed (Tyler 1975). In central California, *zelicaon* is found in a wide variety of habitats from sea level to tree line (Table 1, Fig. 1). Populations at the same latitude exhibit diapause phenologies from univoltine (one generation/yr) to multivoltine (up to four/yr) as a function of habitat elevation, length of growing season, and larval host plant (Sims 1979).

Populations in the Coast Range and the Sierra Nevada above 400 m primarily utilize native Umbelliferae including *Lomatium, Angelica,* and *Cymopterus.* These native plants are available to *zelicaon* larvae from spring to midsummer when the onset of hot, dry weather renders the leaves too hard and dry for the larvae to ingest. These populations are univoltine, though in the montane Sierra a second generation occasionally occurs (Sims 1979, Shapiro unpubl.).

Lowland populations (below 400 m) today feed almost exclusively on sweet fennel (*Foeniculum vulgare* Miller, Umbelliferae), which is common throughout coastal and interior lowland California (Munz 1970), and also on orange (*Citrus sinensis* Osbeck, Rutaceae) which has been grown commercially in California since 1841 (Opitz & Platt 1969). Both plants are available to *zelicaon* 8–12 months per year, allowing these populations to breed continuously (Sims 1983). Fennel and orange were introduced to California by Spanish missionaries in the 18th Century (Hutchinson 1969). Both produce natural compounds similar to those in native Umbelliferae (Dethier 1941). Before this *zelicaon* was presumably univoltine, being limited by ephemeral host plants at low elevations and the short growing season in the mountains (Sims 1983). The introduction of these perennial host plants probably

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enabled *zelicaon* to "switch" its ovipositional preference to the introduced plants or to disperse to areas where only the introduced species were available, or both. This, in turn, allowed multivoltinism to evolve in the lowland areas where these plants are abundant (Shapiro & Masuda 1980, Sims 1983).

Papilio zelicaon populations are consistent with the ecotype concept first proposed by Turesson (1922) for hawkweed (*Hieracium*, Asteraceae): plants from different habitats were shown to be phenotypically distinct even when grown under identical conditions, thus demonstrating a genetic basis for the differences.

Using wild *zelicaon* and a laboratory strain selected for nondiapause, Sims (1979) demonstrated that univoltine *zelicaon* populations have significantly higher diapause incidence (photophase required to induce diapause) and intensity (duration of chilling needed to terminate diapause) than multivoltines, and that this phenomenon is genetically based. Sims (1983) showed that incidence and intensity are polygenically inherited, with intensity being affected by maternal phenotype. These characteristics are maintained under varied environmental regimes (Sims 1979, Shapiro unpubl.).

The present study began as an attempt to use electrophoretic analysis to determine whether orange-feeding *zelicaon* in northern California evolved independently of orange-feeding *zelicaon* in southern California, or had been introduced inadvertently from the south. *Papilio zelicaon* was reported as an orange pest as early as 1909 near Visalia, Tulare Co. (Coolidge 1910), and in the 1960's near Chico, Butte Co. (Shapiro unpubl.). This study also investigates the degree to which differentiation of *zelicaon* into low- and high-elevation diapause ecotypes is reflected by electrophoretically detectable genetic variation.

MATERIALS AND METHODS

Electrophoresis, a commonly used method in biochemical systematics, is based on the movement of charged particles under the influence of an electrical field (Ferguson 1980). Proteins carry a net electrical charge depending on amino acid structures and environmental pH. The rate at which proteins migrate through a support medium is related to their size and shape and is proportional to net charge. Different proteins with different electrophoretic properties migrate at different rates under identical test conditions.

Differential migration of homologous proteins is detectable and of special interest in biochemical systematics. Such differentiation is presumed to reflect differences in nucleic acid sequences that encode proteins. The degree of electrophoretically detected differentiation is thought to reflect the extent of evolutionary divergence between sam-

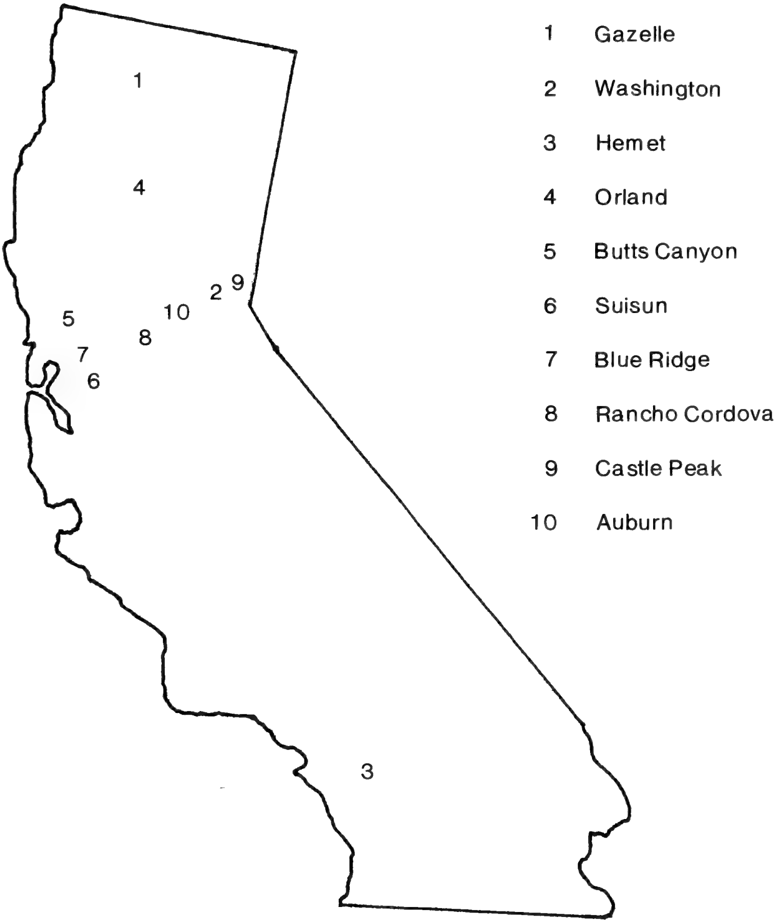

FIG. 1. Location of populations studied.

pled taxonomic groups, although the structural proteins studied represent only one segment of the overall genome.

Adult *zelicaon* were collected during 1984 and 1985 flight seasons at the sites in Table 1. Captured specimens were frozen live and stored at −70°C to prevent protein denaturation.

In preparation for analysis, thoraces were excised and homogenized in 600 μl of glass-distilled water with a Teflon-coated tissue grinder. Homogenate was absorbed onto 2 × 9 mm wicks of #3 Whatman paper and applied to the gels. Horizontal slab gels were made with Sigma starch and were prepared and run for 5 h using methods described in Ayala et al. (1972, 1974a).

After running, gels were cut into four 2-mm-thick slices so that each

TABLE 1. California field site characteristics (Shapiro unpubl.).

Population	Location	Elevation (m)	No. generations/ year	Larval host plant	Habitat
Gazelle	Siskiyou Co.	838	1–2	*Angelica arguta*, *Conium*	Great Basin, grassland, farmland, sloughs
Washington	Nevada Co.	1220	1	*Lomatium*	Sierran W slope, serpentine
Hemet	Riverside Co.	487	>1	*Citrus*	S. California desert, orchards
Orland	Butte Co.	67	>1	*Citrus*	Central Valley orchards
Butts Canyon	Napa Co.	457	1	*Lomatium*	North Coast Range, serpentine
Suisun	Solano Co.	9	>1	*Foeniculum vulgare*, rarely *Cicuta*	Central Valley levees, disturbed areas, near freshwater and tidal marshes
Blue Ridge, +Gates Canyon	Solano Co.	60–762	>1	*Foeniculum vulgare*	Vaca Hills, canyon, riparian
Rancho Cordova	Sacramento Co.	9	>1	*F. vulgare*, rarely *Conium*	Central Valley, riparian forests and gravel beds
Castle Peak	Nevada Co.	2743	1	*Cymopterus*, Umbelliferae spp.	Sierran, alpine
Auburn	Placer Co.	366	1–>1	*Foeniculum vulgare*, Umbelliferae spp. in canyons	Sierran W slope; univoltines: canyon, multivoltines: vacant lots in town

TABLE 2. Enzymes assayed.

Enzyme	Abbreviation	Buffer*
Phospho-glucose isomerase	PGI	REG
Aldolase	ALDO	REG
α-Glycerophosphate dehydrogenase	αGPD	REG
Glutamate-oxaloacetate transaminase	GOT-1	REG
Hexokinase	HK-1	REG
Phospho-gluco mutase	PGM	REG
Fumarase	FUM-2	REG
Mannose phosphate isomerase	MPI	REG
Malic enzyme	ME-1	JRP
Glucose-3-phosphate dehydrogenase	G3PD	DH
Glucose-6-phosphate dehydrogenase	G6PD	DH
Hydroxybutyrate dehydrogenase	HBDH	DH
Esterase	EST-1	DH
	EST-2	DH

* REG: Gel buffer—9 mM Tris, 3 mM citric acid, pH 7.0. Electrode buffer—135 mM Tris, 45 mM citric acid. JRP: Gel buffer—76 mM Tris, 5 mM citric acid, pH 8.65. Electrode buffer—300 mM boric acid, 60 mM NaOH. DH: Gel and electrode buffer—8.7 mM Tris, 8.7 boric acid, 1 mM EDTA, 1 mM β-NAD$^+$, pH 9.0.

sample was tested for four enzymes. Table 2 lists the enzymes assayed. Specific staining systems and gel fixation techniques are described in Ayala et al. (1972, 1974a).

Fixed gels were scored after each run using a light box. Loci were characterized and interpreted as for Pieridae, for which the genetic basis of the electrophoretic banding patterns has been demonstrated in an extensive breeding program (Geiger 1981, Burns & Johnson 1971). Electromorphs were recorded as distance (mm) migrated from the origin.

Electromorph frequencies (considered as allelic frequencies) were used to calculate I, a statistic of genetic identity between taxa (Nei 1972), for all pairwise comparisons of populations. I-values were analyzed using the UPGMA method of cluster analysis (Ferguson 1980).

G-tests (Sokal & Rohlf 1981) were performed on genotype frequencies in the populations represented by large samples ($\geq$14 individuals) to determine whether observed frequencies for each population were consistent with Hardy-Weinberg equilibrium, and whether all populations can be considered to represent a single panmictic population.

RESULTS

Table 3 shows the electromorph frequencies for each population. Of the 14 loci assayed, three are polymorphic: PGI, PGM and MPI.

Results of *G*-tests are displayed in Table 4. Most loci exhibit Hardy-Weinberg equilibrium. However, weighted-average results show that among the populations examined, *zelicaon* does not exhibit Hardy-Weinberg equilibrium and cannot be considered a single, panmictic population. Genotype frequencies are shown in Table 7.

TABLE 3. Electromorph frequencies in 10 *Papilio zelicaon* populations in California.

		Population (n)										
Locus	Allele	Gazelle (8)	Washington (6)	Hemet (19)	Orland (19)	Butts Canyon (14)	Suisun (25)	Blue Ridge (7)	Rancho Cordova (16)	Castle Peak (35)	Auburn (8)	Overall (157)
PGI	13	0	0	0	0.05	0.20	0	0	0.111	0.128	0	0.14
	7	1.0	1.0	1.0	0.95	0.80	1.0	1.0	0.89	0.87	1.0	0.86
ALDO	10	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
αGPD	23	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
GOT-1	27	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
HK-1	40	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PGM	32	0.50	0	0.26	0.10	0.18	0.23	0.25	0.29	0.23	0.15	0.22
	26	0.50	0.20	0.21	0.47	0.18	0.46	0.25	0.35	0.28	0.23	0.33
	23	0	0.40	0.32	0.40	0.45	0.18	0.33	0.23	0.35	0.46	0.31
	20	0	0.40	0.21	0.03	0.18	0.14	0.17	0.03	0.13	0.15	0.13
FUM-2	12	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
MPI	44	0	0	0	0.06	0	0.09	0	0	0.02	0	0.03
	40	0	0	0	0.06	0	0.09	0	0	0.08	0	0.04
	37	0	0	0.30	0.20	0.43	0.18	0.40	0.09	0.30	0	0.22
	33	0.33	0.50	0.57	0.60	0.50	0.64	0.60	0.73	0.52	0.40	0.56
	28	0.67	0.50	0.13	0.06	0.07	0	0	0.18	0.80	0.60	0.15
ME-1	20	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
G3PD	7	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
G6PD	7	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
HBDH	6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
EST-1	22	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
EST-2	14	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

TABLE 4. *G*-test of genotype frequencies in populations ≥14.

	G-statistics for populations						
Locus (df)	Hemet	Orland	Butts Canyon	Suisun	Rancho Cordova	Castle Peak	Average
PGI (1)	0	4.194*	6.605*	0	1.010	2.966	12.776*
PGM (6)	24.349*	20.526*	4.502	13.382*	21.838*	6.846	48.90*
MPI (10)	3.224	3.918	1.582	1.976	10.606	10.334	30.926*

* $P \leq 0.05$. $G = 2\Sigma \text{ OBS} \ln\frac{\text{OBS}}{\text{EXP}}$; $df = \frac{1}{2}(n^2 - n)$ (Ferguson 1980).

Table 5 shows the I-values calculated from electromorph frequencies for each pairwise comparison of populations. The average I-value is 0.980 ± 0.139, indicating a very high level of genetic similarity.

To highlight differentiation without altering phenetic clustering of populations, I-values were recalculated using only data for the three polymorphic loci (Table 6). By excluding the background of monomorphic loci, a more useful graphic analysis can be generated. The UPGMA dendrogram derived from these data is shown in Fig. 2.

DISCUSSION

The high identity values (Table 5) are consistent with similar studies on other insects. Ayala et al. (1974b) reported $\bar{I}$ of 0.970 ± 0.006 for *Drosophila willistoni* populations sampled throughout Central and South America, substantiating previous conclusions about their relatedness based on reproductive relations. Brussard et al. (1985) surveyed genetic identity findings comparing 14 insect taxa (including 3 Lepidoptera), and reported $\bar{I}$ of 0.97 for local populations. It is likely that these values are conservative. Mutants of crucial glycolytic or catabolic enzymes are likely to be eliminated by selection (Bell 1976; Turner 1974; Zera et al. 1985).

Reproductive relations in *zelicaon* are not clear. Breeding trials among

TABLE 5. Genetic identity I-value matrix using 14 loci ($\bar{I} = 0.980 \pm 0.139$).

	Washington	Hemet	Orland	Butts Canyon	Suisun	Blue Ridge	Rancho Cordova	Castle Peak	Auburn
Gazelle	0.97	0.96	0.96	0.95	0.96	0.96	0.98	0.97	0.98
Washington	—	0.98	0.97	0.98	0.97	0.98	0.98	0.98	0.99
Hemet		—	0.99	0.99	0.99	0.99	0.99	0.98	0.97
Orland			—	0.99	0.99	0.99	0.99	0.98	0.97
Butts Canyon				—	0.99	0.99	0.99	0.99	0.97
Suisun					—	0.98	0.99	0.98	0.96
Blue Ridge						—	0.99	0.99	0.97
Rancho Cordova							—	0.99	0.98
Castle Peak								—	0.98
Auburn									—

TABLE 6. I-value matrix using only the three polymorphic ($\bar{I} = 0.867 \pm 0.100$) loci.

	Washington	Hemet	Orland	Butts Canyon	Suisun	Blue Ridge	Rancho Cordova	Castle Peak	Auburn
Gazelle	.765	.713	.707	.656	.723	.676	.807	.730	.853
Washington	—	.855	.830	.842	.795	.812	.849	.850	.950
Hemet		—	.953	.962	.960	.982	.953	.985	.784
Orland			—	.930	.974	.953	.957	.973	.783
Butts Canyon				—	.900	.984	.901	.979	.808
Suisun					—	.952	.966	.964	.719
Blue Ridge						—	.942	.990	.754
Rancho Cordova							—	.757	.822
Castle Peak								—	.808
Auburn									—

multivoltines from northern and southern California and the Central Valley show these populations to be intercompatible (Shapiro unpubl.). Alternatively, Sims (1983) suggests that univoltines and multivoltines are not fully intercompatible because of male-biased hybrid broods. However, control (within-population) data are not available in adequate numbers to validate this conclusion.

While I-values suggest that all *zelicaon* populations are conspecific, the weighted-average *G*-tests show that *zelicaon* is, of course, not panmictic over its entire range. Figure 2 suggests that populations can be clustered on the basis of geographic proximity.

Gazelle (Shasta Valley) is most genetically dissimilar, and is probably more geographically isolated as well. Washington and Auburn are Sierran west slope univoltines. Orland, Suisun and Rancho Cordova are Central Valley multivoltines. Castle Peak, Butts Canyon, Blue Ridge, and Hemet represent univoltine and multivoltine populations in a mixture of very diverse ecological contexts.

The germinal issue is to what degree populations are reproductively isolated by host-plant selection and physical distance. Certainly, the breeding trials and high I-values suggest that all *zelicaon* populations are potentially intercompatible. However, voltinism may be a genetically heritable trait that divides *zelicaon* into low- and high-elevation ecotypes (Clarke & Sheppard 1970).

Our data support Sims's (1983) contention that *zelicaon* diapause physiology and host-plant selection are highly plastic. The clustering of the orange-feeding Orland population with other Central Valley populations rather than with Hemet implies that the northern and southern orange-feeders evolved separately. While fennel is abundant in lowland areas, and is heavily used (Shapiro 1974a, 1974b), the use of orange may allow *zelicaon* to increase its range despite the inferiority of orange as a host plant (Masuda 1981).

TABLE 7. Observed genotype frequencies for the three polymorphic loci in populations where n ≥ 14.

		Populations					
Genotype	(Electromorph-electromorph)	Hemet	Orland	Butts Canyon	Suisun	Rancho Cordova	Castle Peak
PGI	13-13	0	0	0.14	0	0	0.13
	13-7	0	0.05	0.07	0	0.13	0.11
	7-7	1.00	0.95	0.80	1.00	0.89	0.86
PGM	32-32	0.21	0.11	0	0.08	0	0.06
	32-26	0	0	0	0.08	0.31	0.11
	32-23	0.05	0.05	0.17	0.08	0.19	0.11
	32-20	0	0	0.17	0.08	0	0.09
	26-26	0.11	0.21	0	0.21	0.06	0.09
	26-23	0.26	0.53	0.33	0.25	0.19	0.23
	26-20	0	0	0	0.42	0.13	0.09
	23-23	0.21	0.05	0.17	0.42	0	0.14
	23-20	0.05	0	0.17	0	0.13	0.03
	20-20	0.11	0.05	0	0.13	0	0.06
MPI	44-44	0	0	0	0	0	0
	44-40	0	0	0	0	0	0
	44-37	0	0	0	0	0	0
	44-33	0	0.10	0	0.14	0	0.03
	44-28	0	0	0	0	0	0
	40-40	0	0	0	0	0	0
	40-37	0	0	0	0	0	0
	40-33	0	0.10	0	0.14	0	0.10
	40-28	0	0	0	0	0	0
	37-37	0.11	0.10	0.13	0	0	0.13
	37-33	0.32	0.20	0.50	0.29	0.10	0.29
	37-28	0.05	0	0	0	0	0.03
	33-33	0.42	0.40	0.25	0.43	0.70	0.32
	33-28	0.05	0.10	0.13	0	0	0.67
	28-28	0.05	0	0	0	0.20	0.03

Butts Canyon (North Coast Range serpentine) and Castle Peak (Sierran volcanic alpine) probably represent relict *zelicaon* populating rocky, unforested environments with endemic host plants. Other Lepidoptera are known to be similarly disjointly distributed between the Coast Range serpentines and the alpine Sierra; *Papilio indra, Pieris sisymbrii,* and *Euchloe hyantis* all occur obligately in these areas with few or no intervening populations (Shapiro unpubl.). Clustering of Blue Ridge (east of the Vaca Hills, the easternmost part of the Inner North Coast Ranges in Yolo and Solano cos.) with these postulated relict populations rather than with other multivoltines in the Central Valley is especially interesting. *Papilio zelicaon* was not seen in the Vaca Hills during summer in field studies initiated by Shapiro (unpubl.) in 1972. Males were seen on the ridge-tops, but only in spring coinciding with such behavior on Coast Range serpentines to the north. At this time, the site had one patch of 10 fennel plants. In 1975, females were observed

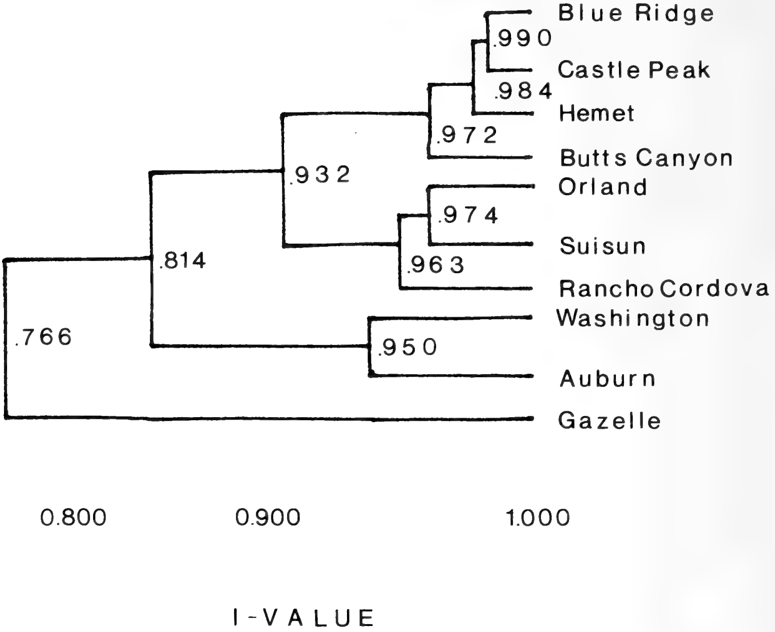

FIG. 2. Phenogram of *P. zelicaon* populations (UPGMA; Ferguson 1980).

ovipositing on fennel. By 1978, fennel was spreading rapidly in disturbed areas and *zelicaon* showed evidence of four generations in one year. Presently, there are over 500 fennel plants along three miles of road in this area, and it continues to spread. It has been presumed that the multivoltine Vaca Hills *zelicaon* are upslope colonists from multivoltine Central Valley populations. Our study suggests, rather, that they are at least partially downslope colonists from univoltine ridge-top (Coast Range) populations. If this is the case, they have very rapidly evolved multivoltinism, apparently as an adaptation to the spread of fennel. This supports the plasticity of host plant- and diapause-"switching" proposed by Sims (1983) to explain the evolution of multivoltinism. Certainly, *zelicaon* is physically capable of having colonized these canyons from the Coast Range. Shields (1967) demonstrated that *zelicaon* is a hilltopping species; adult males and receptive females congregate on summits to mate, thereby promoting gene flow among neighboring populations. Shields determined that adults are capable of traveling several km per day.

Studies by Ehrlich and Raven (1969) and Endler (1973) suggest that populations undergoing sufficiently strong divergent selection will differentiate despite the counter-effects of continuous gene flow. This has been observed in wild Lepidoptera with populations showing differentiation in metrical traits as a result of differential selection, despite close proximity and gene flow (Creed et al. 1959, Clarke & Sheppard 1962). If gene flow along the Coast Range ridge-tops has been continuous, the Vaca Hills population has not only become multivoltine within three years time, but has done so with constant influx of univoltines from the Coast Range. Multivoltinism may be evolving through hybridization, or through selection. Multivoltinism shortens generation time and should, all other factors being equal, be selectively advantageous.

Wright (1943a, 1943b) theorized that a continuously distributed species exposed to different conditions of selection would differentiate if subdivided into partially isolated "islands" separated through inbreeding or limited dispersal ability. *Papilio zelicaon* is certainly distributed throughout habitats with different selection conditions and appears to be sufficiently vagile to be essentially continuous in distribution throughout major portions of its range. More finely focussed studies of nonglycolytic enzymes and mark-release-recapture studies on movement would help to determine the size and location of hilltopping regions and the appropriateness of Wright's "island" models to *zelicaon*.

Papilio zelicaon is composed of low- and high-elevation ecotypes defined by host-plant preferences and diapause physiology. These traits may be determined by a relatively small number of loci that are under strong selection pressure and whose distribution is not reflected by electrophoretically accessible glycolytic enzyme loci, which show great genetic similarity among populations.

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A NEW SUBSPECIES OF *COENONYMPHA TULLIA* (MÜLLER) (NYMPHALIDAE: SATYRINAE) CONFINED TO THE COASTAL DUNES OF NORTHERN CALIFORNIA

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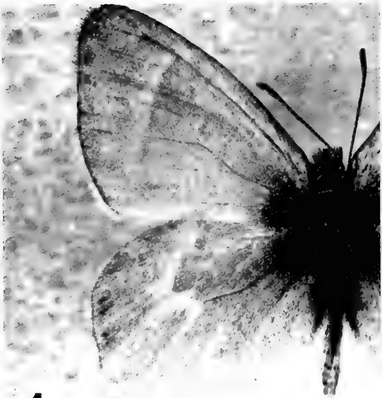
ABSTRACT. *Coenonympha tullia yontocket* is described from a single known population confined to the coastal sand dunes north of Crescent City, Del Norte County, California. It is most similar in phenotype to *C. tullia eunomia* Dornfield, but may be distinguished by wing characters. A population of *C. tullia eryngii* Hy. Edwards occurs ten kilometers away; these two populations show no clear signs of reciprocal introgression in wing characters. Electrophoretic analysis indicates that *yontocket* retains the high genetic variability characteristic of other *tullia*-group taxa, but no diagnostic alleles were found. The high genetic variability is most likely maintained by gene flow from *eryngii*. *Coenonympha tullia* subspecies *yontocket*, *eunomia*, *eryngii*, and *california* Westwood are genetically very similar (Nei's unbiased genetic distance <0.035). The data justify the placement of *yontocket* as a subspecies rather than a species. This subspecies is a likely candidate for listing as threatened in California; collectors and developers are urged to protect this population from extinction.

Additional key words: *Coenonympha tullia yontocket*, taxonomy, electrophoresis, ringlets, threatened species.

Investigation of the coastal dunes of northern California has turned up a unique population of the widespread Ringlet butterfly, *Coenonympha tullia* (Müller). This population occurs in the vicinity of Crescent City, Del Norte Co., and has an ochre ground color; it is wholly contained within the range of *C. tullia eryngii* Hy. Edwards, a widespread subspecies with a whitish ground color. It is quite similar phenotypically to *C. tullia eunomia* described by Dornfield (1967), whose nearest known population is 250 km away in the Umpqua River drainage in southeastern Oregon (Porter & Geiger 1988). This new population flies in the fog belt, and shows the heavy melanization of the wings and body characteristic of butterflies from this type of environment (Hovanitz 1941, McCorkle & Hammond 1988).

Herein, we provide a description of this population as a new subspecies, and justify our taxonomic placement with genetic evidence from electrophoretic analysis. We did not examine genitalic or larval characters: Davenport (1941) indicated that all *tullia*-group taxa were indistinguishable genitalically despite high levels of intrataxon variability, and description of the immature stages would be of little taxonomic use given our small series and the lack of comparative material.

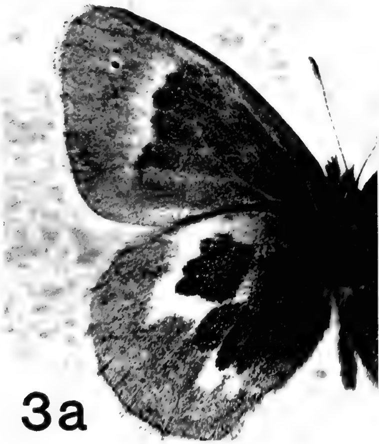


1a

1b

2a

2b



3a

3b

Coenonympha tullia yontocket, new subspecies
(Figs. 1–3)

Description. Holotype (Fig. 1): male; dorsal ground color dull ochraceous; medium to light gray scaling along the costal and distal forewing margins, extending proximally along the veins. Dorsal hindwing with gray scaling along distal margins, stronger in anal area. Eyespots absent; ventral whitish markings barely visible from above. Both dorsal surfaces strongly melanized subbasally. Ventral forewing ground color deep ochraceous, almost orange; medium band whitish, extending from R veins to Cu_2; ground color fades to whitish, then greenish gray in costal and apical regions, becoming strongly suffused with melanized scales; eyespots absent. Ventral hindwing ground color brownish ochre in discal region, fading to greenish gray beyond the median markings. Median band whitish, well marked; absent only between Cu_1 and Cu_2. Whitish basal patch present at radial vein. Eyespots absent. Darkened, single marginal line on all wing surfaces, well expressed ventrally. Head, thorax, and ventral hindwing bases covered with long hairs matching ventral hindwing ground color.

