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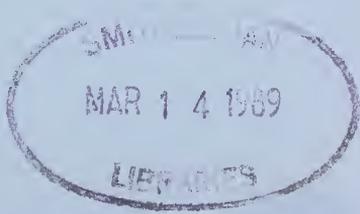
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Cover illustration: Male of the primitive ithomiine *Tellervo zoilus zoilus* (Fabricius) feeding from *Stachytarpheta cayennensis* (Rich.) Vahl (Verbenaceae). Illustration based on observation of three of the butterflies persistently attracted to this 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*, *hydaspes*, *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 un-

desirable 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. pfoutsii (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 *opsis* 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 toptotypical *opsis*, 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 *opsis*, 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 *opsis* 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 *opsis* 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 toptype 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 leg-erdemain 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).

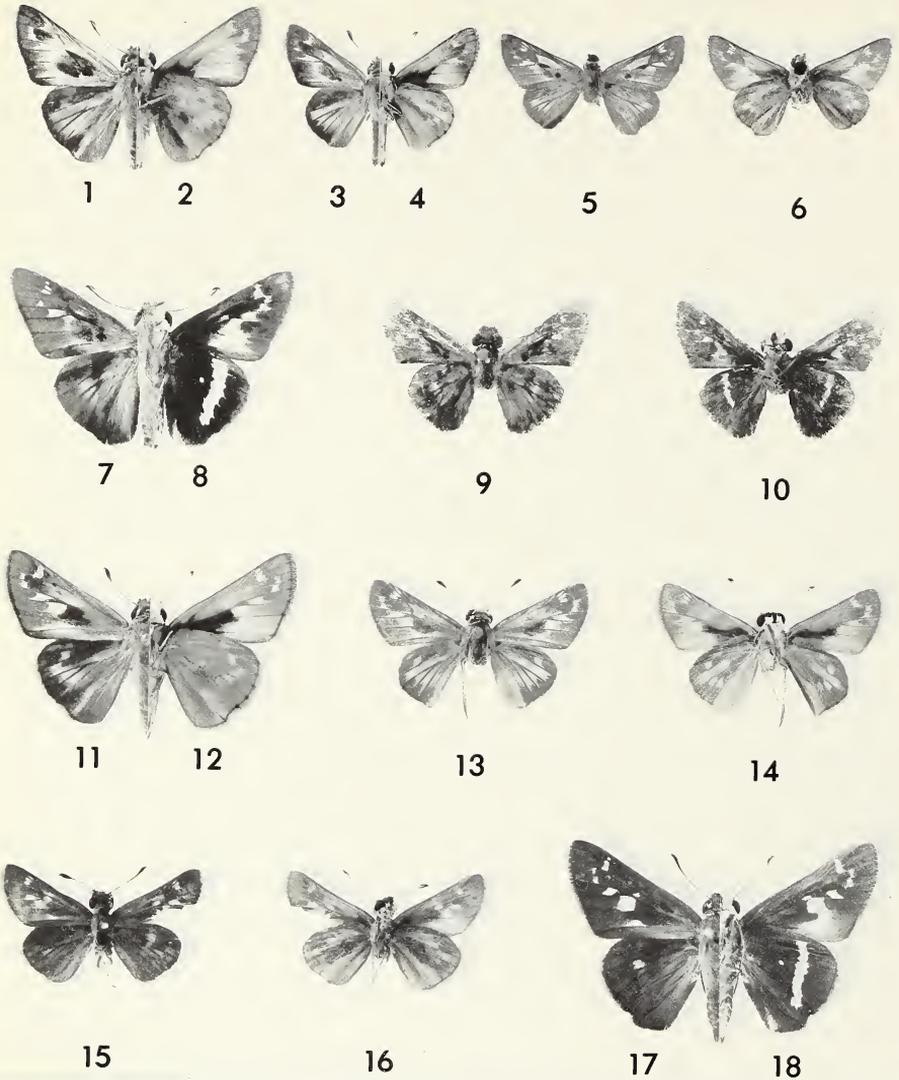
Atalopedes vis-à-vis Hesperia

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 1c 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*.

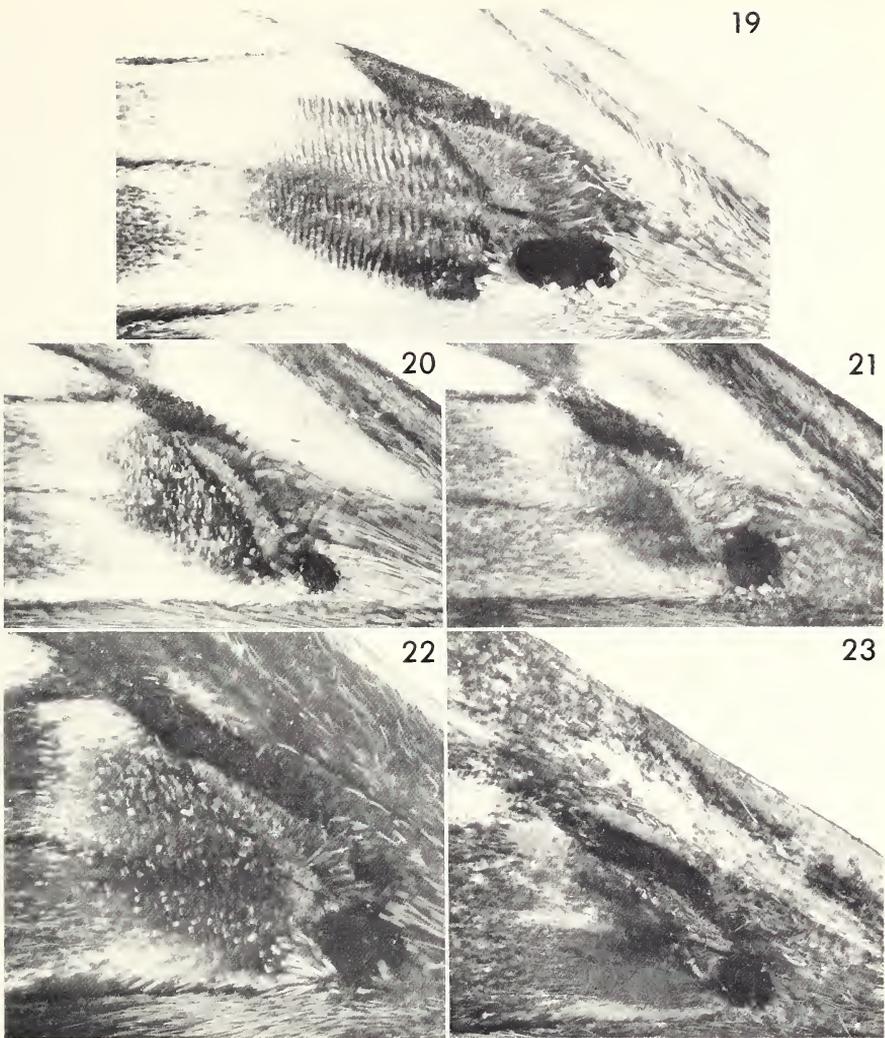
The stigma (Figs. 19–23)—an elaborate communicative device spreading over the dorsal primary of the male from the junction of veins 3 and 4 inward and downward to vein 1—resembles that of *Hesperia* but clearly differs from it. The central, dustlike microandroconial mass (terminology of MacNeill 1964) 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 poststigmatal 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 oversized, titillators and cornuti in such related genera as *Yvretta*, *Polites*, *Ochlodes*, *Poanes*, and *Paratrytone*.

Many genitalic features divide *Atalopedes* from *Hesperia* (Burns

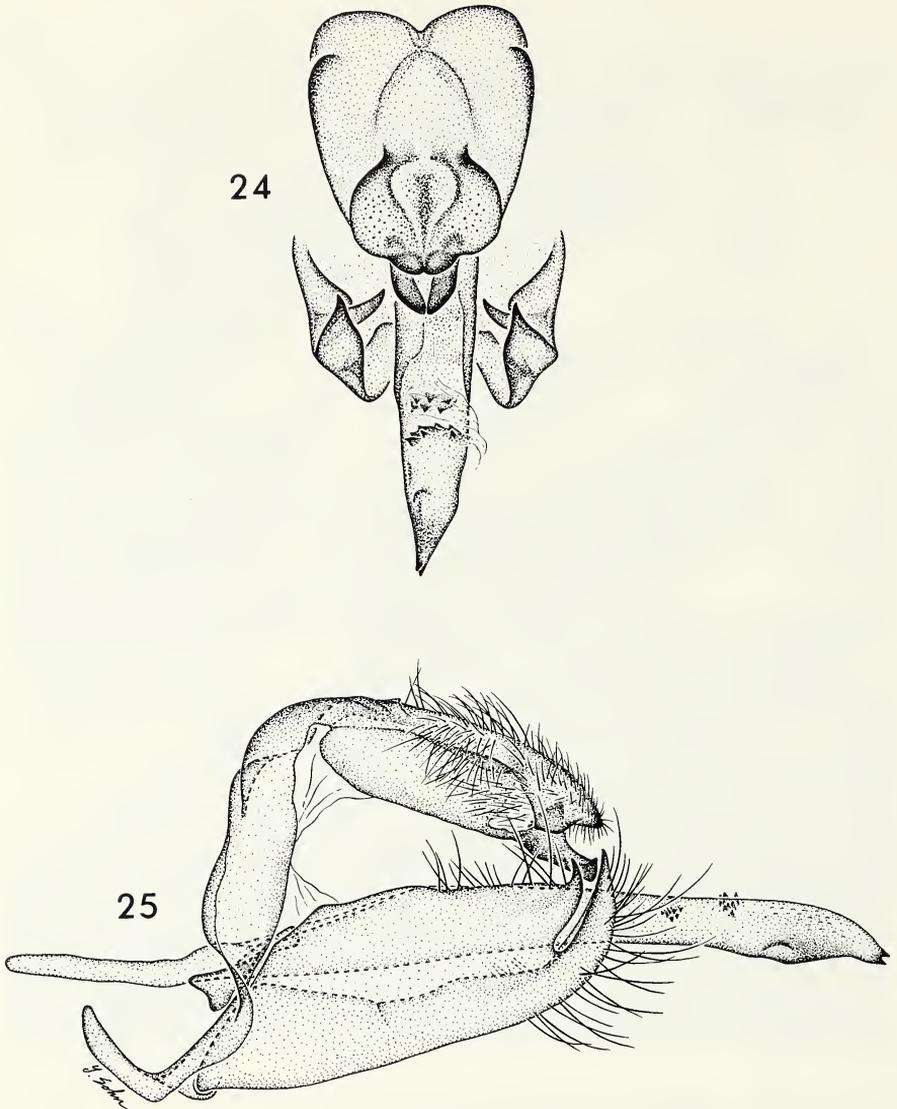


FIGS. 1-18. Adults of *Atalopedes* (all $\times 1$) (in USNM unless otherwise indicated): 1-10, males; 11-18, females; odd numbers, dorsal views; even numbers, ventral views. 1, 2, *campestris*, Charleson St., Annandale, Fairfax Co., Virginia, USA, 1 September 1979, J. M. Burns; 3, 4, *clarkei*, El Morro, 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, Espírito Santo, BRASIL, 25 March 1969, C. & C. T. Eliás (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



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 \pm SE	SD	CV
Margarita I., Venezuela	♂	28	11.0–13.4	12.28 \pm 0.09	0.46	3.70
	♀	1	12.7			
Cartagena, Colombia	♂	8	11.0–13.0	11.88 \pm 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)

Thymelicys [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 poststigmatal 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).

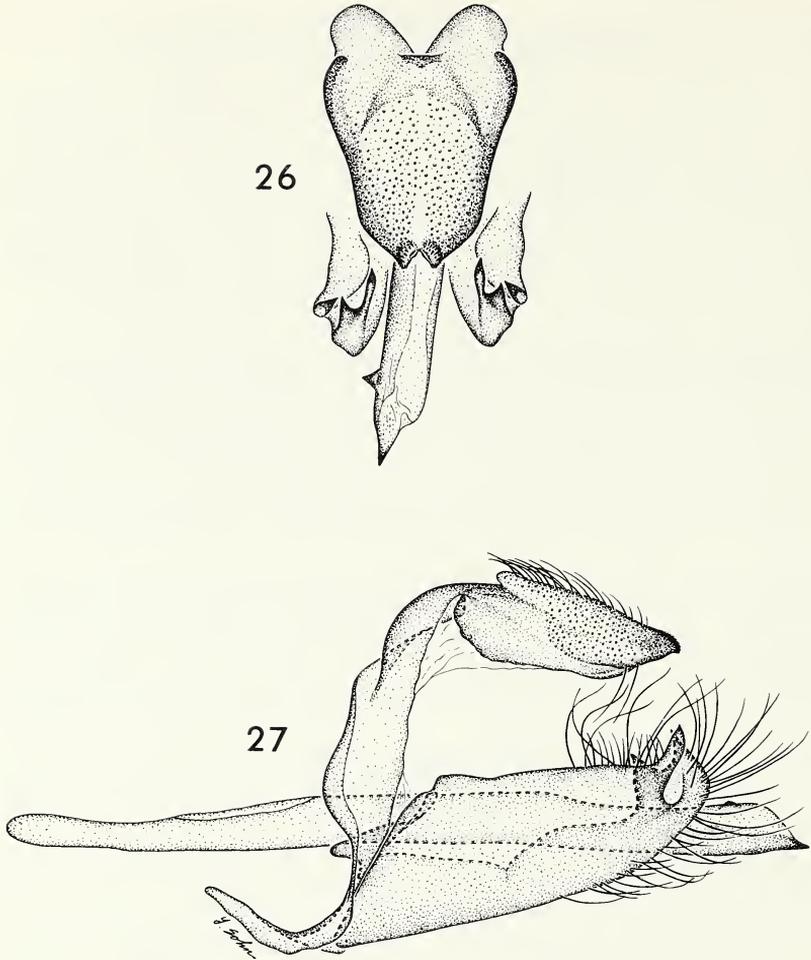
Material examined. Male. Holotype: Bahia, Brazil; Collection W. Schaus; *Thymelicus Bahiensis* Sch[au]s Type [handwritten in black]; Type No. 5999 U.S.N.M. [label red]; Genitalia No. X-2357 J. M. Burns 1987.

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.).

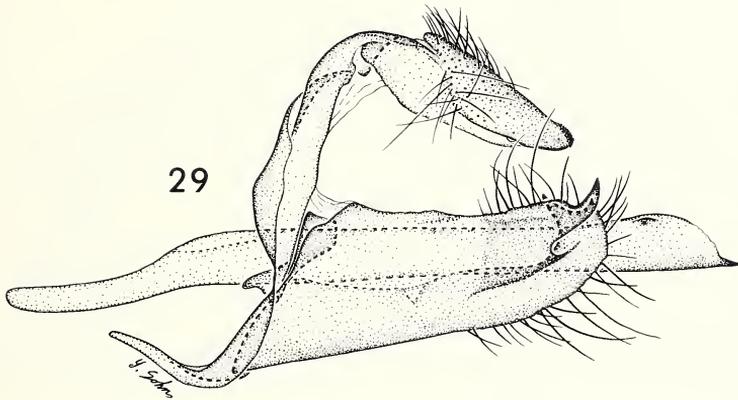
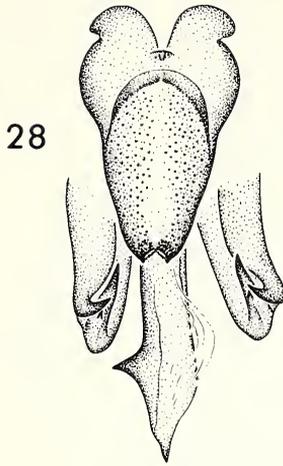
The habitat must have been basically similar, and the population density more or less high, when J. Herrera found *A. clarkei* at the Colombian seaport of Cartagena (see Material examined). During his



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

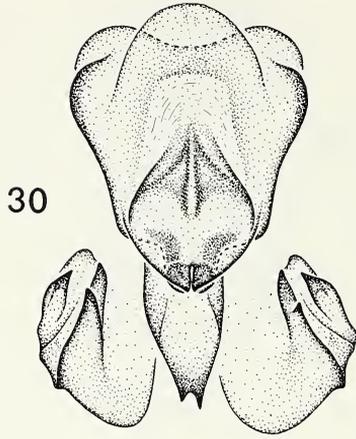


FIGS. 28, 29. Male genitalia of *Atalopedes bahiensis*, holotype, from Bahia, BRASIL (X-2357). **28**, Tegumen, uncus, distal ends of valvae, and distal end of aedeagus in dorsoposterior view; **29**, Complete genitalia (minus right valva) in left lateral view.

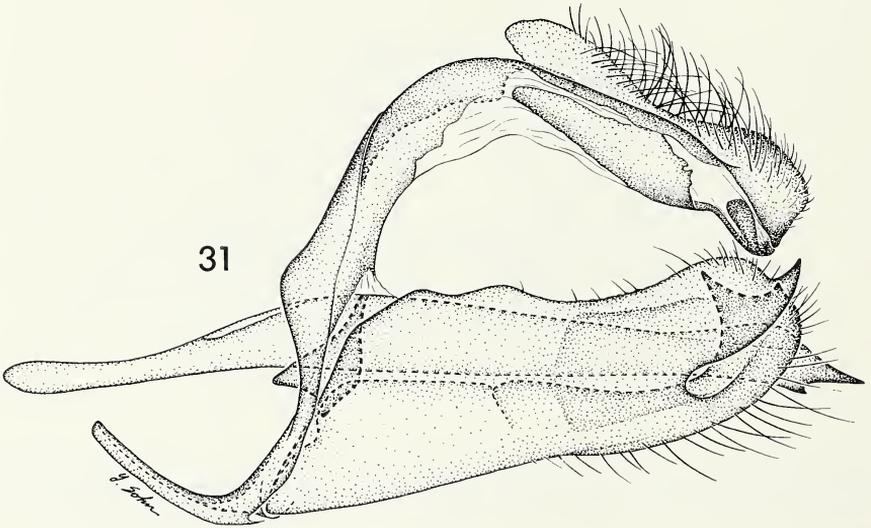
now called Salvador but formerly called Bahia. Restriction to special habitat could explain the scarcity of the skipper in collections.

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



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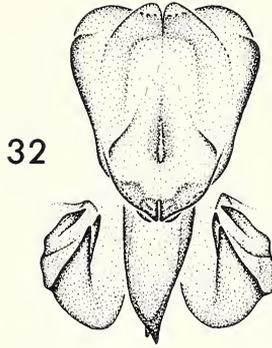


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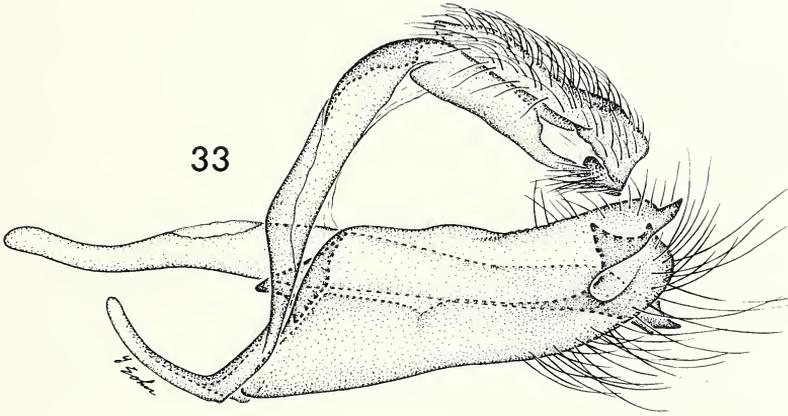
FIGS. 30, 31. Male genitalia of *Atalopedes mesogramma* from Guantánamo Bay, CUBA, 14 September 1943, W. H. Wagner (X-2115). **30**, Tegumen, uncus, gnathos, distal ends of valvae, and distal end of aedeagus in dorsoposterior view; **31**, Complete genitalia (minus right valva) in left lateral view.