Morphological variation (Figs. 2, 3). Forewing length, males: 14–18 mm (n = 65); females: 15–19 mm (n = 10). Spring brood averages slightly larger (males: $\bar{x} = 16.3$ mm; n = 52) than fall brood (males: $\bar{x} = 14.7$ mm; n = 17). Spring brood: gray scaling dorsally along the distal margins of both wings may be almost absent, but may extend proximally in extreme individuals (n = 2) so that the outer third of the wing is pale gray. Ventral forewing median band whitish; extends from R veins to Cu_1 or Cu_2. Single ventral forewing eyespot absent in most individuals, but may be up to 1 mm diameter, unpupilled ochraceous or yellow, or yellow pupilled with black. Ventral hindwing: ground color sometimes obliterated by melanized scaling in discal area; wholly brownish or wholly greenish in some individuals. Median band sometimes weakly expressed between Cu_1 and Cu_2, rarely absent below M_3 (Fig. 3b). Whitish basal patches often present, connecting to median markings via the costa in extreme individuals (n = 2) (Fig. 3a). Eyespots absent in almost all individuals; rarely up to three, yellow or yellow with black pupils, most likely between Cu_1 and Cu_2. Marginal line often double. Females (Fig. 2) tend towards less melanization, broader wings. Fall brood: markings similar to spring brood, more animals with brownish rather than greenish ventral ground color, and more likely expression of ventral basal patches.

Diagnosis. Separable immediately from nearby populations of *eryngii* by the ochraceous ground color. Separable from *eunomia* ventrally by stronger expression of the medial markings; from *eunomia* and *ampelos* ventrally by the frequent occurrence of basal patches, and dorsally by gray scaling along the veins and outer wing edges.

Distribution. Known only from Del Norte Co., California, among the coastal sand dunes north of Crescent City, beginning at the north shore of Lake Earl and extending north 7.5 km to the south bank of the Smith River (Fig. 4). This area is hereby designated as the type locality. Seemingly suitable habitat between Lake Earl and Point St. George may also be populated by *yontocket*. Not present in abutting disturbed habitats to the east (mostly cow pastures), or at the dunes north of Arcata Bay in Humboldt County, California. Replaced by *eryngii* 10 km to the east on exposed serpentine hilltops.

Material examined. Holotype: Male, California, Del Norte Co., 4 km W Fort Dick, 8-IX-1979, leg. S. O. & E. Mattoon. Deposited in the Bohart Museum at the University of California, Davis. Paratypes: California, Del Norte Co., 4 km W Fort Dick, end of Kellogg Rd. S to north shore of Lake Earl, 2-VI-1979 (15 males), 30-VI-1979 (4 males) & 8-IX-

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←

FIGS. 1–3. **1,** *Coenonympha tullia yontocket* holotype male; (a) dorsal and (b) ventral surfaces. **2,** *Coenonympha tullia yontocket* paratype female; (a) dorsal and (b) ventral surfaces. Unlike this specimen, many females do show basal ventral hindwing patches. **3,** *Coenonympha tullia yontocket* ventral surfaces, showing the extremes of expression of maculation. The reduced pattern of (b) is characteristic of *C. tullia eunomia* populations.

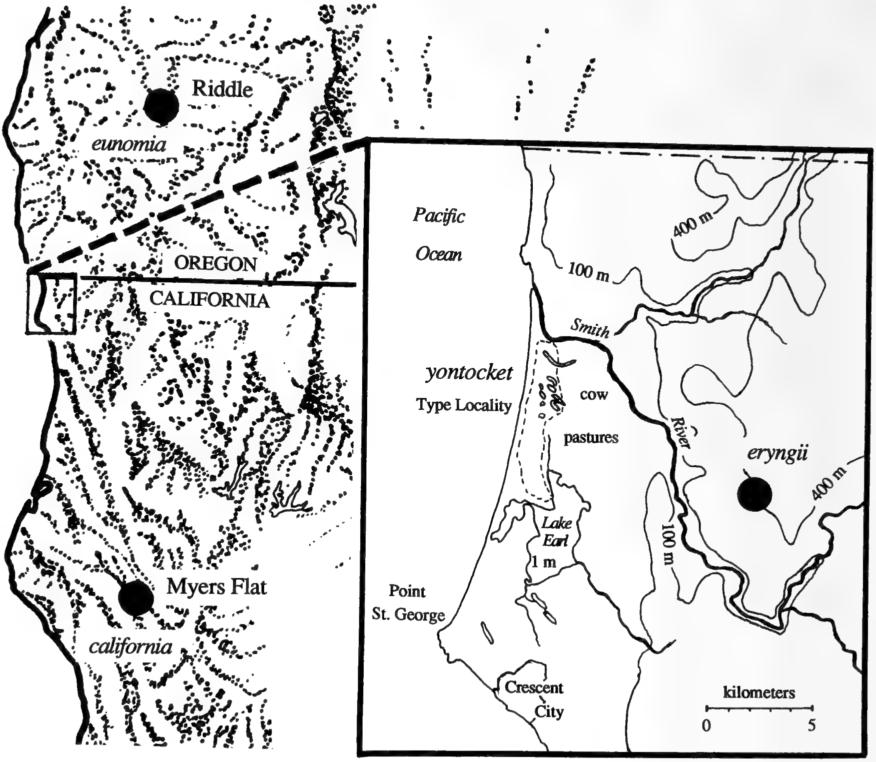

FIG. 4. Map showing localities sampled in northwestern California and southwestern Oregon. Note the close proximity of the *eryngii* population to the type locality of *yontocket* (inset). Neither subspecies occurs in the intervening cow pastures.

1979 (16 males, 2 females), S. O. & E. Mattoon, leg. These will be deposited in the Bohart Museum, the California Department of Food and Agriculture, the California Academy of Sciences, the Los Angeles County Museum, the Allyn Museum, and the National Museum of Natural History, Smithsonian Institution. Additional material: wing vouchers from specimens used for electrophoretic analysis (29 males, 8 females), collected from the Yontocket Archeological Site at the north end of the population range.

Biology. Flight periods May–July and September-October. Habitat: elev. 2 m; in grassy areas among dunes with coniferous lee slopes and grassy exposed slopes, and among dunes on slightly elevated ground around seasonally marshy sphagnum bogs which fill during the rainy season. 2 females oviposited (5 observations) on dry grass stems (mixed species composition) approx. 2–5 cm above soil in areas free from flooding. Larvae and pupa (n = 2 larvae; 1 pupated) are apparently not different from those of *eryngii* (n = 8 larvae; 2 pupated). Larval host(s) presently unknown.

Etymology. *Coenonympha tullia* subspecies are often given American Indian names. This population is dedicated to the memory of the Yontocket tribe, which once had seasonal settlements in these dunes.

In deciding to name this population, we considered two points: (i) is it sufficiently distinct from *C. t. eunomia* to warrant taxonomic recognition?, and (ii) given that an apparently permanent population of

C. t. eryngii occurs in serpentine grassland habitat on a hilltop 10 km to the east and within sight of the *yontocket* population (Fig. 4), should *yontocket* be given species status? To address these questions, we performed starch gel electrophoresis to provide insights into the genetic relationships among the *yontocket* population, the nearby *eryngii* population, a previously studied *eunomia* population from Riddle, Oregon, and a *C. t. california* Westwood population from near Myers Flat, Humboldt Co., California. Each of these populations comes from relatively isolated areas of grassland habitat, providing a control on the potential for genetic differentiation resulting solely from variation in local population structure. Previous work has established that *eryngii*, *california*, and *eunomia* are members of a single polytypic species (Porter & Geiger 1988).

MATERIALS AND METHODS

Butterflies were netted and temporarily stored on wet ice, hand-carried or mailed back to Davis, then frozen alive at −80°C for storage until analysis. Electrophoretic analysis followed the protocol of Ayala et al. (1972) and Geiger and Shapiro (1986), with one modification: rather than using sponge wicks to complete the circuit between the electrode buffer solutions and the gels, gel molds were used which allowed the ends of the gels to contact the electrode buffer directly. We scored 13 loci: adenylate kinase (AK-1), aldolase (ALDO), fumarase (FUM), glutamic-oxaloacetic transaminase (GOT-1, GOT-2), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), α-glycerophosphate dehydrogenase (α-GPDH), isocitrate dehydrogenase (IDH-1), malate dehydrogenase (MDH-1, MDH-2), phosphoglucomutase (PGM), phosphoglucose isomerase (PGI), and superoxide dismutase (SOD-1). Zymograms were scored as described in Porter and Geiger (1988), and data were analyzed using the computer program BIOSYS-1 (Swofford & Selander 1981).

RESULTS

Allelic frequencies for the *yontocket*, *eryngii*, and *california* populations are given in Table 1; allelic frequencies at these loci were previously given for the *eunomia* population in Porter and Geiger (1988). All populations show high levels of genetic variability characteristic of *Coenonympha tullia* populations elsewhere (Table 2; Porter & Geiger 1988); this is an indication that the *yontocket* population has not been through a significant genetic bottleneck in its recent past. Table 3 shows genetic relationships among these populations using Nei's unbiased minimum distance and identity measures (Nei 1978). The phenogram constructed based on these values using UPGMA (Fig. 5; see Sneath &

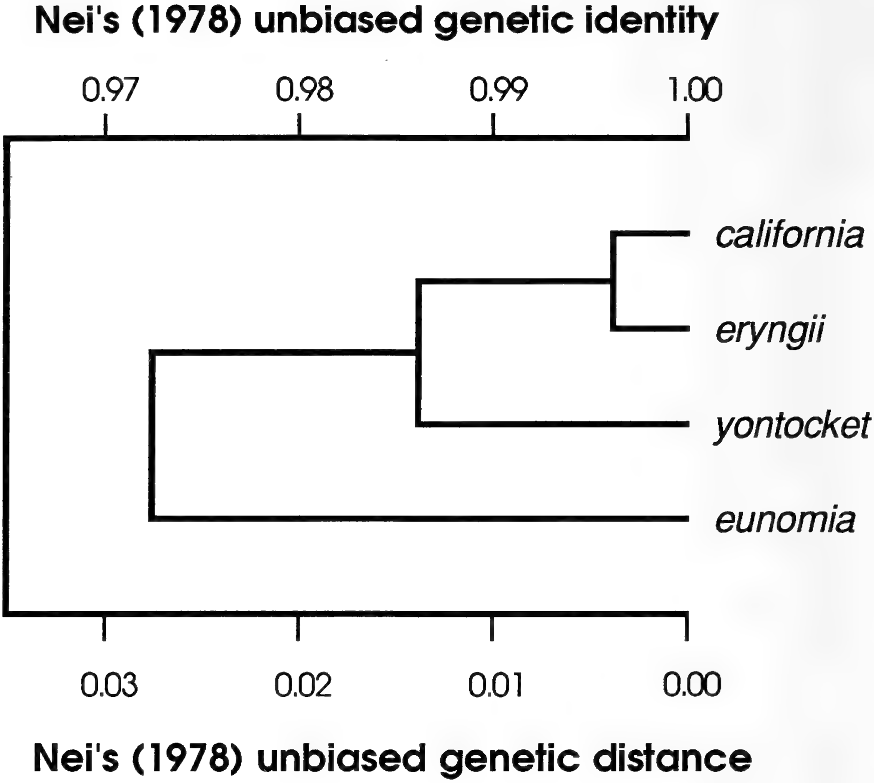

FIG. 5. Phenogram of genetic relationships constructed using the UPGMA algorithm on data from Table 3. *Yontocket* does not cluster with *eunomia*, but all populations are genetically very similar.

Sokal 1973 for methodological details) does not group *yontocket* with *eunomia*, despite their general similarity in wing characteristics. These distance-identity values indicate a very low level of genetic differentiation overall, corresponding to subspecies-level differentiation in most taxa (Thorpe 1983), including butterflies (AHP unpubl. data; H. J. Geiger, pers. comm.).

DISCUSSION

Neither the *yontocket* nor *eryngii* population in Fig. 4 has colonized intervening, non-native grassland presently used for grazing. There is also no clear evidence of introgression in wing pattern traits in the animals we sampled. The pale gray along the veins and wing edges dorsally in *yontocket* may well be evidence of such introgression, but populations from the Pit River drainage in eastern California, where

TABLE 1. Allelic frequencies of *Coenonympha tullia*-group taxa. Population localities and locus abbreviations given in the text.

Locus and allele	Taxon		
	california[1]	*eryngii*[2]	*yontocket*[3]
AK-1			
76	0.056		
86			0.023
90	0.361	0.275	0.500
100	0.556	0.675	0.432
102	0.028		
110		0.050	0.045
ALDO			
100	1.000	1.000	1.000
FUM			
100	1.000	1.000	1.000
GAPDH			
100	1.000	1.000	1.000
GOT-1			
89	0.028	0.014	
91	0.194	0.111	0.135
94			0.041
100	0.778	0.806	0.730
102		0.056	
108		0.014	0.054
110			0.041
GOT-2			
100	0.944	0.944	0.973
112	0.056	0.056	0.027
α-GPDH			
75	0.028		
90		0.042	
96		0.014	
100	0.972	0.931	1.000
110		0.014	
IDH-1			
90	0.028	0.014	
92	0.028	0.028	
100	0.417	0.583	0.730
103	0.194	0.208	0.108
106	0.306	0.125	0.162
111	0.028	0.042	
MDH-1			
91	0.028	0.014	
93	0.028		
100	0.861	0.986	0.932
105	0.028		
110	0.056		0.068
MDH-2			
96	0.028		
100	0.972	0.917	0.932
105		0.069	0.054
110		0.014	0.014
PGI			
81			0.014
88	0.028		0.014
94		0.028	
97	0.083		
100	0.306	0.333	0.284
103	0.056	0.028	
107	0.306	0.389	0.662
105		0.042	
111	0.028	0.069	
114	0.194	0.056	0.027
117		0.014	
121		0.042	
PGM			
90		0.014	
94	0.028	0.042	
97		0.028	0.027
100	0.361	0.486	0.662
106	0.528	0.389	0.311
110	0.083	0.028	
112		0.014	
SOD-1			
89	0.028		
100	0.944	1.000	1.000
120	0.028		

[1] n = 18.

[2] n = 36, except at AK-1, where n = 20.

[3] n = 37, except at AK-1, where n = 22.

california and *eryngii* (white ground color), and *ampelos* (ochre ground color) intergrade, produce many specimens of wholly intermediate background coloration (Porter & Geiger 1988). These observations suggest that differentiation is maintained by behaviors related to habitat and(or) host-plant selection—but not necessarily by reproductive barriers.

Phenograms based on genetic distance-identity indices are often used

TABLE 2. Genetic variability statistics for the three populations given in Table 1. Mean number of alleles per locus = $\bar{x}_{alleles}$. Percent of loci polymorphic = P. Observed heterozygosity = H_{obs}. Heterozygosity calculated from Hardy-Weinberg proportions = H_{exp}. Standard errors in parentheses.

Population	$\bar{x}_{alleles}$	P	H_{obs}	H_{exp}
california	3.2 (0.5)	84.6	0.303 (0.090)	0.283 (0.080)
eryngii	3.5 (0.7)	69.2	0.240 (0.078)	0.246 (0.076)
yontocket	2.5 (0.4)	61.5	0.199 (0.070)	0.210 (0.064)

to approximate phylogenetic relationships between species, but these measures can only reflect overall genetic differentiation within a species. Within a species, the degree of differentiation expressed among populations reflects a balance between the forces of natural selection, genetic drift, mutation, and gene flow acting at each locus. The fact that *yontocket* is more similar to *california* and *eryngii* than to *eunomia* implies that gene flow between *yontocket* and *eunomia* is interrupted: it seems unreasonable to consider them consubspecific. This interpretation is also in agreement with the disjunct distribution of these taxa.

The high level of variability in *yontocket* enzyme characters also requires explanation. The *yontocket* population probably has an effective breeding population of moderate size, and is likely to be affected somewhat strongly by genetic drift. If *yontocket* is fully reproductively isolated from *eryngii,* then *exceedingly* strong selection on these enzymes is required to maintain such high numbers of alleles; on the other hand, infrequent influxes of *eryngii* phenotypes could easily maintain this variability. Given that there is evidence of some gene flow between *eunomia* and *eryngii* in southeastern Oregon (Porter & Geiger 1988) (the subspecies separated by the greatest geographic distances in the phenogram of Fig. 5), and that *yontocket* is of intermediate similarity, we think it is wise to place *yontocket* as a subspecies of *tullia* unless subsequent studies on reproductive biology demonstrate intrinsic barriers to gene flow. The level of current gene flow between these two adjacent *tullia*-group populations, based on their present constellations of allelic frequencies, indicates that these populations exchange between four and five breeding individuals every generation on average (Porter, in prep.), further supporting the taxonomic placement proposed here.

The evolutionary origins of the diagnostic *yontocket* traits are explainable by a number of plausible scenarios (many non-diagnostic traits may be attributable to gene flow from *eryngii*). The most likely scenario is that these traits arose from *eunomia* or even *columbiana* McDunnough, which may have had more southerly distributions during the last glacial stages. A population of *Polites mardon* (Edwards) (Hesperiidae) also occurs in Del Norte Co., California, disjunct from nearest

TABLE 3. Nei's (1978) unbiased genetic identity (above diagonal) and distance (below diagonal) values between population pairs. Populations given in the text.

	Taxon			
Taxon	*california*	*eryngii*	*eunomia*	*yontocket*
california		0.997	0.976	0.982
eryngii	0.003		0.974	0.990
eunomia	0.030	0.035		0.979
yontocket	0.018	0.010	0.026	

known populations in southwestern Washington State (Scott 1986; T. C. Emmel, J. F. Emmel & S. O. Mattoon, in prep.). However, this alone does not explain the high incidence of the basal ventral hindwing patches, a characteristic of populations in the Great Basin and Rocky Mountains. Whether the basal ventral patch is adaptive, ancestral in North America, or exists in *yontocket* as a result of past gene flow from the east, is unknown. Functionally unrelated traits can clearly have independent geographic ranges within a species. Thus, the conclusions we draw concerning the historical biogeography of *tullia*-group traits depend largely on whether or not biological species boundaries exist within the complex (and if they do exist, where they are).

We think it is particularly important to recognize the threat of extinction to *C. t. yontocket* caused by habitat destruction. The southern end of the population distribution occurs in habitat patches within an abandoned gridwork of streets originally intended as a housing development. With the spread of development by the tourist industry around the recently formed Redwood National Park, the *yontocket* habitat is likely to become attractive to developers of beachfront property—both for private and public use. Given the failure of *yontocket* to invade adjacent cow pastures, a habitat used by *tullia* subspecies elsewhere in western North America, it is likely that such development will have severe impact on this population. We urge lepidopterists to refrain from collecting in this fragile ecosystem, and to provide support for groups dedicated to the preservation of this and other threatened taxa along the Pacific Coast.

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A PROCEDURE FOR EXAMINING THE GENITALIC MUSCULATURE OF LEPIDOPTERA

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ABSTRACT. The functional morphology of the genitalia (characteristics of the sclerotized parts and the presence and position of the associated musculature) has been the basis of recent phylogenies of Tortricidae and several other groups of Lepidoptera. Examination of this musculature can be difficult. Procedures for fixing muscles and preserving specimens for future preparation, for dissecting, cleaning and staining the genitalia, and for treating the preparation for viewing are presented. Using these methods, one can stain muscles selectively, minimize handling during cleaning to reduce the potential of physical damage, and view the musculature through transparent sclerotized parts.

Additional key words: functional anatomy, dissection, staining, male genitalia.

The sclerotized parts of the genitalia often are the best or only means of identifying species of Lepidoptera and can provide important characters for determining taxonomic relationships. The associated functional musculature has been used as another source of data on phylogenetic relationships, particularly of higher taxa in Lepidoptera in recent decades.

Forbes (1939) described differences in the male genitalic musculature among six species in five families of Lepidoptera that he examined and two other species illustrated by Snodgrass (1935:fig. 308). Utilization of these characters in taxonomic studies of Lepidoptera was proposed by Stekol'nikov (1965), who examined males of five and females of two species of Noctuidae. Stekol'nikov (1967a, 1967b) constructed a phylogeny of butterflies based on the functional morphology of the genitalia and discussed evolutionary trends in the genitalia of primitive Lepidoptera. An ensuing series of papers by Kuznetsov and Stekol'nikov (1981, 1984, 1985) proposed the higher classifications of various groups of Lepidoptera based largely upon genitalic musculature of the males, and others (e.g., Razowski 1981) have employed these characters in studies of Tortricidae and other Lepidoptera.

Workers wishing to investigate these conclusions further and those intending to use their system to assign troublesome genera to tribe or subfamily may have difficulty preparing specimens for examining musculature, as there is little published information on the methodology. The following procedure, derived by trial and error and from the suggestions of colleagues, may greatly simplify this task. We worked with Tortricidae, and the techniques should be applicable to all Lep-

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idoptera although we did not attempt dissection of smaller moths such as leaf miners. With this procedure, much of the fatty tissue is dissolved, so handling time during cleaning is minimized. The sclerotized parts turn transparent which enables one to view the internal muscles and their connections.

Preparation of Lepidopterous Genitalic Musculature

The best preparations of genitalic musculature result from proper preservation of specimens, from careful dissection, cleaning, and staining, and from treating the stained, dissected genitalia for viewing. Sectioning with a microtome may be necessary for minute Lepidoptera, but the following procedure was effective on a species of *Diactenis,* one of the smallest tortricid moths. Although it was not tried, the procedure should be satisfactory for examination of female musculature as well.

Some internal muscles and their attachment points are seen more easily when the valvae are spread. The valvae of some specimens will spread automatically when killed or immersed live in the preservative, or they can be forced open by squeezing the pregenital segments prior to preservation in fluid. However, using our procedure, the sclerotized parts of the genitalia become transparent, and attachment points can be determined. Consequently, most preparations were of specimens with the valvae closed, because it was easier to position them for dorsal, ventral, or lateral viewing.

Preservation of the specimen: Musculature of dried, pinned specimens can be observed, but better preparations are obtained from specimens preserved in fluid soon after capture. Specimens placed directly into 70% alcohol (we used either isopropanol or ethanol) are usually satisfactory, but the muscle tissue may deteriorate slowly, and older specimens may be unusable.

We obtained better results by first immersing the specimen in Kahle's fluid for 12–24 hours to fix the muscles. Peterson (1964:67–68) and Borror et al. (1976:736) give different, but equally effective recipes for Kahle's fluid.

The moth can be immersed directly into Kahle's fluid; then a few drops of 70% alcohol should be added to enhance wetting. Alternatively, the specimen can be dipped into 70% alcohol or cellusolve (ethylene glycol monoethyl ether) for a few seconds until soaked, then transferred to Kahle's fluid. When it is impractical to preserve specimens immediately, muscles of those killed in dry cyanide vials can be similarly fixed if treated soon after capture.

After fixing the muscles, the specimen can be dissected immediately or retained in 70% alcohol. Specimens transferred from Kahle's fluid to 70% alcohol were in excellent condition more than five years after preservation. Prolonged immersion in Kahle's fluid or preservation in 95% or absolute alcohol makes the muscles brittle and gives them a greater tendency to detach from the sclerotized structures.

A few preparations were made from dried, pinned specimens by removing the abdomen and soaking it in warm water until the viscera softened. The muscles of previously dried specimens are inelastic, sometimes shrunken and contorted, and easily detached, and they do not stain as well as those of specimens preserved in fluid, so results vary.

Dissection and staining: Remove the abdomen from the specimen and place it in 70% ethanol. Shallowly insert the tip of each of two pair of No. 5 jeweler's forceps, one on each side of the pleuron, into the intersegmental membrane anterior to the last or next to last visible pregenital abdominal segment, and carefully peel away the integument. Continue to remove the integument of the pregenital segments from the genitalia until none can be removed without risking damage to the genitalic muscles.

Large agglomerations of fat will inhibit staining, but at this time attempt to remove only the larger looser globules atop the base of the aedeagus to avoid damaging the muscles.

Place the excised genitalia in a drop or two undiluted van Giesen's muscle stain (1 part of 2–3% acid fuchsin and 9 parts of saturated picric acid) on a stain plate for 3–10 minutes or until stain begins to penetrate but does not completely stain the internal muscles of the tegumen. Next, soak the preparation in 70% alcohol for several hours to allow stain to penetrate internal muscles while washing away excess.

After soaking in alcohol, muscles of a properly stained preparation will be red throughout, fat will be paler, and the sclerotized parts should be mostly unstained. Some staining of the sclerotized parts is unavoidable, especially the aedeagus, some of the more membranous parts, and around the margins of other structures.

If too much stain was removed, the exposed muscles on the aedeagus will have lost much of their color while the internal muscles remain red. Place such preparations briefly into a drop of stain then wash off the excess in 70% alcohol.

If understained, stain will not have penetrated the internal muscles, and the staining-soaking step should be repeated. Sometimes, particularly in previously dried specimens, some muscles will not stain well, and additional attempts will only stain the sclerotized structures.

Subsequent steps will remove some additional stain, so slight overstaining is acceptable. If the sclerotized portions are stained excessively, additional soaking in clean 70% alcohol may eventually remove the excess. If still overstained, immerse the preparation in hydrogen peroxide solution, then restain if necessary. Final cleaning follows the next step.

Transfer the preparation to cellusolve and soak for 10 hours or longer. The solvent will dehydrate the preparation and dissolve much of the fat and cause much of the remainder to agglomerate into easily removable globules. The dehydrated remnants of pregenital segments and unwanted extrinsic muscles can be abraded from the genitalia easily with forceps or fine probes, and most of the remaining fat globules can be teased free of the preparation with fine probes. Smaller traces of fat will dissolve or turn transparent in the next step, so it is not necessary to risk damage by trying to remove small bits trapped between muscles.

Preparation for viewing: Place the cleaned preparation in methyl salicylate (oil of wintergreen) for viewing. From about 30 minutes to about five days following immersion, the sclerotized structures will be sufficiently transparent to view the internal muscles, yet will retain enough pigmentation to determine the attachment points of the muscles.

With prolonged immersion in methyl salicylate, the preparation becomes increasingly brittle and more easily damaged during handling, and the sclerotized parts slowly darken, presumably due to infusion of the stain. Partial darkening may help identify sclerotized structures, but after about five days, some musculature may be difficult to see through the sclerotized parts. A darkened preparation can be bleached in hydrogen peroxide after being washed of methyl salicylate in cellusolve then 70% alcohol. It can be restained and treated for viewing as before, but it will be more brittle and somewhat inferior overall.

We positioned preparations for viewing with glass chips in the depression of a culture slide filled with methyl salicylate. A camera lucida attached to a binocular dissecting microscope facilitated sketching the preparation. When necessary, a compound microscope was used to determine musculature attachment points accurately.

After examination, the preparation was washed free of methyl salicylate in cellusolve, then bathed in 70% alcohol. It was preserved in 70% alcohol with the remainder of the specimen. In the alcohol, the stain slowly leaches from the preparation. It can be restained and cleared for re-examination, but will be of lesser quality than after the first treatment.

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GENERAL NOTES

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ON THE LOCATION OF SOME H. A. FREEMAN SKIPPER HOLOTYPES (HESPERIIDAE)

Additional key words: American Museum of Natural History, Mexico.

In "Records, New Species, and a new Genus of Hesperiidae from Mexico," Journal of the Lepidopterists' Society, Vol. 23, Supplement 2, 1969, I stated that the holotypes of most of the species described were to be placed in the United States National Museum, Washington, D.C. Actually, these holotypes were deposited in the American Museum of Natural History (AMNH), New York, in 1981 along with my entire collection of Mexican Hesperiidae. Thus, holotypes of the following species can be found in the AMNH: *Pyrrhopyge tzotzili, Mysoria wilsoni, Epargyreus windi, Epargyreus brodkorbi* (designated in 1969 paper for Museum of Zoology, Univ. of Michigan), *Astraptes louiseae, Astraptes gilberti, Polythrix mexicanus, Aethilla chiapa, Mimia chiapaensis, Windia windi, Staphylus veytius, Staphylus zuritus, Quadrus francesius, Enosis matheri, Dalla ramirezi, Vettius argentus, Niconiades comitana, Anthoptus macalpinei, Cynea nigricola, Pheraeus covadonga, Carystoides escalantei, Carystoides abrahami, Carystoides floresi, Carystoides mexicana, Atrytone mazai, Atrytone potosiensis, Mellana montezuma, Euphyes chamuli,* and *Tirynthia huasteca.*

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EFFECTS OF HANDLING ON *EUPHYDRYAS EDITHIA* (NYMPHALIDAE)

Additional key words: Mark-release-recapture, wing wear, aging.

A central component of most studies of insect population dynamics is mark-release-recapture (MRR). It is generally assumed that handling insects during MRR does not affect either their survival or behavior, but rarely have these assumptions been tested. Several previous studies have looked at possible effects of handling on recapture probabilities. R. H. T. Mattoni and M. S. B. Seiger (1963, J. Res. Lepid. 1:237–244) compared observed with expected values of multiple recaptures of *Philotes sonorensis* and found no decrease in observed recaptures, as would be expected if repeated handling had a negative effect on recapture probability. Other studies, however, found reduced probabilities of recapturing handled butterflies in the area of first capture (Singer, M. C. & P. Wedlake 1981, Ecol. Entomol. 6:215–216; Morton, A. C. 1982, Oecologia 53:105–110; Gall, L. F. 1984a, Biol. Conserv. 28:139–154).

Studies attempting to determine the age-structure of butterfly populations commonly use wing-wear as an indicator of age (Watt, W. B., F. S. Chew, L. R. G. Snyder, A. G. Watt & D. E. Rothschild 1977, Oecologia 27:1–22; Ehrlich, P. R., A. E. Launer & D. D. Murphy 1984, Am. Nat. 124:525–539; Gall, L. F. 1984b, Biol. Conserv. 28:111–138). Butterflies captured with undamaged (fresh) wings are considered young, while butterflies with worn wings are scored as old. In such studies, it is important to determine whether the MRR technique itself measurably wears the insects; such an effect would increase age estimates of repeatedly handled butterflies and possibly decrease survival. In this

TABLE 1. Linear regression of change in condition on number of handling events, by days in residence (males).

Days in residence	Sample size	Slope (m)	95% confidence limits for the slope		Correlation coefficient (R)	Power* (1 − β)
3	24	0.08	−0.30	0.47	0.10	0.12
4	30	0.00	−0.29	0.30	0.01	0.13
5	32	−0.18	−0.39	0.04	0.29	0.52
6	28	−0.21	−0.41	0.00	0.37	0.71
7	25	0.12	−0.13	0.37	0.20	0.25
8	27	0.07	−0.11	0.26	0.17	0.27
9	25	−0.03	−0.19	0.13	0.08	0.12
10	19	0.09	−0.10	0.28	0.23	0.21

* Power values for correlation coefficients from Cohen, J. 1977, Statistical power analysis for the behavioral sciences, rev. ed., Academic Press, New York, 474 pp.

study, we attempt to determine if handling during MRR studies causes an increased rate of wing-wear.

At Stanford University's Jasper Ridge Biological Preserve, *Euphydryas editha bayensis* (Sternitzky) populations have been under experimental observation since 1960. In the past twenty-eight years, extensive data from MRR studies have been collected (Ehrlich, P. R. 1965, Evolution 19:327–336; Ehrlich, P. R., R. R. White, M. C. Singer, S. W. McKechnie & L. E. Gilbert 1975, Science 188:221–228; and Baughman, J. F., D. D. Murphy & P. R. Ehrlich 1988, Oecologia 75:593–600).

In 1981, an intensive MRR study was carried out at the Jasper Ridge Area H demographic unit from 23 March to 1 May (Ehrlich et al. 1984, above). Butterflies were handled on all of the days that they flew; a total of 478 individuals were handled at least once during the season (310 males and 168 females). Males are more likely to be caught than females because of differences in flight behavior. Three experienced field workers attempted to capture all of the butterflies present on each day of the flight season. The MRR protocol followed that of P. R. Ehrlich and S. E. Davidson (1960, J. Lepid. Soc. 14: 227–229), with each individual given a characteristic mark with a felt-tipped, permanent-ink pen. Between capture and release, individuals were kept in glassine envelopes with their wings together to keep them from moving; these envelopes were then placed in slotted boxes appropriately marked by sex and area of capture. After collecting was completed, butterflies were removed from the envelopes with forceps, marked (on initial capture), examined, and released.

At capture and at each subsequent recapture, the individual's age, as estimated by wing-wear, was recorded on a scale of 0.5 to 3.5, in increments of 0.5, with 0.5 indicating a newly emerged individual and 3.5 a very worn one (for an alternate technique, see Watt et al., above). In this study, both loss of scales and nicks were used as indicators of wear. When making age estimates, an effort was made to ignore obvious handling damage (such as fingerprints) and to score only naturally induced wear. For consistency, the same three people performed all of the sampling and two checked each rating.

TABLE 2. Linear regression of change in condition on number of handling events by days in residence (females).

Days in residence	Sample size	Slope (m)	95% confidence limits for the slope		Correlation coefficient (R)	Power (1 − β)
3	18	0.22	−0.07	0.52	0.37	0.54
4	20	0.02	−0.21	0.24	0.04	0.11
5	14	0.20	−0.19	0.59	0.30	0.28
6	13	−0.12	−0.54	0.30	0.19	0.16
7	11	0.02	−0.41	0.44	0.03	0.09

Field records indicate how many times each individual was captured, the day each capture or recapture occurred, and the estimated condition at the time of each handling. From these data, the length of time between first and last capture (days in residence), the number of handling events that occurred (initial capture plus total number of recaptures), and how much the butterfly aged (change in condition), were determined for each individual.

To determine if handling the butterflies influenced the rate at which they aged (as indicated by wing-wear), a linear regression of change in condition on number of handling events was performed (Model I linear regression with >1 value of Y for each value of X; for details, see Sokal, R. R. & F. J. Rohlf 1981, Biometry, 2nd ed., W. H. Freeman and Co., New York, 859 pp.). Previous studies (Ehrlich et al. 1984, above) have shown that male and female *Euphydryas* wear at significantly different rates; therefore, the data were pooled by sex. For each sex, individuals were pooled by number of days in residence in order to separate natural wear from wear induced by handling. Individuals captured only once were not included in the analysis. Only males in residence between 3 and 10 days (210 individuals), and females in residence 3 to 7 days (76 individuals), were considered. Too few were in residence for longer and shorter periods to make analysis reliable.

The results of the regressions are summarized in Tables 1 and 2. In all cases, regression line slopes are not significantly different from zero. Although with small sample sizes it is not possible to affirm the null hypothesis at a satisfactory power (only males 6 days in residence had a test power >0.70; for most of the other regressions, the probability of rejecting a false null hypothesis ($1 - \beta$) was <0.30), the results suggest that there is no significant relationship between amount of handling and change in condition. In addition, a linear regression of change in condition on days in residence was performed for each sex, pooling across number of handling events. In both cases, slopes were significantly different from zero (males, $m = 0.12$, $P < 0.001$; females, $m = 0.13$, $P < 0.001$), indicating a significant relationship between time and change in condition, as would be expected. The majority of males (157 of 210) and females (56 of 76) had an initial condition of 0.5 and over half of the remaining individuals in each case had initial conditions of 1.0; consequently, further subdividing the butterflies into wing-wear cohorts (grouping by initial condition) did not change the significance of any of the results.

It is doubtful, however, that handling never causes wear. Different investigators, because of varying amounts of practice or ability, probably cause different amounts of wear to the butterflies they handle. The same person may occasionally cause a great deal of wear to a single butterfly (due to difficulty in disintangling the butterfly from the net, for example) while normally causing very little wear. It is probable that the greatest handling-induced change in condition occurs during the initial capture and marking. Subsequent recaptures may not greatly affect overall condition. Singer and Wedlake (above) found that *Graphium sarpedon* (L.) handled while being marked were much less likely to be recaptured than those not handled while marked, which they interpreted as a change in dispersal behavior due to the initial capture. A marking effect limited to the date of capture was found in *Boloria acrocnema* (Gall & Sperling) by Gall (1984b, above). Capturing and marking the butterflies disrupted their flight activity immediately following release, but this effect did not appear to last beyond the marking date. Wear induced by initial capture and marking would not cause an increased rate of wing-wear, but possibly could affect survival.

The conclusion that increased handling does not significantly change the amount of wear observable on *Euphydryas editha* has two important implications for MRR studies. First, it indicates that handling may not significantly "age" *Euphydryas editha* individuals. Secondly, it suggests that, when done carefully, it is possible to estimate age reliably using wing-wear as an indicator.

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PERFORATED CUPOLA ORGANS ON LARVAE OF EUSELASIINAE (RIODINIDAE)

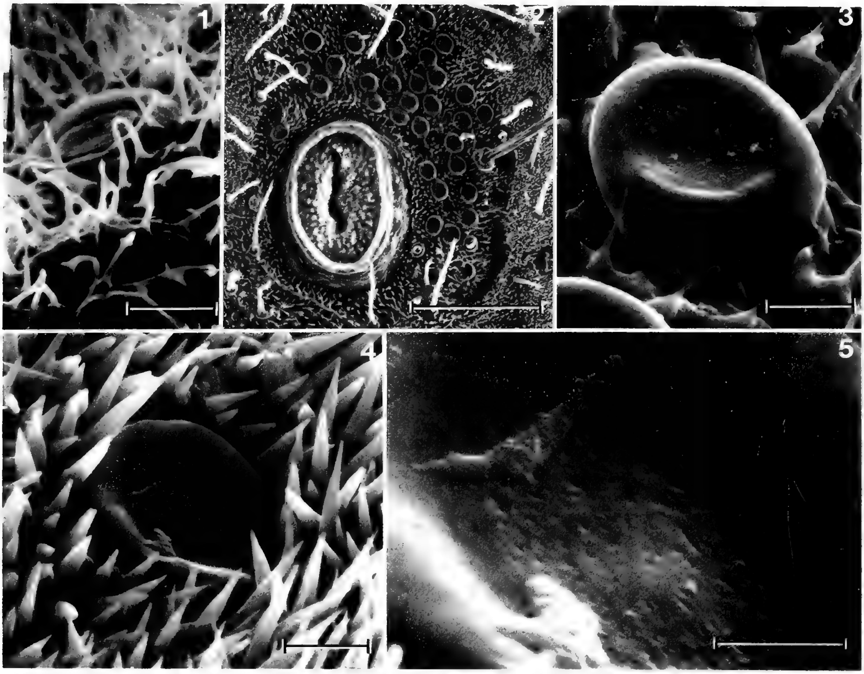
Additional key words: *Euselasia aurantiaca, E. mystica, Hades noctula,* ultrastructure.

Perforated cupola organs (PCO's) are minute, epidermal secretory organs, homologous to setae, found on larvae of many Lycaenidae (Malicky, H. 1970, J. Lepid. Soc. 24:190–202). They also occur on larvae of Riodinidae. These organs are known to secrete amino acids in some species (Pierce, N. E. 1983, Ph.D. Thesis, Harvard University, Cambridge, Massachusetts, 286 pp., Diss. Abs. Int. 44:1708B), and are thought to be involved in maintenance of ant associations in myrmecophilous species even though they are also found on amyrmecophilous larvae (Malicky, above; Kitching, R. L. & B. Luke 1985, J. Nat. Hist. 19:259–276). These organs have been relatively well-studied in Lycaenidae (DeVries, P. J., D. J. Harvey & I. J. Kitching 1986, J. Nat. Hist. 20:621–633 and included references; Kitching, R. L. 1987, J. Nat. Hist. 21:535–544), but there is little information on their occurrence in Riodinidae (sometimes considered a subfamily of Lycaenidae). They have been illustrated using scanning electron microscopy in one amyrmecophilous species of Old World Hemearinae, *Hamearis lucina* (L.) (Kitching & Luke, above), and one myrmecophilous species of New World Riodininae, *Pandemos palaeste* Hewitson (Harvey, D. J. & L. E. Gilbert, J. Nat. Hist. in press). They have not been illustrated, however, for larvae of a third subfamily, Euselasiinae, although their presence in this group has been alluded to (Harvey, D.J. unpubl., cited *in* DeVries et al., above). Larvae of the remaining subfamilies, the monotypic Styginae and Corrachiinae, are unknown (Harvey, D. J. 1987, pp. 446–447 *in* Stehr, F. (ed.), Immature insects, Vol. 1, Kendall/Hunt, Dubuque, Iowa, 754 pp.).

Euselasiinae consists of three genera: *Euselasia* with over 130 species, *Hades* with 2 species, and the monotypic *Methone* (Harvey, D. J. 1987, Ph.D. Thesis, University of Texas, Austin, Texas, 216 pp., Diss. Abs. Int. 49:625B). Distribution and morphology of PCO's on mature larvae of three euselasiines, *E. mystica* (Schaus), *E. aurantiaca* (Godman & Salvin) and *H. noctula* Westwood, are described here.

Larvae were examined with a Wild stereomicroscope. Material for scanning electron microscopy was coated with gold-palladium in a Hummer V sputter coater, and micrographs taken with an ISI Super IIIA.

All three species have the same distribution pattern of PCO's. Some are scattered along lateral and posterior margins of the prothoracic shield (Fig. 1). All remaining PCO's on larvae are restricted to clusters around abdominal (A) spiracles (Fig. 2). Long, tactile setae, present elsewhere on the larvae are absent from these clusters, though they may be immediately adjacent. The PCO's are set in fields of microtrichia (Figs. 2–4). The numbers of abdominal PCO's on larvae of the three species are as follows (A segment



FIGS. 1–5. Scanning electron micrographs of perforated cupola organs (PCO's) on larvae of Euselasiinae (Riodinidae). **1,** *Euselasia mystica,* PCO on prothoracic shield (scale bar = 10 μm); **2,** *Hades noctula,* cluster of PCO's around spiracle on A4, left side (scale bar = 200 μm); **3,** *H. noctula,* individual PCO (scale bar = 10 μm); **4,** *E. aurantiaca,* PCO in field of microtrichia, near spiracle on A4, left side (scale bar = 10 μm); **5,** *E. aurantiaca,* sieve plate of PCO showing pores (scale bar = 4 μm).

number : number on right and left side; "?" denoting larva damaged and PCO's present but uncountable):

E. mystica: A1:15,17; A2:33,31; A3:24,27; A4:18,15; A5:14,10; A6:17,14; A7:22,26; A8: 26,21.

E. mystica: A1:?,49; A2:55,52; A3:?,45; A4:?,?; A5:?,35; A6:39,?; A7:53,?; A8:70,?.

H. noctula: A1:36,38; A2:86,91; A3:47,56; A4:34,36; A5:33,28; A6:29,27; A7:42,51; A8: 45,47.

In addition to identical placement of PCO's, all three species also show a similar pattern in relative numbers of PCO's on different segments: maximum numbers on the anterior segments are found on A2, usually followed by A3; and on the posterior segments, on A7 and A8.

Diameters of the PCO's average 21 μm for *E. mystica* (on prothoracic shield), 27 μm for *E. aurantiaca* (on A4), and 28 μm for *H. noctula* (on A4). Minute pores are visible on the central "sieve plate" of the PCO's (Figs. 1, 5). No pores are evident on sieve plates of *H. noctula,* which have minute crenulations (Fig. 3), of unknown function.

Larvae of *Euselasia* and *Hades* are amyrmecophilous; ant mutualisms are restricted to the subfamily Riodininae (Harvey, above; Harvey & Gilbert, above).

PCO's of Riodininae differ from those on larvae of the amyrmecophilous *H. lucina,* which lack pores, are not clustered, and are more sparse (Kitching & Luke, above). PCO's are also present on first instars of both myrmecophilous (*Eurybia, Calospila* among others) and amyrmecophilous (*Apodemia, Calephelis* among others) riodinines, where they form a regular component of chaetotaxy (Harvey unpubl.). Despite broad taxonomic occurrence of PCO's, their function (if any) in euselasiines and other amyrmecophilous riodinids is obscure.

Pattern of PCO distribution in Euselasiinae examined in this study is consistent, and may be taxonomically significant. It resembles that described for the curetine lycaenid *Curetis regula* Evans (DeVries et al., above), where PCO's are also clustered near abdominal spiracles. However, *Curetis* differs in having PCO's near the prothoracic spiracle (rather than on the shield), and in their closer spacing (without intervening microtrichia). In addition, their form is more elevated, and waxy exudates are present on sieve plates. On the other hand, Euselasiinae differ from observed Riodininae, which usually have PCO's (when present) in several pairs of clusters per segment, or if single clusters are present (as in Euselasiinae), they are more dorsal on segments (Harvey & Gilbert, above; Harvey unpubl.). Restriction of PCO's to clusters around spiracles and prothoracic shield may be the primitive configuration in Riodinidae, perhaps also in Lycaenidae. In light of this possibility, description of PCO's from additional members of Hamearinae, from *Styx infernalis* Staudinger and *Corrachia leucoplaga* Schaus, and from the lycaenid subfamilies Lipteninae and Poritiinae, would be of interest.

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BOOK REVIEWS

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CATALOGUE OF LYCAENIDAE & RIODINIDAE (LEPIDOPTERA: RHOPALOCERA), by Charles A. Bridges. 1988. Printed by the author. 816 pp.: vi, ii + 377 pp., ii + 115 pp., ii + 140 pp., ii + 100 pp., ii + 37 pp., ii + 1 p., ii + 10 pp. 21 × 28 cm, hardcover. $95.00 in North America, $97.50 elsewhere.

Bridge's *Catalogue of Lycaenidae and Riodinidae* is an extremely useful publication for any lepidopterist interested in the systematics of these two families. It provides information on original descriptions and other literature, authors, periodicals, and the current systematic placement of taxa. I have found the catalogue easy to use and a great time-saver for tracking down names and references.

The catalogue is divided into a brief introduction, six parts and two appendices, each with separate pagination. Part I consists of an alphabetic list of species-group names. Each entry includes the author, date of publication, abbreviated literature citation (cross-referenced to Part IV), and the original genus for each species-group name. The status of each name (i.e., available and valid species, subspecies, or synonym; available invalid; or unavailable) is indicated by a letter code. For species subsequently transferred to other genera, the current genus is given along with a reference(s) (cited in full in Part IV) for the transfer. In addition, many entries include information on the type locality, location of type specimen, its sex, and/or references to life history. Part II is an index to genera that includes a list of species-group names under each genus. Part III is the index to the bibliography. Publications are listed by author, date, and journal (cross-referenced to the full citation in Part IV). Under each publication, species group names are listed, along with reference to volume and page number, and to plate and figure numbers if the taxon is illustrated. Part IV, the bibliography, lists complete citations for 4258 publications. Each publication is given a unique number by which it is cross-referenced in other parts. This part also provides information on when and where some authors were born and died, and the disposition of their collections. Part V, the index to journals and serials, lists them by abbreviation and includes their full titles. Under each is a list of included papers (cross-referenced to Part IV) with the author, date, volume and page numbers. Part VI, the index to the bibliography by year, lists the unique numbers of each publication in Part IV under its year of publication. Appendix I is a synonymic list of family-group names. Appendix II is a synonymic list of genus group names arranged according to family, subfamily, tribe, subtribe (if any) or section (if any). Although not explicitly stated, the higher classifications follow Eliot for the Lycaenidae and Stichel for the Riodinidae.

There are some problems with the first 40 copies that will be corrected in later editions. In Part I, a block of 290 names is missing "between" pages 275–276, and a block of names is duplicated on pages 287–293. In addition, some changes in format also will be made: in Part II each genus will have an indication of its place in the higher classification that will facilitate finding it in Appendix II, and Part VI will include the names of authors. A series of annotations is being issued which lists additions and corrections to the catalogue.

The catalogue appears to contain relatively few errors for a work of its size. I found two typographical errors in the Introduction (misspellings of Julian P. Donahue's and Jacqueline Y. Miller's names). The authorships of riodinid taxa described by Le Cerf and by Lathy in a paper by Rebillard are incorrectly attributed to Rebillard in the catalogue. The generic name *Balocna* Moore is listed as a synonym of *Zemeros* Boisduval in Appendix II but it is actually a synonym of *Dodona* Hewitson. Although the author states in the introduction that no new names are introduced in the catalogue, the subtribe Sarotiti is apparently proposed in Appendix I as a replacement name for Charitini Stichel. These problems are minor, and the author is to be commended for providing a mechanism for correcting such errors.

The catalogue holds at least one nomenclatorial surprise. The name *Orimba* Herrich-Schaeffer (1858), used by Stichel and all subsequent authors for a genus of neotropical riodinids, is actually a synonym of *Setabis* Westwood (1851).

The amount of time and effort required to produce this catalogue must have been immense, and such enterprises are often thankless tasks. Bridges has done us a great favor by providing a careful, well-planned and exhaustive work. This catalogue is an indispensible reference that belongs in the library of all who work on the systematics of lycaenids and riodinids.

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PAPILLONS ET CHENILLES DU QUEBEC ET DE L'EST DU CANADA [Lepidoptera and Larvae of Quebec and of Eastern Canada], by Jean-Paul Laplante, 1985. 280 pp., 65 color plates, with many other color figures in text. Editions France-Amerique, 170 Benjamin Hudon, Montreal, Quebec H4N 1H8, Canada. Hardcover. About $25.00.

This beautiful book makes an important contribution to our knowledge of the butterflies and moths of Quebec and of eastern Canada in general. Covering more than 300 species and subspecies of Lepidoptera with illustrations of the adults, eggs, larvae, pupae, and habitats (over 1000 separate color figures), this book would be of value to anyone with an interest in the Canadian fauna. It is currently available only in a French edition, but Latin insect and plant names, locality names that can be identified on any map, etc., make it readily usable even if one should not know French.

The author has worked for more than 30 years on the lepidopteran fauna of eastern Canada, especially Quebec, and has collaborated with many workers in Canada to assemble the knowledge and photographs displayed in this volume. He begins with a general introduction to the evolution and biogeography of butterflies and moths, their ecology, and life history. Excellent text drawings and scanning electron micrographs, as well as color photographs, illustrate scale structure and other features. Concise but well-done summaries of geographic and genetic variation of butterflies and moths are presented, along with a fascinating discussion of mimicry that includes unusual illustrations not appearing in any other book. Likewise, a short section is devoted to the enemies and diseases of Lepidoptera, and there is a valuable descriptive section on the characteristics of each family of butterflies and some of the major moth groups.

The author then presents a quite usable key to the species of diurnal Lepidoptera in Quebec as well as to species of certain genera in major moth families (Sphingidae, Lasiocampidae, Saturniidae, Arctiidae, Agaristidae, Notodontidae, and Lymantriidae). The last key, interestingly enough, is solely to the larvae of the species in the genus *Dasychira* in Quebec, because they offer the best distinguishing characters for the genus.

The outstanding and immaculately reproduced color plates, however, carry the major load of identification of specimens. The male, female, and underside of each species is shown, along with seasonal and geographic variation across eastern Canada. The plates are among the very best ever produced for a book on a North American faunal region. After the 34 color plates of adult specimens, photographed crisply on a blue background, the author includes a series of 30 plates of eggs, larvae, and pupae of the illustrated butterflies and moths, as well as a plate of eight habitat photographs. Technically, it would be hard to suggest any improvement that could be made in the beautiful photography that illustrates this book.

The author discusses in detail the vegetation zones of Quebec and northeastern Canada, north to Hudson Bay and west into Ontario as well as east into Labrador and Newfoundland. One of the most interesting features is a complex yet highly readable table presenting a summary of biological notes on 282 species and 11 subspecies of Lepidoptera, including 134 butterflies and 159 moth species. This table neatly shows the distribution, flight period, abundance in habitat, cross-references to illustrations in the text, number of annual generations, the hibernation or aestivation stage, and the larval characteristics, including host plants, period of activity, living habits (solitary, gregarious, etc.), and the average body length, as well as cross-references again to the illustrations in the main text. The book closes with a brief but very adequate discussion on how to collect, prepare and preserve butterflies and moths. An excellent glossary and selected bibliography, as well as a comprehensive index, close the book.

Jean-Paul Laplante has produced an excellent book on the butterflies and many of the interesting larger moths found in Quebec and the other areas of eastern Canada. The wonderful color illustrations of the larvae of virtually all the species of butterflies and major moth groups in Quebec would make this book a sound investment on that basis alone. The extraordinarily low cost of this beautiful book and its ready intelligibility even to readers lacking a good reading knowledge of French should prompt many lepidopterists to purchase it for their personal libraries.

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SLUG AND NETTLE CATERPILLARS: THE BIOLOGY, TAXONOMY AND CONTROL OF THE LIMACODIDAE OF ECONOMIC IMPORTANCE ON PALMS IN SOUTH-EAST ASIA, edited by M. J. W. Cock, H. C. J. Godfray, and J. D. Holloway. 1987. 270 pp., 18 color plates. CAB International, Wallingford, Oxon, UK. Hardcover. $99.00.

This book is an invaluable tool for tropical biologists in the coconut and oil palm industries of South-east Asia. It also is important in a broader geographic and economic sense because the larvae of Limacodidae, which are highly polyphagous, are pests of palms and other tropical plantation crops worldwide. Although less than comprehensive, the work presents a review of recent literature on natural enemies of New World limacodid palm pests along with a wealth of information on Limacodidae in general.

The organization of the book is as follows: chapters 1 and 2 present introductory information on Limacodidae; chapter 3 provides systematic accounts of palm pests of South-east Asia; and chapter 4 is a short, preliminary account of tropical Australasia pests. Chapters 5–17 deal with aspects of pest management and include systematic accounts of parasitoids and predators, and fungal, viral, and chemical control. Most of these final 13 chapters are brief, encompassing about half of the total text.

The book includes 36 plates comprising genitalic preparations, color photographs of spread specimens (with useful, identified black and white duplicates on facing pages), and striking photographs of live larvae, cocoons, natural enemies, and adults in natural postures.

As one who has reared limacodids for several years, I can appreciate the amount of intensive labor that the book represents. I found the information on rearing methods (chapter 2) particularly enlightening. A minor shortcoming, however, is a sense that larvae were reared by someone other than the authors. The statement that larvae appear "remarkably stupid" because they must be manually transferred to new host material is absurd, as this is a manifestation of rearing these specialized larvae in captivity. Slug caterpillars, especially in early instars, have a difficult time moving from one leaf to another because of the small thoracic legs and absence of abdominal prolegs. Difficulties in rearing slug caterpillars that the authors fail to mention include: 1) their tendency to become immobilized with frass due to the sticky nature of their ventral surface; and 2) their movement off the host material and onto the container, perhaps a preference for the smoothest available substrate (most limacodids are found on hosts with smooth leaves).

Chapter 3 on systematics of the South-east Asian pest species considerably expands our knowledge of the region's fauna, with 35 new species and four new genera described by Holloway, and 28 new synonyms, new combinations, and other nomenclatural changes. Relationships among genera are proposed on the basis of the signum type of the female genitalia as in Holloway (1986, The moths of Borneo: Key to families; Cossidae, Metarbelidae, Ratardidae, Dudgeoneidae, Epipyropidae and Limacodidae, Malay. Nat. J. 40: 1–166). While the family represents a well defined monophyletic group, there is no widely accepted supergeneric classification for the world fauna. Use of the signum in relating genera may have merit, but caution should be exercised since the congruence of this character with other morphological and/or behavioral characters has not been examined in a phylogenetic (cladistic) context.