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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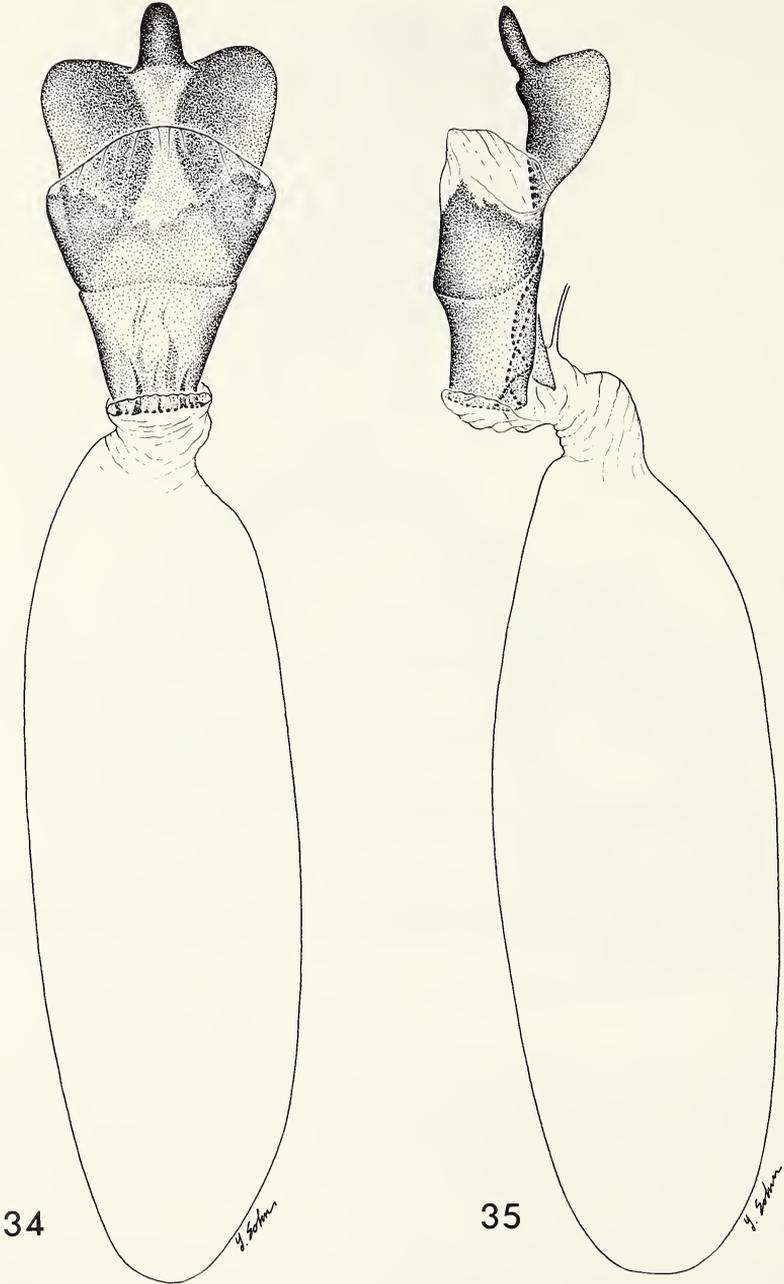


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FIGS. 32, 33. Male genitalia of *Atalopedes carteri* from Nassau, BAHAMAS, 1 February 1898, H. G. Dyar (X-2116). **32**, Tegumen, uncus, gnathos, distal ends of valvae, and distal end of aedeagus in dorsoposterior view; **33**, Complete genitalia (minus 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*



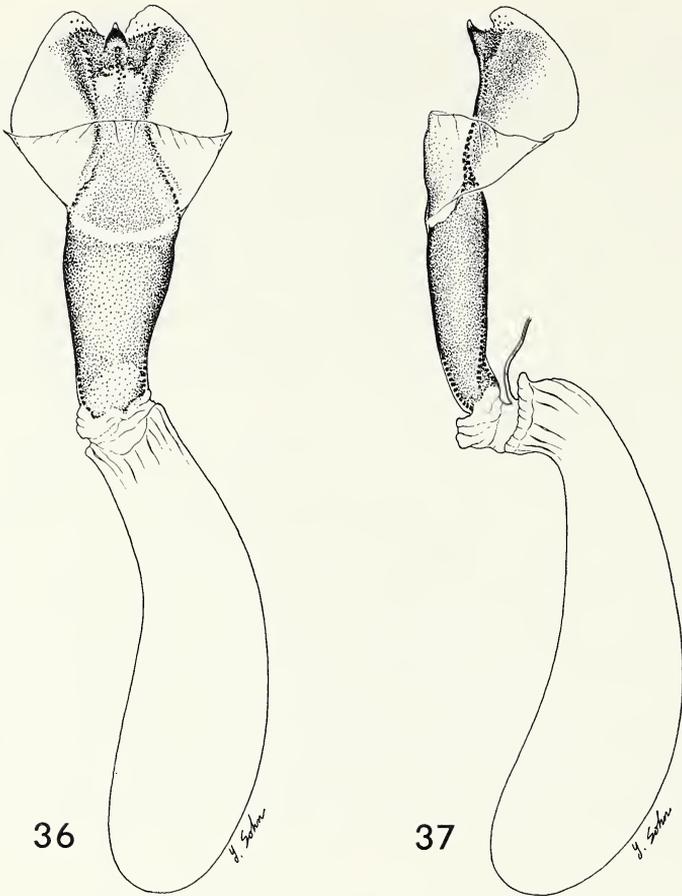
FIGS. 34, 35. Female genitalia of *Atalopedes campestris* from Skippers, Greenville Co., Virginia, USA, 30 September 1981, J. M. Burns (X-2169). **34**, Sterigma and bursa copulatrix in ventral view; **35**, The same, plus part of the ductus seminalis, in right lateral view.

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.

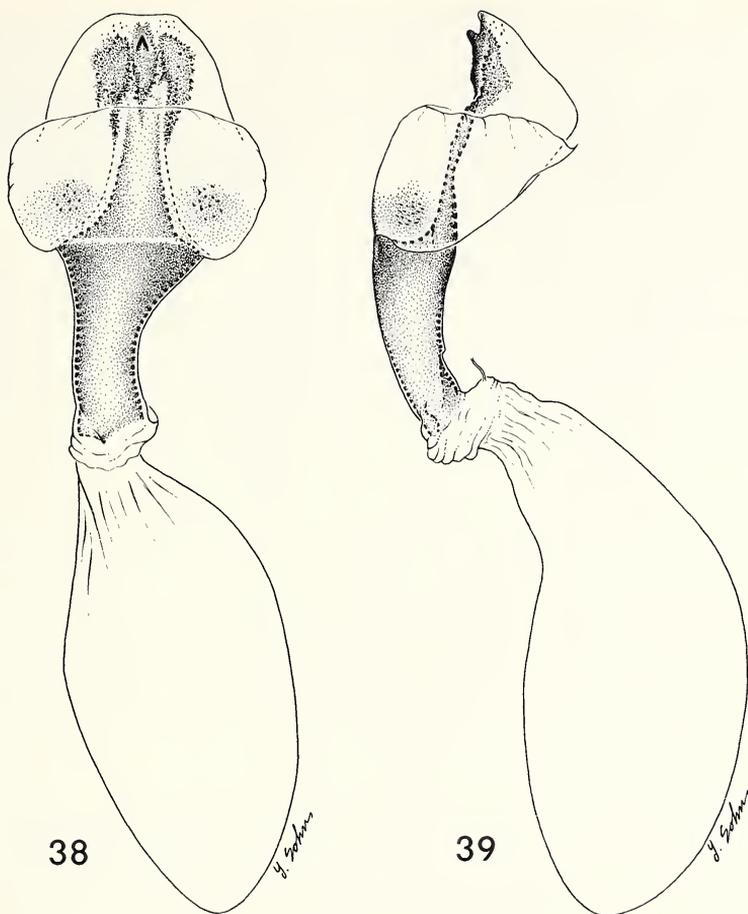
Other male genitalic characters bolster the sequence that puts the *mesogramma* group between *campestris* and the *clarkei* group. The strangely protuberant uncus of the *mesogramma* group (Figs. 30–33) relates clearly to that of *campestris* (Figs. 24, 25), though differing in many details and appearing, 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.

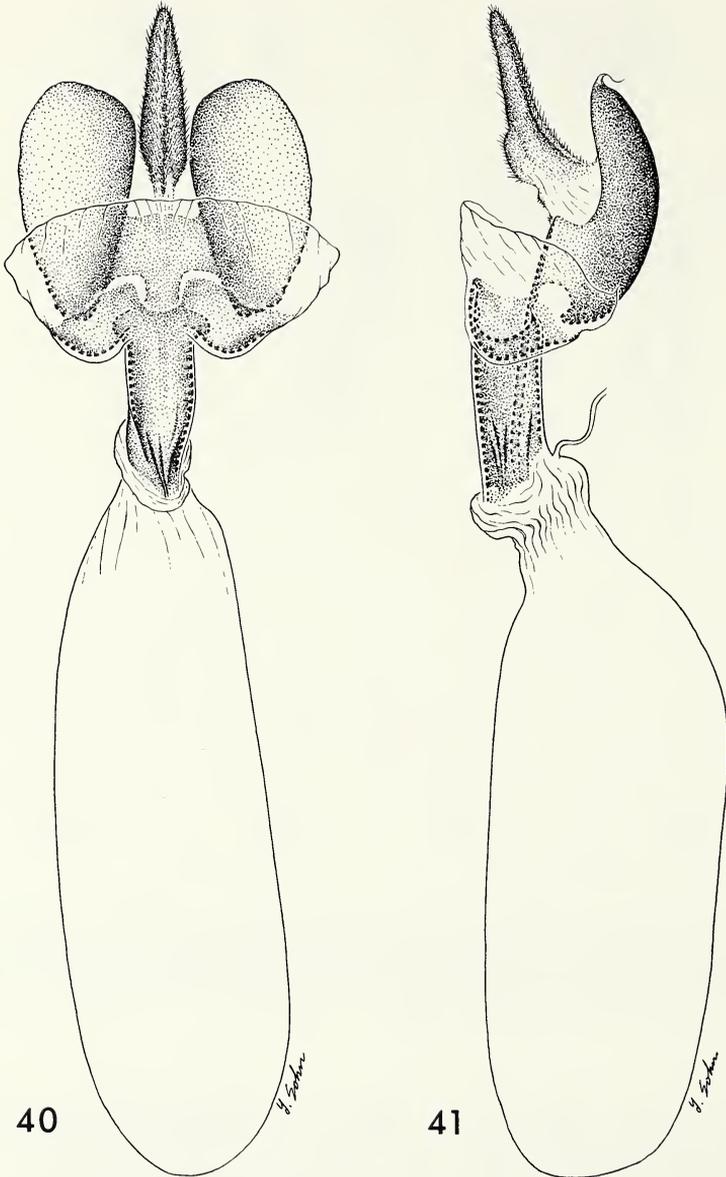
Size is another labile character of little value in working out low-level skipper phylogeny. In *Atalopedes* size varies from medium in



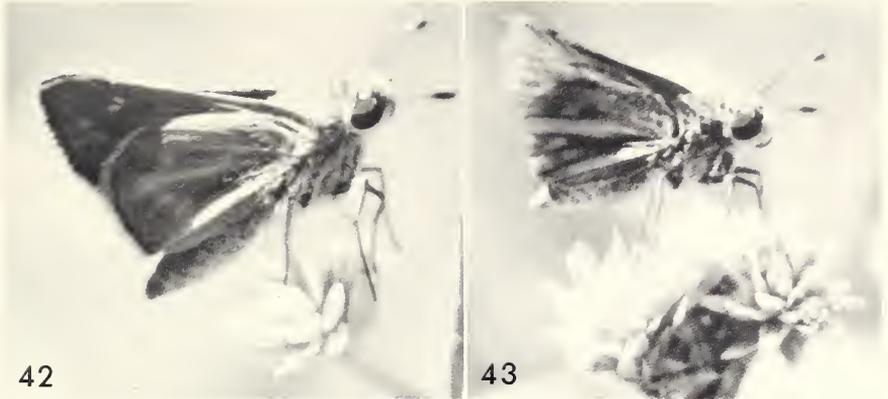
FIGS. 38, 39. Female genitalia of *Atalopedes bahiensis* from Conceição da Barra, Espírito Santo, BRASIL, 25 March 1969, C. & C. T. Elias (X-2390) (collection of O. H. H. Mielke). **38**, Sterigma and bursa copulatrix in ventral view; **39**, The same, plus part of the ductus seminalis, in right lateral 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.

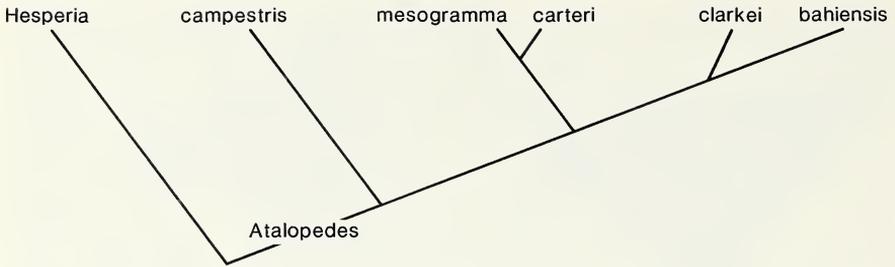


FIG. 45. Phylogeny of the bigger and better genus *Atalopedes*.

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 distri-

bution 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. alipha* 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. alipha* (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 alipha* 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 heliconine 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:		No. territorial expulsions	No. expulsions/h*
					Arrival	Departure		
<i>Heliconius sara</i>	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†
<i>H. leucadia</i>	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)
<i>Eueides tales</i>	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†
<i>E. alipha</i>	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.

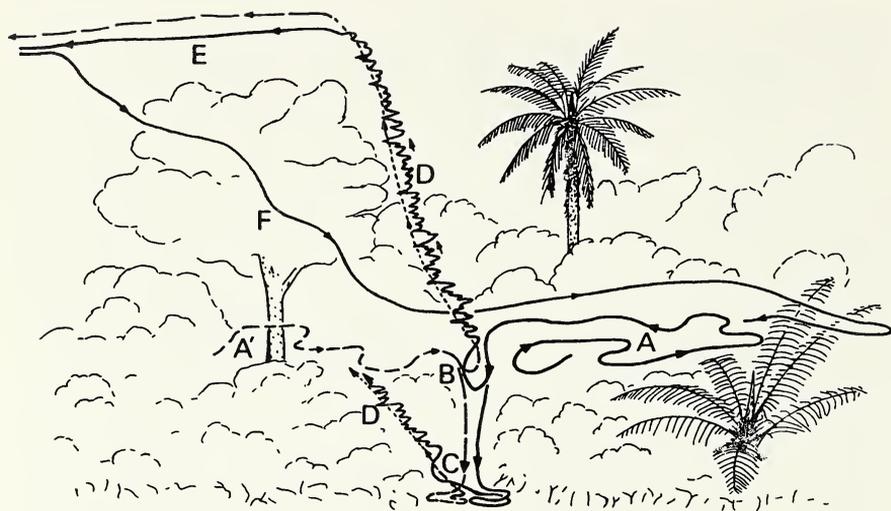


FIG. 1. Typical territorial interaction in *Heliconius sara* at Serra dos Carajás, Pará, Brazil. Resident *H. sara* (solid line) promenades (A) or perches on territory while intruder (broken line, segment length approximately proportional to intruder velocity) patrols along forest margin (A'). One or 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 $\frac{1}{2}$ 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 resident	Behavior of intruder			
	Interaction initiated by resident		Interaction initiated by intruder	
	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*

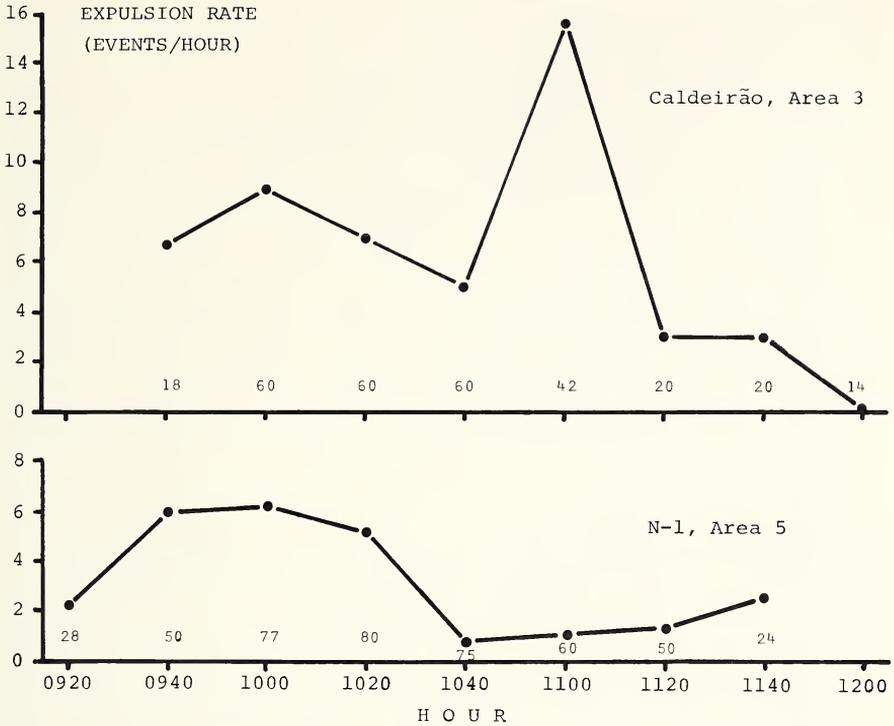


FIG. 2. Expulsion rates for territorial *Heliconius sara* at Serra dos Carajás, Pará, Brazil. Results grouped for intervals of 20 min. Numbers above abscissa show minutes of observation in time interval.

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. alipha* 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. alipha* contained larval food-plant (*Passiflora oerstedii* Mast. in Mart.) with immature stages. An *E. alipha* observed in August 1985 near Serra Norte, Brazil, promenaded above a roadside tangle of *Passiflora* vines on which *E. alipha* larvae were also feeding. The territories of other heliconiines studied at Cal-

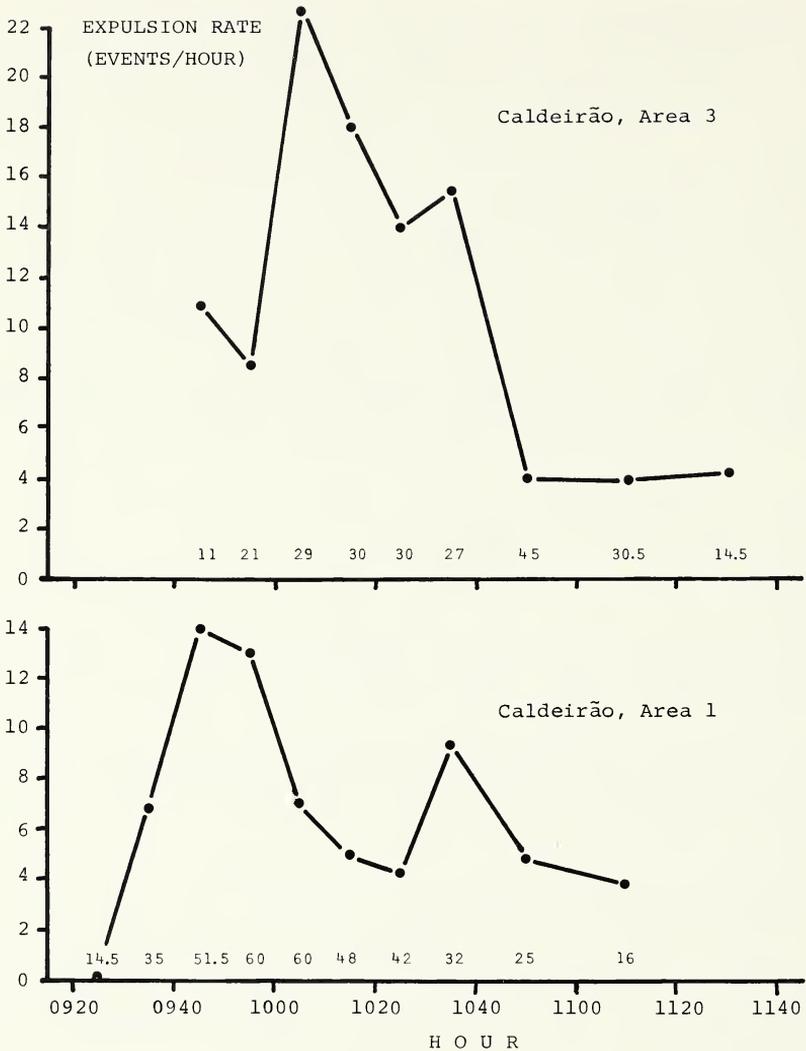


FIG. 3. Expulsion rates for territorial *Heliconius leucadia* at Caldeirão, Serra dos Carajás, Pará, Brazil. Results grouped for intervals of 10 or 20 min. Numbers above abscissa show minutes of observation in time interval.

Caldeirão lacked larval food-plants, although at N-1 an *H. sara* host, *Pasiflora (Astropea)* 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 dis-

covering 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 entrenched 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. alipha* 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 receptacle 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 \pm 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 ob-

tained 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-

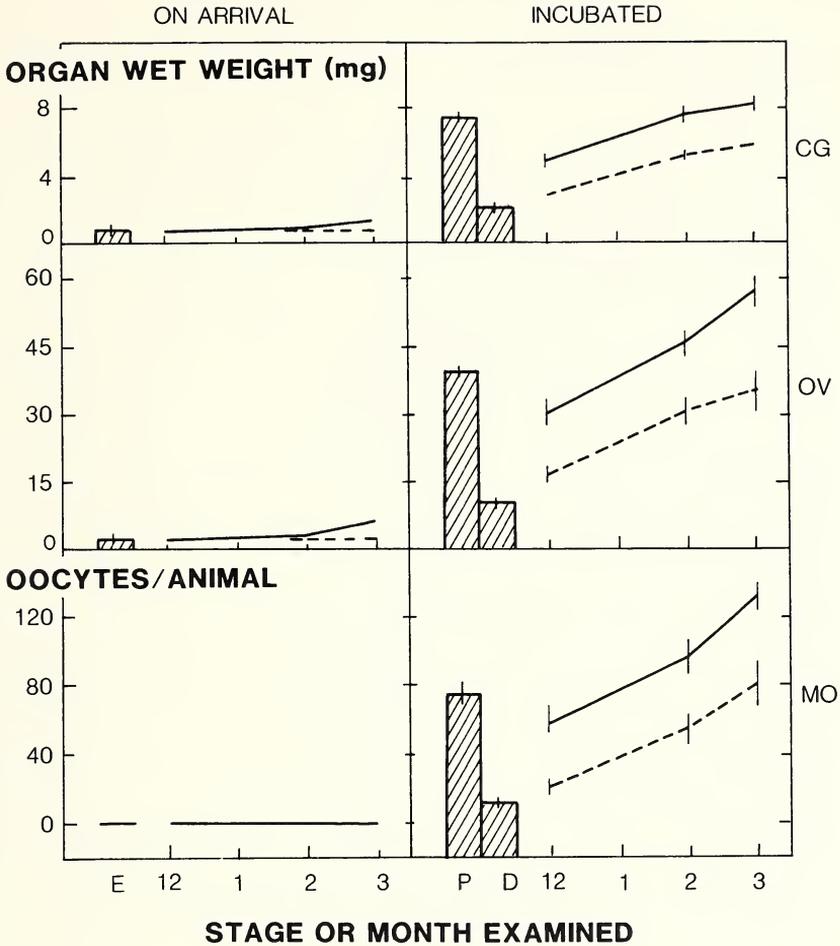


FIG. 1. Wet weights of colleterial glands (CG) and ovaries (OV), and total number of mature oocytes (MO) in females collected in Californian (solid lines) and Mexican (dashed lines) overwintering colonies. On-arrival data obtained from at least 17 animals/data point, and incubated data obtained from 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

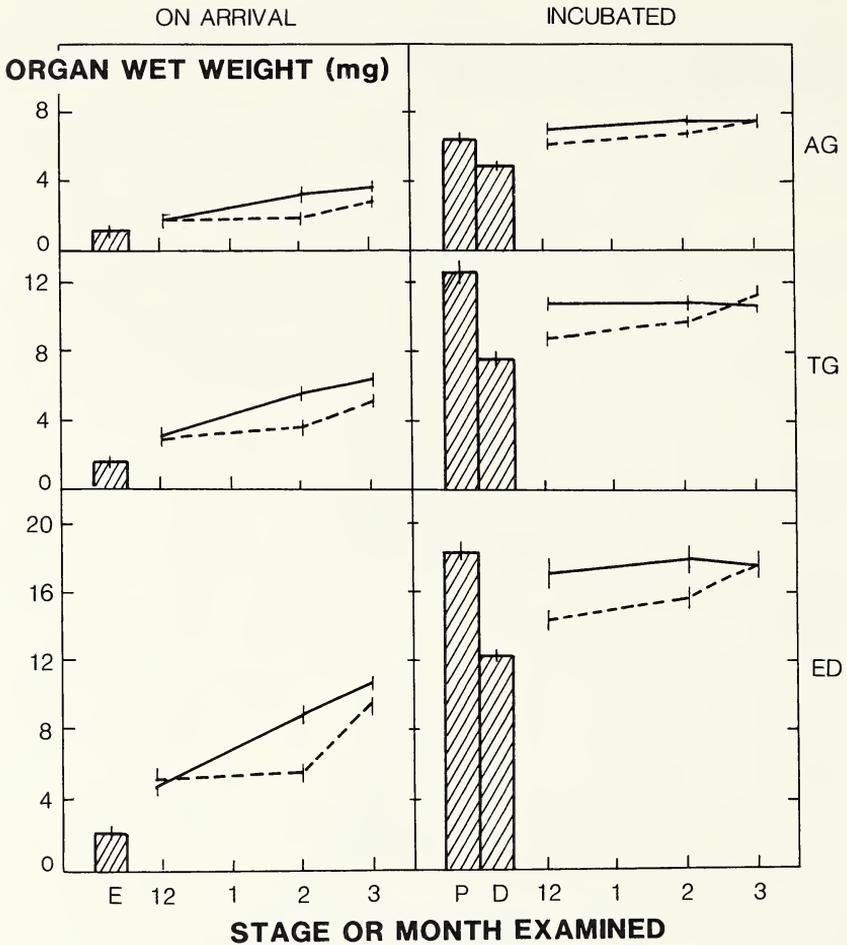


FIG. 2. Wet weights of accessory glands (AG), tubular glands (TG), and ejaculatory ducts (ED) from monarch males collected in Californian and Mexican colonies. On-arrival data obtained by dissection of at least 27 animals/data point, and incubated data obtained from at least 24 animals/data point. Data 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

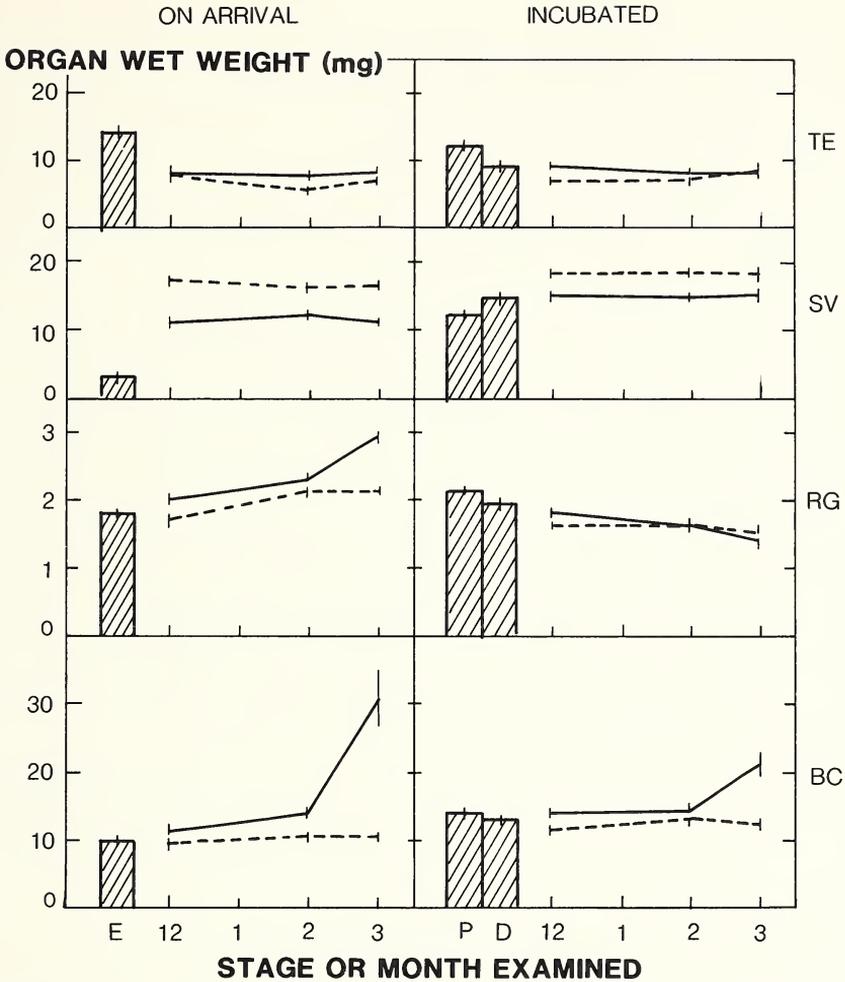


FIG. 3. Wet weights of testes (TE) and seminal vesicles–vas deferens complexes (SV) from males, and of receptacle glands (RG) and bursae copulatrix (BC) from females, collected in Californian and Mexican colonies. Other abbreviations, data presentation, and n values in Figs. 1 and 2.

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 $25 \pm 3^\circ\text{C}$ (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 \pm SD of larval instars					Mean larval stage (days \pm SD)		Mean pupal stage (days \pm SD)
			First	Second	Third	'Extra'	Last	Last	Last	
Male	4	1	4.0	6.0	8.0	—	5.0	23.0	8.0	
Female	4	6	3.3 \pm 0.5	6.0 \pm 1.7	5.2 \pm 1.5	—	6.0 \pm 1.3	20.5 \pm 4.0	8.2 \pm 1.2	
			Long-day ova							
Male	4	2	4.5 \pm 0.7	7.0 \pm 0	13.5 \pm 0.7	—	7.5 \pm 0.7	32.5 \pm 0.7	8.0 \pm 0	
Female	4	4	5.0 \pm 2.2	6.8 \pm 1.9	6.0 \pm 2.6	—	6.3 \pm 1.0	24.0 \pm 6.1	7.8 \pm 0.5	
Male	5	12	4.5 \pm 0.7	7.8 \pm 1.9	13.2 \pm 1.8	11.1 \pm 6.7	7.3 \pm 1.8	43.8 \pm 8.2	8.8 \pm 1.0	
Female	5	5	4.2 \pm 0.5	8.0 \pm 1.2	11.2 \pm 1.6	6.2 \pm 3.2	6.2 \pm 0.8	35.8 \pm 3.4	8.2 \pm 0.8	

¹ Egg hatch to pupation.

TABLE 2. Mean head width of *Lycaena phlaeas hypophlaeas* larvae reared indoors at 25°C.

Oviposition day length	Mean head width \pm SD of larval instars									
	First	N	Second	N	Third	N	'Extra'	N	Last	N
Long	0.24 \pm 0.01	14	0.43 \pm 0.02	17	0.72 \pm 0.06	18	0.89 \pm 0.01	2	1.25 \pm 0.04	8
Short	0.26 \pm 0.01	21	0.43 \pm 0.02	23	0.72 \pm 0.03	23	0.87 \pm 0.03	17	1.22 \pm 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 multi-voltine *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:

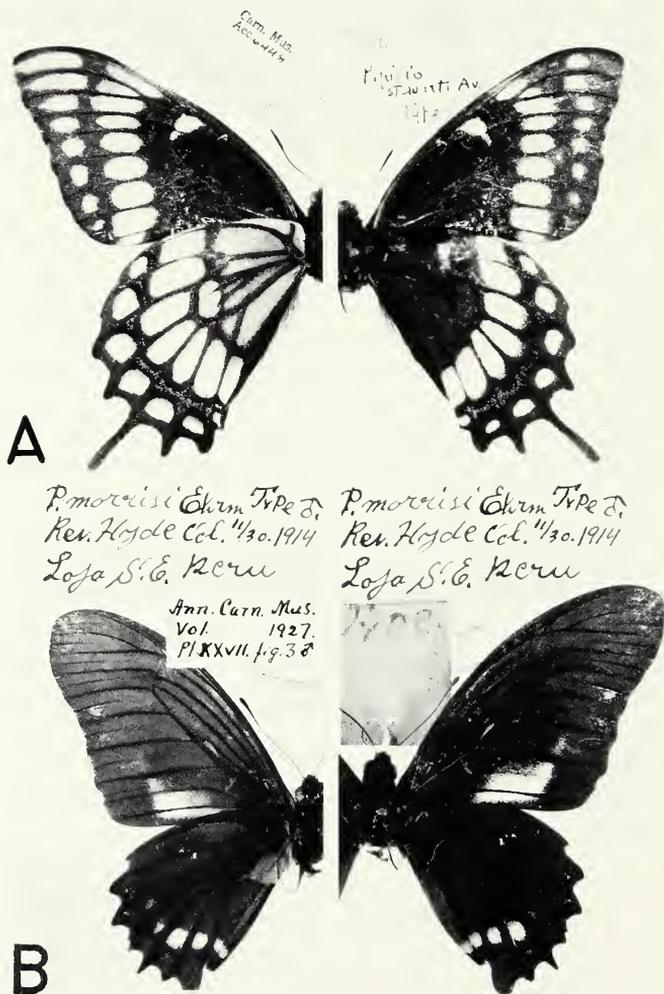


FIG. 1. *Papilio* holotype males. A, *P. stewarti*, upper surface on right, under on left; forewing expanse, base to apex, 50.0 mm; B, *P. morrиси*, as above; forewing expanse 40.0 mm.

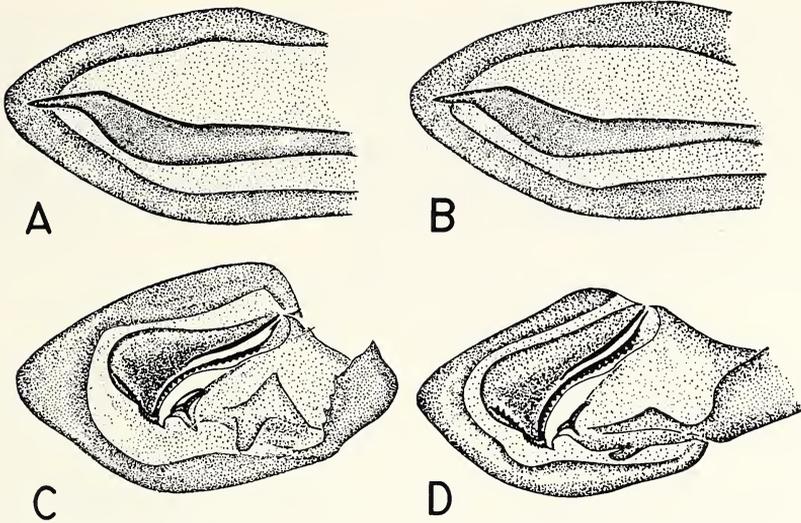


FIG. 2. Papilionid male genital valves, inner lateral view. **A**, *Papilio stewarti* holotype male; **B**, *P. scamander joergenseni*, Tucumán, Argentina (David Matusik Collection); **C**, *P. morrissi* holotype male; **D**, *Protesilaus xenoides*, Rio Pastaza, Ecuador (Am. Mus. Nat. Hist., New York).

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. morrissi* 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, *Catálogo 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 morrissi (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. morrissi* belongs to the “*lysiouthus* 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. morrissi* specimens labelled “Rio Bamba, Ecuador”) indicate *P. morrissi* is a synonym of *Protesilaus xenoides* (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. morrissi*, 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. Wakabayashi & 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

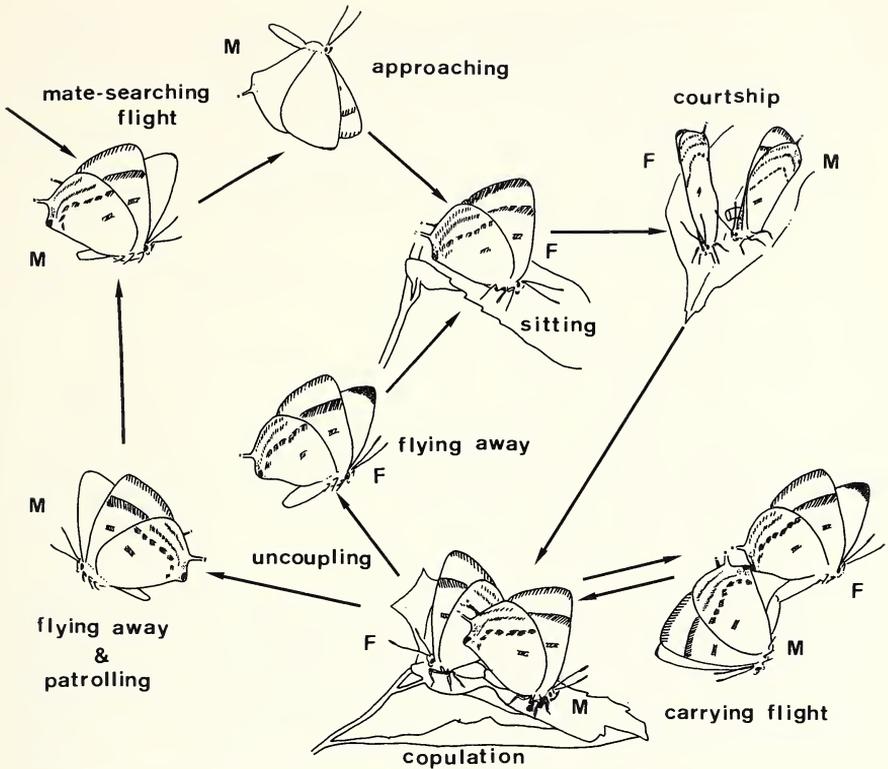


FIG. 1. Sequence of repeated copulations in *S. janasi*. M: male, F: female. Further details in text.

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 (Svård & 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. saepestrata* (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).

I thank B. A. Drummond and an anonymous referee for valuable comments on the manuscript.

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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 Entomología, Universidad Metropolitana de Ciencias et la Educación, 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 "Taracapa" 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. Gumpfenberg, 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 Pylalidae. 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.

EVERETT D. CASHATT, *Illinois State Museum, Springfield, Illinois 62706.*

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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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.

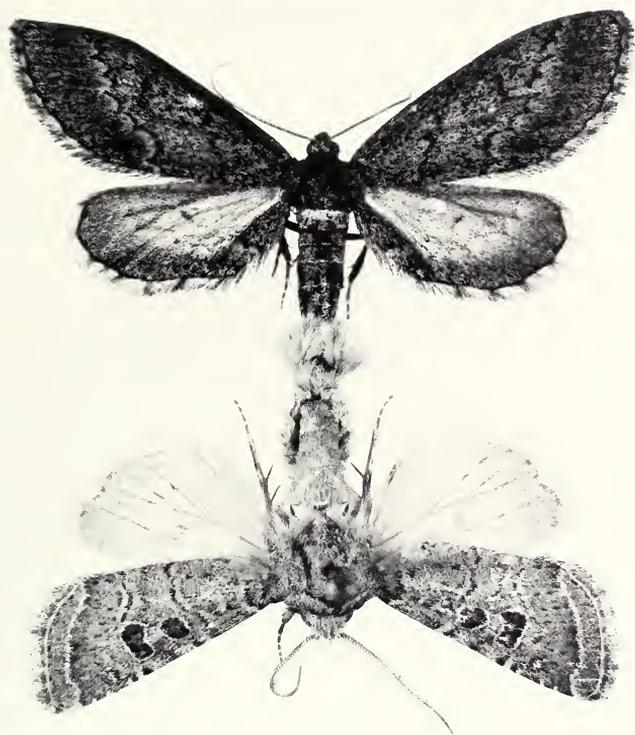
There are no keys to genera of Lepidoptera. However, for Noctuidae, Pyralidae, and Tortricidae, three of the five most speciose families, there are keys to selected species. The pyralid keys treat stored product and corn-sugarcane pests; the tortricid keys treat pine feeders, soybean-alfalfa-cultivated 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.

WILLIAM E. MILLER, *Department of Entomology, University of Minnesota, St. Paul, Minnesota 55108.*

FEATURE PHOTOGRAPH



▲ rare and perhaps unique interfamily mating between a female *Glaucina erroraria* Dyar (Geometridae) (upper) and a male *Protorthodes melanopis* (Hampson) (Noctuidae) (lower) shown $2.8\times$ 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.

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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.

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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 (Avisé 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

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)	hexokinase (HK)
aldolase (ALD)	indophenol oxidase (IPO)
arginine kinase (APK)	isocitrate dehydrogenase (IDH-1, IDH-2)
fumarase (FUM)	malate dehydrogenase (MDH-1, MDH-2)
glutamate-oxaloacetate transaminase (GOT-1, GOT-2)	malic enzyme (ME-1, ME-2)
glutamate-pyruvate transaminase (GPT)	phosphoglucomutase (PGM)
glyceraldehyde-phosphate dehydrogenase (GAPDH)	6-phospho-gluconate dehydrogenase (6-PGD)
α -glycerophosphate dehydrogenase (α -GPDH)	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.

<i>Vanessa carye</i> , 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 Infernillo, 3300 m, i.20.86 (n = 1); Tafi del Valle, 2100 m, i.23-27.86 (n = 7); San Miguel de Tucumán, i.29-iii.9.86 (n = 5 + 1 reared ex <i>Sida</i>).
<i>V. annabella</i>	
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).
<i>V. cardui</i>	
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. Hérault: Oppidum d'Enserune, vi.2.79 (n = 1).
<i>V. virginiensis</i>	
CALIFORNIA, USA:	Nevada Co.: Donner Pass, ix.4.86 (n = 3).
<i>Polygonia zephyrus</i> W. H. Edwards	
CALIFORNIA, USA:	Nevada Co.: Donner Pass, ix.25.85 (n = 2).
<i>Nymphalis milberti</i> 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	
<i>annabella</i>	100	100	100	100	100	100	103	100	100	100	100	100	100	100	104	107	100	100	100	100	100	96	100
<i>carye</i>	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
<i>cardui</i> France	100	100	100	101	110	100	112	100	100	94	90	100	102	100	93	103	100	100	120	110	95	100	100
<i>cardui</i> USA	100	100	100	101	110	100	105	100	100	94	90	100	102	100	93	103	100	100	120	110	95	100	100
<i>virginiensis</i>	100	100	100	96	110	100	109	100	100	94	98	100	103	100	90	107	100	100	120	110	100	100	100
<i>zephyrus</i>	100	100	100	88	100	100	102	89	100	94	90	100	95	96	85	105	100	100	120	110	104	110	110
<i>milberti</i>	100	100	100	84	90	100	102	89	100	105	90	100	107	92	102	105	100	100	100	100	110	110	110

^aCommon allele of *carye* always designated "100."

TABLE 3. Allelic frequencies at loci with high variability between *Vanessa annabella* and *V. carye*.