Chapters 5–9 deal with parasitic Hymenoptera associated with South-east Asian Limacodidae. The chapters on Ichneumonidae, Braconidae, and Chalcidoidea, constituting nearly a fourth of the book, have keys to the parasitoids, with scanning electron micrographs and line drawings of the former two families. I found chapter 5 very informative in its division of the life styles of ichneumonid wasps by taxonomic groups. Chapters 10 and 11 summarize dipteran parasitoids in the Tachinidae, Sarcophagidae, and Bombyliidae, and chapter 12 reviews hemipteran predators. Chapter 13, a half page description of a pyralid cocoon predator, *Ectomyelois ceratoniae* (Zeller), would have been better summarized in the introductory matter or mentioned with other predators. Reviews of classical biological control, fungal pathogens, viruses, and chemical control of limacodids are presented in the final four chapters.

Although the book is full of important life history information and literature citations, several important references on limacodid life histories are not included. In the 60th anniversary since the passing of Harrison G. Dyar (1866–1929), it seems appropriate to mention his contribution to this subject. Even though Dyar described the early stages of primarily Nearctic species, many of these taxa have obvious phylogenetic connections with the Asian fauna. Reference to Dyar's work would have added support to statements on the origin of non-stinging, smooth ("gelatine") types of caterpillars from those with stinging scoli. Dyar recognized the ancestral plan of Limacodidae as possessing two rows of scoli, and hypothesized two independently derived lineages of smooth larvae (Dyar, H. G. 1899, The life-histories of the New York slug caterpillars, J. N.Y. Entomol. Soc. 7: 234–253, pls. 6–8). Each of these lineages possess rows or rudiments of scoli in the first instar that are lost in later instars.

While I applaud the information on rearing methods, there is no mention of obtaining life-history data by capturing adult females and inducing oviposition. This is a viable alternative, particularly since most if not all limacodids can be reared on palm without previous knowledge of the host owing to their polyphagous nature. This procedure, used by Dyar, is practical for associating adults with larvae and obtaining good series of both.

Appendix 1 is a list of host plants of South-east Asian limacodids mentioned in the text. Unfortunately, this information is not indexed, making it difficult to find the species of limacodids associated with each plant.

The price of this book may be prohibitive to those with only a casual interest in Limacodidae or without an economic stake in the subject. However, since the work represents a significant contribution to our knowledge of the early stages, behavior, and systematics of Limacodidae, it is indispensible for the serious student.

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THE GUILD HANDBOOK OF SCIENTIFIC ILLUSTRATION, edited by Elaine R. S. Hodges, 1989. xv + 575 pp. Van Nostrand Reinhold, 115 Fifth Avenue, New York, New York 10003. 22 × 29 cm, hardcover. $79.95.

In 1968 U.S. natural science illustrators organized themselves professionally; since then, the Guild has brought to a formerly disconnected occupation a unity of strength and purpose. The *Guild Handbook of Scientific Illustration* is one very tangible result of this union, its high-tone pages bringing together in one volume the wide variety of principles and procedures that define the field of natural science illustration (practiced by scientific illustrators dedicated to biological and medical subjects).

In five major parts, 30 chapters introduce the reader first to the "Basics:" steps in the process of illustration, outfitting the studio, materials, and the play of light on subjects. "Rendering Techniques" follow: an in-depth survey of the use of media from simple line and ink to complex color applications. The majority of the text consists of 11 chapters covering the special problems and approaches to the principal "Subject Matter:" plants, fossils and extinct vertebrates, invertebrates (including insects), fishes, amphibians and reptiles, birds, mammals, animals in their habitats, humans and their artifacts, and medical subjects. Several advanced topics follow in "Beyond Basics:" using the microscope, charts and diagrams, cartography, copy photography, and the printing process. Finally, the "Business of Scientific Illustration" is given attention, where copyright law, making contracts and operating a free-lance business are discussed. Included are a Bibliography and Appendix with names of sources of supplies and other compact information.

The voluminous text is generally well written by 45 motivated and capable authors and is fully illustrated with over 600 clean, instructive figures in black and white and color. The matter discussed is immense in depth and diversity, requiring and receiving a masterful editing job by Hodges.

It is hard to find fault in a work obviously so lovingly and meticulously produced. I would, perforce, comment on a few minor imperfections, mostly trivial, which mar only slightly an otherwise superior technical publication:

1. While the somewhat varied approaches taken by authors to accommodate the quirks of their disciplines are highly appropriate, they allowed for some redundancy (e.g., where techniques overlap) and at least one contradiction (sans serif lettering advocated by Allen on p. 500, the contrary by Lynch on p. 459).
2. I find some bothersome pedantries and truisms, the most common being the oft repeated statement that taking classes in this or that discipline of biology makes one a better illustrator. I think that many items in the lists of instruments and materials in Part 3 are part of any studio; mention of such items as magnifiers, rulers, a camera, French curves, etc., could give way to more discussion of things peculiar to the subjects at hand. It does not seem necessary to say, on p. 394, right column: "The illustrator may be called upon to work on a wide range of subjects in a variety of settings." Or on p. 376, middle column: "There is considerable variety in the field of illustrating mammals."
3. Some confusing statements have crept into the text: p. 23, left column: "To this end, adaptations of some traditional drawing media have been developed in some techniques." Also, on p. 264, first sentence: "Invertebrates that are not arthropods do not have jointed legs."
4. I miss discussion on some important issues: Nowhere is perspective or the problem of parallax discussed, yet lighting is given a detailed treatment. Needed is a more unified review of the types of symmetry, axes, planes, and regions in organisms, and terms pertaining thereto. A glossary would be a welcome addition to the next edition.
5. Some authors fail to include mention of those involved in the historical development of their field. While this may be excused by the primarily prosaic purposes of the book and the availability of other works on the history of biological illustration, the omission is definitely to the detriment of the reader, especially when classic examples are not shown.
6. Much of the flavor of the book is towards drawing for taxonomy. I would like to have seen more shift given to the branches of anatomy and behavior (especially regarding insects).
7. The list of suppliers in the index leans heavily toward the eastern U.S.; we out west have many fine outlets too.
8. Some errors bear noting: p. 197, right column: "Plants having roots, stems, leaves, and a vascular system are called gymnosperms." should read ". . . are called *thallophytes*." The sentence is repeated on p. 199, left column but ends in "angiosperms." also erroneously. In the list of types of specimens given on p. 4, left column, *mounted* specimens are illogically omitted (see #6 below).

As an entomological illustrator myself, I have a bit more to say of the pages dealing with insects. These are small issues, as those above, the treatment on the whole being excellent.

1. I notice again the lack of acknowledgment of achievements of historical workers. Superb examples date back as far as Hooke's louse and Lyonnet's goat moth larva of the early 18th century. In my opinion the finest entomological illustrator was Hermann Weber. His rendering of homopteran mouthparts are masterpieces of analytical anatomical graphics. Others important in establishing the field were E. O. Detmold, A. J. E. Terzi, and G. Ferris. Some useful and important technical publications might have been cited [Edy, R. 1968, Some illustrations of microsculpture in the Hymenoptera, Proc. Entomol. Soc. London, ser. A 43:66f.; King, R. & H. Akai (eds.) 1982, 1984, Insect ultrastructure. Vols. 1–2; Catts, E. & J. Young 1959, A chalkboard technique for making illustrations, Pan-Pac. Ent. 35:163f.]. A nice little book that teaches much on the art of posturing for live insect illustrations is N. Weaver's How to draw insects (Studio Pub., London. 1958).
2. Some additional techniques are: individual sand grains are suggested for propping specimens; a bed of fine silica sand gives an even more versatile matrix for holding specimens in any position. Specimens may also be embedded temporarily in clear gelatin to hold them for drawing. Insect membrane is commonly indicated by light stippling while sclerites are left clear in anatomical works. Precautions for putting away microscope slides are given on p. 261; I would add that the box or tray should be stored so that the slides are flat, with specimen on top, to prevent gravity from tugging at the medium.
3. There are a few mistakes: p. 290, first paragraph of left column: ". . . a dorsal segment is a tergum or tergite"; . . . , should read, "a dorsal *sclerite* is a tergum or tergite;" p. 289, top of middle column: Myriapoda is a category that *contains* millipedes (Diplopoda) and is not synonymous with them; p. 297, center column: carbolic acid or phenol crystals, not naphthalene, are usually added to relaxers to inhibit mold growth. Instructions for calibrating microscope micrometers in the "Eyepiece Scale Value Method" (p. 31), transpose "stage micrometer" for "ocular micrometer (reticle)".
4. Terms that need more explanation are "sclerotized" (used to infer hardness and/or pigmentation); "spines" (as distinct anatomically from setae); "minutens" (unfamiliar to the non-entomologist).
5. Some indefensible or inane statements appear: p. 293, center column: "Tarsal structure is second in importance only to antennal form in many insects . . . for identification to family." And on p. 301, last paragraph: "Because these animals vary so widely in size, appearance, anatomy, and requirements for preservation, the techniques for handling and drawing them also vary."
6. There seems to be a confusion of what is meant by "mounting" and "propping" (p. 260). In entomology a "mounted" specimen is one that has been prepared in some way (on pin, wings spread, etc.). These may need propping as much as an unmounted specimen.

In summary, this fine work is encyclopaedic and copies will no doubt be put on the reference shelf by many librarians. But more than that, it is also a voluptuous handbook, so full of practical data and sound conceptual advice, and beauty as well, that most copies sold will surely never be found far from the illustrator's hand.

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BUTTERFLIES OF NEPAL (CENTRAL HIMALAYA), by Colin Smith. 1989. 352 pp., 355 color figures, 3 maps. Tec Press Service L.P., 487/42 Soi Wattanasilp, Pratunam, Bangkok, Thailand. 15 × 23 cm, hardcover. $50.00 U.S., plus $5.00 airmail postage.

The Central Himalaya Mountains have always held a fascination for lepidopterists interested in both temperate and tropical butterflies. At last, we have a field guide to the butterfly fauna of Nepal—and one to match the demands of its incredible diversity.

The great number of butterfly species known to occur in Nepal and the rugged mountains culminating in Mt. Everest, along with adjacent rich tropical lowlands, have brought many biologists to this landlocked country to explore and enjoy its natural history and scenic beauty. The country is partitioned lengthwise into Palearctic and Oriental sets of floral and faunal provinces. It ranges in elevation from some 500 feet above sea level on the Ganges plain to the highest peaks in the world in the Central Himalaya (to over 29,000 feet on Mt. Everest in northeastern Nepal). It is little wonder that altitude seems to be the critical factor for butterfly distribution here. In fact, a significant dividing line (shown in Smith's map on p. 31) appears at about 3000 meters elevation (between 9000 and 10,000 feet); some 90% of the species above this line show Palearctic affinities, while below it, about 90% of the species are of Oriental origin. Although many references to this diverse fauna have been made in books on high-altitude entomology and in scattered publications on the characteristics of different groups of butterflies from Nepal, Smith's book is the first to cover this extremely interesting fauna in a comprehensive format.

In this new publication Colin Smith has set forth an outstanding introduction to the 614 species known to occur in Nepal. The illustrations cover more than 70% of the species (90% of the 266 genera), using more than 200 photographs of butterflies in their natural living state and another 100 photographs of mounted specimens to show uppersides and undersides. In addition to the extensive taxonomic section, Smith includes a general discussion of the biology of butterflies, including particular examples of migration, mimicry, etc. from Nepal. He also presents a fascinating introduction to the country of Nepal and to the natural geographic divisions of the Central Himalaya region, including climate, seasonality, ecology, habitats, and other attributes. The book thus provides an indispensable introductory guide to the natural history of Nepal, as well as the sole popular introduction to the butterfly fauna of that country.

For the lepidopterist, the innovative features of this book include a classification chart at the beginning of each family that shows nicely in columnar format a series of facts (subfamilies, tribes, genera, new genera, subgenera, region of origin, total number of species worldwide, and number of species in Nepal) about the classification and status of that family. Additional tables are offered to help in the identification of certain complex groups, such as the Lycaenidae. A general summary for the identification of the Nymphalidae is presented in a running tabular form. Each genus is numbered within a family, and author's name, date, type species, and general diversity worldwide are given. For each individually numbered species account, Smith gives the complete species and subspecies name, author, date of publication, common name if available, range of wingspan, comments on distribution (usually to district within Nepal), seasonality, elevational range, distribution outside Nepal, and the species' relative abundance.

Following the taxonomic section, the author traces the history of butterfly collecting in Nepal and includes a summary of species and subspecies endemic to the country, a record of principal collectors who have taken Nepalese butterflies and the species and subspecies they have taken, and a list of the butterflies recorded from Nepal (based on all authenticated Nepal records known to the author) with their habitats, altitude, seasonality, and common name. The book concludes with a selective bibliography of 48 publications on the butterflies of Nepal, indices to scientific and common names, and a brief biography of the author.

Overall, this book represents a remarkable individual accomplishment in its presentation of the first general faunal coverage of the butterflies of Nepal and the Central Himalaya. Exploration of the Palearctic high country of the Central Himalayan and Trans-Himalayan regions has lagged far behind that of the Oriental region in Nepal. Some Himalayan areas such as border districts and national parks are often closed to collecting, and limited access by road or air-strip often necessitates carefully-planned, multi-man expeditions by backpack or porters. The incredibly diverse fauna and terrain will undoubtedly produce many more species with further lepidopterological exploration of the country, as the author is the first to admit (he added two Nepalese species new to science in 1986 alone). Overall, the book is well designed and printed. Although some of the color photographs are not reproduced as clearly or as crisply as would be desirable, the overall impression of the book is quite favorable and the illustrations can be used to identify specimens.

Perhaps most importantly, the beautiful photographs of habitats throughout Nepal, coupled with the author's enthusiasm for photographing living butterflies and studying their natural history, will help to engender greater worldwide interest in the wilderness conservation programs and butterflies of this fascinating country of the Central Himalaya. This book belongs on the library shelf of any lepidopterist interested in temperate and tropical Old World faunas, or in beautiful butterfly books in general. The book also will be of interest to biogeographers, ecologists, and conservationists worldwide.

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FEATURE PHOTOGRAPH

Split-level Dining: Three female *Godyris zavaleta amaretta* (Haensch, 1903) (Nymphalidae: Ithomiinae) share a piece of fruit in the interior of primary rainforest in eastern Ecuador. The leaf on which these three are perched is 1.5 m above the forest floor. In the canopy 60 m overhead is a flock of yellow-headed parrots (*Amazona ochrocephala*) gorging themselves on fruit, fragments of which fall to the forest understory below, providing a food source for deep forest Lepidoptera and other insects. Male *Godyris* visit tree-fall gaps and stream margins to seek flowers for nectar, while females remain in the forest interior and feed on detritus. Photograph taken at Limoncocha, Napo Province, Ecuador (0°24'S, 76°38'W; 280 m elev.) on 26 July 1974 with a Pentax SP-1000 with a 50 mm macrolens (Kodak Plus-X, natural light: $\frac{1}{30}$ sec f4.0).

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ANNOUNCEMENT

COLOR ILLUSTRATIONS IN THE *JOURNAL*

Many Lepidoptera are colorful animals, both as juveniles and adults, and black and white illustrations rarely do them justice. Color illustrations accompanying some articles in the *Journal* should enhance both the information content and the esthetic quality of our publication. Fortunately, the cost of color printing has declined in recent years, now making the use of color in the *Journal* financially feasible. Although author page charges for color illustrations will always be significantly higher than regular page charges, the Executive Council of the Society recently approved a policy of subsidizing part of the cost of appropriate color illustrations in the *Journal*. As a result, authors are encouraged to submit color illustrations for publication in the *Journal*.

The cost of color printing varies with the size and format of the color illustration, so authors who wish to use color should contact the Editor *before submission* to discuss the nature of the illustration, the special submission requirements, and the cost. Please note that the newly established FEATURE PHOTOGRAPH category will also accept color submissions, although no Society financial subsidy is available for color illustrations in this category.

Society support for the appearance of color in the *Journal* will come from the Society's Color Illustration Fund, which gladly accepts donations both private and corporate. Contributions to the Color Illustration Fund may be sent to the Treasurer of the Society.

BOYCE A. DRUMMOND, Editor

NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of Lepidoptera study. Categories are Articles, General Notes, Technical Comments, Book Reviews, Obituaries, Feature Photographs, and Cover Illustrations. Reviews should treat books published within the past two years. Obituaries must be authorized by the President of the Society. Requirements for Feature Photographs and Cover Illustrations are stated on page 203 in Volume 42(3). *Journal* submissions should be sent to the editor at the above address. Short manuscripts concerning new state records, current events, and notices should be sent to the *News*, June Preston, Editor, 832 Sunset Drive, Lawrence, Kansas 66044 U.S.A. *Journal* contributors should prepare manuscripts according to the following instructions, and submit them flat, not folded.

Abstract: An informative abstract should precede the text of Articles.

Key Words: Up to five key words or terms not in the title should accompany Articles, General Notes, and Technical Comments.

Text: Manuscripts should be submitted in *triplicate*, and must be typewritten, *entirely double-spaced*, with wide margins, on one side only of white, letter-sized paper. Titles should be explicit, descriptive, and as short as possible. The first mention of a plant or animal in the text should include the *full scientific name* with *author*, and *family*. Measurements should be given in metric units; times in terms of the 24-hour clock (0930 h, not 9:30 AM). Underline only where *italics* are intended.

Literature Cited: References in the text of Articles should be given as Sheppard (1959) or (Sheppard 1959, 1961a, 1961b) and listed alphabetically under the heading LITERATURE CITED, in the following format without underlining:

SHEPPARD, P. M. 1959. Natural selection and heredity. 2nd ed. Hutchinson, London. 209 pp.

——— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10:165–216.

In General Notes and Technical Comments, references should be shortened and given entirely in the text as P. M. Sheppard (1961, Adv. Genet. 10:165–216) or (Sheppard, P. M., 1961, Sym. R. Entomol. Soc. London 1:23–30) without underlining.

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FACTORS IN ECLOSION OF PIERIS RAPAE
BUTTERFLIES FROM COAHUILA
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LIFE HISTORY OF CHLOSYNE FULVIA

(Complete contents on back cover)

15 November 1968

THE LEPIDOPTERISTS' SOCIETY

Editorial Committee

Executive Council

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THE EVOLUTIONARY AND BIOLOGICAL SIGNIFICANCE OF MULTIPLE PAIRING IN LEPIDOPTERA

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The frequency of pairing in Lepidoptera may be related to population structure (Labine, 1964), to courtship behavior (Marshall, 1901) or to the balance of a polymorphism in a mimetic population (Burns, 1966). In this paper a sample of female *Utetheisa ornatrix bella* (L.) (Arctiidae) from the polymorphic Florida population is analyzed by phentotpye and pairing frequency for evidence of sexual selection; data taken from the literature are summarized; and the importance of mating frequency for the evolution of behavior and of population structure is discussed.

Studies of copulation have shown that in many Lepidoptera the male constructs a sperm containing bag (spermatophore) in the genitalia of the female (Callahan and Cascio, 1963: Callahan and Chapin, 1960; Khalifa, 1950; Norris, 1932; Weidner, 1934). Mating refers to copulation; successful mating requires transfer of at least one spermatophore. Since spermatophores remain in the bursa copulatrix, the number of successful pairings can be ascertained by dissecting the bursa and counting spermatophores. The spermatophore is reported to disintegrate as soon as it is formed in certain Microlepidoptera (Callahan and Casico, 1964: 554). While spermatophore remnants are difficult to count, the hardened duct (collum) through which sperm pass from the spermatophore to the ductus seminalis is retained more or less complete in *Utetheisa ornatrix*, and the number of colli is an index of pairing frequency. At most one spermatophore is produced during a single copulation of this species. Of twelve virgin females mating once in controlled breeding experiments in 1961, all had one and only one spermatophore in the bursa copulatrix.

In the pink bollworm, *Pectinophora gossypiella* (Saunders) (Gelechiidae), spermatophores were formed in 199 of 219 laboratory matings of virgin females (Ouye, *et al.*, 1965, experiment 1). Seventeen of the

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20 pairs which did not form spermatophores remained in copulo no longer than 30 minutes. Thus, a certain minimum time is required for spermatophore construction and no more than one spermatophore is formed during a single copulation.

The distribution of spermatophore frequencies in a sample of 89 females of *U. o. bella* collected in Florida is tabulated in Table 1. One bursa was lost in the process of dissection. Fifty-three males were collected with the females. The mean number of spermatophores was 3.489 with standard deviation 2.656. One individual had copulated at least 11 times, and eight had not mated successfully.

Before dissection, the condition (fresh vs. worn) of each specimen was estimated on the basis of external appearance and graded A, B, C, or D. Not unexpectedly, the mean number of spermatophores increases from 1.455 for very fresh (A) individuals to 6.250 for very worn (D) individuals (Table 2). Moths reared under constant conditions (80°F, 12–16 hours light per day) usually mated at night although a few males collected in the field mated in the afternoon by artificial light. Diurnal mating may be an adaptation to the Florida winter season with its cold nights and warm days. A refractory period may follow copulation during which time the male will not mate successfully (cf. Khalifa, 1950: 39, *Galleria mellonella* (L.) (Pyralidae); Ouye, *et al.*, 1965 experiment 2, *Pectinophora gossypiella*).

The sample was tabulated separately for five wing pattern characters and tested for differences in mean spermatophore number between categories (Table 3). The characters were subdivided into categories as follows: (1) forewing ground color—*yellow* or *orange, red orange* and *orange red,* or *red*; (2) the distribution of forewing ground color—*colored* or *streaked, intermediate* and *white*; (3) black spotting on forewing—*spotted* or *unspotted*; (4) hindwing black markings—*wide, semi* or *narrow*; (5) hindwing ground color—*red, pink* and *flush* versus *white* (Pease, 1968).

When the t-test was applied independently to each of the five characters in Table 3, only the difference between the mean number of individuals with spotted *versus* unspotted forewings was statistically significant with probability less than .02 of a difference between the means as large or larger. However, the probability is about ¼ that one or more of five independent tests is significant at the .05 level, $(1 - .95^5)$. Since the statistical hypothesis was formulated after looking at the data, the result does not favor a hypothesis that wing pattern is a factor determining mating frequency. This is consistent with the observation that this species mates at night and that the bright pigmentation serves as a warning stimulus (aposematic coloration) to potential diurnal predators. Toxic substances have been found in the haemolymph by M. Rothschild. The species exudes a frothy bubble at the tegulae when seized suddenly (reflex bleeding).

The average number of spermatophores in the tiger swallowtail (*Papilio glaucus* L.), a species with dimorphic females, was greater for yellow females than for dark females in samples from Mountain Lake, Virginia and Baltimore, Maryland (Burns, 1966). The resemblance of dark females to the unpalatable blue swallowtail (*Battus philenor* (L.)) is believed to confer protection from predators whose vision enables them to distinguish the two forms. The population frequencies of dark and yellow females are affected by two antagonistic forces of natural selection (an example of disruputive selection). An extra-specific environmental factor, mimicry, favors the mimetic dark female; an intra-specific factor, sexual selection, favors the yellow female.

The preference of the male tiger swallowtail, which is always yellow, for the yellow female is relatively independent of the frequencies of dark and yellow females. At Baltimore the frequency of dark females is .4483 and the mean number of spermatophores was .3366 greater in yellow than in dark females. At Mountain Lake, Virginia where the frequency of dark females is almost doubled (.8571) the difference in mean spermatophore number between yellow and dark females is nearly the same (.3889) (Burns, 1966 Tables 1 and 2).

The difference in means for spermatophores in dark and yellow forms is significant at the 0.2 level for the sample from Mountain Lake, Virginia and is significant between the 0.2 and 0.3 level for the sample from Baltimore County, Maryland (Appendix 1). The "true" difference between the means is important to the theory of polymorphic populations. The experimental biologist can determine the correct sample size to prove or disprove the theory by using the data given below.

Population parameters for the frequency of dark and yellow forms of the tiger swallowtail and the mean number of spermatophores for each follow (Burns, 1966):

	Mountain Lake, Virginia			*Baltimore County, Maryland*		
	Frequency of Female Type	*Mean number of Spermatophores Per Female*	*Standard Deviation-(s)*	*Frequency of Female Type*	*Mean number of Spermatophores Per Female*	*Standard Deviation-(s)*
Dark	.857	1.694	.781	.448	1.538	.776
Yellow	.143	2.083	1.379	.552	1.875	.619
Combined Data	–	1.750	.890	–	1.724	.702

For an assessment of how many specimens should be collected from each population so that the estimated difference in the average number

TABLE 1. DISTRIBUTION OF SPERMATOPHORES IN FIELD SAMPLES OF VARIOUS LEPIDOPTERA AND EXPERIMENTS ON MATING BEHAVIOR

N—sample size; $\overline{X}$—mean or average; s^2—sample variance, mean square or square of the sample standard deviation.

Number of spermatophores	*N*	*0*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	$\overline{X}$	s^2
Utetheisa ornatrix bella (L.) (Arctiidae)—Archbold Biol. Station, Lake Placid, Florida (net collection)	88	8	12	15	20	11	5	4	4	2	3	3	1	3.4886	7.0573
Pseudaletia unipuncta (Haw.) (Noctuidae)—Louisiana Callahan and Chapin (1960) Table 1—p. 779 (light trap)	417	182	107	76	36	14	2	–	–	–	–	–	–	1.0384	1.3447
Peridroma saucia Hbn. (= *margaritosa* Haw.) (Noctuidae)—Louisiana Callahan and Chapin (1960) Table 2—p. 780 (light trap?)	239	203	16	5	8	6	1	–	–	–	–	–	–	.3305	.8525
Heliothis zea (Boddie) (Noctuidae)—Louisiana Callahan (1958) Table 6—p. 427 (light trap)	1295	519	455	227	77	16	1	–	–	–	–	–	–	.9336	.9338
	N		*less than 2*							*2 or more*					
Euphydryas editha (Bdv.) (Nymphalidae)—California Labine (1964)	23		14							9					
	N	*0*	*1*	*2*	*3*	*4*	*5*							$\overline{X}$	s^2
Battus philenor (L.) (Papilionidae)—Mtn. Lake Biol. Sta., Virginia Burns, 1966—table 2.	33	0	17	11	3	1	1							1.7273	.9545
Papilio glaucus L. (Papilionidae) Burns, 1966—table 2.															
Mtn. Lake Biol. Station, Virginia															
dark females	72	0	33	30	8	–	1							1.6944	.6095
yellow females	12	0	6	2	2	1	1							2.0833	1.9015
Total	84	0	39	32	10	1	2							1.7500	.7922
Baltimore County, Maryland															
dark females	13	0	8	3	2	–	–							1.5385	.6026
yellow females	16	0	4	10	2	–	–							1.8750	.3833
Total	29	0	12	13	4	–	–							1.7241	.4926

TABLE 1 Continued

Pectinophora gossypiella—(Saunders)

1. Number of copulations (spermatophores not counted) during the lifetime of individual pairs maintained in laboratory population cages.

No. of copulations	*No. of moths in Population Cage:* ♂	♀	*N*	*0*	*1*	*2*	*3*	*4*	$\bar{X}$	s^2
Lukefahr and Griffin (1957, 1967)	1	1	100	72	16	3	3	1	.3500	.5934
Ouye, *et al.* (1964) Ouye, (*in litt.* 1967)	1	1	94	24	50	14	5	–	.9894	.6343

2. Number of spermatophores produced during lifetime exposure to moths of opposite sex under laboratory conditions (Ouye, *et al.*, 1965, experiment 4—table 3; experiment 5—table 4, and Ouye, *in litt.* 1967).

No. of spermatophores formed during lifetime	*No. of Moths in Pop. Cage* ♂	♀	*N*	*0*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	$\bar{X}$	s^2
Males	$\overline{3}$	$\overline{1}$	206*	10	19	20	25	41	29	29	16	9	5	3	4.2524	5.3116
Females																
(A) Crowded	75	25	196	3	49	74	45	22	2	1	–	–	–	–	2.2245	1.1186
(B) Uncrowded	1	6	266	8	64	83	69	34	6	1	–	1	–	–	2.3195	1.4334
Combined (A+B)			426	11	113	157	114	56	8	2	–	1	–	–	2.2792	1.2993

* Amends N in experiment 4 and table, Ouye, *et al.*, 1965.

3. Spermatophore formation during the first 24 hours after eclosion of females (Ouye, *et al.*, 1965, experiment 3 table 2, Ouye, *in litt.* 1967).