Sample	PGM											GPT				6PGD			HK			
	N	95	100	103	107	60	100	104	100	107	110	107	100	104	107	110	110	107	100	96	100	
Davis	10			1.0				1.0						1.0	1.0			1.0			1.0	
Donner Pass	9			1.0				1.0						1.0	0.06			0.94			1.0	
Ball Mt.	7			1.0				1.0						1.0				0.86			1.0	
Σ <i>annabella</i>	30	0.02		0.98				1.0						1.0	0.02			0.95			1.0	
Tucumán	5		0.70		0.30	0.10		0.70					0.20	1.0								1.0
Tafi	7	0.17	0.50		0.33			0.21					0.79	1.0								1.0
Σ <i>carye</i>	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. manni* 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. (Danidae) (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.*

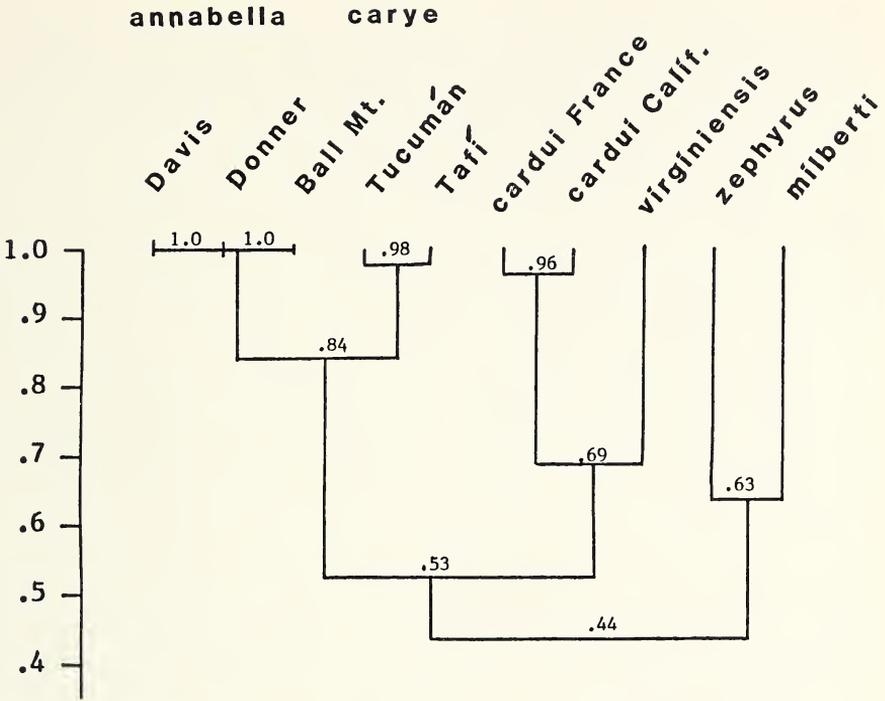


FIG. 1. Dendrogram illustrating clustering among three populations of *Vanessa annabella*, two of *V. carye*, and small samples of *V. cardui*, *V. virginiensis*, *Polygonia zephyrus* and *Nymphalis milberti*, using Nei's statistic \bar{I} .

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 geo-historical 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 dif-

ferences 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.

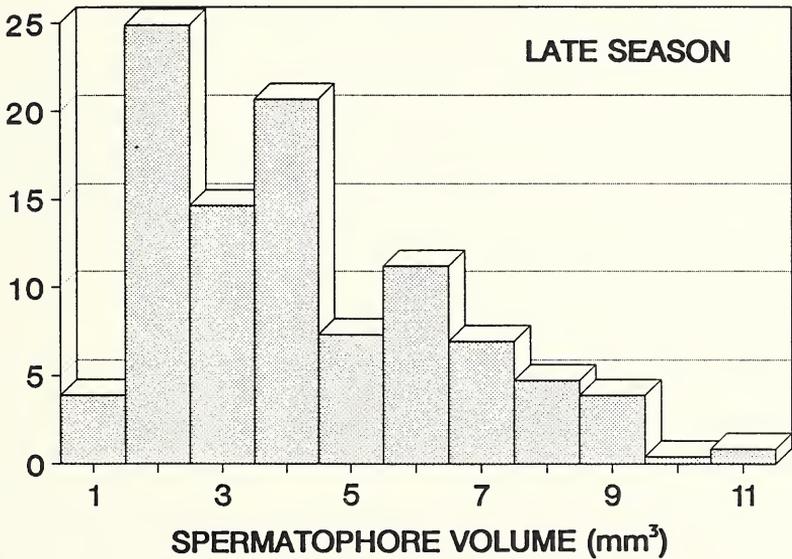
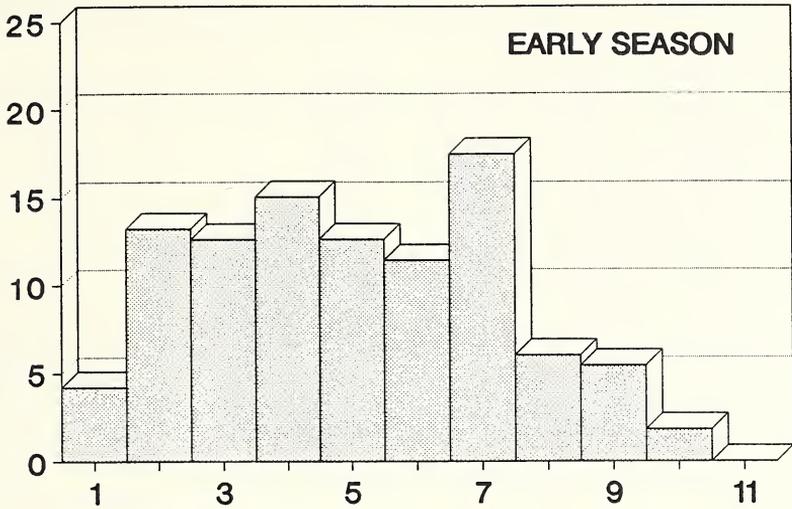
Comparisons of mating histories for different female morphs within a population must control for female age. Pliske (1972) questioned the importance of sexual selection in maintaining the frequency of the yellow female phenotype in a Florida population of *P. glaucus* because

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 mm³) result from males' first matings and the smaller ones (about 4 mm³) 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 mm³) carried more than one spermatophore compared with 63% of 70 females that had a small first spermatophore (≤ 4 mm³). 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

FREQUENCY (%)



SPERMATOPHORE VOLUME (mm³)

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 \times 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-

PERCENT MULTIPLE MATINGS

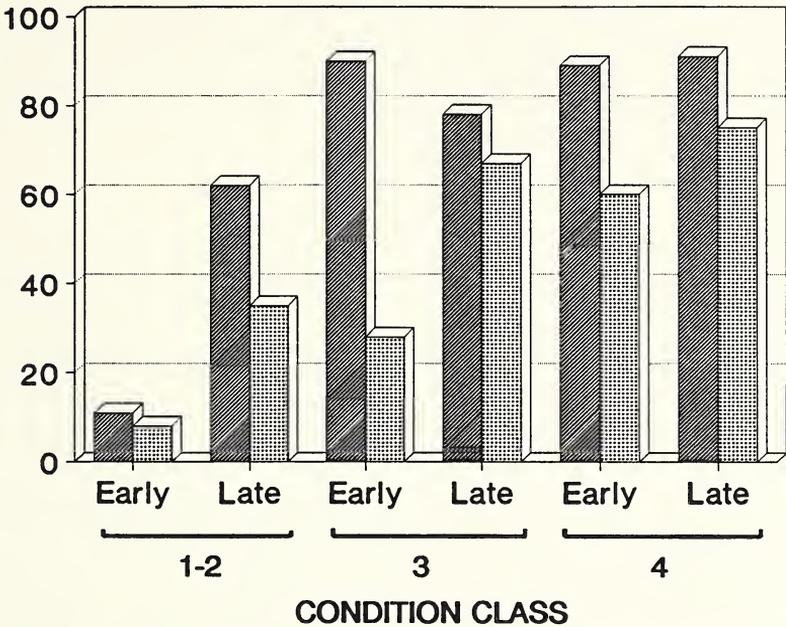


FIG. 2. Probability of remating in Wisconsin *Papilio glaucus canadensis* females as influenced by first spermatophore size, date of collection, and condition class. In 6 of 6 comparisons females receiving a small 1st spermatophore (hatched bars) were more likely to remate than females receiving a large 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 m² 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 leaf-tiers and leaf-miners, 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 systematic 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.



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

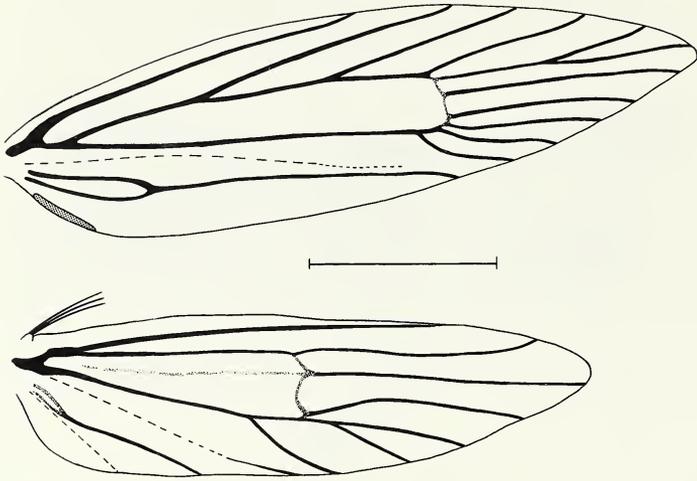


FIG. 2. Wing venation of *Anoncia crossi*. Scale line = 2.0 mm.

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

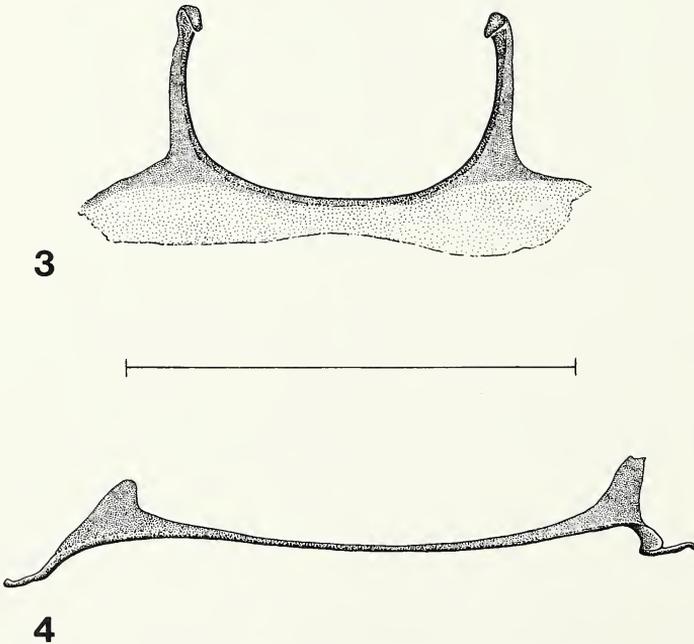


FIG. 3. Eighth tergum of male *Anoncia crossi* (dorsal view). Scale line = 0.5 mm.

FIG. 4. Eighth sternum of male *Anoncia crossi* (dorsal view). Scale line = 0.5 mm.

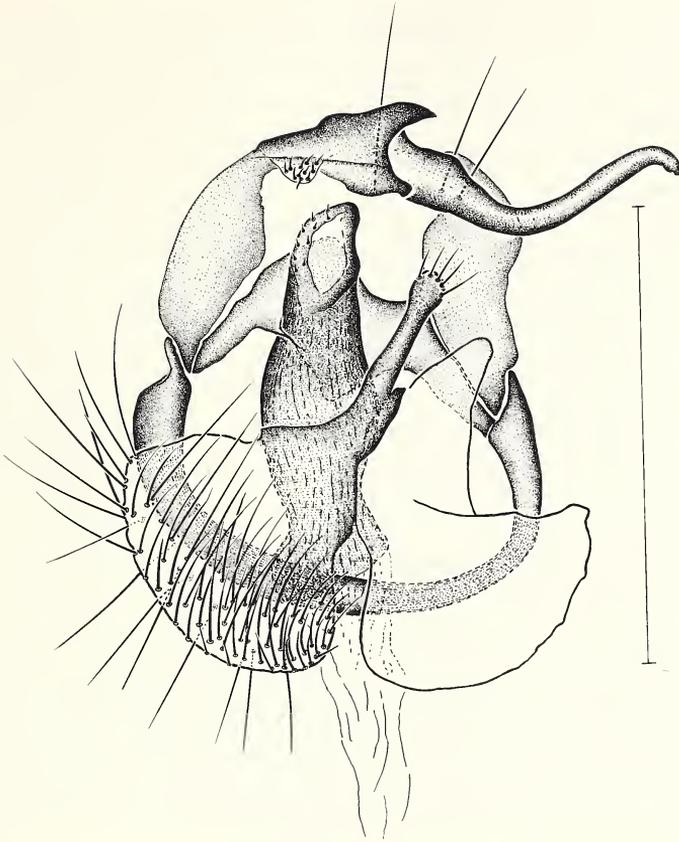


FIG. 5. Male genitalia of *Anoncia crossi* (posterior view). Scale line = 0.5 mm.

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 Eguale, 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.

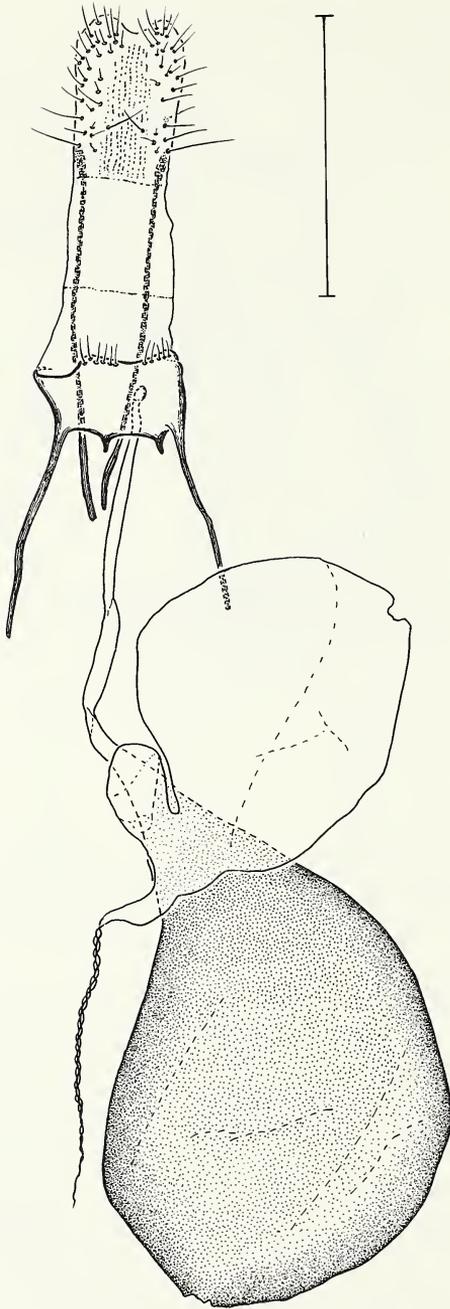


FIG. 6. Female genitalia of *Anoncia crossi* (dorsal view). Scale line = 1.0 mm.

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 ½ 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-

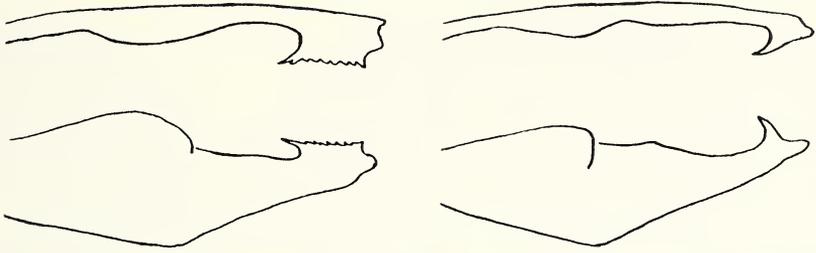


FIG. 1. Top left and right lateral views of *Neonympha* male valvae. Left, *N. mitchellii*, Jackson Co., Michigan; right, *N. areolatus*, Fort Bragg, North Carolina.

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	<i>m. francisci</i> (North Carolina)		<i>m. mitchellii</i> (Michigan & New Jersey)	
	Male	Female	Male	Female
Left forewing length				
Mean \pm SD	16.7 \pm 0.8	18.8 \pm 0.8	16.4 \pm 0.75	18.3 \pm 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 \pm SD	3.3 \pm 0.7	4.0 \pm 0.65	3.7 \pm 0.5	5.9 \pm 0.7
Range	2-5	3-5	2-4	5-6
N	35	12	44	31
No. hindwing ocelli				
Mean \pm SD	5.5 \pm 0.6	5.75 \pm 0.4	5.5 \pm 0.55	5.9 \pm 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

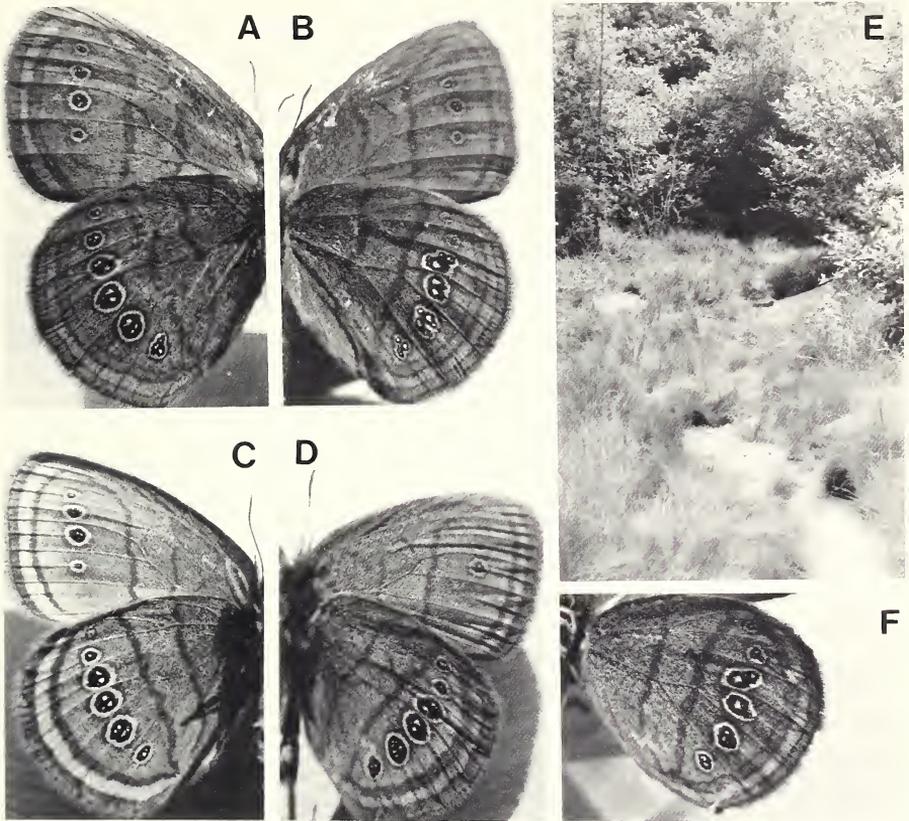


FIG. 2. *Neonympha mitchellii*. A, *N. m. francisci* female paratype, Fort Bragg, North Carolina, 31 August 1984. B, *N. m. francisci* holotype male. C, *N. m. mitchellii* female, Jackson Co., Michigan, 5 July 1984 leg. D. K. Parshall. D, *N. m. mitchellii* male, Springdale, New Jersey, 12 July 1970 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 pro-

nounced 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* (Walk.) 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 Wilschmann 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 sub-

species. 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 post-median 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.

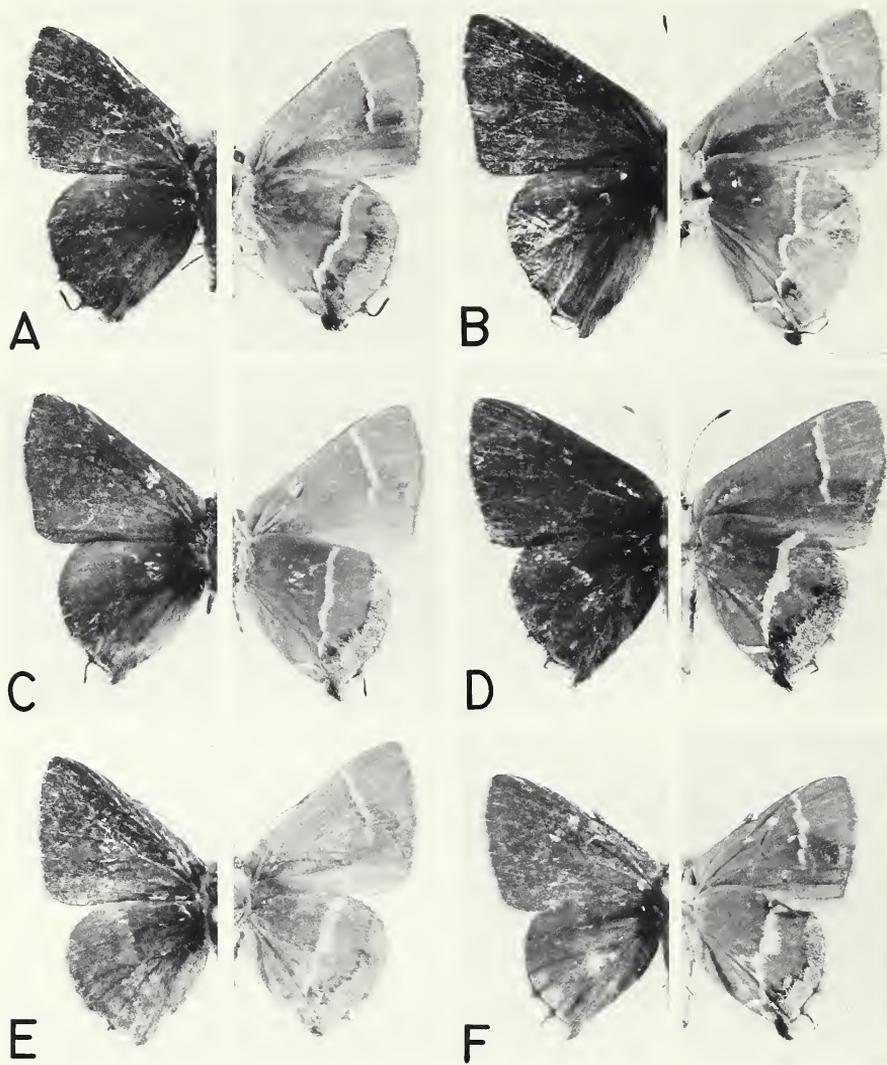


FIG. 1. Adult male *Chlorostrymon simaethis* (left, upper surface; right, under surface) (AMNH except as noted). A, *C. s. simaethis*, proximate topotype (TL given as generalized locality), Basseterre, St. Kitts. B, *Thecla s. jago*, holotype. C, *C. s. sarita*, proximate topotype, San Antonio, Texas, 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.