No. of spermatophores Time exposed to males in population cages	*N*	*0*	*1*	*2*	*3*	*4*	$\bar{X}$	s^2
15–21 hours	373	89	222	44	16	2	.9812	.5776
9–15 hours	118	65	42	7	4	–	.5763	.5711
3–9 hours	16	14	1	–	1	–	.2500	.6000

4. Distribution of spermatophore number in a sample of females collected at light traps in the vicinity of Brownsville, Texas (Graham, *et al.*, 1965; and Ouye, *in litt.* 1967).

No. of spermatophores	*N*	*0*	*1*	*2*	*3*	*4*	*5*	*6*	$\bar{X}$	s^2
No. of moths	2570	284	1872	332	65	13	3	1	1.0911	.4067

of spermatophores lies within .05 of the "true" value 95% of the time, see Appendix 2.

Disruptive selection in the tiger swallowtail may be an example of evolutionary homeostasis at the population level; that is, constant intraspecific factors of selection counterbalance variable extra-specific environmental factors and tend to restore primitive population conditions.

TABLE 2. *Utetheisa ornatrix bella* IN EACH OF FOUR GRADES OF CONDITION WITH MEAN NUMBER OF SPERMATOPHORES PER FEMALE

Condition	*# Individuals*	*Mean Number of Spermatophores*
A	22	1.455
B	32	2.781
C	26	5.231
D	8	6.250

If this is true, when the environment ceases to favor the evolutionary novelty (the dark female), the force of sexual selection will restore a uniformly yellow population. This hypothesis is consistent with the observed correlation between the distribution of the blue swallowtail and a high frequency of the dark female form of the tiger swallowtail.

Data on spermatophore frequency in Lepidoptera are summarized in Table 1. The maximum number of spermatophores counted in a female was 11 (*Utetheisa ornatrix*). The maximum number of spermatophores formed by a male was 11 (*Pectinophora gossypiella*—Ouye, *in litt.* 1967).

The mating habits of the pink bollworm moth (*Pectinophora gossypiella*) have been thoroughly studied (Lukefahr and Griffin, 1957; Ouye, *et al.*, 1964; Ouye, *et al.*, 1965; Graham, *et al.*, 1965; Ouye, *in litt.* 1967). Data are summarized in Table 1. Pairs of moths copulated an average of .350 times during their lifetime in the experiments of Lukefahr and Griffin and .989 times in the experiments of Ouye and his workers (spermatophores were not counted). The two means are different (Appendix 3).

Females mate successfully as many as four times during the first 24 hours after eclosion; males produce no more than one spermatophore in a 24 hour period. The average number of spermatophores formed during the life of a male is 4.252 under laboratory conditions. This is almost double the lifetime average of 2.279 for the combined data of females in crowded (A) and uncrowded (B) population cages. (Table 1, experiments 2 and 3) (Appendix 4).

Thus, while the female pink bollworm moth mates successfully more often in one day, the male can mate successfully almost twice as many times as the female in the moths' lifetimes.

The greater number of spermatophores formed by the male is consistent with a hypothesis that natural selection acts more strongly on the male than on the female. Two factors reduce the male's average under the competitive conditions in the field. Males may compete more actively for females than females compete for males (intra-specific sexual selection). Extra-specific factors of natural selection sometimes

TABLE 3. NUMBER OF INDIVIDUALS AND MEAN NUMBER OF SPERMATOPHORES IN EACH CATEGORY OF THE FIVE CHARACTERS FOR WING PATTERN AND PIGMENTATION IN *Utetheisa ornatrix bella* FROM FLORIDA

Character	*Phenotype*	*Number of Individuals*	*Mean Number of Spermatophores*
1	Colored/streaked	36	3.750
	Intermediate	22	3.136
	White	30	3.433
2	Yellow/orange	76	3.526
	Red/orange red/red orange	10	3.100
	("Redless" Aberration)[1]	2	4.000
3	Spotted	69	3.145
	Unspotted	19	4.737
4	Wide	55	3.618
	Semi	30	3.367
	Narrow	3	2.333
5	Red/pink/flush	82	3.304
	White	4	2.000
	("Redless" Aberration)[1]	2	4.000

[1] Specimens in which the red pigment is missing on both the upper and under surface of the wings.

favor survival of the female at the expense of the male, as for example, when the female is protectively colored. Thus, at the population level, the male's greater reproductive potential compensates for individual competition among males and for the greater risk involved in being a male.

It seems intuitive that the competition for mates affects the distribution of spermatophores formed by the two sexes, perhaps, by increasing the variation in the number of spermatophores formed by the males. However, the design of a practical experiment to collect data, and a method of analysis are a challenge to the ingenuity of the experimental biologist.

In samples of Lepidoptera collected at light traps, the average number of spermatophores varies from 1.0911 (*Pectinophora gossypiella*) to .3305 (*Peridroma saucia* Hbn. (Noctuidae)). The average number of spermatophores in a collection made with a net was 3.4886 for *Utetheisa ornatrix.* These data are not comparable to laboratory data because of the mixed age distribution in feral populations.

Some calculations (by Graham, *et al.,* 1965) suggest that the first mating of the pink bollworm is density dependent, but that multiple paring is density independent. This hypothesis is based on a correlation (or absence of) between the log of the number of moths collected in light traps and (a) the proportion of moths which had mated, (b) the

TABLE 4. SPERMATOPHORE NUMBER IN FALL-WINTER VERSUS THE OVERWINTERING SPRING POPULATIONS OF *D. plexippus* IN CALIFORNIA (DATA FROM TABLE 16, WILLIAMS, *et al.*, 1942)

Date	*Location*	*N*	*0*	*1*	*2*	*3*	*4*	*5*	$\overline{X}$	s^2
Oct. 1938—Feb. 1939	Pacific Grove San Diego El Carrito	38	17	19	2	0	0	0	.605	.353
April 1939	San Francisco	5	0	0	2	0	1	2	3.600	2.300

proportion of once mated or multiply mated moths, (c) the mean number of spermatophores for mated and unmated moths combined, and (d) the mean number of spermatophores for mated moths.

Observations on the sex ratio, migration, spermatophore number, adult activity and mating behavior of the winter population of the monarch butterfly (*Danaus plexippus* (L.) (Nymphalidae)) in California are reported by J. A. Downes (Williams *et al.*, 1942: 160–165). No more than two spermatophores were found in any female until after February (Table 4). Although both sexes migrate, the estimated male: female ratio in the population remaining at Pacific Grove in winter quarters was 1000 to 1 by the second week in May. Females apparently migrate first. Some mating occurs in the hibernating population at Pacific Grove (no reports from November to January, however) even though egg follicles remain unripe until the last week in March.

Species in which both sexes pair several times contrast with those in which the female is prevented from multiple insemination by a sphragis or plug which the male constructs in the genitalia (*Acraea* : Marshall, 1901, 1902, and Eltringham, 1912; *Parnassius* : Eltringham, 1925; *Bombyx mori* L. : Omura, 1938). Marshall hypothesized that differences in courtship behavior separate sphragis building genera (e.g., *Acraea* and *Parnassius*) from many other butterflies, "marriage by capture" (Poulton, 1911) *versus* "marriage by courtship." In other words, sphragis construction complements a behavior pattern in which the male "grapples" with the female after a rudimentary display; in species with more complex behavior patterns, courtship may be terminated at any of several stages (e.g., Brower, *et al.*, 1965).

Eltringham (1912) suggests that the sphragis may block the release of a chemical attractant which serves to assemble males. If this hypothesis is correct, the "capture" system may represent only the final stages of courtship.

In terms of evolutionary potential, no matter how effective "no" signals are, the rare male which succeeds in breaking through the defense mechanisms of an already mated female will leave more offspring than the male which does not mate under such circumstances. Unless there is a selective advantage to multiple insemination such as a short life span of sperm or a prolonged oviposition period, the balance between multiple versus single copulation should occur when the effort required to copulate with an already mated female will reduce, first, the probability of insemination of unmated females and, second, the males contribution to the gene pool of the next generation. For multiple insemination to persist under such circumstances, the number of fertile offspring left by the more versatile male should outnumber those left by the virgin inseminator.

If this were not so, the evolution of more effective mechanisms against multiple pairing would be expected.

A relationship between mating frequency and interpopulation gene flow has been suggested (Labine, 1964—*Euphydryas editha* (Bdv.) (Nymphalidae)). Populations in which the female mates before migration and only once can be contrasted with those in which the female mates several times and especially with endemic males after migration. In the first instance, a migrating female produces offspring with a gene complement derived exclusively from the parent population while all offspring produced by migrant males mated to endemic females receive half their genes from the parent population and half from the other. In contrast, if both sexes mate after migration, essentially, all offspring are interpopulation hybrids. Thus, multiple pairing may increase the proportion of hybrid offspring among progeny of migrants and hasten the breakdown of introduced gene complexes. On the one hand multiple pairing may increase variation through recombination between the two gene pools and thereby influence the speed of adaptive change. On the other hand, if the crossing of the two gene pools proves deleterious and non-adaptive, F_1 offspring of migrants will be at a competitive disadvantage even though offspring homozygous for genes from the parent population compete successfully in the new habitat. *Thus, hybridization is an effective strategy on the part of the endemic population for increasing the probability of beneficial combinations, and at the same time, serves to reduce the competitive advantage of a closely related invading species provided that the reproductive potential of the endemic population is great enough to prevent swamping.*

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APPENDIX

Statistical Notes (Anderson and Bancroft, 1952: Fraser, 1958)

1. Tests for equality of the average number of spermatophores in samples of dark and yellow females of *Papilio glaucus* L. (Burns, 1966).

Hypothesis	*Test*	*Degrees of Freedom*		*Value of Experimental Statistic*	*Value of Tabulated Statistic*	*Significance Level*	*Conclusion*
Mountain Lake Biological Station, Virginia							
		Dark	*Yellow*				
$\mu_{\mathrm{D}} = \mu_Y$	t′	71	11	.13496	$1.980 < t' < 2.201$	.05	means equal
	(Cockran and Cox)						

(Note: a value of the experimental statistic as large or larger is expected on the basis of chance alone about .8 of the time).

Baltimore County, Maryland

		Dark	*Yellow*				
$\mu_{\mathrm{D}} = \mu_Y$	t′	12	15	1.090	$2.131 < t' < 2.179$	.05	means equal

(Note: a value of the experimental statistic as large or larger is expected on the basis of chance alone between .7 and .8 of the time).

2. An approximate solution can be found using the following expression for the confidence limits for the difference of two means (Fraser, 1958: 281):

$$\overline{X}_d - \overline{X}_y \pm t_{.05}\left(\frac{1}{DN}+\frac{1}{YN}\right)^{\frac{1}{2}} s$$

$t_{.05}$ —is the t statistic with $N-2$ degrees of freedom but evaluated here for an infinite number of degrees of freedom since the sample size is large but unknown.
N —Sample size.
D —frequency of dark females in sample.
Y —frequency of yellow females in sample.
s —square root of the variance. Since the variance for spermatophore numbers may differ in the two types of females, an approximate solution is obtained by using the population variance calculated from the combined data.

The solution is obtained by choosing N such that

$$t_{.05}\left(\frac{1}{DN}+\frac{1}{YN}\right)^{\frac{1}{2}} s = .05$$

or

$$N = 400s^2(1.96)^2\left(\frac{1}{D}+\frac{1}{Y}\right).$$

The answer depends on the relative frequencies of dark and yellow females in the sample. The smallest adequate sample is one in which the frequencies of dark and yellow females are equal (*i.e.*, $D = Y = .5$). When equal numbers of both types of female are collected, 3028 females comprise an adequate sample in Maryland and 4870 in Virginia.

3. Means differ at the .02 level of significance, but variances are equal for the two sets of data.

Lukefahr and Griffin, 1957	$N_L = 100$	$\overline{X} = .350$	$s^2_L = .593$
Ouye, *et al.*, 1964	$N_o = 94$	$\overline{X} = .989$	$s^2_o = .635$

Hypothesis	*Test*	*Degrees of Freedom*	*Value of Experimental Statistic*	*Value of Tabulated Statistic*	*Significance Level*	*Conclusion*
$\sigma_L^2=\sigma_o^2$	F-test	93, 99	1.070	$1.59 < F_{.02} < 1.87$	.02	variances equal
$\mu_L = \mu_o$	t-test	192	7.256	$2.33 < t_{.02} < 2.36$	.02	means not equal

4. Data for females in crowded (A) versus uncrowded (B) population cages were tested for equality of means and variances. Combined data for females under both conditions were compared with the data from males for equality of means and variances.

Crowded females (A)	$N_A = 196$	$\overline{X}_A = 2.224$	$s^2_A = 1.146$
Uncrowded females (B)	$N_B = 266$	$\overline{X}_B = 2.320$	$s^2_B = 1.433$
Combined data for females	$N_C = 462$	$X_C = 2.279$	$s^2_C = 1.299$
Males	$N_M = 206$	$\overline{X}_M = 4.252$	$s^2_M = 5.315$

Hypothesis	*Test*	*Degrees of Freedom*	*Value of Experimental Statistic*	*Value of Tabulated Statistic*	*Significance Level*	*Conclusion*
$\sigma_A^2 = \sigma_B^2$	F-test	265,195	1.251	$1.28 < F_{.02} < 1.59$	.02	variances equal
$\mu_A = \mu_B$	t-test	460	.770	$2.33 < t_{.02} < 2.36$	.02	means equal
$\sigma_C^2 = \sigma_M^2$	F-test	205,461	4.091	$1.00 < F_{.02} < 1.48$	.02	variances unequal
$\mu_C = \mu_M$	t′ (Cockran and Cox)	205,461	11.664	$2.33 < t'_{.02} < 2.35$	.02	means unequal

LEONARD STEVENS PHILLIPS (1908–1968)

Leonard Stevens Phillips was born December 4, 1908 at Le Claire, Iowa. He died suddenly in Chicago, Illinois, February 13, 1968. He was the son of Clyde and Winifred Phillips. His marriage to Merle Olive Garton took place May 26, 1937. She survives him; there were no children.

He attended the public schools of Le Claire and received his B.A. degree from the State University of Iowa in 1932. He did graduate work there and at the Iowa State University of Agriculture, and received his teacher's certificate from the Iowa State Teachers' College in 1938.

He engaged in private business from 1936 to 1946, then became a laboratory assistant in the Stritch School of Medicine, Loyola University, Chicago, a position which he held until 1950. Following a period as laboratory technician with Swift and Company in Chicago, he became Assistant Biologist at the Illinois Institute of Technology Research Institute. Here he was in charge of the animal room and worked on many projects involving the use of small animals in behavioral studies and biochemical research. In 1965 he joined the Loop City College of Chicago as a laboratory assistant, and in 1967 returned to private business, in which he was engaged at the time of his death.

Leonard was an active and enthusiastic collector of Lepidoptera. He collected personally in every state of the continental United States and maintained an active correspondence and exchange with fellow lepidopterists throughout the world. He contributed several papers to the pages of this *Journal*; a bibliography is given below. His collection of some 5,600 specimens of worldwide Lepidoptera is being retained by his widow for the present, but will be presented to Buena Vista College, Storm Lake, Iowa.

Among his other interests were collections of pressed plants, minerals, and stamps; woodworking, and amateur art. He was active in Boy Scout, boys' club, and church work. He was a member of the Chicago Entomological Society, and had been a member of the Lepidopterists' Society since 1948.

Leonard's many friends and correspondents will miss his friendly, outgoing personality, his enthusiasm for his avocation, and his willingness to be of service to others.

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THE EFFECT OF BAROMETRIC PRESSURE AND OTHER FACTORS ON ECLOSION OF THE CABBAGE BUTTERFLY *PIERIS RAPAE* (PIERIDAE)

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The literature describes various effects of barometric pressure on insects. For example, there is evidence that slightly reduced pressure increases the rate of development of insects while slightly increased pressure has no positive influence (Wellington, 1946). *Pieris rapae* (L.) is said to lay more eggs when the barometric pressure is low (Stephens and Bird, 1949), while low pressure appears to be disadvantageous to at least one insect activity in that a slight depression is reported to prevent the silkworm from secreting silk (Markovic-Giaja, 1957).

Of particular interest is the assertion that lowering of the barometric pressure is necessary for successful eclosion of butterflies (Pictet, 1933), including *Pieris rapae* and *Pieris brassicae* (L.); it was recorded that 91.3% of 1758 pupae eclosed during atmospheric depression. Also, certain Lepidoptera are supposed to be so sensitive to the effect of barometric pressure that they eclose when the pressure falls only 1.7–3.4 mm of mercury below the daily maximum (Mell, 1939).

The present work is in large part an evaluation of the effect of pressure on eclosion of the subject species by means of observations at ambient conditions and also by controlled experiments.

Eclosion under ambient conditions

The pressure in the central area of a typical "high" is about 765–773 mm, while a "low" is normally 743–750 mm (Anonymous, 1960). In the New York City area the mean pressure in summer generally is about 762 mm.

The data of Table 1 are for successive broods in a culture started with eggs laid by *Pieris rapae* taken at Flemington, New Jersey on May 1, 1965. It is apparent that the barometric pressure was relatively high, and certainly not considerably depressed, during eclosion. The impression is that the time of eclosion was controlled simply by the time required for maturation of the pupa (7–10 days, approximately). The possibility would seem to remain that eclosion might be delayed by an unusually high pressure, e.g. 788 mm as recorded in New York City for record highs in 1927 and 1949 (Hansen, 1961), and the effect of extremely high pressures was studied in the experiments discussed below.

TABLE 1. BAROMETRIC PRESSURE DURING ECLOSION UNDER AMBIENT CONDITIONS

				Conditions during eclosion[1]		
Number eclosed	Pupation (day)	Eclosion (day)	Date eclosion started	Relative humidity (%)	Temperature (°F)	Barometric pressure (mm)
38	0–6	9–15	June 6, 1965	38–55	75–90	754–766[2]
51	0–5	14–18[3]	July 11, 1965	49–62	77–87	758–766
37	0–3	7–10	Aug. 11, 1965	48–60	78–89	761–765
16	0–5	9–13	Sept. 16, 1965	60–65	72–84	760–770

[1] The barometric pressure readings are corrected to 0°C and sea level.
[2] The pressure was in the 759–766 mm range except for the last day.
[3] The pupae had been refrigerated from day = 6 to day = 12.

ECLOSION UNDER CONTROLLED CONDITIONS—EXPERIMENTAL

Rearing of larvae.—Larvae were reared in cardboard boxes with gauze windows and fed cabbage leaves from refrigerated heads as in previous work (Kolyer, 1966).

The pupae used for experiment 1 derived from eggs laid on August 6 and 7, 1966 by females taken at Berkshire Valley and Morristown, New Jersey. Pupation took place 17–21 days after the inception of hatching on August 9. The larvae were reared in a room at 73–91°F and 40–70% relative humidity.

The pupae for the remaining experiments were reared from eggs obtained from N. R. Spencer of the U. S. Department of Agriculture (see Acknowledgment). A minor portion of the final-instar larvae evidenced black spots on the integument, but fortunately there was no effect on pupation or eclosion. Pupation took place 26–29 days after the inception of hatching on April 7, 1967. The room was at 67–79°F and 25–34% relative humidity during the larval period. Incidentally, two male adults from this brood were of the canary-yellow form (one eclosed in experiment 2 and one in experiment 5).

TABLE 2. SUMMARY OF EXPERIMENTAL CONDITIONS

Experiment Number	Pressure (mm)	Photoperiod[1]	Relative Humidity (%)
1	735–740 and 765–770[2]	no	43 at 72°F
2	735–740 and 765–770[2]	yes	43 at 72°F
3	690–700 and 790–800[2]	no	43 at 72°F
4	825–830	yes	43 at 72°F
5	ambient	yes	87 at 75°F
6	ambient	yes	43 at 72°F

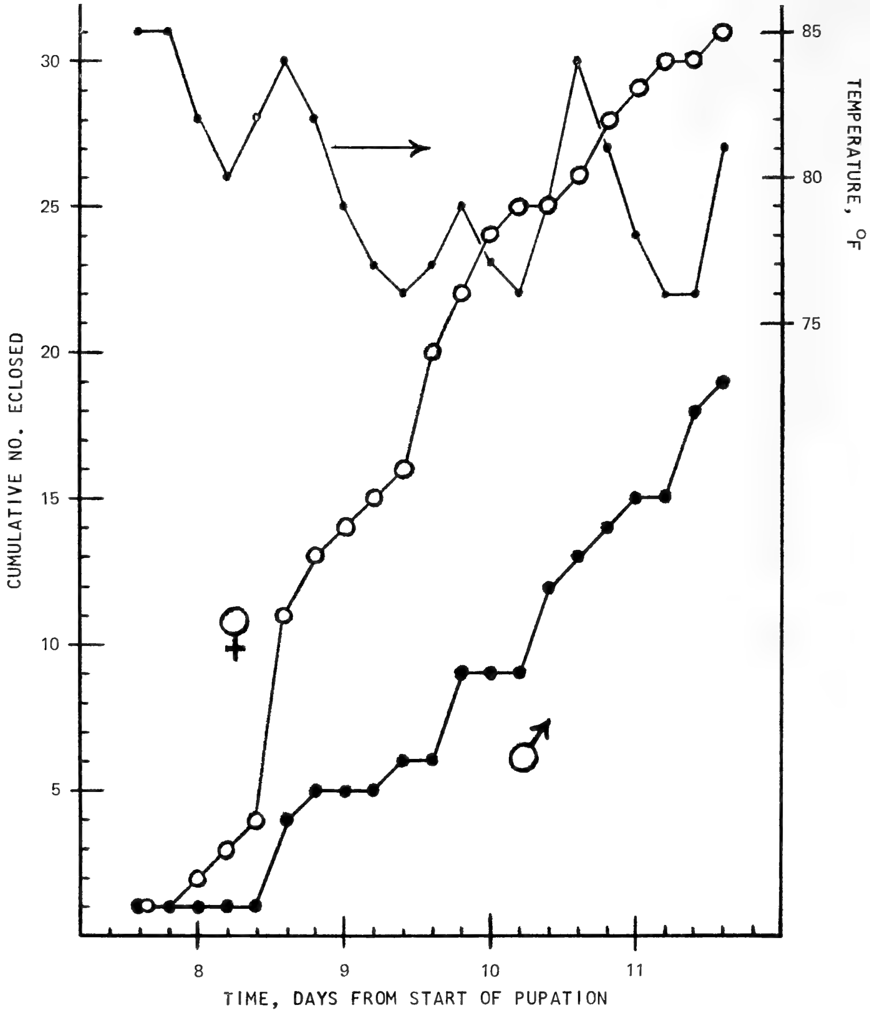
[1] Diffuse sunlight (from windows with southern exposure) from 7:27 AM to 5:03 PM.
[2] Cycled from one range to the other every 4 hours and 48 minutes (five times per day).

Fig. 1. Apparatus used for experiments 1–4.

Final-instar larvae were sorted quite reliably into males and females by means of the testes visible in the male as done in previous work (Kolyer, 1966), and the sexes were allowed to pupate in separate boxes.

Apparatus and procedure.—The apparatus shown in Figure 1 was used for experiments 1–4 (summarized in Table 2). This consisted simply of two one-liter flasks connected through their side-arms and fitted with a stopcock (and pinch clamp, not shown, for perfect seal) and mercury-containing manometer open to the atmosphere. Gauze was provided in the flasks so that the emerging butterflies could climb up and expand their wings.

Vials (approximately one inch inside diameter) containing saturated potassium carbonate solution in contact with solid potassium carbonate hydrate were suspended inside the flasks to regulate the relative humidity. A value of 42.8% relative humidity at 77°F is given by Stokes and Robinson (1949), and 43% at 72°F was found experimentally by confining a calibrated hygrometer with the potassium carbonate system. The capacity of the system to absorb water was demonstrated by introducing one milliliter of water into a one-gallon jar containing a hygrometer and the regulating system in a 2.5 inch diameter dish. In about five

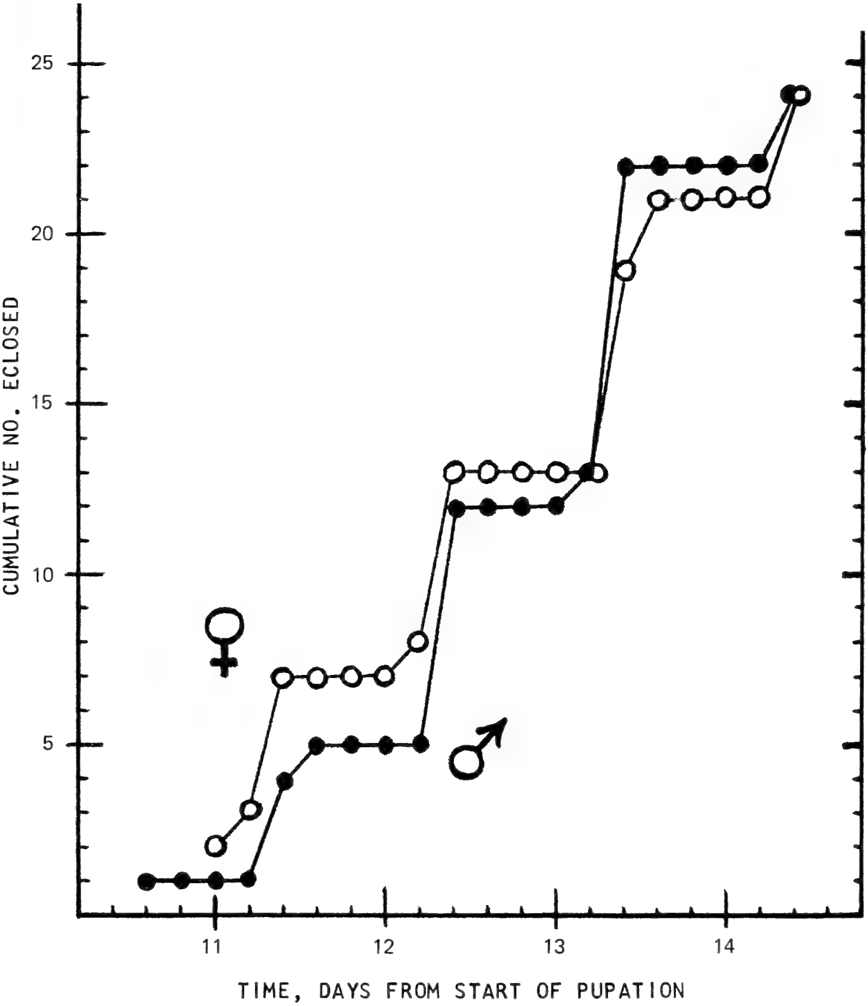


EXPLANATION OF GRAPH 1

Cumulative number eclosed vs. day from start of pupation for experiment 1. A record of temperature is included.

hours the relative humidity had risen to a maximum of 81% and at 50 hours it had fallen back to 50%; in the absence of the system 100% relative humidity was attained about 10 hours after adding the water.