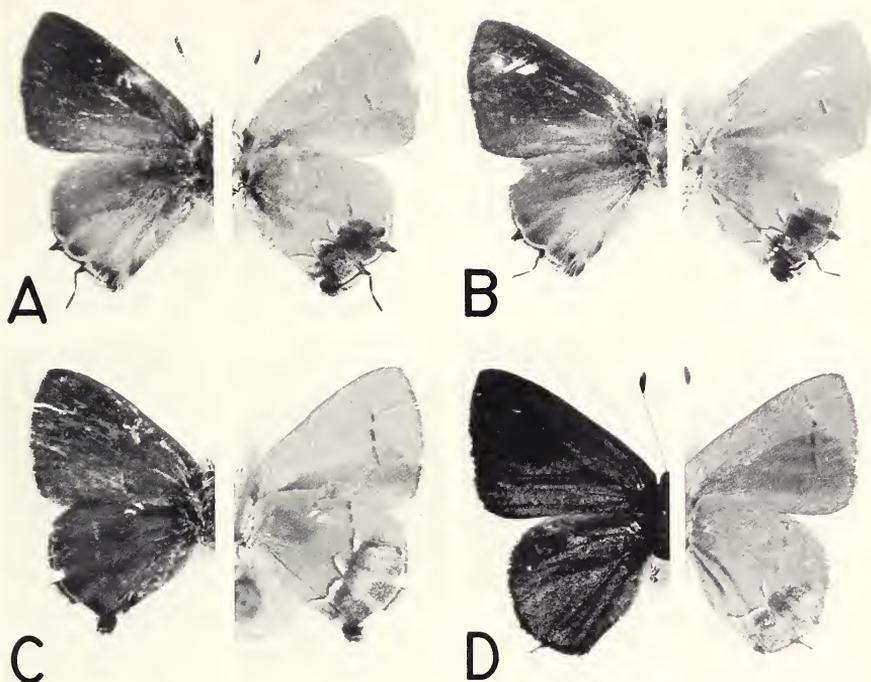


FIG. 2. Adult female *Chlorostrymon telea* and *C. maesites* (left, upper surface; right, under surface) (AMNH except as noted). A, *C. telea*, proximate topotype, Obidos, Amazonas State, Brazil. B, *C. telea*, Villa Ana, Santa Fe Province, Argentina, 26 February 1927 (BMNH). C, *C. maesites*, proximate 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 postdisical band distinctive across entire wing | 2 |
| | VHW postdisical 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 postdisical band distinctive only costad vein M_3 | <i>chileana</i> , new species |
| | VHW postdisical band distinctive only caudad vein M_3 and with the costal fold of
forewing extremely wide (≥ 1 mm) and rufous colored | <i>patagonia</i> , new species |
| 4 | VHW limbal patch extending costad to M_1 ; postmedian line forming a distinct
"W"; VFW postmedian line very faint to absent | <i>telea</i> |
| | VHW limbal patch extending costad to M_3 ; postmedian line not forming a "W";
VFW postmedian line black | <i>maesites</i> |

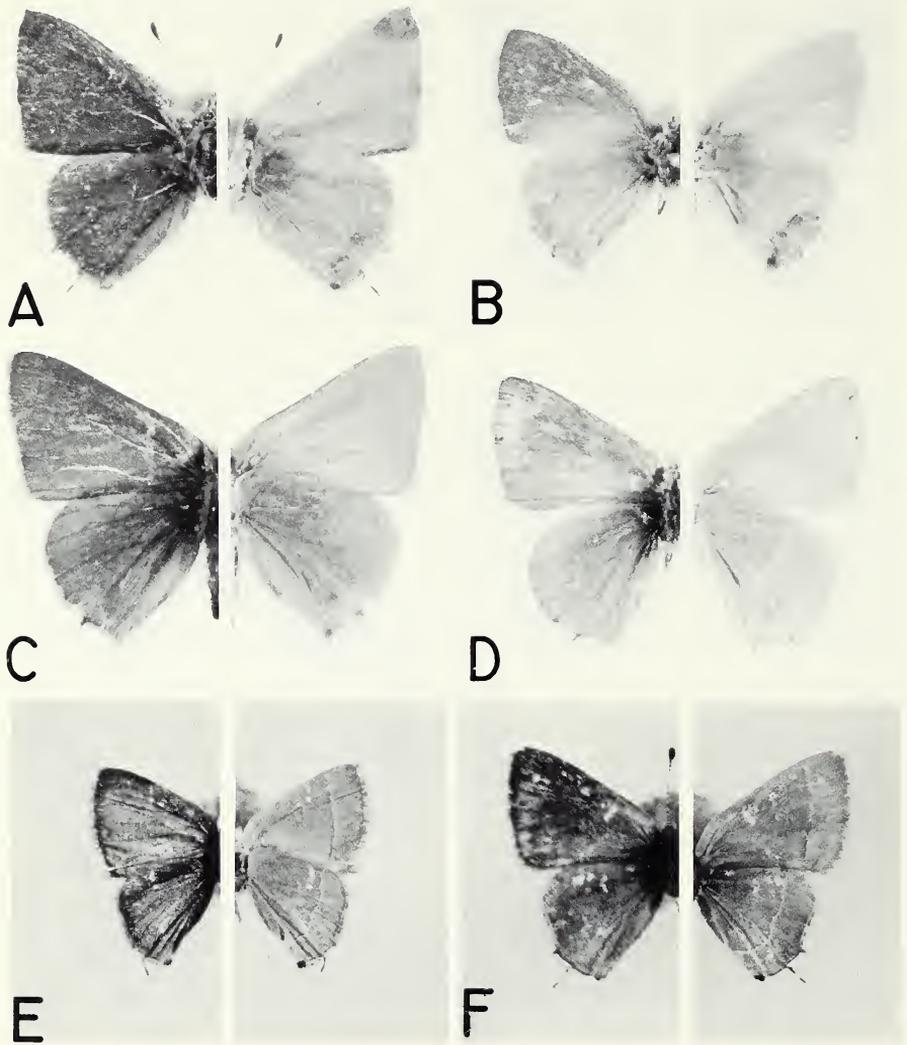


FIG. 3. Adults of austral South American *Chlorostrymon* (left, upper surface; right, under surface). A, *C. patagonia*, allotype male. B, *C. patagonia*, holotype female. C, *C. chileana*, allotype male. D, *C. chileana*, holotype female. E, *C. kuscheli*, paratype male. F, *C. kuscheli*, female, data 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) *chilleana*, 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-*

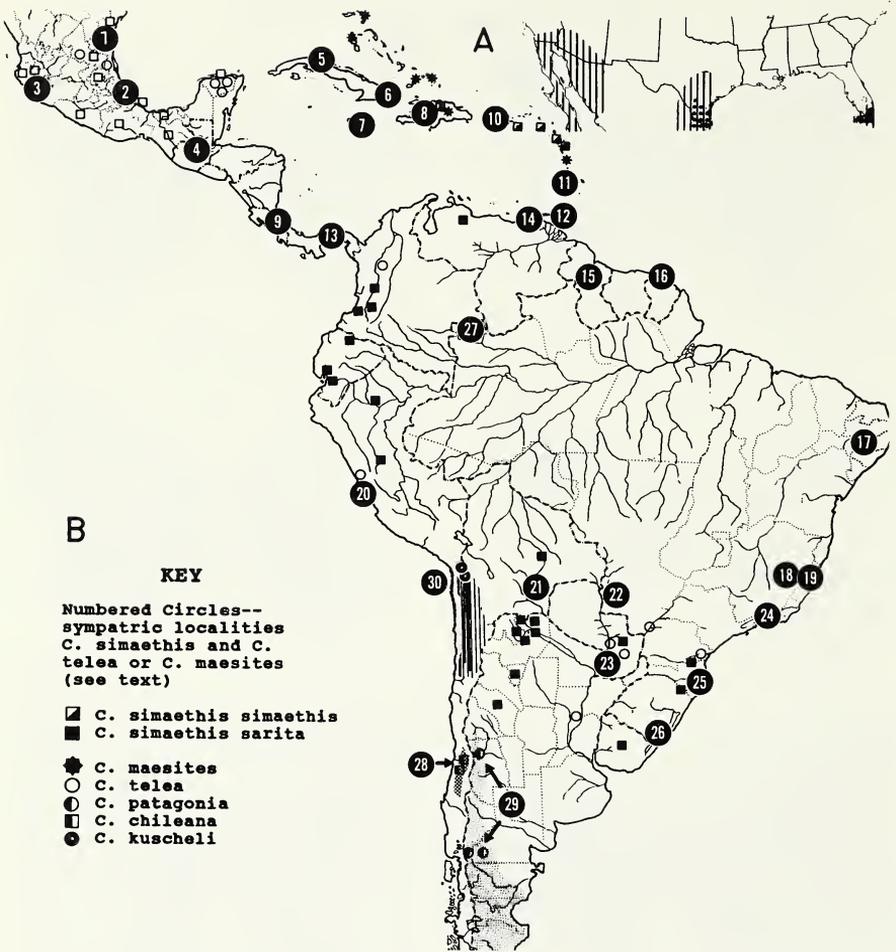


FIG. 4. Geographic ranges of *Chlorostrymon* species. A, United States and northern Mexico distributions of *C. simaethis* (vertical hatches), *C. telea* (stippled), and *C. maesites* (black), from localities assembled by Scott (1986) and Opler and Krizek (1986). B, Neotropical and austral distributions (specimens in AMNH except as noted). Numbers 1-27: sympatric Neotropical localities of *C. simaethis* and *C. telea* (mainland) or *C. maesites* (Antilles). 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. chilleana*, 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. Giacomelli (BMNH, IML). Austral South America: Pata-

gonia; C. Larsen (MNHN). (28) Chile (Valparaíso, Santiago); R. Martin (MNHN). General collections of CECUC, MNHC.

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 *lycus* 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

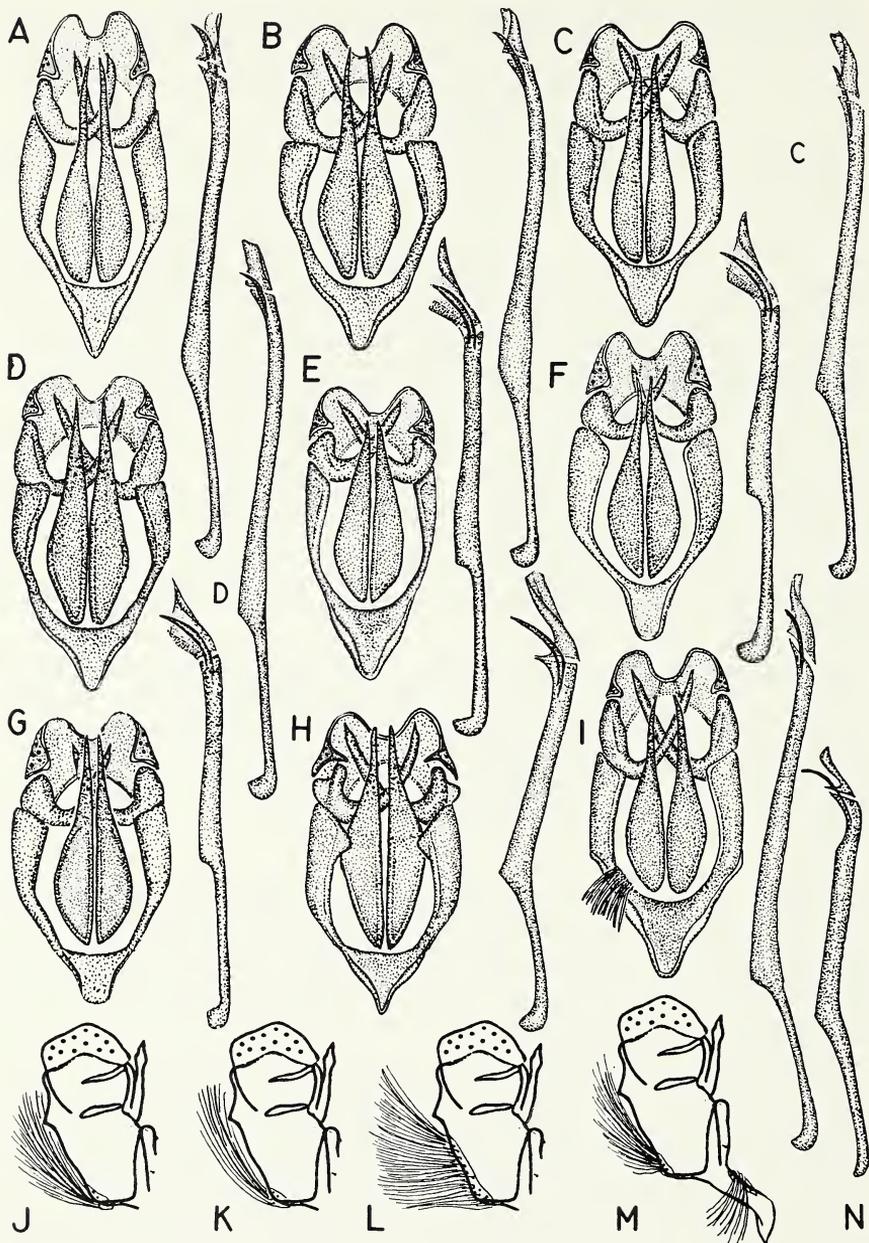


FIG. 5. Male genitalia (A-I, N) and brush organs (J-M) of *Chlorostrymon*. Genitalia shown in ventral view at left without aedeagus, aedeagus in lateral view at right (specimens in AMNH unless otherwise noted here or in text). A, *Thecla simaethis jago*, holotype. B, C, *simaethis sarita*, proximate 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 (♂), Guantanamo 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 (Banós: AMNH, CMNH; Aguatico, 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 $\frac{1}{2}$ that of lamella; normally about $\frac{1}{3}$). From Guatemala S through Panama, females are more locally variable in antral 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 recurvature. In South American females the antrum is usually outstanding and greatly flared (most often from about half the distance between the lamellar 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 abutment 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).

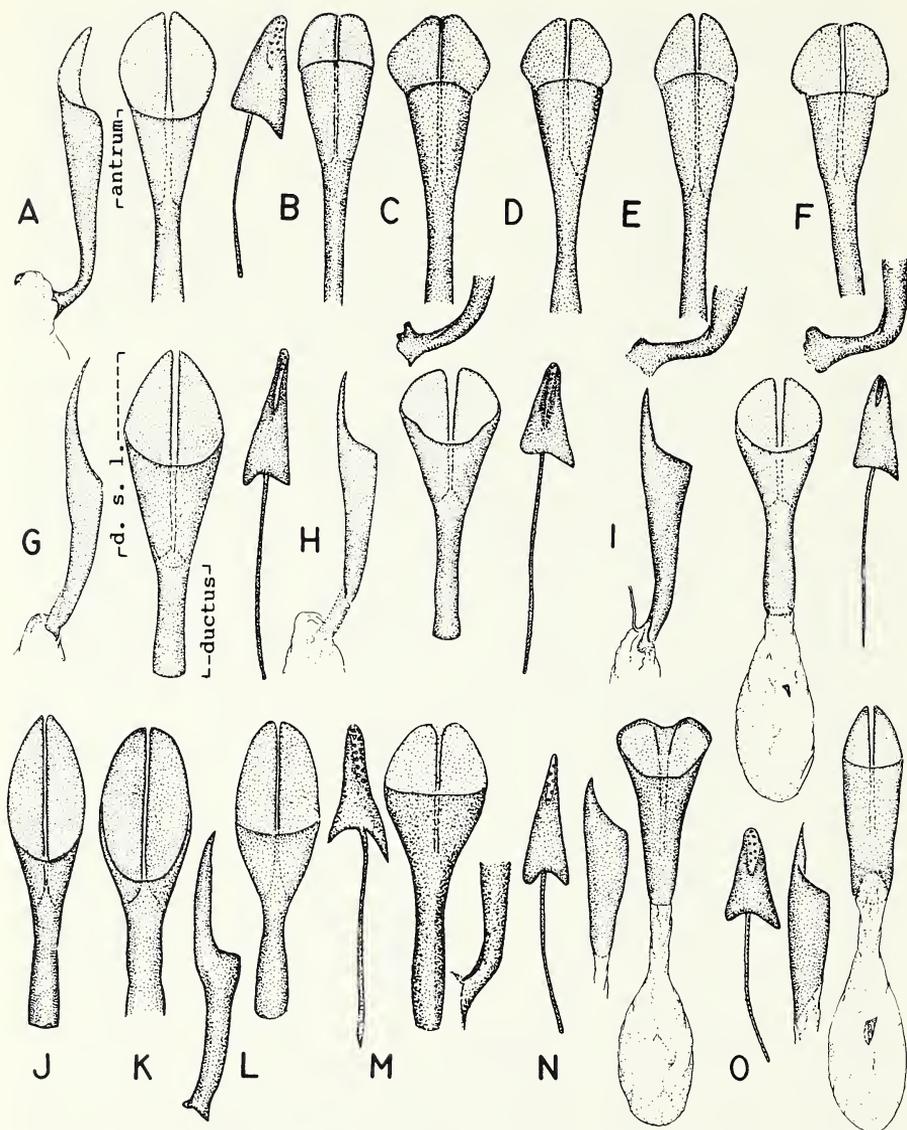


FIG. 6. Female genitalia of *Chlorostrymon*. Unless otherwise indicated, lateral view at left; ventral view at center (antrum indicated in A; dorsal suture line, d.s.l., and ductus indicated in G); lateral view of papillae anales and their apophyses at right (specimens in AMNH unless indicated otherwise 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, Yariquenda (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: Banões, 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, Parapanura 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 ECADOR (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. chilleana*, 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 post-median 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 lamellar configuration than *C. telea* (Fig. 6G, J-L). As Nicolay (1980) noted, the lamellar 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: Caldas, 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

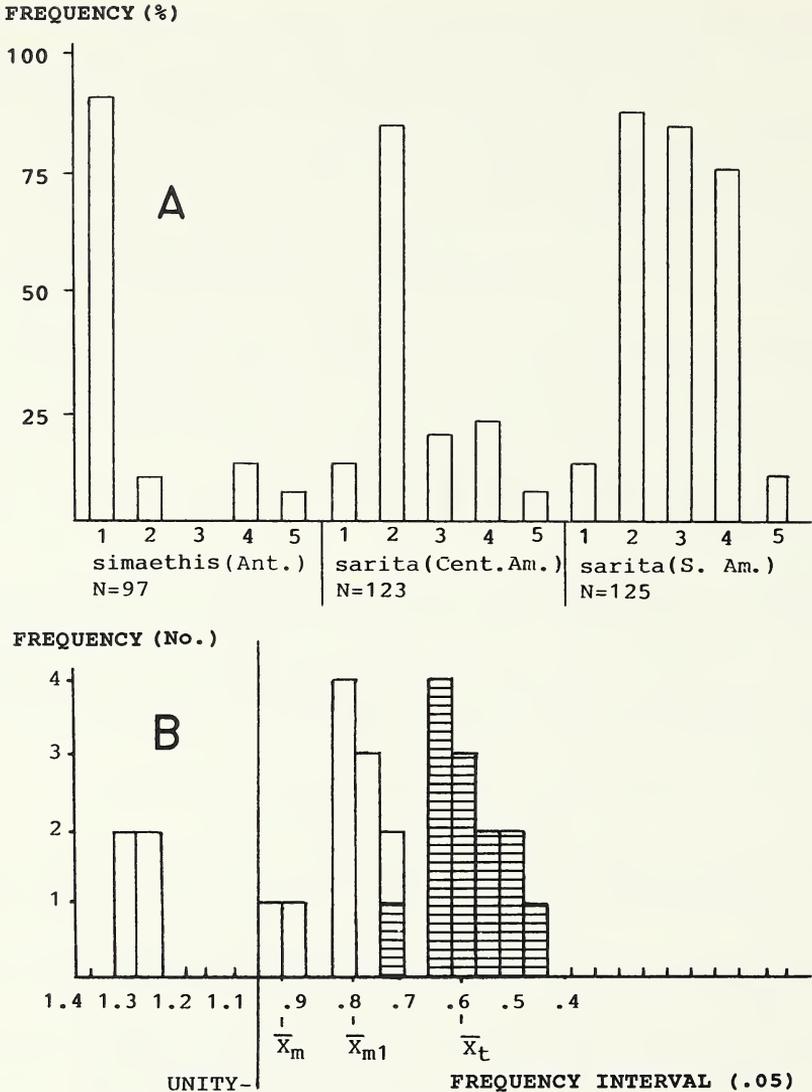


FIG. 7. Frequencies of characters in certain *Chlorostrymon* populations. A, Wing characters in *C. simaethis simaethis* (Antilles) and *C. s. sarita* (Central America, South America). Characters: 1, VHW postdiscal band undulate (angles of band, along inner surface at consecutive veins, changing at least 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 genital 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}_{m1} 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 $3\times$ maximum width of vincular arc (in *C. simaethis*, $3.5\text{--}4.0\times$), and (b) with terminal $\frac{1}{4}$ 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 (noticeable 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. 5C] 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 antrunal 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. chilleana*, with sclerotized components including only the antrunal 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 antrunal 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. chilleana*. 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. chilleana*) duplicate only the antrunal structure of other *Chlorostrymon* species. The ductal area of *C. patagonia* (and *C. chilleana*) is wholly 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. chilleana* are autapomorphic, as discussed under *C. chilleana*.