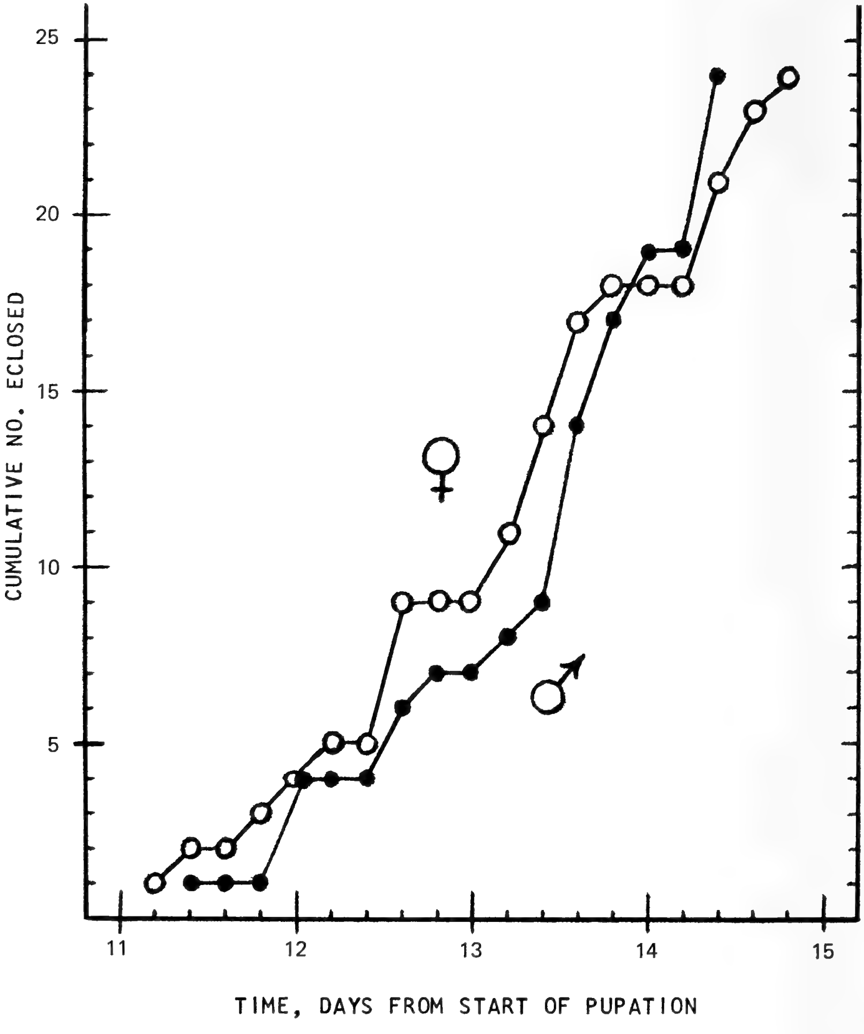
Pupae, detached by clipping the silken girths and pulling free from the silk button at the caudal end, were dropped into the flasks (males in one flask, females in the other) three days before eclosion began, and maintenance of conditions as defined in Table 2 was initiated.



EXPLANATION OF GRAPH 2

Cumulative number eclosed vs. day from start of pupation for experiment 2.

In the graphs and tables each day is arbitrarily taken to begin at 2:39 AM and is divided into five equal periods (beginning at 2:39 AM, 7:27 AM, 12:15 PM, 5:03 PM, and 9:51 PM). At the start of each period the barometric pressure and the room temperature were noted, and the pressure was cycled in the case of experiments 1–3. The object of cycling was to give the pupae a choice of high or low pressure every five hours.

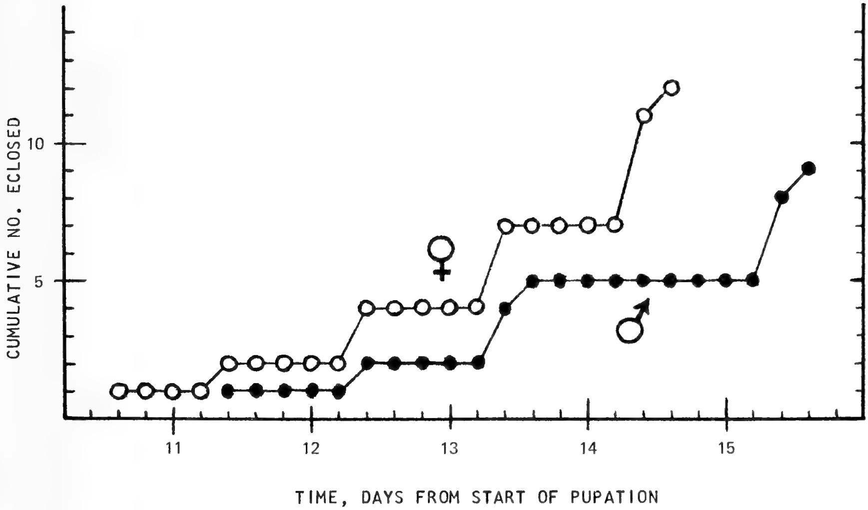


EXPLANATION OF GRAPH 3

Cumulative number eclosed vs. day from start of pupation for experiment 3.

For reference, the first period of the 8th day on Graph 1 was a high cycle, as was the first period of the 11th day for Graphs 2 and 3.

The data are presented in Graphs 1–7. The temperature record for experiment 1 is included in Graph 1, while the temperature record for experiments 2–6 (all done at the same time) and the barometric pressure record applicable to experiments 5 and 6 are shown in Graph 7.



Explanation of graph 4

Cumulative number eclosed vs. day from start of pupation for experiment 4.

The barometric pressure readings in Graph 7 were used to adjust the pressure in the flasks. For example, if the atmospheric pressure was 760 mm and a pressure of 740 mm was desired in the flask, a differential of 20 mm on the manometer was produced by drawing out air by lung power and closing off the stopcock and the pinch clamp. A rubber bulb was used to pressure the flasks in the high cycles. To correct the pressure readings, which were taken at Convent, New Jersey at an elevation of 290 feet, to 0°C and sea level, approximately 4 mm must be added (Perry, 1950). The flask pressures listed in Table 2 are ranges because some fluctuations necessarily accompanied temperature variations.

In experiments 5 and 6, wide-mouth jars (approximately 3.5 inches inside diameter by 5 inches deep) contained the pupae and humidity-regulating system. The jars were closed tightly enough to maintain regulated humidity but not to hold a pressure differential relative to the atmosphere. The potassium carbonate system was used in experiment 6, while in experiment 5 a saturated sodium carbonate solution in contact with solid hydrated sodium carbonate was included. The sodium carbonate system gave 87% relative humidity at 75°F experimentally; Lange (1946) lists 92% at 65°F.

ECLOSION UNDER CONTROLLED CONDITIONS—RESULTS AND DISCUSSION

The five factors considered were barometric pressure, light, tempera-

TABLE 3. ECLOSION DURING ALTERNATING CYCLES OF HIGH AND LOW PRESSURES

Experiment Number	Pressure	Number Eclosed			Theoretical Random Distribution
		Male	Female	Total	
1	low	7	16	23	25
	high	12	15	27	25
2	low	13	13	26	24
	high	11	11	22	24
3	low	7	13	20	24
	high	17	11	28	24

ture, relative humidity, and sex. The results are discussed in terms of each of these.

Barometric pressure.—The data summarized in Table 3 show no significant trend with respect to barometric pressure. By the chi-square method of testing goodness of fit (Sinnott and Dunn, 1939) it is found that the differences observed in the total numbers eclosed at high vs. low pressure can very possibly be explained by chance alone (Table 4).

In experiment 3 the low pressure was below one of the lowest on record (721 mm) for New York City (Hansen, 1961), and the high pressure was above a record high (788 mm). In experiment 4, in which the pressure was held constant at an abnormally high level, the butterflies had no notable difficulty in eclosing (one unexpanded and one with shriveled forewing vs. two imperfect specimens in experiment 1, three in experiment 2, and one in experiment 5). Also, eclosion in experiment 4 was not delayed and proceeded over about the same time interval as in experiments 2, 3, 5, and 6.

In experiment 1 the larvae were diseased, and only 11 specimens (4 males and 7 females) expanded normally. It is interesting that 7 of these (all but 4 of the females) eclosed during the high pressure cycle, showing the lack of advantage of low pressure even when expansion ability was marginal.

TABLE 4. SIGNIFICANCE OF DATA (TOTAL ECLOSED) OF TABLE 3

Experiment Number	χ^2	Approximate Probability of Observed Deviation by Chance Alone[1]
1	.320	58
2	.333	57
3	1.33	25

[1] For one degree of freedom.

TABLE 5. ECLOSION VS. TIME OF DAY

	Experiment 1			Experiment 2			Experiment 3		
Period[1]	Male	Female	Total	Male	Female	Total	Male	Female	Total
1	0	4	4	1	2	3	1	4	5
2	7	2	9	21	18	39	7	7	14
3	6	14	20	2	2	4	7	9	16
4	5	6	11	0	2	2	4	3	7
5	1	5	6	0	0	0	5	1	6

	Experiment 4			Experiment 5			Experiment 6		
Period[1]	Male	Female	Total	Male	Female	Total	Male	Female	Total
1	0	0	0	0	1	1	2	0	2
2	7	10	17	9	6	15	4	7	11
3	2	2	4	1	4	5	3	2	5
4	0	0	0	0	0	0	1	0	1
5	0	0	0	0	0	0	0	2	2

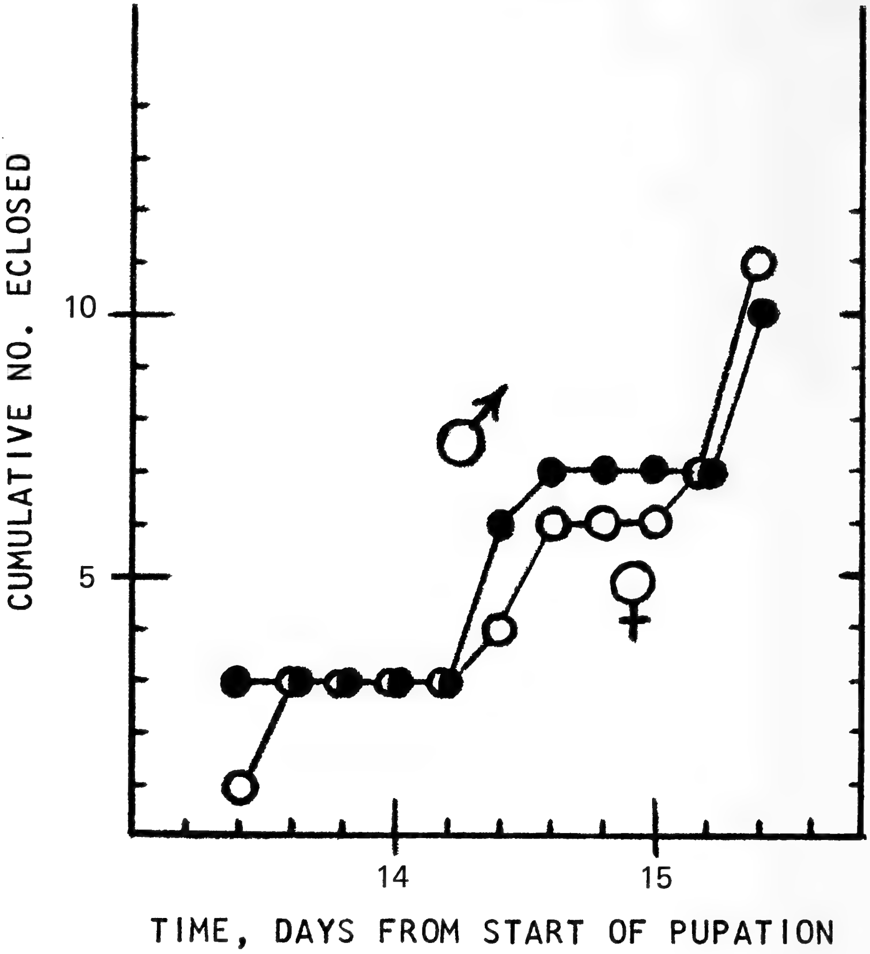
[1] The day was divided into five equal periods beginning at 2:39 AM.

Pupae which are prepared to eclose appear to be able to wait several hours for the stimulus of light and so might have been expected to take advantage of the occurrence of low pressure cycles every four hours and 48 minutes if reduced pressure also is a stimulus.

As expected, there was no real correlation of eclosion with ambient barometric pressure in experiments 5 and 6. For example, eclosion in experiment 5 was concluded at the high point of the pressure record. In view of the data of Table 1 and the results of experiments 1–4, the fortuitous drop in pressure seen in Figure 7 probably had no bearing on eclosion.

Light.—In experiments 1 and 3 the pupae were kept in darkness except for brief intervals of light when the pressure was adjusted between periods. The data (Table 5) indicate a preference for periods 2–4 (7:27 AM—9:51 PM) in experiments 1 and 3, and the chi-square test (four degrees of freedom) shows less than a 5% probability that the results are due to chance alone. It is possible that temperature variation and/or brief admission of diffuse sunlight at the beginning of the favored periods was responsible. However, David and Gardiner (1962) report a rhythm of eclosion for *Pieris brassicae* in darkness.

In experiments 2, 4, 5, and 6, in which diffuse sunlight was available during periods 2 and 3, there resulted a very marked preference for eclosion during the photoperiod. Only 40% of the pupae should have eclosed during the photoperiod by chance, while the result was 90%. The chi-square test shows that in all cases the deviation from chance



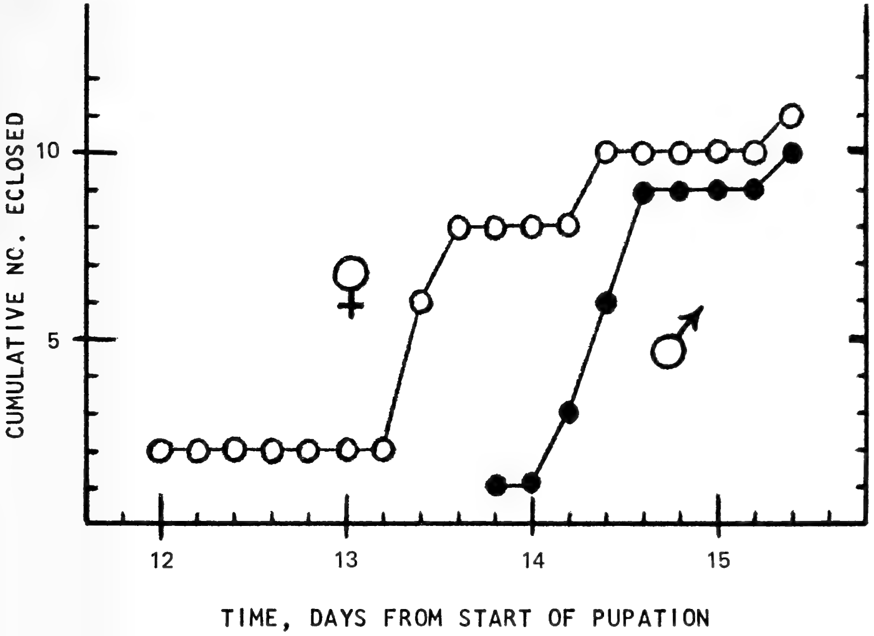
Explanation of graph 5

Cumulative number eclosed vs. day from start of pupation for experiment 5.

distribution is highly significant. Graphically, the stepwise nature of the curves for experiments 2, 4, 5, and 6 is conspicuous.

The impression is that the mature pupa can wait several hours for the arrival of the photoperiod before eclosing, and it is reported (Mell, 1939) that butterflies generally eclose in the early morning and that the coming of light seems to be the stimulus. In a study including *Pieris rapae*, 85.9% of 1758 pupae eclosed from 8 AM to 6 PM and the remaining 14.1% at night (Pictet, 1933).

Temperature.—In experiments 2–6 the temperature varied over a



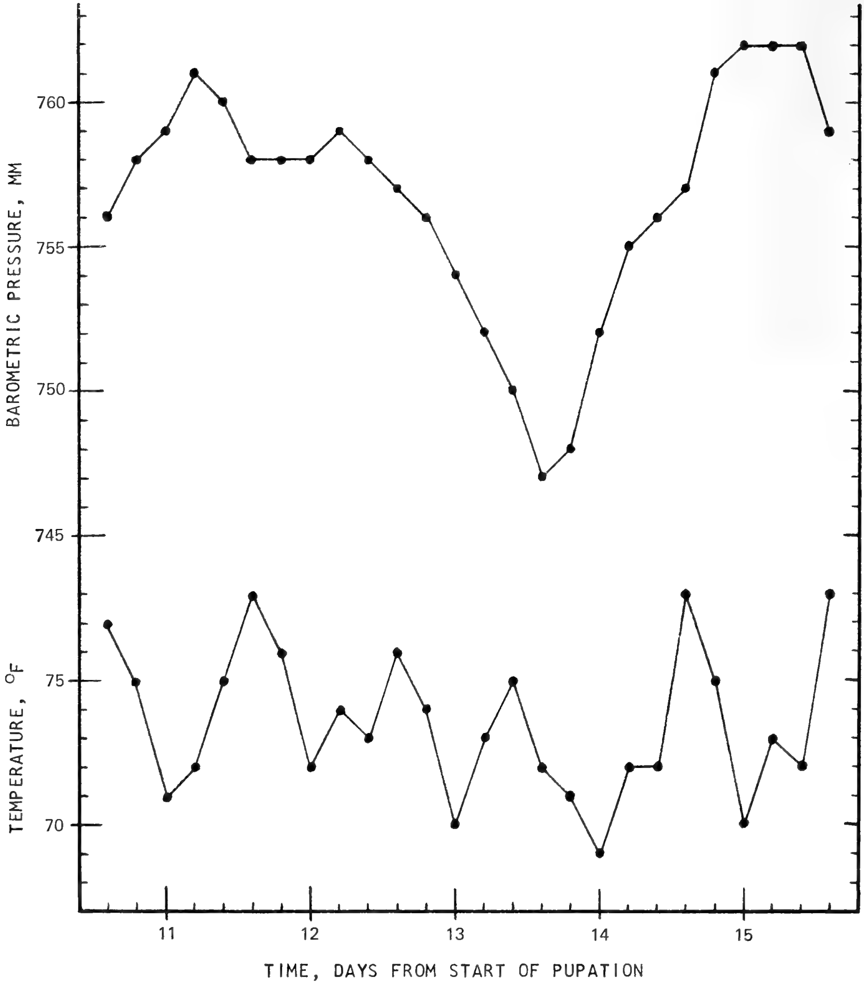
Explanation of graph 6

Cumulative number eclosed vs. day from start of pupation for experiment 6.

range of 9°F (Graph 7). Low points occurred at the beginning of period 1 (2:39 AM) in all cases, and high points occurred at the beginning of periods 3 or 4. The fluctuations were similar in magnitude, though less regular, in experiment 1 (Graph 1).

It would seem that the effect of light as a factor is predominant in the experiments having a photoperiod (2, 4, 5, and 6), but some temperature fluctuation may be required for photoperiod to promote eclosion; David and Gardiner (1962) report that for *Pieris brassicae* eclosion takes place in the dark period with photoperiod 6 AM—10 PM when the temperature is constant but that eclosion is delayed until morning or afternoon when the temperature fluctuates.

Relative humidity.—Very high humidity may delay eclosion of certain moths (Mell, 1939). However, in experiment 5 eclosion at 87% relative humidity was certainly not hindered, nor was it judged significantly accelerated or delayed vs. eclosion at 43% relative humidity. As in the other experiments, light appeared to be the dominant factor (though possibly through interaction with temperature fluctuation pattern). Eclosion of the males was completed during the highest phase (763–766 mm, corrected to 0°C and sea level) of the ambient pressure record,



Explanation of graph 7

Record of barometric pressure and temperature during experiments 2–6.

and it is suspected, though it was not experimentally demonstrated, that controlled variations of the pressure would have had no more effect at 87% relative humidity than they were found to have in experiments 1–3 at 43%.

At a lower relative humidity under ambient conditions (23–34% relative humidity, 72–76°F), five males eclosed at 764, 763, 761, 766, and 759 mm (corrected to 0°C and sea level). Again, reduced pressure was not required.

Sex.—In *Pieris napi* (L.) and *P. bryoniae* (Ochs.) the males are said to tend to emerge before the females (Bowden, 1953). However, in experiments 1–3 the sexes eclosed over almost exactly the same time interval and at about the same rate; if anything, the females tended to eclose a little earlier in experiments 2 and 3. In experiments 4 and 6 the females tended to eclose considerably earlier, though the significance of this is dubious because of the limited numbers involved. Certainly, there was no trend for the males to emerge before the females in any of the experiments. This conclusion is, of course, applicable *only* to the specific conditions of the tests.

Conclusion

Care must be taken in drawing generalized conclusions from the data because of the possibility of the interaction of factors, the possibility of discontinuities in cause-effect relationships, and the possible effect of rate of change of variables. For example, at some critical values for the three variables the relative humidity, temperature, and barometric pressure might interact so that the pressure *does* influence eclosion. Or the effect of pressure might be nil at slight or major depressions but unexpectedly apparent at medium depressions. Or eclosion might be promoted not simply by low barometric pressure but by the dynamic factor of *falling* pressure.

Therefore, the present work does not prove that barometric pressure cannot influence eclosion of *Pieris rapae* but only that it does not influence eclosion under specific ambient conditions or in certain controlled environments. In fact, even the strain of a species conceivably could have an effect. Still, it seems a reasonable conclusion that light is a principal factor (as appears in the literature) and that barometric pressure is not a significant factor under certain typical summer ambient conditions or when cycled between extreme values, or held at a constant high value, in experiments at constant relative humidity, slightly fluctuating temperature (9°F maximum variation), and controlled photoperiod.

The indication is that the time of eclosion was controlled to the nearest day or so simply by the rate of development of the pupa (in turn controlled by the temperature history; David and Gardiner (1962), for example, list a pupal period for *Pieris brassicae* of 40 days at 54.4°F and only 7.5 days at 86°F). Then, under the particular conditions of the tests, which involved some temperature fluctuation, the mature pupa showed a strong tendency to await the coming of light as stimulus for eclosion. No obvious effect of sex, relative humidity, or barometric pressure upon this process was seen.

SUMMARY

Under typical summer conditions, pupae of *Pieris rapae* (L.) were observed to eclose at up to 770 mm barometric pressure with no apparent preference for atmospheric depression, although reduced pressure has been described in the literature as a requirement for eclosion of certain Lepidoptera.

Under controlled conditions, male and female pupae were studied separately. The relative humidity was held constant, the temperature fluctuated over a maximum of 9°F with minima at night, and a photoperiod (diffuse sunlight) of either 0 or 9.6 hours was provided. The barometric pressure was held at a constant high level (approx. 830 mm) or cycled from approx. 735 to 770 mm or from approx. 690 to 800 mm five times per day to give eclosing pupae a choice of high or low pressure. No significant dependence of eclosion on barometric pressure or sex was found, but light stimulated eclosion under the test conditions. There was no notable difference in eclosion at 87% vs. 43% relative humidity.

The indication is that the time of eclosion was controlled within a day or so simply by the rate of development of the pupa (dependent on temperature history), and that light, if available, then was the immediate stimulus for eclosion in a very significant proportion of cases. It is emphasized that conclusions must be confined to the particular experimental conditions.

ACKNOWLEDGMENT

We wish to acknowledge the aid and advice of Mr. N. R. Spencer, U. S. Department of Agriculture, Entom. Res. Div., Columbia, Missouri, who kindly supplied us with eggs from his *Pieris rapae* culture.

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FOODPLANTS OF *CALLOPHRYS* (*INCISALIA*) *IROIDES*

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In contrast with other members of the subgenus, which are restricted in host selection, *I. iroides* (Boisduval) is polyphagous. The diverse host plants credited to this West Coast butterfly are summarized by Clench (1961), who indicates some of the early records are doubtful.

Recorded foodplants for *iroides* include "young apples" (*Malus,* Rosaceae) in British Columbia (Bethune, 1904) and both *Ceanothus* (Rhamnaceae) and *Cuscuta* (Polemoniaceae) in southern California (Comstock and Dammers, 1933). Field oviposition was observed and larvae reared on *Cuscuta,* a leafless, parasitic plant which lacks chlorophyll. Clench also lists *Gaultheria* and *Arbutus* (Ericaceae) as hosts but does not cite the original source of these records.

Recent investigations during California Insect Survey activities confirm use of two of these foodplants in central and southern coastal California and have disclosed the use by *I. iroides* of *Chlorogalum pomeridianum,* a monocotyledenous plant in the foothills of the Sierra Nevada.

A nearly mature larva was collected on *Arbutus menziesii* at China Camp, Marin County, June 3, 1964, from which an adult *iroides* was reared, emerging on April 19, 1965. *Ceanothus* probably is commonly used by *iroides* over much of its range. One larva was swept from *C.*

cuneatus near Middletown, Lake County, on May 14, 1966. It fed on the green fruit of this plant in the laboratory prior to pupation in mid-June. Emergence did not occur, but a fully developed adult was dissected from the pupal shell in May, 1967. Additional larvae were taken on an unidentified species of *Ceanothus* at the north end of Casitas Reservoir, Ventura County, on March 15, 1967, by P. A. Opler. One *iroides* emerged April 16, 1967, suggesting, as did Comstock and Dammers' observations, that populations in southern California develop two spring generations.

Six larvae of varying ages were found on *Chlorogalum pomeridianum* (Liliaceae) about two miles south of Grass Valley, Nevada County, California, on July 3, 1967. They were located on lateral branches in the spreading inflorescences, feeding on the flowers and buds. Pupation occurred by late July and adults emerged April 21 and May 15, the following year.

Incisalia iroides was early reported to feed on *Sedum* (Crassulaceae) in California. Comstock (1927) states that the larva and pupa were described by Henry Edwards (1878) from this plant. Possibly this record refers to *I. fotis* (Strecker), which is represented by a recently rediscovered *Sedum*-feeding race near San Francisco, where Edwards did much of his work. Adults of the two butterflies are similar in appearance.

It is curious that *I. augustinus* (Westwood) of the eastern United States is restricted to Ericaceae (Cook & Cook, 1904, 1906; Clench, 1961), yet is considered by Clench to comprise with *iroides* a single widespread, polytypic species. Other workers have treated *augustinus* and *iroides* as closely related species, each with its own subspecific diversity (*e.g.*, dos Passos, 1964). Perhaps further data on host selection by the various races of this complex will help clarify taxonomic relationships.

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BUTTERFLIES FROM COAHUILA, MEXICO

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Carnegie Museum, Pittsburgh, Pennsylvania

Dr. C. J. McCoy is Assistant Curator of Amphibians and Reptiles at Carnegie Museum. In June, 1966, accompanied by Mr. Arthur Bianculli, he made a trip[1] to central Coahuila to collect and study these animals. Dr. McCoy also maintains a considerable interest in butterflies and, as his regular work permitted, made a collection of them in the area. Because almost nothing is known about Coahuilan butterflies, a list of his captures should be useful.

The collection was made in three different localities, all in the vicinity of Cuatro Ciénegas de Carranza (about 70 airline km west of Monclova), central Coahuila, Mexico. A sketch map of the area, additional description and some landscape photographs may be found in Taylor (1966). Muller (1947) gives a general description and map of the regional vegetation, also accompanied by photographs.

The three localities are as follows, bracketed portions not being repeated in the species list below:

1. Rio Cañon [ca. 1000 m., 3 mi N Cuatro Ciénegas]

Collecting was done along the river, a spring-fed permanent stream in a deep, narrow canyon with precipitous walls up to 500 feet high. The narrow part is about five miles long and opens at either end onto broad desert basins. Vegetation in the canyon consists of bunch grasses with scattered willows and narrow-leaf cottonwoods along the river, and thickets of mesquite and acacia on higher ground. In side canyons there are hackberry trees and some oaks. Most of the smaller butterflies were taken at the flowers of a low Verbenaceous plant (*Phyla lanceolata*). Lower Sonoran zone: Chihuahuan Desert Scrub (Muller, 1947).

The butterflies here (31 species taken, three others seen) are typical of the Lower Sonoran facies of the Chihuahuan Desert fauna, which extends with little variation over much of the lower elevations on the northern Mexican Plateau and into western Texas, southern New Mexico and southeastern Arizona. With progressive depletion it also occurs in arid and semi-arid Upper Sonoran regions of the southern Plateau and also well into the prairie regions of central United States, and in very dilute form even into eastern United States.

A striking feature of this fauna is the large proportion of known or probable wanderers (species that migrate regularly, whether or not they do so *en masse*): *K. lyside* and *castalia*, *E. nicippe* and *lisa*, *P. protodice*,

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[1] Supported by funds from Carnegie Museum and a research grant-in-aid from the Society of the Sigma Xi.

D. gilippus, A. vanillae, E. claudia, V. atalanta, Libytheana sp., *H. isola, L. marina, B. exilis, H. phyleus*. These total 14 species, or about 41% of all species taken or seen. In addition to their regular and often long migrations, these wanderers share (a) broad environmental tolerance, both to temperatures and to vegetation type; (b) generally high levels of abundance, some of them inclined to frequent eruptions; (c) broad choice of larval food plant species; and (d) frequent occurrence in disturbed environments. The combination is conspicuously one of opportunistic species, capable of rapidly exploiting a region where conditions are stringent and suitable environments few, widely scattered, and often transient.