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 chilleana*, 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 CuA₁ and CuA₂. Female genitalia sclerotized only in terminal antrimal 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 CuA₁ and CuA₂ slightly suffused reddish to grey distad, silver basad; stubby tail at terminus of HW vein CuA₂. 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 $\frac{2}{3}$ 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 antrimal 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. coeruleascens* (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

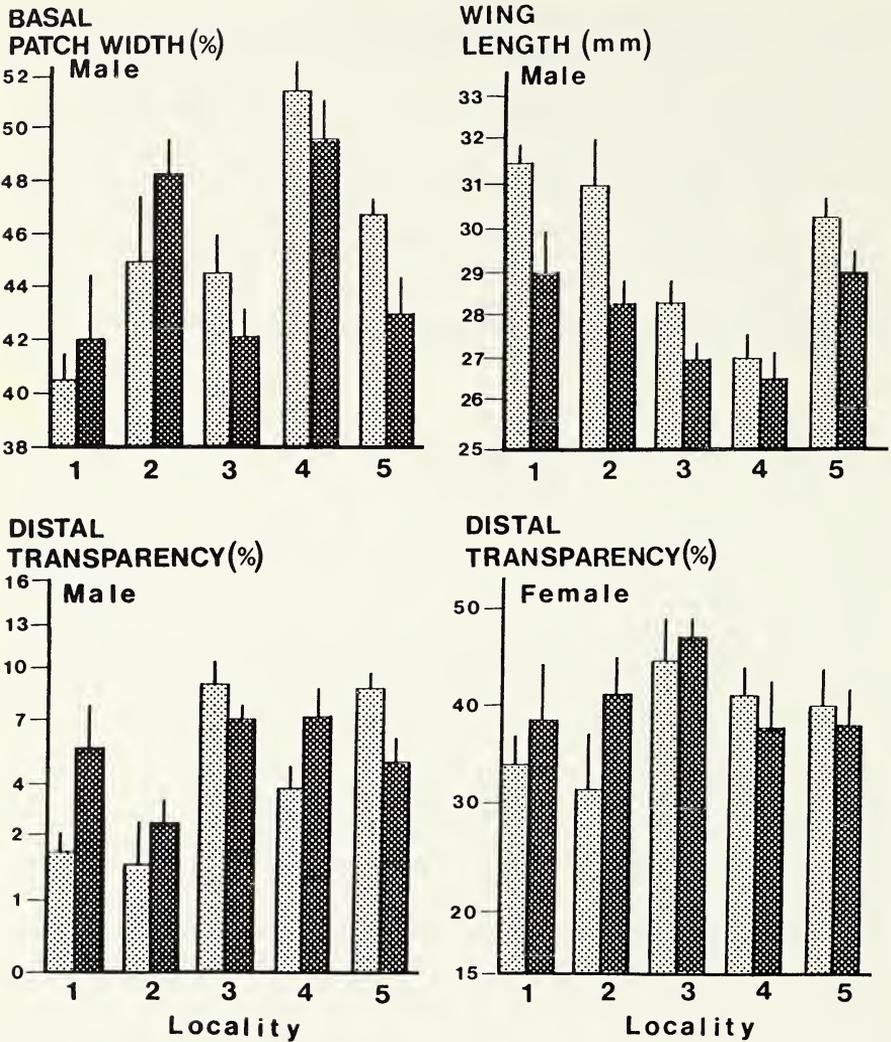


FIG. 1. Characters of *Parnassius phoebus* for which a genetic basis was detected. Dark bars, reared samples; light bars, wild samples. Vertical lines represent 1 SE. Sample origins and sizes are given in Table 1.

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 basal 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 ($39 \pm 4^\circ\text{C}$). 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 ($31 \pm 2^\circ\text{C}$) 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 $10 \pm 1^\circ\text{C}$, 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 $7 \pm 2^\circ\text{C}$ 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 macro lens. 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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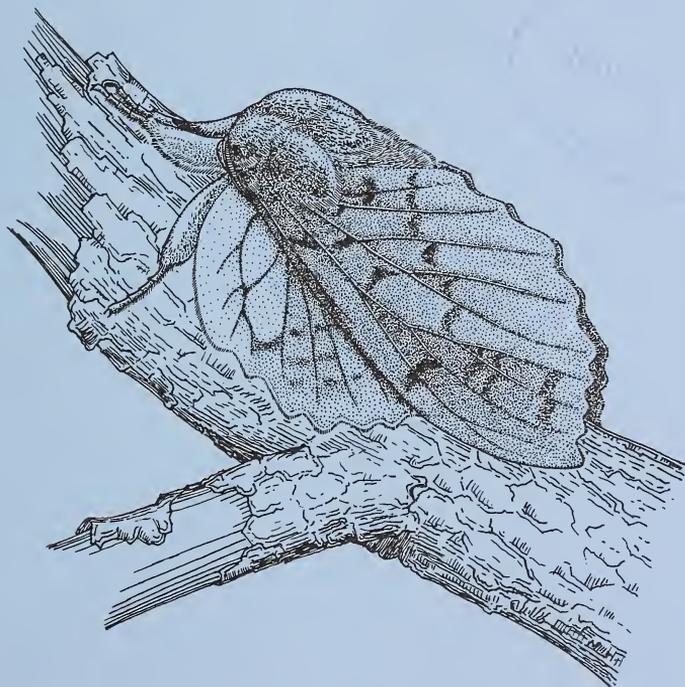
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Cover illustration: Female of *Gastropacha populifolia* (Esper) (Lasiocampidae) in natural resting position on a dead branch, Beijing, China. Submitted by Yu Xiangming, No. 31, Qian Men Wai Zhu Bao Shi, Beijing, China.

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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

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, sea-shells, 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 *Apo-demia phycioides* 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 $\frac{3}{4}$ 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 geometrid 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 ovarian 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 cm² 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 cm² 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 \pm , range in parentheses.

Attribute	Mean		Departure from plain-water group (%)
	Plain water [19 pairs]	Honeydew-water [9 pairs]	
Oviposition span, days ¹	8.8 \pm 1.8 (6-12)	10.3 \pm 4.1 (5-17)	17 ^a
No. eggs and oocytes			
Total	326 \pm 46 (243-395)	339 \pm 75 (204-446)	4
Matured	200 \pm 46 (134-291)	245 \pm 71 (109-350)	22 ^b
Laid	197 \pm 46 (130-289)	235 \pm 76 (98-348)	19
Change in no. laid (L) as function of forewing length (W)	28.2	102.8	264 ^c
Unlaid immature	127 \pm 28 (88-176)	94 \pm 58 (0-184)	-26 ^a
Egg viability, %	75 \pm 20 (28-97)	81 \pm 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 cm² yucca leaf segments were weighed (weight *x*), misted as for imbibing, reweighed (weight *y*), thoroughly washed, towel-dried, and again reweighed (weight *z*). These weighings 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

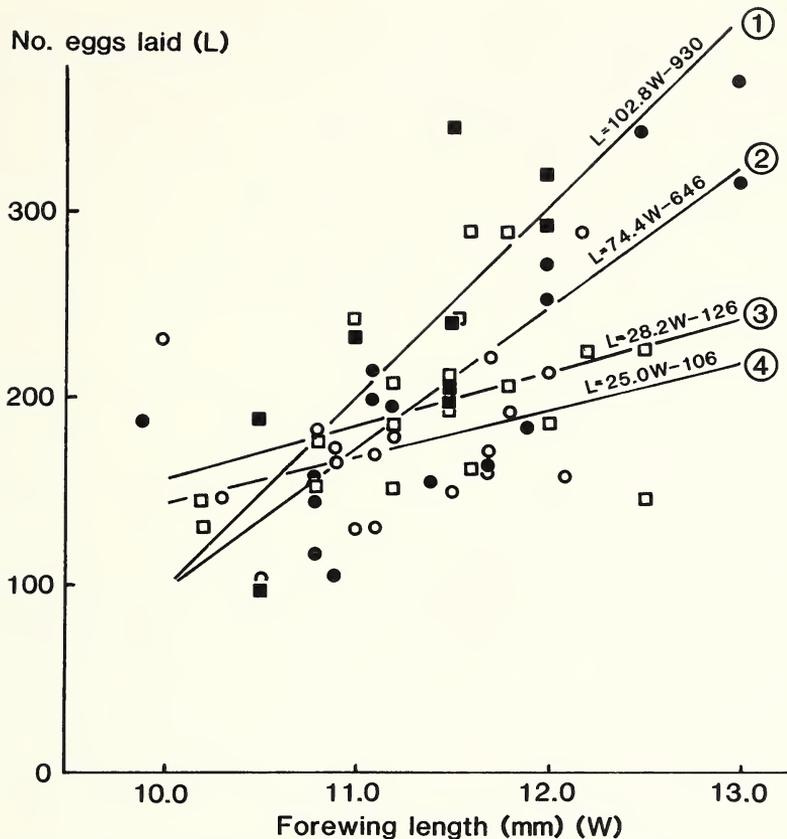


FIG. 1. Role of spruce budworm female body size in determining number of eggs laid in response to honeydew- and plain-water imbibing treatments. Each symbol represents one female. Line ① (closed squares) and line ② (closed circles) depict honeydew-water imbibers in the preliminary and main experiments, 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 ($11.0 \times 102.8 - 930 = 200.8$) while one on plain water laid 184 ($11.0 \times 28.2 - 126 = 184.2$) (9% difference); but a 12.5-mm female on honeydew-water laid 355 eggs ($12.5 \times 102.8 - 930 = 355.0$) while one on plain water laid 226 ($12.5 \times 28.2 - 126 = 226.5$) (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 ($11.0 \times 74.4 - 646 = 172.4$) while one on plain water laid 169 ($11.0 \times 25.0 - 106 = 169.0$) (2% difference);

TABLE 2. Performance of spruce budworm pairs imbibing plain water and honeydew-water in the main experiment. SD preceded by \pm , 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 \pm 0.7 (1-3)	2.3 \pm 0.8 (1-4)	
Lifespan, days			
Female	10.7 \pm 2.0 (7-14)	11.4 \pm 3.4 (6-17)	6 ^a
Male	9.4 \pm 2.8 (5-14)	8.7 \pm 3.8 (4-17)	-7
Oviposition period, days	7.7 \pm 2.2 (4-11)	9.5 \pm 3.6 (4-15)	23 ^b
No. eggs and oocytes			
Total	238 \pm 60 (104-332)	233 \pm 80 (126-404)	-2
Matured	177 \pm 43 (104-288)	214 \pm 78 (111-372)	21
Laid	175 \pm 43 (102-288)	210 \pm 79 (104-370)	20
Change in no. laid (L) as function of forewing length (W)	25.0	74.4	198 ^c
Viable	156 \pm 36 (98-245)	181 \pm 78 (59-325)	16
Unlaid immature	60 \pm 41 (0-134)	19 \pm 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

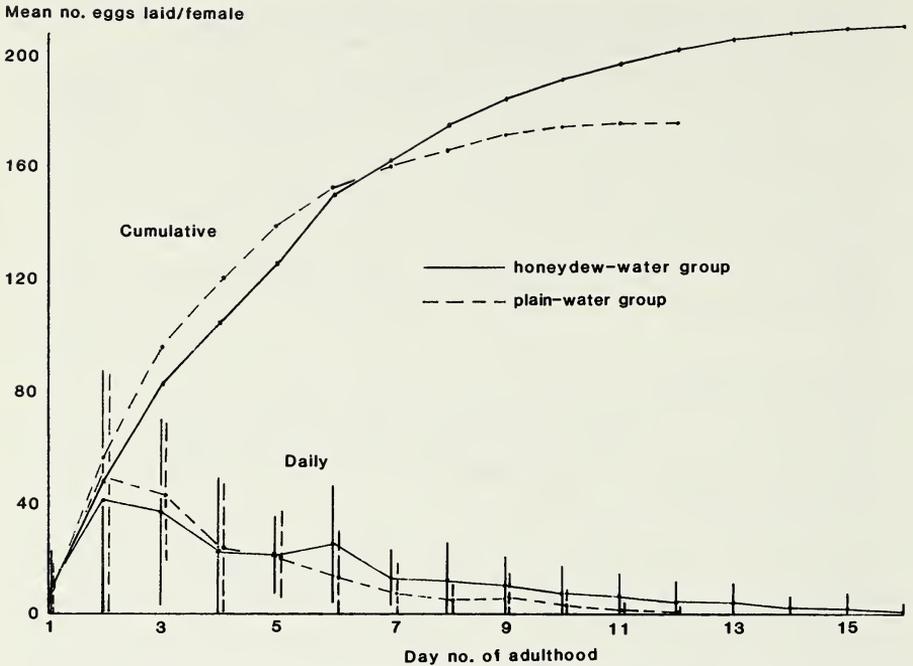


FIG. 2. Oviposition records for fertile spruce budworm females in the main experiment. Sixteen females in the honeydew-water group, 18 in the plain-water group. Vertical bars represent SD.

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 \pm , range in parentheses.

Fertility status	No. observed	Mean age (days)	Mean forewing length (mm)	Amount imbibed (mg)
Plain-water imbibers				
Fertile	9	8.1 \pm 2.4 (5-12)	11.1 \pm 0.3 (10.5-11.7)	3.9 \pm 2.3 (0.9-8.1)
Infertile	5	4.6 \pm 1.8 (3-7)	10.7 \pm 0.6 (9.8-11.2)	4.3 \pm 1.5 (2.7-6.5)
Honeydew-water imbibers				
Fertile	7	8.0 \pm 1.0 (7-10)	11.7 \pm 0.8 (10.8-13.0)	5.2 \pm 2.5 (1.7-10.0)
Infertile	7	5.1 \pm 1.3 (4-7)	10.8 \pm 0.5 (9.8-11.2)	3.0 \pm 1.8 (1.0-6.5)
All imbibers				
Mixed	28	6.7 \pm 2.3 (3-12)	11.1 \pm 0.7 (9.8-13.0)	4.5 \pm 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 ($31.6 \times 0.065 = 2.05$). 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 Hesperiiidae 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 Hesperinae (greater than 2000), followed by Pyrginae, Polyommatainae, 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 (Hesperiiidae, 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, Hesperinae, Megathyminae, Satyrinae, Morphinae (in part), and Brassolinae. The world species richness of butterflies, 17,280, when divided by 128,811,340 km², the total land area of the earth excluding Antarctica and inland waters, yields an average density of 0.000134 species per km². 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, Polyommatainae, 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 I. 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
Polyommatainae	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
Argynniinae ³	155	Warren 1944, 1955; dos Passos & Grey 1945; Grey <i>in litt.</i> ; 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 Moults 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 \pm 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, Gynaecini, Cyrestini (=Marpesiini), Epicaliini (=Callicorini, Catagrammini, Catonephelini, Dynamini, Epiphilini, Eunecini), Limenitidini (=Abrotini, Adelphini, Bebeariini, Chalingini, Euthalini, Neptini, Neurosigmatini, Parthenini, Pseudacraeini), Nymphalini (=Araschini, Cynthini, Diademini, Doleschallini, Euphydryini, Hypolimnini, Junonini, Kallimini, Melitaeini, Phycodini, Vanessini), Pseudergolini.

* Includes Heliconiinae, Cethosini.

* 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'Abreia 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 (*vide* 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).

* Includes Charaxinae.

* 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.

* Includes Amathusiinae. Parsons (1984) estimates there are ca. 100 species of Amathusiinae. Morphinae now includes the Neotropical genera *Morpho*, *Antirrhoea*, and *Caerots* (DeVries et al. 1985). D'Abreia (1984) lists 31 species of *Morpho*, 21 *Antirrhoea*, and 3 *Caerots*. Smart (1977) estimates about 80 species of *Morpho*, probably too many (*cf.* D'Abreia 1984).

* 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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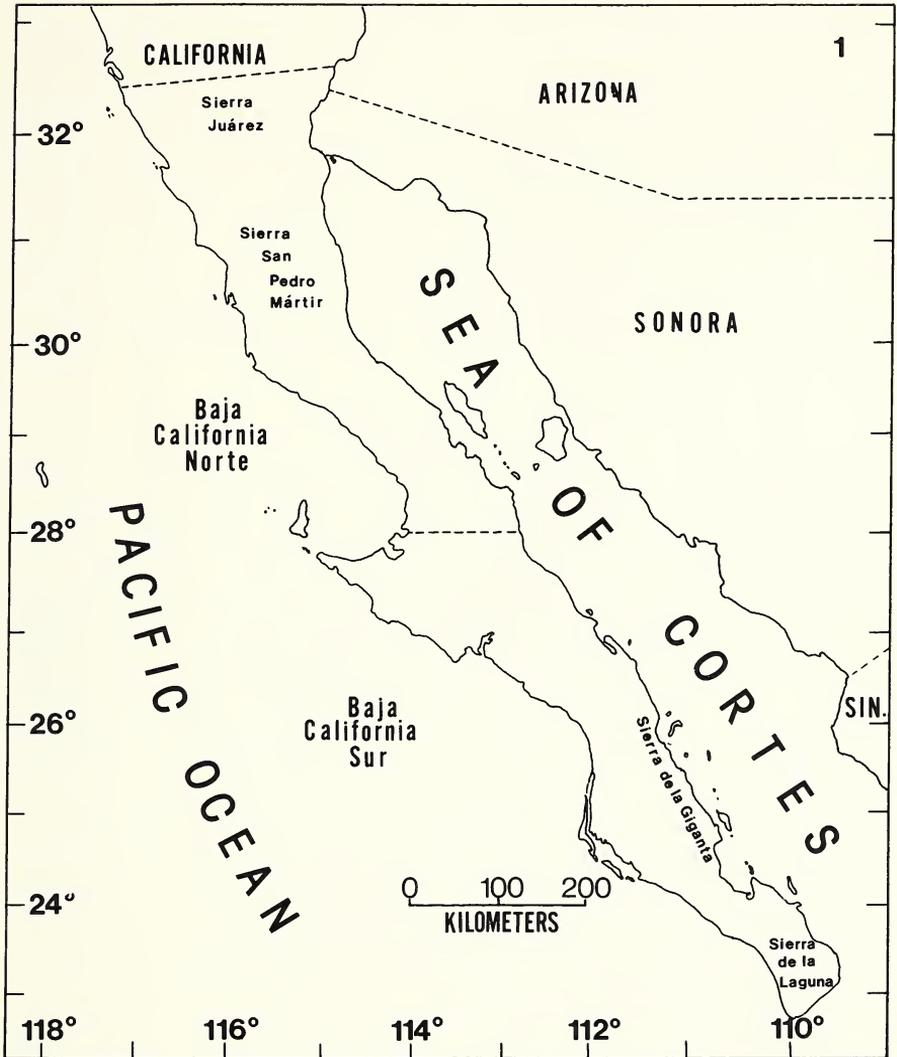


FIG. 1. The peninsula of Baja California and adjacent areas.

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 repre-

senting 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.

number of
species

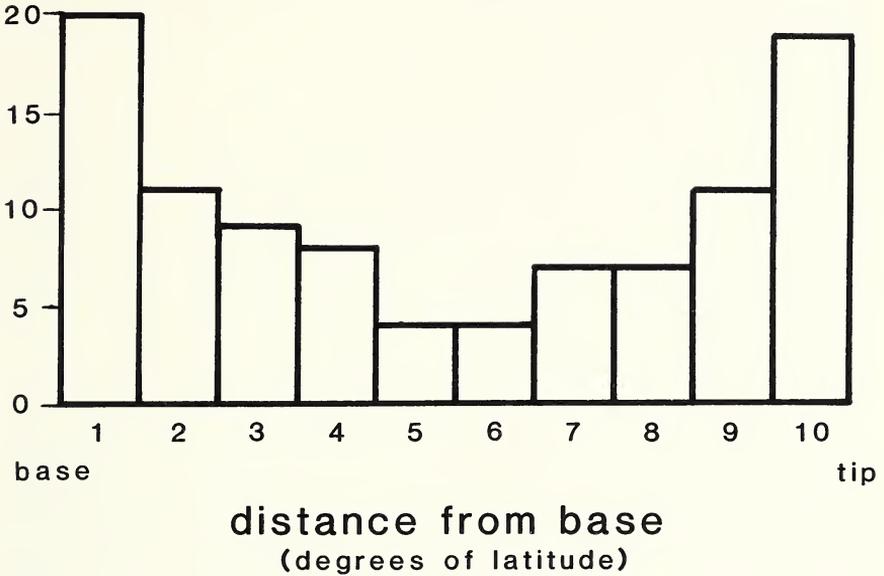


FIG. 2. Species density histogram for Baja California SpHINGIDAE (base = north end of peninsula; tip = southern extremity).

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* (Verbenaceae), 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, 11/2-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 dollii 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, 78-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, Indigenus 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 Cavatiña, 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 genitally 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); Bahía 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 (SDNHM). 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 Bartolo, 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, 11/2-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, 2023-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.

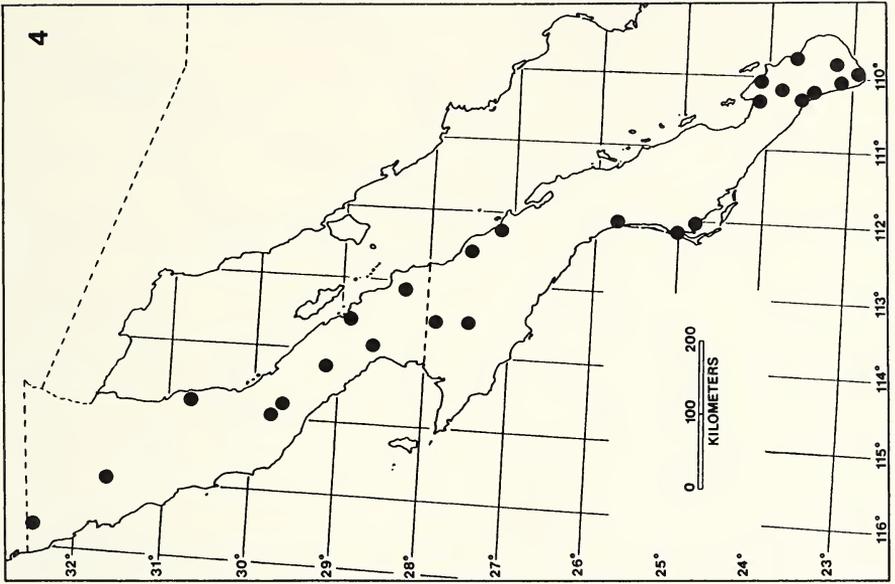
Celerio lineata; Cary, 1963:153.

Hyles lineata; Hodges, 1971:153.

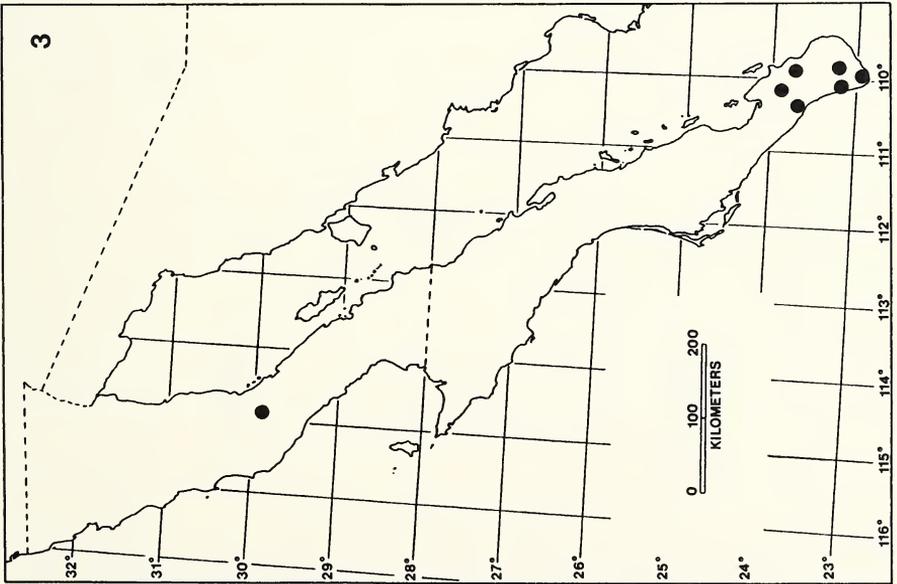
H. lineata is by far the most common and widespread sphingid in Baja California. It ranges from the coastal lowlands to the mountains; it is common in the desert areas; it is also known from several islands both in the Sea of Cortés (e.g., Isla Angel de la Guarda and Isla Mejía) and along the Pacific 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

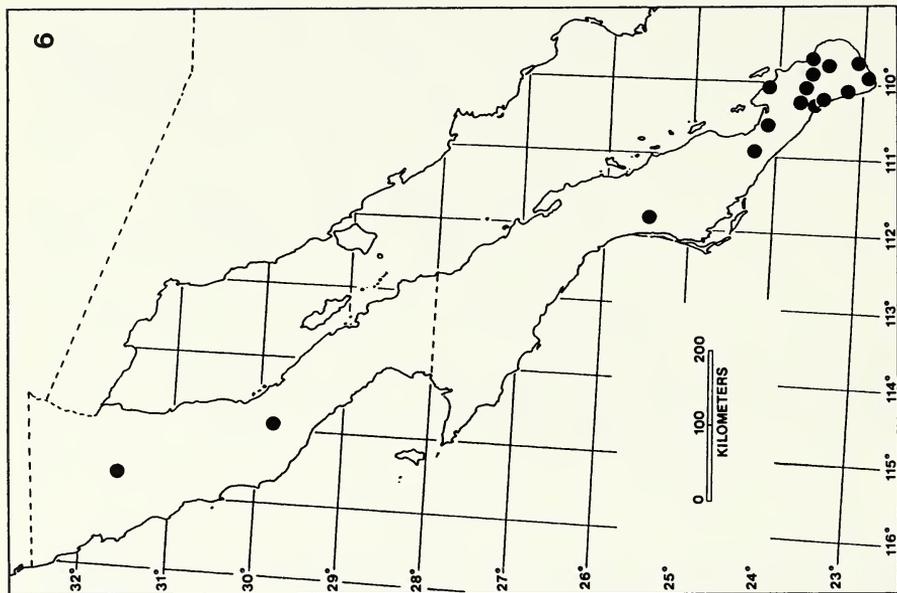
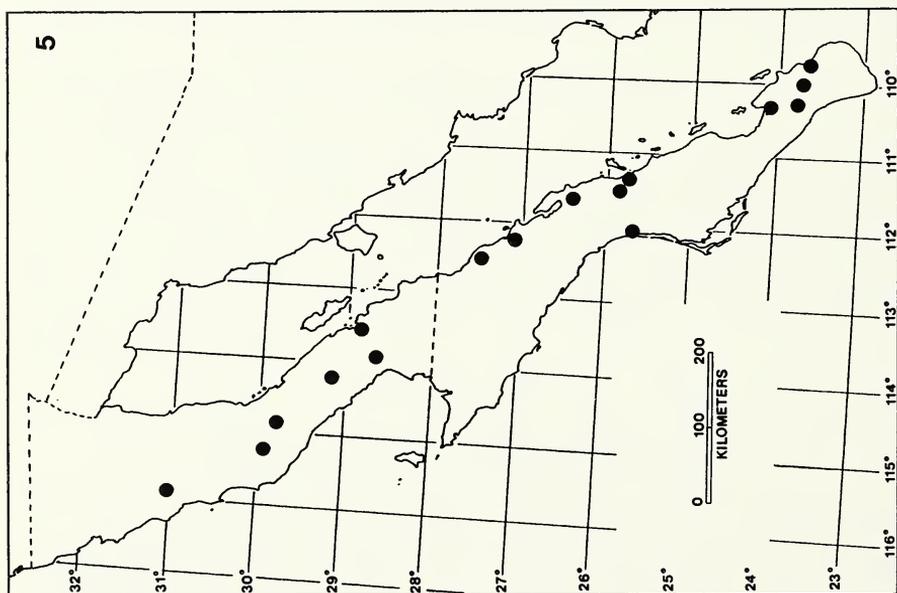
The Californian Province in the northwestern portion of the peninsula represents a significant southern intrusion of Nearctic elements, both floral and faunal. Physiographically, this region is an extension of the area to the immediate north. Most of the sphingids present in southern California occur 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-

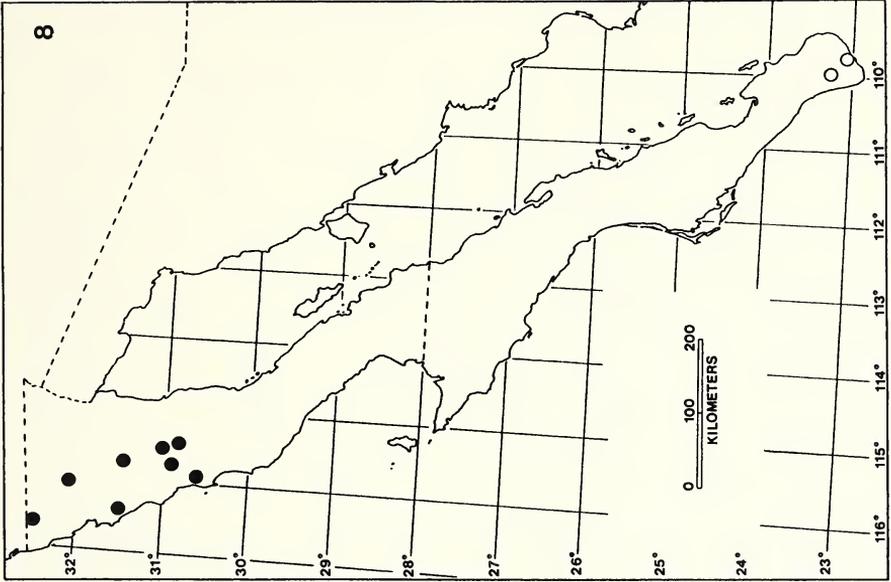


4. Distribution of *Manduca sexta*.

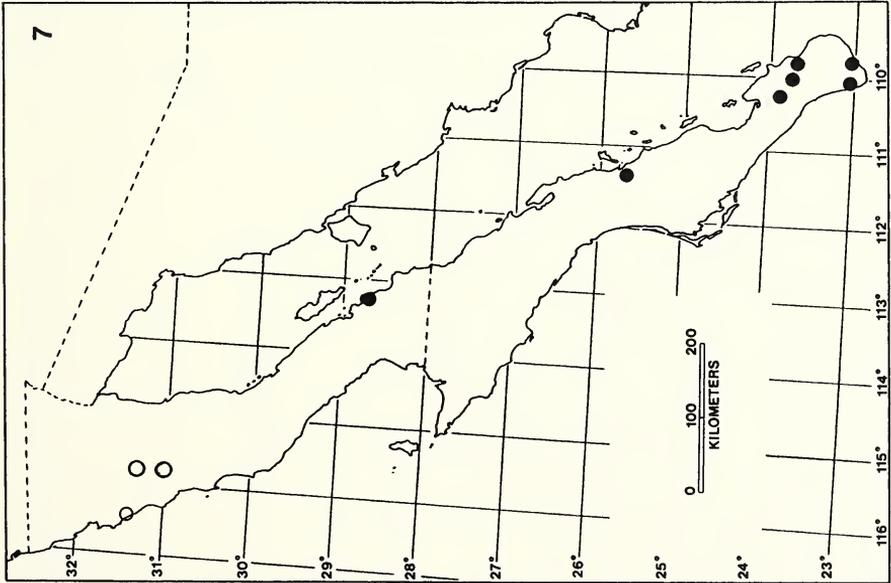


3. Distribution of *Agrilus cingulatus*.

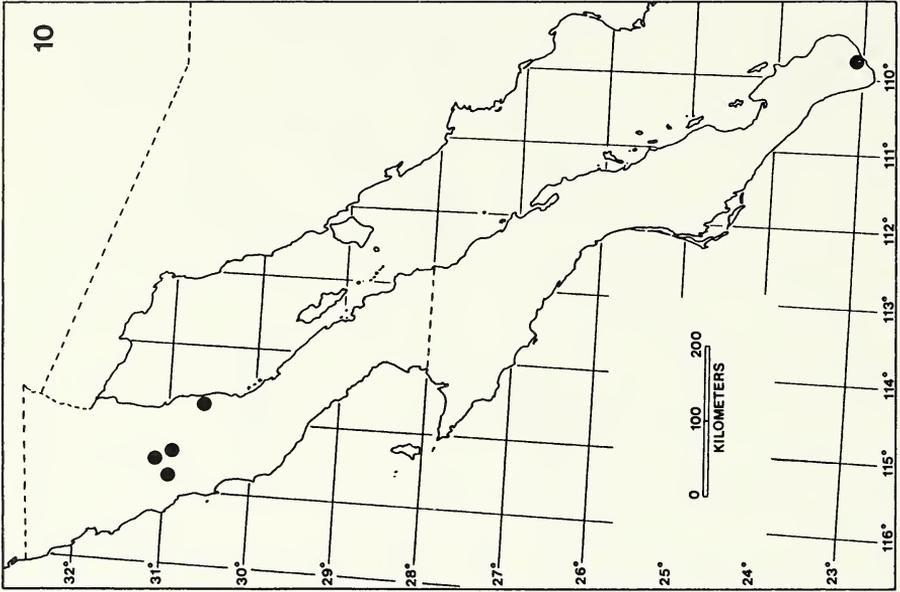
6. Distribution of *Manduca rustica*.5. Distribution of *Manduca quinque maculata*.



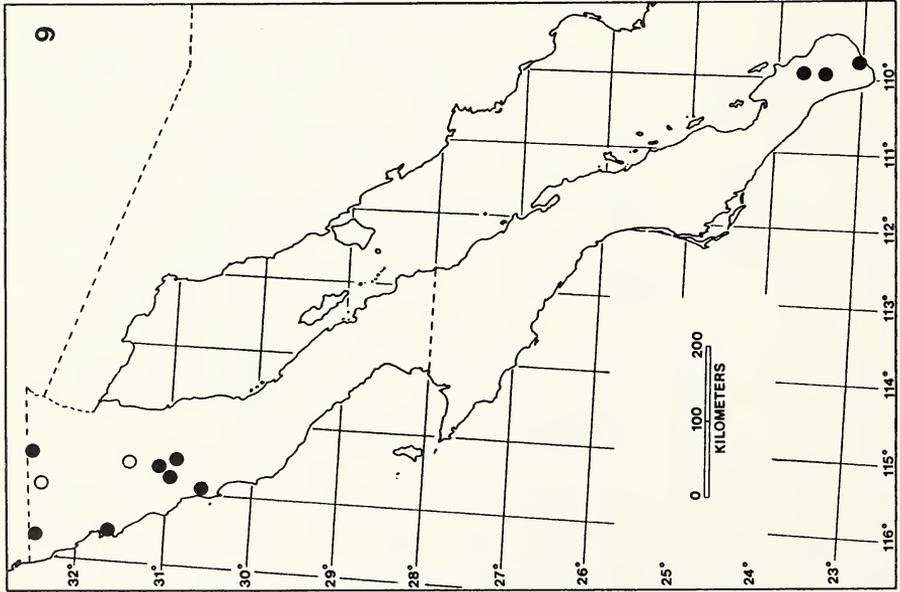
8. Distribution of *Sphinx libocedrus* (open circles) and *S. perelegans* (closed circles).



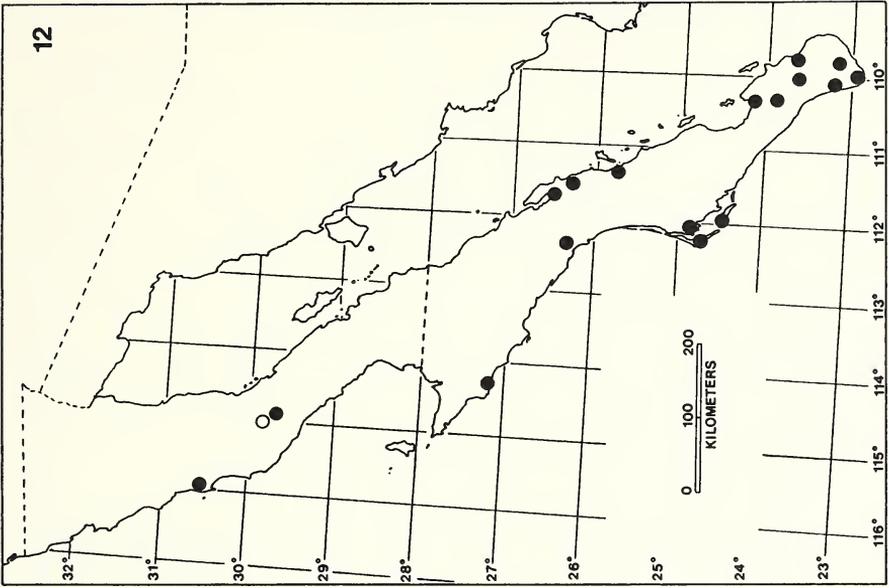
7. Distribution of *Sphinx xantus* (closed circles) and *S. chersis* (open circles).



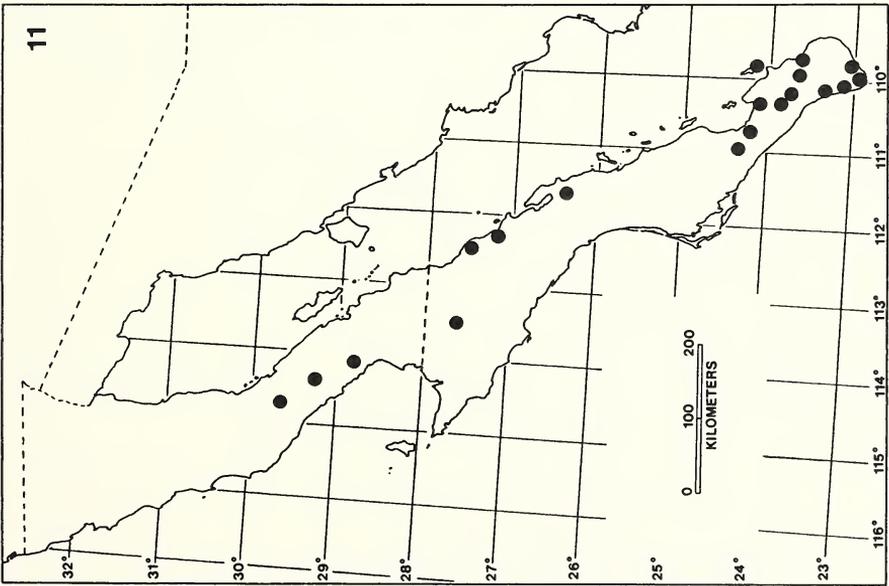
10. Distribution of *Pachysphinx occidentalis*.



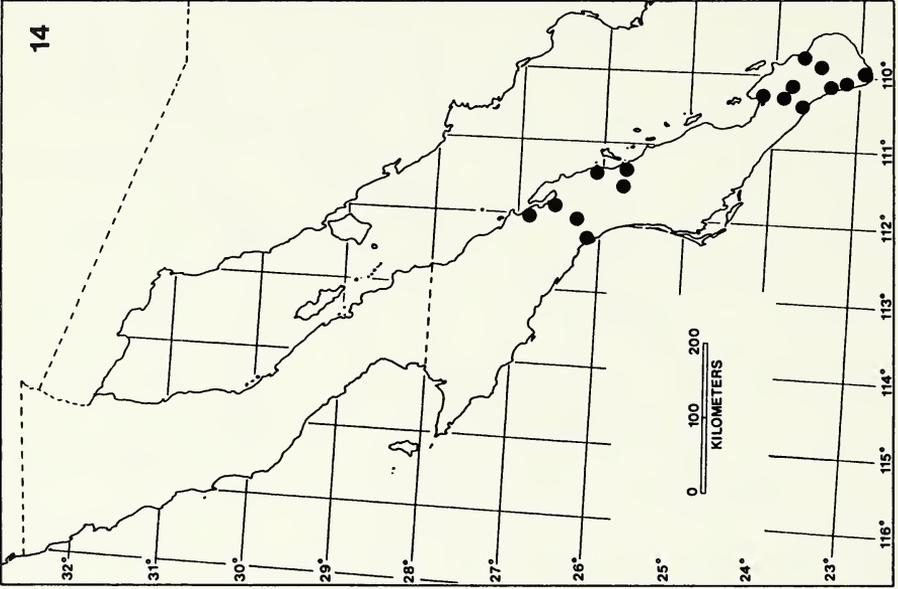
9. Distribution of *Sphinx sequoiatae* (open circles) and *Smerinthus certsiyi* (closed circles).



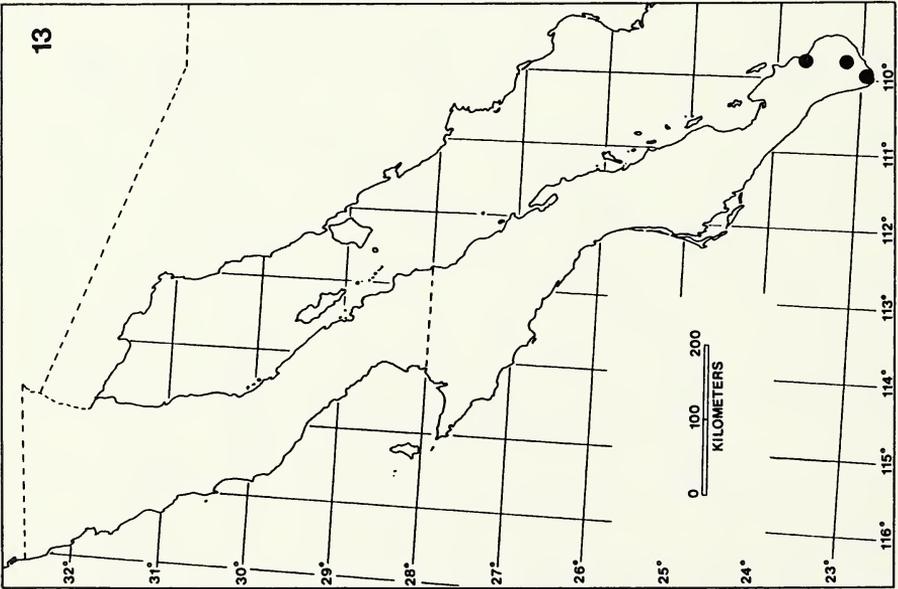
12. Distribution of *Erinnys crameri* (open circles) and *E. obscura* (closed circles).



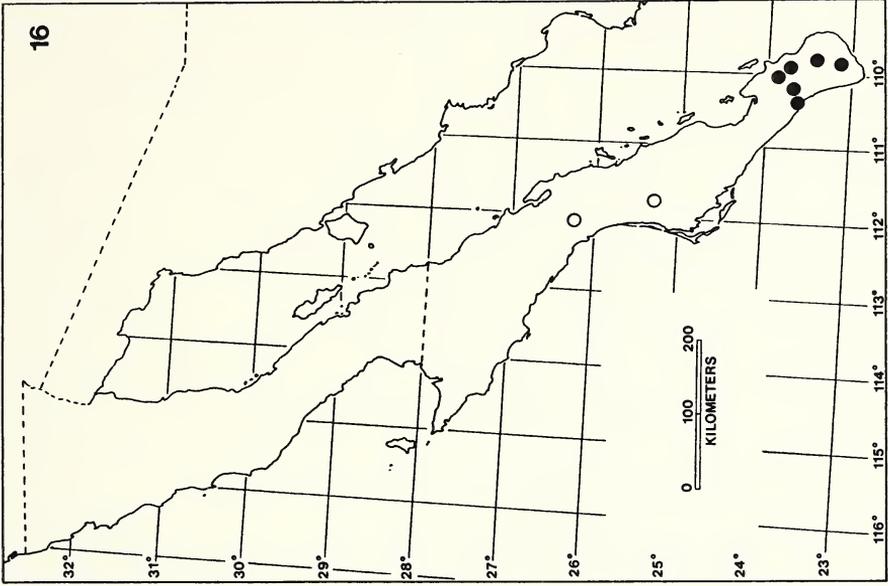
11. Distribution of *Erinnys ello*.