It is worth noting that there is no trace of regional endemism in this fauna, such as occurs in some degree in the reptiles, and to a truly remarkable degree in the fresh water fish and especially the fresh water mollusks (Taylor, 1966).

2. Rio Salado [de los Nadadores, 7.3 mi W Sacramento, 650 m.]

The area is extensively farmed, part of a large desert basin. Collecting was done along the man-made channel of the river and along the edges of fallow, weed-grown fields. Hedgerows of fig and pomegranate were present, and scattered cottonwoods along the river. Most of the butterflies were taken from the yellow-and-pink flowers of *Cryptantha*. The locality appears to be in the Subtropical zone: Tamaulipan Thorn Scrub (Muller, 1947).

Twelve species were taken here, and two others seen. Despite more intensive and prolonged collecting, five of these 14 were not found at Rio Cañon: *P. sennae, P. tharos, B. hyperia, M. amymone, S. columella*. In this latitude, all of these are regional residents of the Subtropical zone. *P. tharos* ranges far into cooler zones in eastern United States, but not locally. *P. sennae* and *M. amymone* are wanderers, but do not appear to reside anywhere in cooler zones, though they may sometimes occur as transients. *B. hyperia* and *S. columella* are both regionally confined to the Subtropical zone. *S. columella* especially is a good zonal indicator regionally: it is fairly common, multiple brooded, tolerates arid and semi-arid conditions, and is not known to wander at all. On the basis of these species, particularly *columella*, I conclude that this locality lies in the Subtropical zone, but probably near its boundary with the Lower Sonoran.

3. El Capriño [2.4 mi E Sacramento, 550 m.]

A few butterflies were collected at weeds along the roadside, in mesquite grassland. The land is open, rocky, hilly, grazed by goats but not farmed. Probably Subtropical zone.

The Rio Cañon is only about 16 airline miles from the Rio Salado locality. Nonetheless, Muller (1947) shows that they are in different vegetation zones and the butterflies, as described above, indicate different life zones. Dr. McCoy tells me that there is also a striking difference in the herpetofaunas of the two localities. This difference in the localities is explained in part by elevation (Rio Cañon is about 350 meters—1,100 feet—higher than Rio Salado), and in part by the westward decrease in precipitation. The Rio Cañon is itself a well-watered locality, so the latter effect may be less important to the butterflies than the former.

SPECIES LIST

Papilio polyxenes asterius Cramer
Rio Cañon 9–12.VI (3♂ 2♀)
Nathalis iole Boisduval
Rio Cañon 10–19.VI (7♂ 11♀); Rio Salado 30.VI (2♂)
Kricogonia lyside (Godart)
Rio Cañon 9–19.VI (5♀)
This is a known migrant and probably is non-resident.
Kricogonia castalia (Fabricius)
Rio Cañon 9–26.VI (8♂: 2, no apical hind wing black bar; 1, very thin bar; 5, normal bar); Rio Salado 30.VI (1♂, no bar).

I am not convinced of the distinctness of this and the preceding species, but follow Comstock (1944: 515) in discriminating them. Like the preceding, *castalia* is a renowned migrant, probably nonresident at the Rio Cañon at least.

Eurema mexicana (Boisduval)
Rio Cañon 18.VI (1♂)
Eurema nicippe (Cramer)
Rio Cañon 10–22.VI (4♂ 2♀)
Eurema lisa lisa Boisduval & LeConte
Rio Cañon 26.VI (1♂)
Eurema nise (Cramer)
Rio Cañon 18.VI (1♂)
This may be a stray from the Subtropical zone.
Phoebis sennae (Linnaeus)
Rio Salado (seen, not taken)
Pieris protodice (Linnaeus)
Rio Cañon 8–18.VI (3♂ 9♀); Rio Salado 30.VI (2♂ 2♀)
Danaus gilippus strigosus (Bates)
Rio Cañon 9–19.VI (2♂ 2♀)
Agraulis vanillae incarnata (Riley)
Rio Cañon 9.VI (1♂)
Euptoieta claudia (Cramer)
Rio Cañon 9.VI (1♀ ?)
A pair *in copula* (10:30 A.M., ♂ flying) was also taken in Nuevo Leon: 6 mi S Villa de Garcia (25° 49′ N, 100° 35′ W), 770 m., 2.VII.
Chlosyne lacinia adjutrix Scudder
Rio Cañon 10–19.VI (1♂ 5♀); Rio Salado 30.VI (1♂ 1♀); El Capriño 23.VI (2♂ 1♀)

To judge by the condition of the specimens, a brood was just coming to an end in late June, represented almost entirely by badly worn females. At the same time a new brood was beginning to appear, represented chiefly by fresh males.

Phyciodes vesta (Edwards)
Rio Cañon 16–18.VI (2♀); Rio Salado 30.VI (3♂ 1♀)
Phyciodes tharos (Drury)
Rio Salado 30.VI (1♀)
Phyciodes phaon (Edwards)
Rio Cañon 9–26.VI (10♂ 7♀); Rio Salado 30.VI (4♂);
El Capriño 23.VI (2♂ 1♀)
Phyciodes (*Tritanassa*) *texana texana* (Edwards)
Rio Cañon 10.VI (1♀)
Nymphalis antiopa (Linnaeus)
Rio Cañon (seen, not taken)
Vanessa atalanta (Linnaeus)
Rio Cañon (seen, not taken)
Mestra amymone (Ménétriés)
Rio Salado 30.VI (1♀ ?)
Biblis hyperia (Cramer)
Rio Salado (seen, not taken)
Asterocampa leila (Edwards), subspecies
Rio Cañon 9–19.VI (9♂ 5♀)
Anaea aidea (Guérin-Méneville)
Rio Cañon 18.VI (1♀)

A female was also taken in Nuevo Leon: 6 mi S Villa de Garcia (25° 49′ N, 100° 35′ W), 770 m., 2.VII.

Libytheana carinenta mexicana Michener
Rio Cañon (a *Libytheana,* probably this, seen but not taken);
Rio Salado 30.VI (1)

I am not certain that this entity is really distinct from *L. bachmanii larvata* (Strecker). It is a well known migrant and perhaps not resident.

Calephelis species
Rio Cañon 15 specimens

These will be determined by Mr. W. S. McAlpine.

Strymon melinus franki Field
Rio Cañon 10–26.VI (2♂ 19♀); Rio Salado 30.VI (1♂ 4♀)

Dr. McCoy tells me that when he arrived in the area (Rio Cañon) in early June there were no *melinus* at all, but that they became common towards the end of the month. Curiously, however, the few early specimens are all rather fresh, the late ones much worn. Perhaps these latter are immigrated, rather than newly emerged, specimens.

Strymon columella istapa (Reakirt)
Rio Salado 30.VI (1♂ 1♀)
Hemiargus (*Echinargus*) *isola alce* (Edwards)
Rio Cañon 9–25.VI (12♂ 6♀)
Leptotes marina (Reakirt)
Rio Cañon 9–18.VI (2♂); El Capriño 23.VI (1♂)
Brephidium exilis exilis (Boisduval)
Rio Cañon 9–18.VI (6♂ 4♀)
Systasea evansi (Bell)
Rio Cañon 9–19.VI (2)
Pyrgus oileus philetas Edwards
Rio Cañon 9–10.VI (1♂ 2♀)

Pyrgus sp. (group of *P. communis* (Grote))
    Rio Cañon 12–19.VI (4♂ 2♀); Rio Salado 30.VI (2♀)
Pholisora catullus (Fabricius)
    Rio Cañon 10.VI (1)
Ancyloxypha arene (Edwards)
    Rio Cañon 16–18.VI (1♂ 1♀)
Copaeodes aurantiaca (Hewitson)
    Rio Cañon 18–26.VI (6)
Hylephila phyleus (Drury)
    Rio Cañon 10.VI (1♂ 1♀)
Amblyscirtes nysa Edwards
    Rio Cañon 26.VI (1♀)

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CONTINUOUS VARIATION IN RELATED SPECIES OF THE GENUS *CATOCALA* (NOCTUIDAE)

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The genus *Catocala* has been extensively studied for more than a century. In fact, at the turn of the century, American journals dealing with the Lepidoptera sometimes devoted the bulk of their coverage to this genus. Even with all this attention many taxonomic problems remain. These problems have defied classical morphological techniques, perhaps because they centered around characters differing in kind rather than amount. This study is, in the main, descriptive of the variation existing in several frequently used diagnostic characters. However, the species used in the examples were selected to suggest the utility of these statistical descriptions in taxonomic studies. They may supplement a knowledge of classical morphology and ecology.

METHODS

An unselected sample of over 1500 *Catocala* of 30 species was taken during the summer of 1961 at a Mercury vapor light operated on the edge of a deciduous wood at the University of Michigan, Edwin S. George

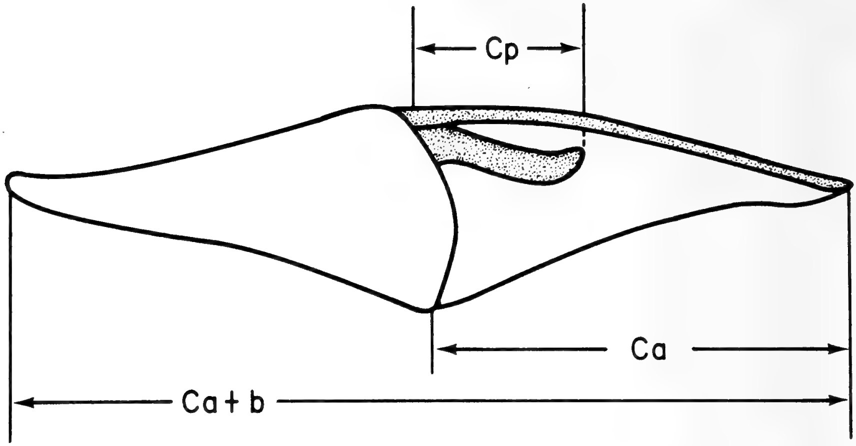

Fig. 1. Schematic diagram of the right clasper of the genus *Catocala*, showing the measurements used.

Reserve, Pinkney, Michigan. From this sample the following series were studied:

78 male *C. ilia* Cramer
25 male *C. palaeogama* Gueneè
25 male *C. retecta* Grote
17 male *C. sordida* Grote[1]
7 male *C. gracilis* Edwards[1]

The following measurements were made on each of the 152 specimens: wing span (WS), total right valva (clasper) length (C a + b), length of distal clasper segment (Ca) and length of clasper projection (Cp) (Fig. 1). The measurement WS was considered a reflection of the overall size of the moth. Cp and Ca, being heavily sclerotized, are more reliable measures than C a + b.

Results

Table 1 presents the mean and standard deviation of the four variables for the five species considered.

Table 2 presents the coefficients of correlation of each of the variables on all other variables. The overall size of the moth as measured by WS is not significantly correlated to the size of the genitalia. However, the various genitalia measurements are not independent. Cp was chosen for further analysis.

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[1] Determined by A. E. Brower, Augusta, Maine, to whom we are grateful for many helpful comments.

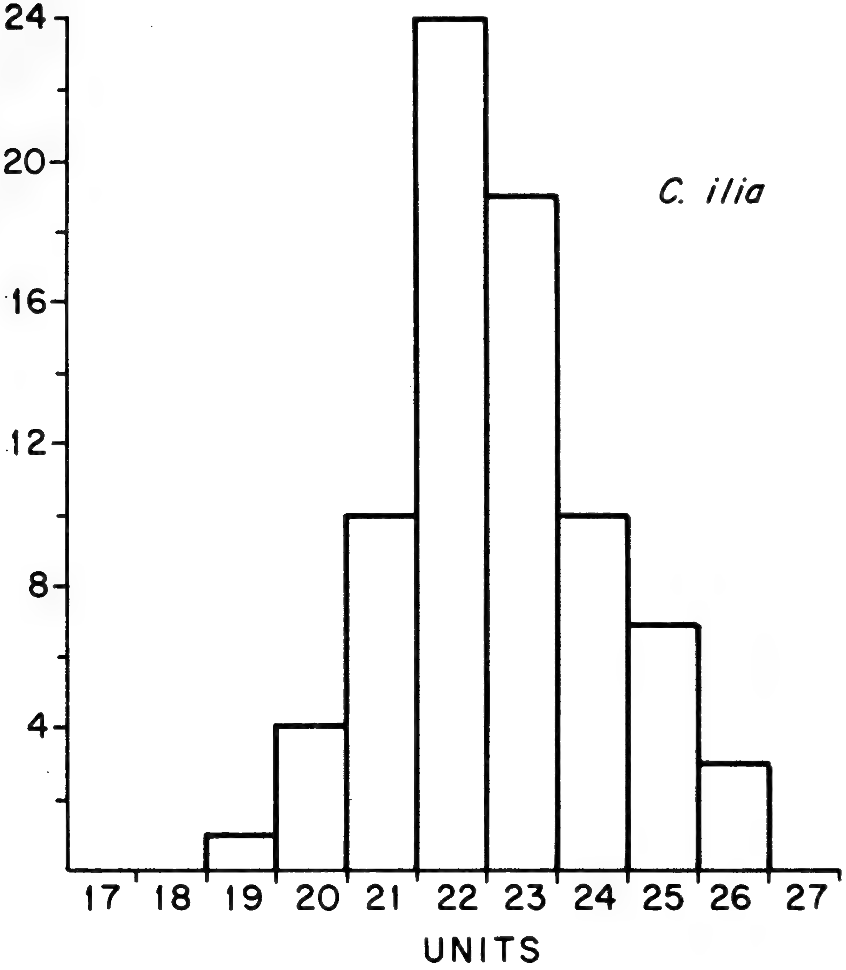
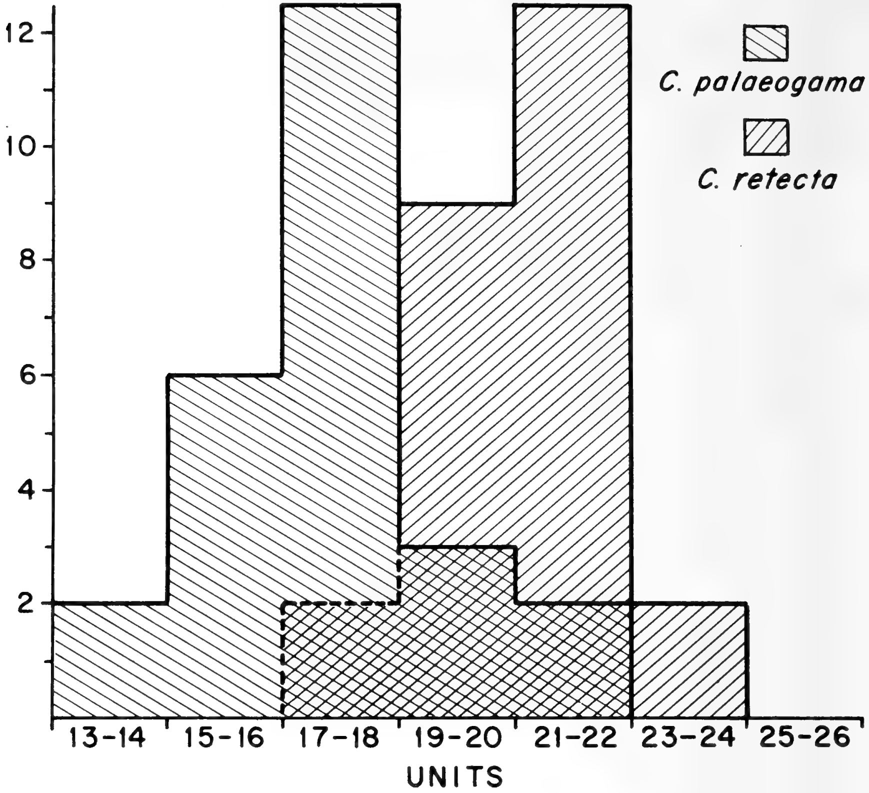


Fig. 2. Frequency distribution of the clasper projection (C p) in *Catocala ilia*.

Figure 2 presents the frequency distribution of Cp for *Catocala ilia*. It approaches the normal distribution.

Figure 3 presents the frequency distribution of Cp for *C. palaeogama* superimposed on *C. retecta*. These two species are closely related but distinct species. The measurement of Cp definitely indicates two populations with some overlap. The "t" test of difference of the means is significant at a $P < 0.001$.

Figure 4 presents the frequency distribution of Cp for *C. gracilis* superimposed on *C. sordida*. These species are closely related and individual specimens are often impossible to determine with certainty.


12
10
8
6
4
2
13-14
15-16
17-18
19-20
21-22
23-24
25-26
UNITS
C. palaeogama
C. retecta

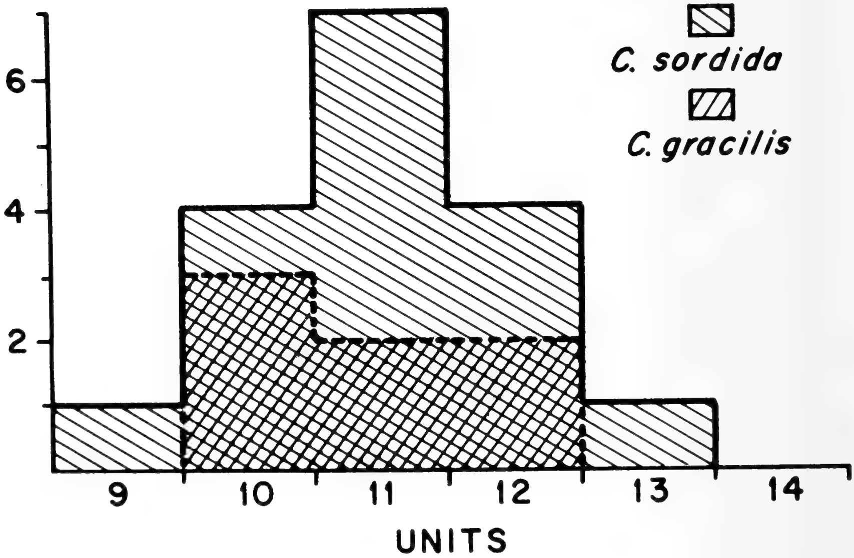

6
4
2
9
10
11
12
13
14
UNITS
C. sordida
C. gracilis

Table 1: Mean and Standard Deviation of Four Variables for Five Species of *Catocala*[1]

		Mean	Standard deviation
ilia	WS	77.14103	2.97926
	C a + b	78.20513	4.95003
	C a	40.02564	2.61849
	C p	22.64103	1.51164
palaeogama	WS	67.96000	2.09126
	c a + b	59.20000	4.46281
	C a	32.88000	3.07300
	C p	17.24000	2.14632
retecta	WS	71.48000	2.90287
	C a + b	71.64000	4.51738
	C a	40.68000	3.36304
	C p	20.68000	1.46401
gracilis	WS	41.71429	1.25357
	C a + b	35.42857	2.63674
	C a	20.14286	1.57359
	C p	10.85714	0.89974
sordida	WS	41.70588	1.21268
	C a + b	38.64706	2.64436
	C a	20.23529	1.25147
	C p	11.00000	1.00000

[1] (WS measured in mm.; Ca and Cp measured in units, 50 units = 7 mm.)

Here the measurement of Cp does not indicate two populations and the "t" test is not significant, P—0.50–0.80.

Discussion

Variation in the clasper of these five species of the genus *Catocala* is clearly continuous. The frequency distributions are nearly normal, implying that the character is controlled by small additive contributions from many genetic factors, no one of which is individually measurable (*i.e.*, multifactorial inheritance).

It is not surprising that closely related but distinct species (*C. retecta* and *C. palaeogama*) showed some overlapping values. The bulk of their genetic contribution is probably of identical origin. It is even less sur-

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Fig. 3. Frequency distribution of the clasper projection (C p) in *Catocala palaeogama* and *C. retecta.*

Fig. 4. Frequency distribution of the clasper projection (C p) in *Catocala gracilis* and *C. sordida.*

TABLE 2: CORRELATION COEFFICIENTS FOR FOUR VARIABLES IN FIVE SPECIES OF *CATOCALA*[1]

		WS	C a + b	C a	C p
ilia	WS	1.0000	0.24635	0.19764	0.16711
	C a + b		1.00000	0.76008	0.31197
	C a			1.00000	0.34030
	C p				1.00000
palaeogama	WS	1.00000	–0.15536	0.44011	0.14147
	C a + b		1.00000	0.26007	0.16008
	C a			1.00000	0.50362
	C p				1.00000
retecta	WS	1.00000	0.37913	0.54990	0.53767
	C a + b		1.00000	0.45561	0.00076
	C a			1.00000	0.57073
	C p				1.00000
gracilis	WS	1.00000	–0.10805	0.70007	0.25332
	C a + b		1.00000	0.38448	0.45163
	C a			1.00000	0.48769
	C p				1.00000
sordida	WS	1.00000	0.55031	0.25436	0.15462
	C a + b		1.00000	0.61213	–0.04727
	C a			1.00000	–0.04994
	C p				1.00000

[1] (WS measured in mm.; Ca and Cp measured in units, 50 units = 7 mm.)

prising that *C. gracilis* and *C. sordida* completely overlap, since they are of similar size, shape and coloration. Their eggs and larvae are nearly identical. They feed on the same food plant (*Vaccinium*). Several possibilities exist to explain this degree of overlap. The sample may be too small to demonstrate a difference. However the frequency distributions give no evidence that these samples are abnormal. There may be hybridization in Michigan. This is very possible if the two species are isolated mainly by weak ecological factors which may be ineffective in this area where *C. gracilis* is on the very edge of its range. Finally it is recognized that parallel varietal forms occur (*e.g.*, some specimens of both species may have a dark shade along the inner third of the forewing). It is possible that these two species are in fact a single breeding population which has been artificially separated on the basis of monomeric traits having diverse gene frequencies in various geographic areas.

The study of continuously varying characters, such as those considered in this report, is unlikely to give definitive results. However it is likely that most adaptive radiation is on the basis of quantitative rather than monomeric traits. Thus such characters are appropriate material for the study of racial and geographic variation.

THE LIFE HISTORY AND HABITS OF *CHLOSYNE FULVIA* (NYMPHALIDAE)

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In the summer of 1961 two larvae were found on paintbrush, *Castilleja integra* A. Gray, west of Pueblo, Pueblo County, Colorado. They were reared and found to represent *Chlosyne fulvia* (Edwards). In order to obtain a more complete description of the life history, the author confined several females with the foodplant on May 16, 1964. Four females laid approximately 100 eggs on May 16 and 17. Descriptions of the egg and larvae from 1964 specimens and a description of the pupae from 1961 specimens follow. In addition, notes on the foodplant and field habits of the species have been included.

FIELD HABITS

C. fulvia flies in juniper woodland in the Upper Sonoran Zone wherever its foodplant abounds, usually on low hills formed from gypsum-rich shale. Adults fly slowly and alight often on the ground, and are thus easy to capture. Males enjoy the few flowers available. Males are not hilltoppers. There are three broods at Pueblo, May 5 to June 10, a second flight occurs in July, and the third from August 23 to September 2. Adults are most abundant in late May and late August.

FOODPLANT

Castilleja integra has crimson bracts and slender leaves one inch in length. It is the only species of paintbrush at the localities near Pueblo where *C. fulvia* flies. Two other undetermined species of *Castilleja* from the Wet Mountains in Pueblo County were offered to the larvae but were refused.

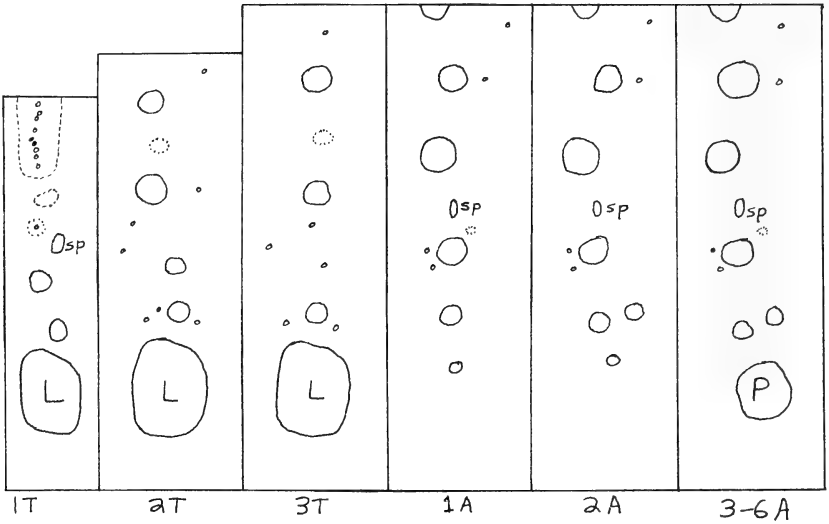
Larvae consume only the fleshy bracts; when the fleshy parts of transplanted plants dried, larvae ate the leaves. One larva devoured part of the ovary and some of the premature seeds.

Eggs are laid in clusters of ten to 30 on stem, leaves, or bracts. Eggs may be laid singly in the field, however. Most of the eggs laid May 16 and 17 hatched May 21.

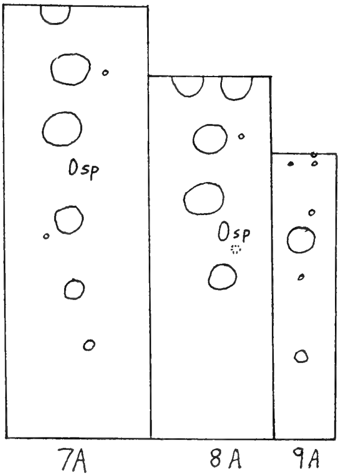
DESCRIPTION OF EARLY STAGES

EGG: Pale yellow. Spherical, with slightly flattened base, diameter 0.5 mm; upper half with approximately 18 vertical ridges, lower half pitted with many small, roughly pentagonal cavities.

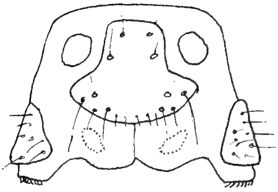
FIRST INSTAR: Length 1.5 mm. Cylindrical, pale grayish green, first two thoracic



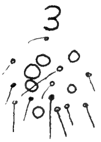
1



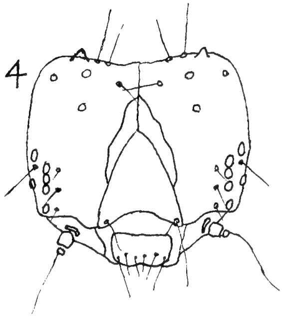
2



3



4



EXPLANATION OF FIGURES

Figs. 1–4. Mature larva of *Chlosyne fulvia* Edwards. 1, setal map; 2, posterior view of larva; 3, ocelli and ocellar setae; 4, frontal view of head. In figs. 1–2 tiny circles represent unbranched setae, and larger circles represent branching spines; dotted lines delineate borders of sclerotized areas.

EXPLANATION OF FIGURES

Figs. 5–7. Pupa of *Chlosyne fulvia* Edwards. 5, ventral view; 6, lateral view; 7, dorsal view.

segments darker. Head black. Body covered with dark setae, arranged on I–VIII abdominal segments, as follows: one long (1 mm) dorsolateral seta, one short (0.5 mm) lateral seta just below and slightly posterior to dorsolateral seta, one long seta below the short seta, in line with dorsolateral seta; below and slightly behind the spiracle two short setae, one below the other, on thoracic and IX abdominal segments the supraspiracular setae consist of two long setae, forming four equally-spaced setae on the top half of larva in dorsal view. An additional short dorsolateral seta between VIII and IX segments. Larvae molted mostly on May 23.

SECOND INSTAR: Length 2.5 mm. Anterior half pale green, posterior half pale yellow. Pinaculi black, the largest around the longest setae. Prothoracic shield with six long setae and two shorter setae posteriorly. Setae arranged as in first instar. White internal structures appear around each setae in late stages lending a slightly more mottled appearance. Most larvae molted May 26.

THIRD INSTAR: Length 4.5 mm. Similar to mature larva, dull green fading to greenish yellow at end of abdomen, becoming yellow prior to molting. Setae replaced by branched spines (scoli). Base of spines reddish brown, distal portion black. Larvae appear very black and spiny, spines almost as large as those of mature larvae. Each spine with approximately six setae. Dark patches surrounding spines almost touch, forming thin dorsal line along length of larva. Spines arranged as in mature larva. Larvae molted mostly on June 3.

FOURTH INSTAR: Length 8 mm. Ground color ochre yellow, vented surface darker. Spines arranged as in mature larva. Thin, dark dorsal line as in mature larva. Dark patches surrounding spines; in abdominal segments I–VIII and thoracic segments 2–3 both lateral spines above spiracles surrounded by a common dark pinaculum. Most larvae molted June 12.

FIFTH INSTAR: Length 14 mm. Similar to mature larva. Ground color ochre-yellow. Spines arranged as in mature larva. Thin brown line connecting subdorsal as well as dorsal brown pinaculi. Most larvae molted on June 18.

MATURE LARVA: Length about 25 mm. Ground color ochre-yellow; spines black, slightly brownish at base. Body tapering anterior to thoracic segment 3 and posterior to abdominal segment VII. Dark pinaculi surrounding dorsal spines on abdominal segments I–VIII, and much larger dark brown pinaculi surround both dorsolateral spines on these segments. A narrow dorsal line from thoracic segment 2 to abdominal segment VIII. Thoracic segments 2–3 with dark brown pinaculi around upper dorsolateral spine. A heavy line connecting subdorsal dark pinaculi from thoracic segment 2 to abdominal segment VIII. Ventral surface light brown; boundary between brown and ochre yellow occurring between the upper and lower rows of subspiracular spines. Ventral surface, especially prolegs, covered with small reddish brown setae and hundreds of smaller transparent setae. Arrangement of spines (scoli) as in Figure 1. Setae of the most ventral spine in abdominal segments I, II, and VII unpigmented. Each large spine on dorsal half of body covered with about 20 minute setae, the longest (about 1.3 mm) at base and shortest at distal end of spine. Shorter spines with fewer setae. Leg with black trochanter and tarsal claw, other segments reddish brown. Ventral surface of legs covered with setae. Crochets biordinal, forming a lateral penellipse. Anal plate shown in Figure 2. Anterior lobe of anal plate dark brown, remainder reddish brown. Head reddish brown. Adfrontal sutures darker, separated from rest of head by pale sutures (Fig. 4). Ocelli and ocellar setae shown in Figure 3. Head with many dorsal and lateral setae; only those which have a constant position shown in Figure 4. Larvae began wandering on June 24; most pupated the following day.

PUPA: Length 15 mm. White, mottled with black stripes and spots as in Figures 5–7. Degree of melanism variable; in one individual many black areas were broken into separate spots, presenting a lighter appearance. Light brown showing faintly on dorsal surface: between black spots that are close together; in grooves between segments of abdomen (especially the grooves posterior to wing cases and one groove anterior to these grooves); and outlining wing cases. Light brown not showing on dorsum in a median one mm-wide strip except a few days before eclosure, when the segments posterior to the wing cases turn reddish brown. Ventral surface with light brown in the small spaces between the black in the space between the wing cases. Pupal stage lasts about eight days.

ADDENDUM

In the article "Study of fluorescent pigments in Lepidoptera by means of paper partition chromatography" by George W. Rawson (*J. Lepid. Soc.*, 22 (1): 27–40, 1968), the following additions and corrections should be made.

On page 31, the author of *Melanargia galathea* is Linnaeus, not Seitz.

On page 36, the names of the 14 *Phyciodes* and allies were omitted in the explanation of Plate 2. These are as follows: 1) *Chlosyne janais* (Drury); 2) *C. californica* (Wright); 3) *Phyciodes* (*Eresia*) *claudina guatemalena* Bates; 4) *P.* (*Phyciodes*) *tharos tharos* (Drury) form "*marcia*" Edw.; 5) *P.* (*P.*) *t. tharos* form "*morpheus*" F.; 6) *P.* (*P.*) *batesii* (Reakirt); 7) *Chlosyne i. ismeria* (Bdv. & LeC.); 8) *P.* (*P.*) *mylitta* (Edwards); 9) *P.* (*P.*) *campestris* (Behr); 10) *P.* (*Tritanassa*) *ptolyca* (Bates); 11) *P.* (*Eresia*)*frisia* (Poey); 12) *P.* (*Tritanassa*) *myia* (Hewitson); 13) *P.* (*Eresia*) *phillyra* (Hewitson); 14) *P.* (*Tritanassa*) *texana* (Edwards).

The color representation of the boxed symbols, A–F, accompanying this plate is as follows: A) Bright violet fluorescence; B) dull blue-violet; C) pale yellow; D) pale blue; E) grayish green; F) pinkish (in the basal portion of nos. 5 and 11).

A TAXONOMIC LIST OF PHILATELIC LEPIDOPTERA

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Many lepidopterists are also philatelists. This includes professional entomologists, some of whom are those actually responsible as instigators or consultants for the many butterfly and moth postage stamps that have of late years appeared around the world.

The first philatelic lepidopteran was issued in 1890 as an ornament in the hair of Hawaiian Queen Liliuokalani. Although one may speculate that it is the beautiful *Vanessa tameamea* Esch., it was not until 1930 when Lebanon honored the silk industry that a definitely determinable species was depicted. Stylized figures had appeared in the interval. In these instances the insects were, of course, incidental. Sarawak in 1950 was the first with nomenclature, *Troides brookiana* Wallace, which was figured unicolorous gray. It remained for the Swiss Pro Juventute issue of 1950 to honor the insect exclusively and in full color. This was largely the work of Dr. Loeliger, a member of our Society until his death and an important force in the Pro Juventute youth movement. The issue was accompanied by a brochure about the insects and was a most noteworthy effort towards stimulation of interest in Lepidoptera in that country.

From this beginning, at first slowly, but with accelerated frequency, over 65 countries have "honored" species of Lepidoptera by 310 butterfly and 115 moth stamps, a total of 425 major varieties by the end of 1966. These embrace 248 species divided 181 and 67 respectively between butterflies and moths. *Papilio machaon* L. with 12 instances leads the list. In most cases the insect is well depicted and the species pertinent to the issuing country. A few are monstrous viz. Lebanon and Togo with *Morphos* and other distant species, San Marino also with inappropriate selections and Albania and Somalia with flying butterflies both upside down and half "inside out." This presents the showier surfaces. Some fine endemics have been chosen (Madagascar, Jamaica *et al.*). All families of butterflies are now represented together with 21 moth families.

Japan 1966 (879) is the only stamp with more than one species. It is a large stamp artistically presenting a girl amidst a veritable swarm of flying butterflies. Ten species can be recognized with reasonable confidence and are included in the list although this stamp does not truly serve as a satisfactory portrayal of the subject species.

It is apparent that the raison d'etre in may cases is the fiscal benefit to the country of issue. Nevertheless, the popularization of the subject has worthy aspects. Flagrant abuses are discussed in the philatelic press and need not be pursued here.

Only those species determinable, at least speculatively, are considered in the body of the taxonomic list which follows. Only stamps recognized by the International Postal Union are included.

As to be expected, nomenclature presents a troublesome problem, the same species often appearing under different names. Frequently a racial name has been elevated to specific status.

The issuance of the Cuban 1961 stamp portraying "*Othreis toddi* Zayas (in litt.)" has a particular interest. Inasmuch as the species had not theretofore been described it would appear to represent a most novel medium for publication and be vested with priority standing. Correspondence (January 1964) with Dr. E. L. Todd who is honored in the naming of the striking new species advised that to the best of his knowledge publication had not yet appeared in orthodox channels. He goes on to state, however, that the illustration on the stamp does not constitute one of the requirements for "availability" and quotes the new Code of Zoological Nomenclature requiring that after 1930, in addition to other requirements, there must be a statement of characters differentiating the taxon, or at least reference to such (Article 13a). So the first sortee of philate-lepidopterology into the intricasies of zoological nomenclature is adjudged invalid on a technicality.

There is, of course, difficulty in arranging a list embracing all world faunal zones. Remington (1954) is followed to the family level, modified by Ehrlich (1958) for butterflies to subfamily. For genera and species the sequence follows Munroe (1960) for the Papilionidae, Rothschild & Jordan (1903) for Sphingidae, Peters (1952) for African Rhopalocera, Forster & Wohlfahrt (1955, 1960) for most European Lepidoptera, and various sources including the many volumes of G. F. Hampson's *Catalogue of the Lepidoptera Phalaenae in the British Museum* and of *Macrolepidoptera of the World* (edited by A. Seitz) for other groups and regions. Nomenclature roughly follows these same sources but is modified by work of more recent authors in limited categories and faunas. The checklist is presumed complete through 1966.

Latin names in square brackets appear if nomenclature on the stamp differs from that in the list. In such instances the inscriptions are not necessarily deemed erroneous though such is usually the case. In any event, somewhat arbitrary procedure cannot be avoided to conform to the authorities chosen and to combine examples of the same species under one name. Scott's Standard Postage Stamp Catalogue (1966) numbers and monthly Journal for later assignments are indicated by parentheses. Scott's numbers prefixed by "B" are semi-postal issues;

"C", airmail; "RA", postal tax stamps; "J", postage due. There are no Scott's numbers for North Korea, Red China, Cuba or Mongolia for recent years; numbers are published in foreign catalogues. The United States Treasury Department through its Foreign Assets Control Section, and Pres. Kennedy, by proclamation of Feb. 7, 1962 have forbidden importation of stamps of these countries after that date. Numbers lacking in other instances were not available at the time of preparation of the list.

Grateful acknowledgment is made to Prof. Charles L. Remington of the Department of Biology, Yale University, for his many helpful suggestions, particularly concerning pertinent literature. Thanks are offered also for his counsel in the matter of troublesome determinations. More than once I observed him turning stamps over in his eagerness to detect significant ventral characters.

MOTHS

COSSIDAE	
Cossus Pulchra Rothschild	Spanish Sahara [*C. pulcher*] 1964 (143)
PSYCHIDAE	
Manatha microcera Bourgogne	Mali 1964 (J14)
GELECHIIDAE	
Pectinophora gossypiella Saunders	Central African Rep. 1965 [*Platyedra*] (55)
ZYGAENIDAE	
Zygaena carniolica Scop.	Switzerland 1956 (B258) Hungary 1966 (1730)
Arniocera ericata Btlr.	Mozambique 1953 (376)
Erasmia pulchella Hope	China 1958 [*E. p. chinensis*] 1958 (1186)
Amesia sanguiflua Drury	Lebanon 1965 [*Erasmia*] (C434)
CASTNIIDAE	
Castnia eudesmia Gray	Chile 1948 (C124) (254) (255)
PYRALIDAE	
Sylepta reginalis Cramer	Cuba 1965
GEOMETRIDAE	
Dysphania militaris L	Laos 1965 (103)
?	Dubai 1963 (21) (C12)
Abraxas grossulariata L.	Switzerland 1957 (B269)
URANIIDAE	
Chrysiridia madagascarensis Less.	Malagasy Rep. [*C. madagascariensis*] 1960 (C64)
Urania boisduvalii Guer.	Cuba [*Uranidia*] 1961
DREPANIDAE	
Epicampoptera strandi Bryk	Central African Rep. 1965 (53)
BOMBYCIDAE	
Bombyx mori L.	Lebanon 1930 (108–13) Japan 1947 (383) Trieste Zone B 1950 (30) Zone A 1953 (187)–Overprint Italy (640) Italy 1953 (640) Afghanistan 1963 (640) (641) (C38) (C40)

	Romania 1963 (1582–4)
	Lebanon 1965 (439–445)
	Libya 1964 (249–51)
	Afghanistan 1966 (731)
Brahmaeidae	
Dactyloceras widenmanni Karsch	Central African Rep. 1960 (8)
Saturniidae	
Saturniinae	
Epiphora bauhiniae Guer.	Senegal 1963 (224)
Argema mittrei Guer.	Malagasy Rep. 1960 (65)
mimosae Bdv.	Mozambique (*Aigenia*) 1953 (371)
Bunaea alcinoe Stoll	Togo 1964 (466)
	Rwanda 1966 (118A)
Attacus atlas L.	China 1958 (1185)
	Ryukyu Islands 1959 (57)
	Laos 1965 (C46)
Nudaurelia hersilia Westw.	Mozambique 1953 [*N. h. dido* M&W] (370)
Athletes ethica Westw.	Mozambique 1953 (373)
gigas Sonth.	Rwanda [South] 1965 (119)
Pseudaphelia apollinaris Bdv.	Mozambique [*P. pollinaris*] 1953 (377)
Saturnia pyri Schiff.	Switzerland 1951 (B211)
	France 1956 (790)
	Romania 1960 (C89)
	Jugoslavia 1964 (728)
Gynanisa maja Klug	Mali 1964 (J9)
Gonimbrasia hecate Rougeot	Mali 1964 (J17)
Lobobunea phaedusa Drury	Rwanda 1966 (116A)
christyi Sharpe	Mali 1964 (J18)
Lasiocampidae	
Lasiocampa quercus L.	Switzerland 1952 (B221)
Sphingidae	
Acherontia atropos L.	Hungary 1959 (C207)
	Romania 1960 (C93)
	Poland 1961 (1036)
	Albania 1963 (694)
Polyptychus roseus Druce	Mali 1964 (J7)
Cephonodes hylas L.	Central African Rep. [*Cenophodes*] 1965 (54)
Daphnis nerii L.	Jugoslavia 1964 (726)
	Mali 1964 (J8)
	Israel 1966 (306)
Celerio lineata Fabr.	Spanish Sahara 1964 (142) (144)
Noctuidae	
Catocalinae	
Mormonia dilecta Hbn.	Bulgaria [*Catocala*] 1962 (1242)
Catocala fraxini L.	Switzerland 1950 (B198)
	Czechoslovakia 1961 (1088)
nupta L.	Switzerland 1957 (B271)
Egbolis vaillantina Stoll	Mozambique 1953 (378)
Metopta rectifasciata Men.	South Korea 1954 (202A)
[*Othreis toddi* Zayas]	Cuba 1961
Agaristidae	
Xanthospilopteryx mozambica Mab.	Mozambique 1953 (380)
Aegocera frevida Wlk.	Mozambique 1953 (383)

ARCTIIDAE	
Lithosiinae	
Chionaema saalmeulleri Btlr.	Malagasy Rep. [*C. pauliani*] 1960 (309)
Arctiinae	
Carathis gortynoides Grt.	Cuba 1965
Holomelina heros Grt.	Cuba [*Eubaphe*] 1965
disparilis Grt.	Cuba [*Eubaphe*] 1965
Rhyparioides metelkana Led.	Romania 1964 (1618)
Pericallia matronula L.	Lebanon 1965 (C426B)
Arctia caja L.	Switzerland 1954 (B238)
	Yemen 1966
flavia Fuessl.	Switzerland 1955 (B250)
villica L.	Czechoslovakia 1966 (1396)
Ammobiota festiva Hufn.	Hungary [*Arctia hebe*] 1959 (1269)
	Bulgaria [*Arctia hebe*] 1962 (1243)
Panaxia dominula L.	Hungary [*Callimorpha*] 1966 (1726)
	Czechoslovakia 1966 (1395)
quadripunctaria Poda	Albania [*Callimorpha hera*] 1963 (692)
Amphicallia thelwalli Drc.	Mozambique 1953 (365)
pactolicus Btlr.	Rwanda 1965 (116)
NYCTEMERIDAE	
Nyctemera leuconoe Hpffr.	Mozambique 1953 (381)
PERICOPIDAE	
Phaloe cubana H-S.	Cuba 1961
CTENUCHIDAE (SYNTOMIDAE)	
Syntomis alicia Btlr.	Ifni 1966 (137) (139) same design
Syntomidopsis variegata Wlk.	Cuba 1965
Ctenuchidia virgo H-S.	Cuba 1965
Metarctia lateritia H-S.	Mozambique 1953 (379)
LYMANTRIIDAE	
Lymantria monacha L.	Switzerland 1953 (B228)
dispar L.	Romania 1964 (1619)

BUTTERFLIES

HESPERIIDAE	
Capila translucida Leech	Red China 1963
PAPILIONIDAE	
Parnassiinae	
Parnassius phoebus L.	East Germany 1964 (684)
jacquemontii Bdv.	Red China 1963
nomion Hbn.	North Korea 1963
apollo L.	Finland 1954 (B127)
	Switzerland 1955 (B251)
	Poland 1961 (1038)
	Czechoslovakia 1961 (1084)
	Bulgaria 1962 (1238)
	Germany 1962 (B380)
	Czechoslovakia 1963 (1165), 1966 (1394)
	Mongolia 1963
	Jugoslavia 1964 (727)
mnemosyne L.	Poland 1961 (1035)
Allancastria cerisyi Gdt.	Bulgaria [*Thais*] 1962 (1239)
Serecinus telamon Dvn.	North Korea 1962
	South Korea 1966 (501)
Zerynthia hypermnestra Scop.	Czechoslovakia [*Z. hypsipyle* Sch.] 1961 (1083)

Luehdorfia puziloi Ersch.	North Korea 1962
Bhutanitis thaidina Blanch.	Red China 1963
Papilioninae	
Lamproptera meges Zink.	Red China 1963
Teinopalpus aureus Mell	Red China 1963
Eurytides pausianus Hew.	Ecuador [*Graphium*] 1961 (680), 1964 (711)
molops R&J	Ecuador [*Graphium*] 1961 (682), 1964 (712)
protesilaus L.	Venezuela [*P. p. leucones* R&J] 1966 (889)
Iphiclides podalirius L.	Switzerland 1951 (B209) Poland [*Papilio*] 1961 (1037) Germany 1962 (B383) Albania [*Papilio*] 1963 (691) Hungary 1966 (1729) Czechoslovakia 1966 (1391)
Graphium weiskei Ribbe	Indonesia 1963 (B158) Papua & New Guinea 1966 (212)
doson Felder	Red China 1963
antheus Cramer	Mozambique [*Papilio a. evombaroides* Eim.] 1953 (372)
policenes Cramer	Guinea 1963 (294) (299) (C48)
mandarinus Oberthur	Red China 1963
Papilio memnon L.	China 1958 (1188) Togo 1965 (486) (489) Japan 1966 (879)
elwesi Leech	China 1958 (1184)
euchenor Guer.	Papua & New Guinea 1966 (216)
menestheus Drury	Guinea 1963 (297) (302) (C49)
lormieri Distant	Somalia 1961 (C77) Central African Rep. 1963 (31)
ophidicephalus Obert.	Malawi [*P. o. mkuwadzi*] 1966 (37)
demodocus Esper	Mozambique 1963 (364) Guinea 1963 (292, 293) (298) (303)
alexanor Esper	Israel [*P. a. maccabeus*] 1966 (305)
machaon L.	Switzerland 1954 (B241) Czechoslovakia 1955 (714) Hungary 1959 (1268) Romania 1960 (C92) Czechoslovakia 1961 (1085) Mongolia 1963 East Germany 1964 (685) Jugoslavia 1964 (729) Lebanon 1965 (C431) Albania 1966 (927) Yemen 1966 Japan 1966 (879)
bianor Cramer	Japan 1966 (879)
hoppo Mats.	Red China 1963
blumei Bdv.	Indonesia 1963 (B156)
?*lorquinianus* Fldr.	San Marino 1963 (568)
ulysses L.	Papua & New Guinea [*P. u. autolycus*] 1966 (209)
zalmoxis Hew.	Central African Rep. 1963 (32)
antimachus Drury	Spanish Guinea 1953 (332) (B28)

	Central African Rep. [*Drurya*] 1960 (11)
	Somalia 1961 (C78)
dardanus Brown	Mozambique [*P. d. tibullus* Kirb.] 1953 (369), (369) as stamp on stamp (384) (385)
	Central African Rep. 1963 (30)
	Rwanda 1966 (117A)
	Yemen 1966
phorcas Cramer	Mozambique [*P. p. ansorgei* Rtsch.] 1953 (375)
	Somalia [*P. ansorgei*] 1961 (C80)
hesperus Westw.	Rwanda 1966 (114A)
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magdae Gifford	Malawi 1966 (38)
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Troides aeacus Fldr.	Red China 1963
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myrmidone Esp.	Bulgaria [*C. balcanica*] 1962 (1244)
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FIRST RECORDS OF TWO BUTTERFIES IN WISCONSIN (NYMPHALIDAE, PIERIDAE)

I collected in northern Wisconsin in quick hit and run fashion on June 2nd, 3rd, and 4th of 1967. My collecting objective was to document the widespread occurrence of *Erebia discoidalis* (Kirby) in northern Wisconsin, but incidental to my objectives, I uncovered two butterflies previously unreported from the state.

BOLORIA FREIJA (Thunberg)

A single male of this species was taken in an open bog containing sphagnum, labrador tea, cranberry, cottongrass and a sparse growth of black spruce on June 2. After entering the bog, located on highway 17 about five miles north of Rhinelander, Oneida county, I quickly collected three specimens of *Erebia discoidalis* and was about to leave when I noticed and captured the *freija.* A second *freija* was sighted but not captured. I had found *freija* very common in Minnesota bogs the previous week and after capturing this specimen I expected to obtain others as I searched other Wisconsin bogs, but I failed to do so. The abundance of *freija* in Minnesota had been quite surprising since it was first reported from that state only two years previously. The only other butterfly found in the bog was *Incisalia augustinus* (Westwood) which was common.

PIERIS VIRGINIENSIS Edwards

Later on June 2 I was collecting just south of Presque Isle, Vilas County, Wisconsin, on a small side road leading into a rich maple forest and captured three specimens (2♂♂, 1♀) of *Pieris virginiensis.* Other species taken in the same vicinity include *Euchloe olympia* (Edwards), *Papilio glaucus canadensis* Rothschild & Jordan, *Nymphalis j-album* (Boisduval & LeConte) and *Polygonia satyrus* (Edwards). My three specimens of *virginiensis* are the first documented captures from Wisconsin; however Mr. James R. Neidhoefer of Milwaukee reports (*in litt*) that he collected a specimen (23-V-1961) near Hazelhurst, Oneida County—about 25 miles directly south of my locality. Still later on June 2, 1967, I found *P. virginiensis* very abundant in a maple forest about five miles south of White Pine, Ontonagon County, Michigan and captured about 40 specimens in an hour. These are the westernmost records for *virginiensis* in Michigan, which had previously been reported from Mackinac, Emmet and Benzie counties by Voss and Wagner (1956).[1]

I am indebted to Dr. Alexander B. Klots of the American Museum for confirming my determinations. The three specimens of *Pieris virginiensis* and the one of *Boloria freija* have been donated to the American Museum Collection, New York.—JOHN H. MASTERS, *Box 7511, St. Paul, Minnesota.*

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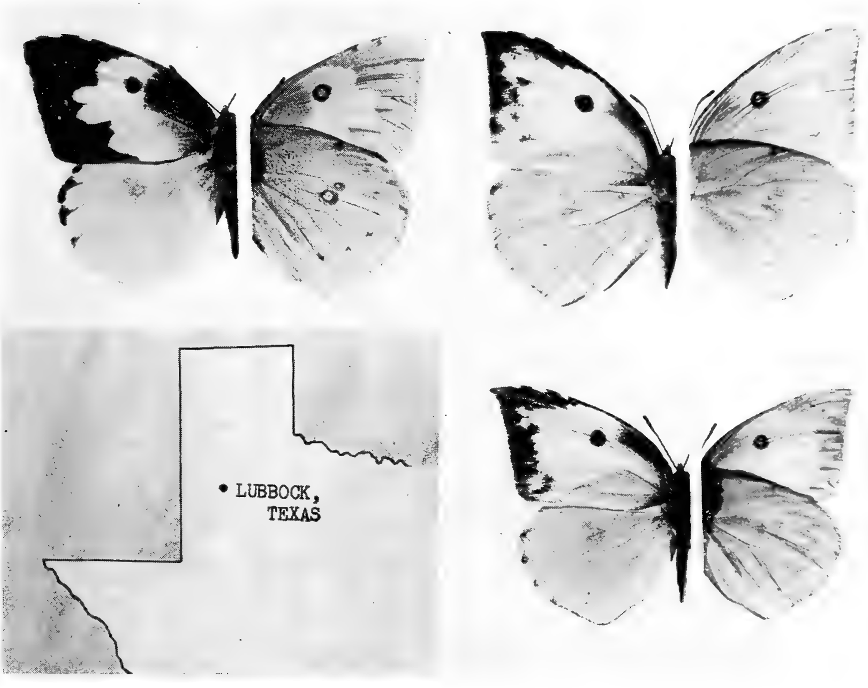
[1] Voss, E. G. and W. H. Wagner, Jr. 1956. Notes on *Pieris virginiensis* and *Erora laeta*—two butterflies hitherto unreported from Michigan. Lepid. News, 10: 18–24.

TWO VARIANT FEMALES OF *COLIAS* (*ZERENE*) *CESONIA* (PIERIDAE)

The southern dogshead, *Colias* (*Zerene*) *cesonia* (Stoll), is a fairly common visitor in the Lubbock, Texas area. Fellow collectors and myself who have been collecting in this area for years know the species well. I was quite surprised during the months of October and November, 1966, to find two aberrant *C. cesonia*. Both were collected in my back yard at flowers. The striking feature of both specimens was the great reduction of black bordering on the dorsal side of the forewing. Females of this species commonly have less black bordering than males, but the reduction is slight and primarily in the border of the hind wings.



Colias (*Zerene*) *cesonia* (Stoll). Upper lefthand—typical male, upper and underside; upper right—aberrant female, upper and underside; lower right—aberrant female, upper and underside; lower left—location of capture.

The first of the two females (lower right in photograph) was captured on October 24, 1966; the weather was still very mild and that particular day was sunny and warm. During the previous month we had experienced three mild frosts. October 23 I had taken a perfect male specimen (upper left) on the same flowers. The second aberrant specimen (upper right) was taken 14 days later, November 7, 1966, following another frost. The black border on this female's forewings was even more greatly reduced than in the first specimen. The variations could have been caused by genetic mutations but more likely were related to environmental factors such as a rapid change in temperature during pupation.—Dwight Bennett, *2808-I Street, Lubbock, Texas 79415.*

SOUNDS PRODUCED BY *NEPTIS HYLAS* (NYMPHALIDAE)

While in South Viet-Nam between 1955 and 1959, I witnessed two occasions on which specimens of *Neptis hylas* (L.) produced noises which were not incidental to normal movement, as are the clicking sounds made during flight by some of the robust-bodied Nymphalids such as *Charaxes* and *Euthalia*.

On the first of these occasions, in December of 1956, a specimen of *Neptis hylas* alighted in my Saigon garden on a hibiscus leaf four feet from the ground and about six feet away from me. It flattened its wings against the horizontal upper surface of the leaf (a position commonly assumed by this species and others of the genus), extended its reduced foremost pair of legs, and began to snap them together rapidly so that the tarsi met to produce a sharp click which would have been audible even at a distance several times greater than the two yards between myself and the butterfly. In quality, the sound was identical to that made by tapping a fingernail edge against a sheet of paper resting on a resilient surface. The legs were partially extended on a horizontal plane, the angle between femur and tibia being about ninety degrees, and the gesture which brought the tarsi together was similar to that of a child clapping its hands.

The movement was very rapid, the insect giving three successive clicks within less than a second; it paused for about two seconds and then repeated the series of three clicks. After this it flew to a leaf on a level with my head and repeated the performance for a third time before flying away.

The second occasion was three weeks later when another specimen (with fresher coloring) came to almost the same spot on the hibiscus hedge. It settled in the same posture on a leaf five feet up and about eight feet away, turned itself through 180 degrees until it faced me, and produced three rapid clicks. In this instance, the insect's position and its greater distance from me made it difficult to be sure which pair of legs was employed; however, the movement of the legs coincided with the clicks. In an effort to approach more closely I frightened it away.

On neither day was I able to capture the butterfly, or to determine its sex. Both of these incidents occurred between 10:00 and 11:00 A.M., on hot sunny mornings with no wind. I never noticed the presence of a second specimen to which either of the two could have been signaling, although this is inconclusive. Possibly, the behavior was an attempt to dislodge clinging parasites. I subsequently examined every fresh capture of this species for signs of ectoparasitism but found nothing.—Frederick W. Scott, *P. O. Box 19, Chester, Nova Scotia, Canada.*

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