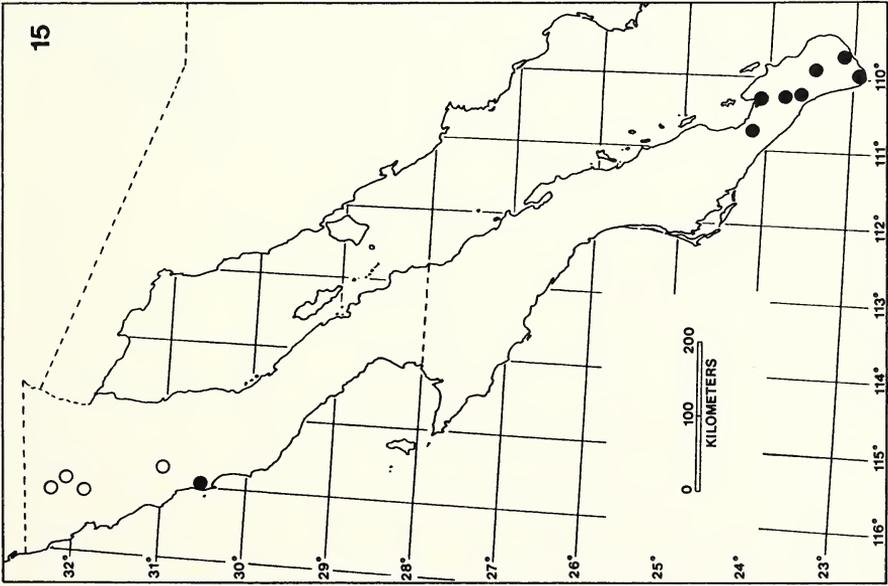
14. Distribution of *Callionima falcifera*.



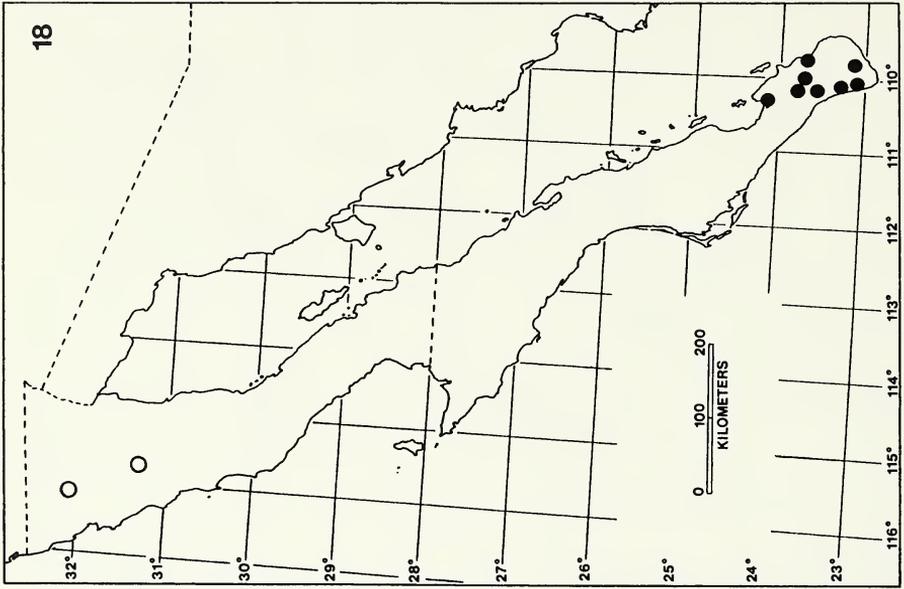
13. Distribution of *Pachylia syces*.



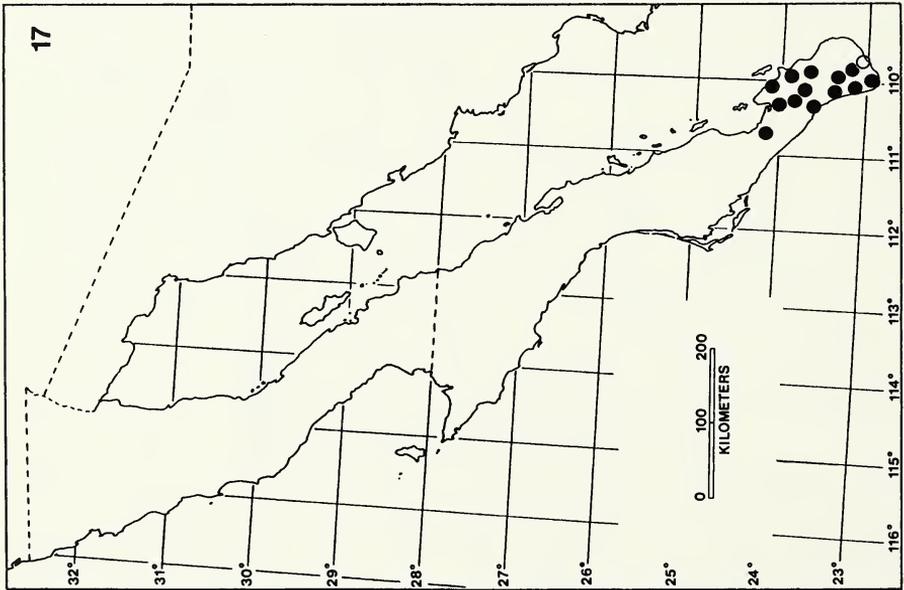
16. Distribution of *Eumorphia satellitia* (closed circles) and *E. achemon* (open circles).



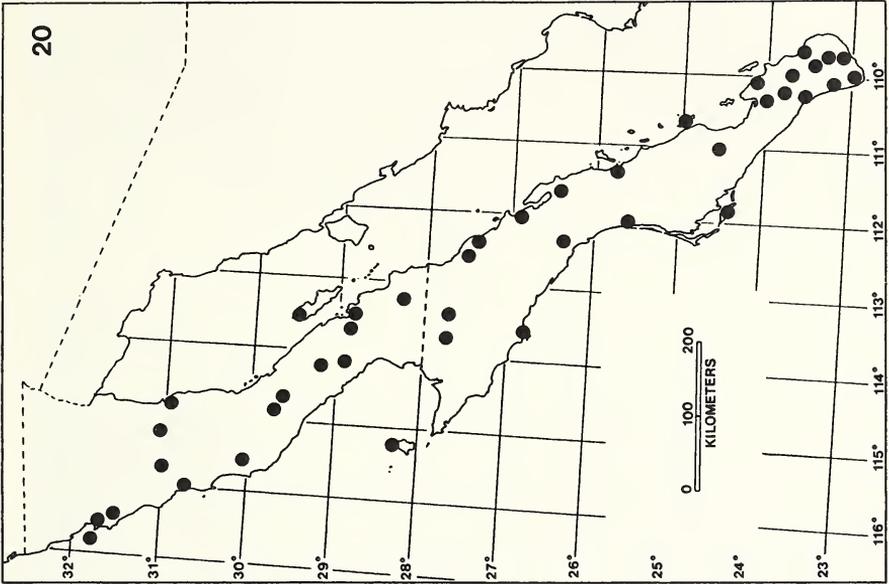
15. Distribution of *Aellopos clavipes* (closed circles) and *Hemaris diffinis* (open circles).



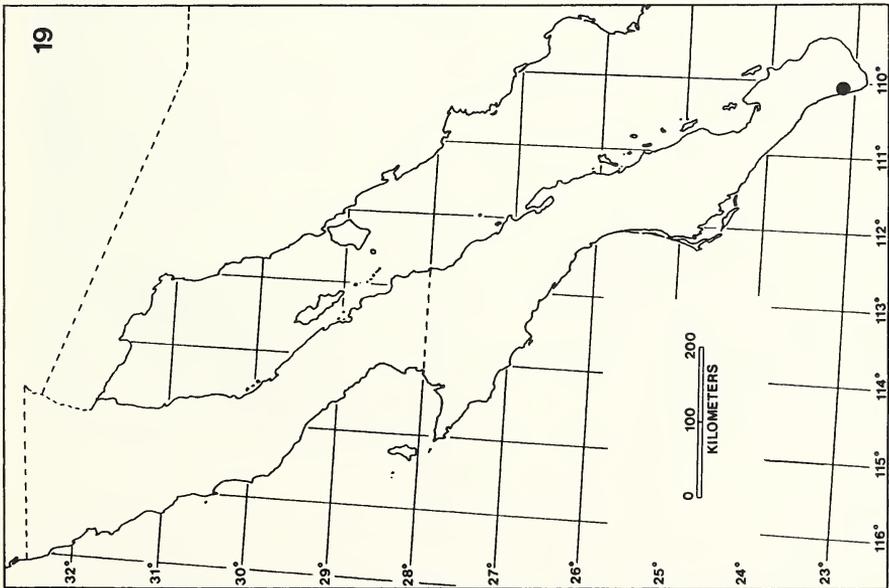
18. Distribution of *Euproserpinus phaeton* (open circles) and *Xylophanes tersa* (closed circles).



17. Distribution of *Eumorpha vittis* (closed circles) and *E. fasciata* (open circles).



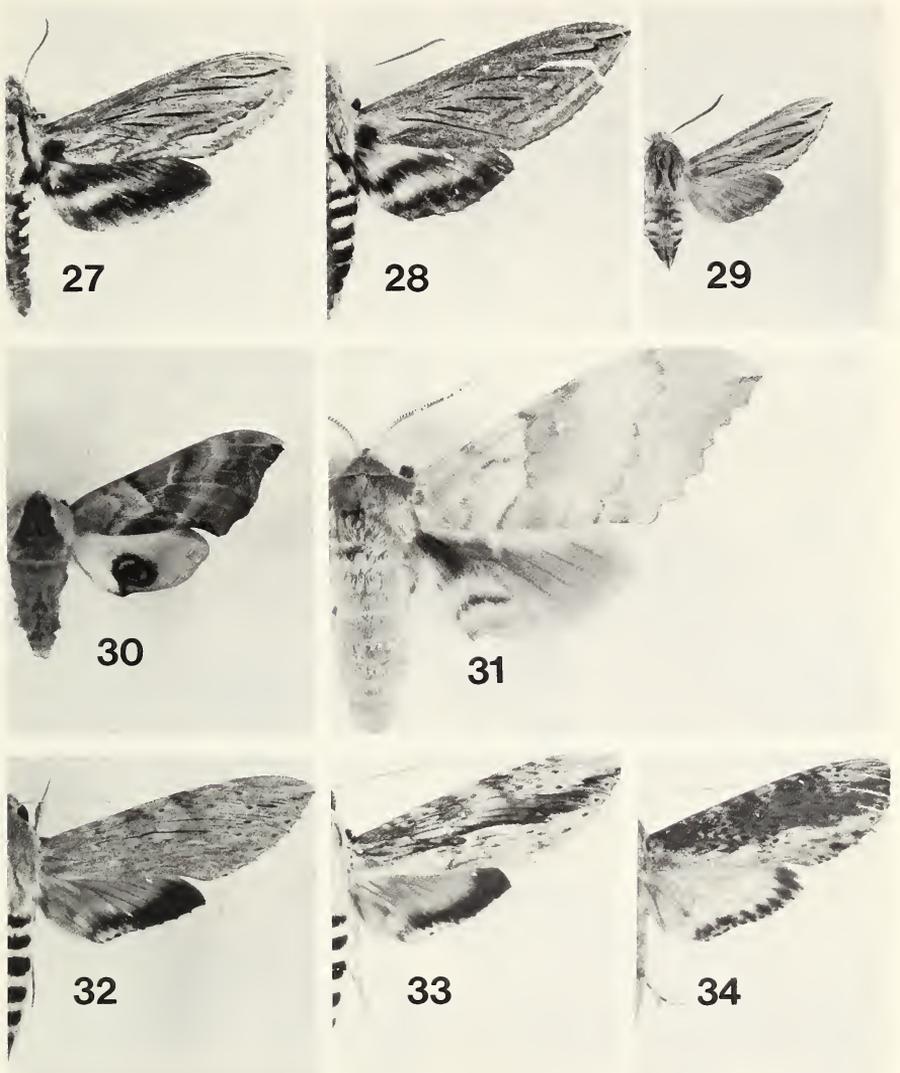
20. Distribution of *Hyles lineata*.



19. Distribution of *Xylophanes pluto*.

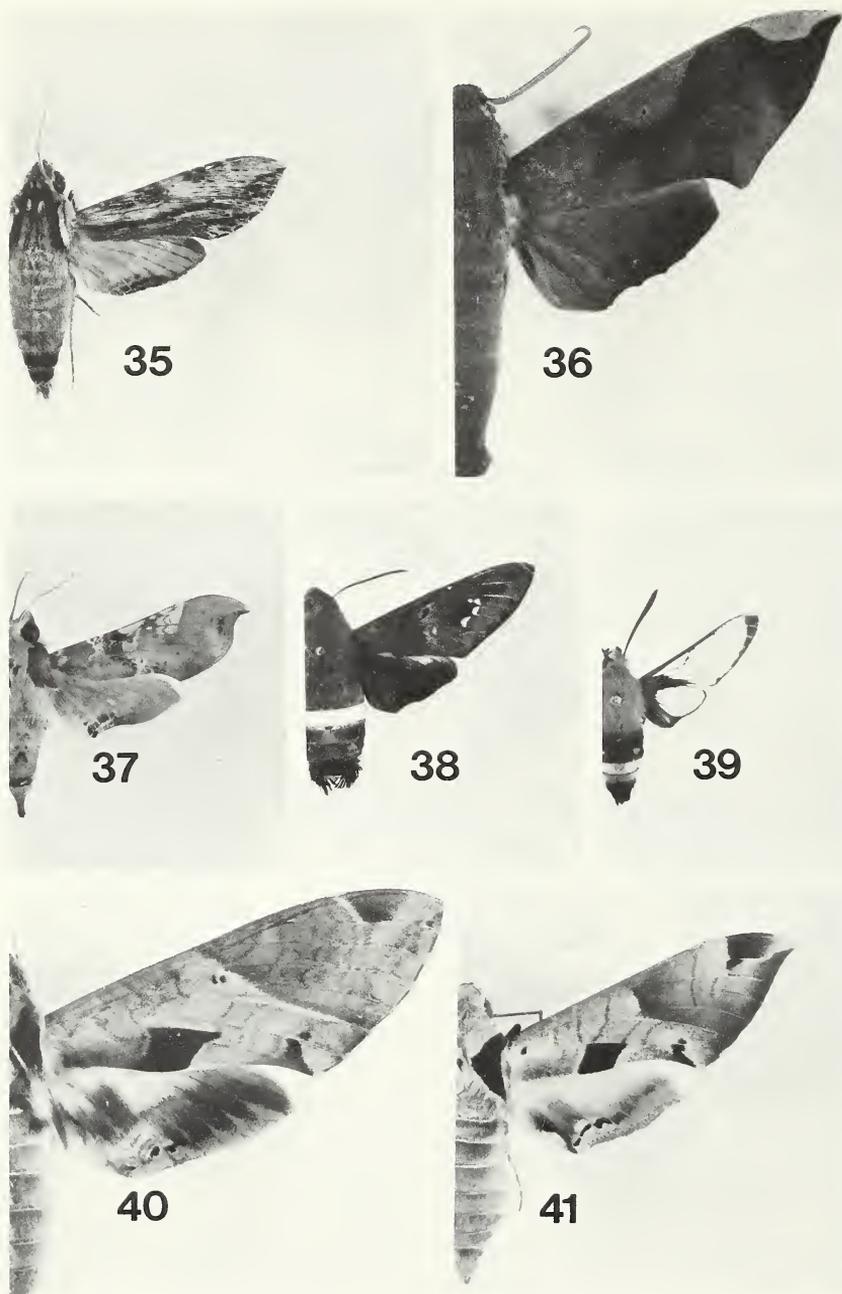


FIGS. 21-26. 21, *Agrius cingulatus*. 22, *Manduca sexta*. 23, *Manduca quinque-maculata*. 24, *Manduca rustica*. 25, *Sphinx xanthus*. 26, *Sphinx perelegans*.



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



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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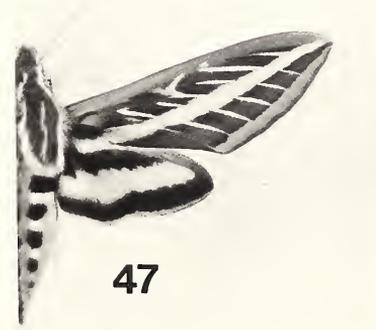
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FIGS. 42-47. 42, *Eumorpha vitis*. 43, *Eumorpha fasciata*. 44, *Euproserpinus phaeon*. 45, *Xylophanes tersa*. 46, *Xylophanes pluto*. 47, *Hyles lineata*.

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), *Eumorphia 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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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*, Heliiothinae.

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* ($n \cong 400$ 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 tunneled 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.

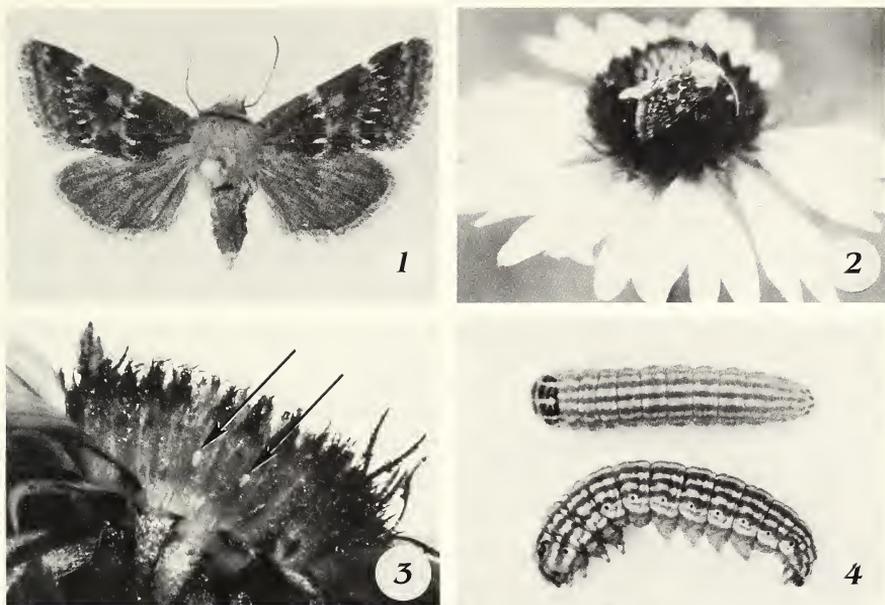
Larvae burrowed into the soil to pupate. Pupae removed from sandy soil in the laboratory had bound soil particles together with silk to a distance of approximately 5 mm in all directions to form a weak pupation chamber ($n = 16$). This species appears to be univoltine.

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, dis-

tinguishes *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* Fougereux, 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 *zelicaton* 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 zelicaton 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 *zelicaton* and a laboratory strain selected for nondiapause, Sims (1979) demonstrated that univoltine *zelicaton* 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 *zelicaton* in northern California evolved independently of orange-feeding *zelicaton* in southern California, or had been introduced inadvertently from the south. *Papilio zelicaton* 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 *zelicaton* 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 $600\ \mu\text{l}$ of glass-distilled water with a Teflon-coated tissue grinder. Homogenate was absorbed onto $2 \times 9\ \text{mm}$ 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	<i>Angelica arguta</i> , <i>Conium</i>	Great Basin, grassland, farmland, sloughs
Washington	Nevada Co.	1220	1	<i>Lomatium</i>	Sierran W slope, serpentine
Hemet	Riverside Co.	487	>1	<i>Citrus</i>	S. California desert, orchards
Orland	Butte Co.	67	>1	<i>Citrus</i>	Central Valley orchards
Butts Canyon	Napa Co.	457	1	<i>Lomatium</i>	North Coast Range, serpentine
Suisun	Solano Co.	9	>1	<i>Foeniculum vulgare</i> , rarely <i>Cicutia</i>	Central Valley levees, disturbed areas, near freshwater and tidal marshes
Blue Ridge, +Gates Canyon	Solano Co.	60-762	>1	<i>Foeniculum vulgare</i>	Vaca Hills, canyon, riparian
Rancho Cordova	Sacramento Co.	9	>1	<i>F. vulgare</i> , rarely <i>Conium</i>	Central Valley, riparian forests and gravel beds
Castle Peak	Nevada Co.	2743	1	<i>Cymopterus</i> , <i>Umbelliferae</i> spp.	Sierran, alpine
Auburn	Placer Co.	366	1-→1	<i>Foeniculum vulgare</i> , <i>Umbelliferae</i> 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	α GPD	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	HBDDH	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 (≥ 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 6. I-value matrix using only the three polymorphic ($\bar{I} = 0.867 \pm 0.100$) loci.

	Wash- ington	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 *zelicæon* populations are conspecific, the weighted-average G-tests show that *zelicæon* 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.

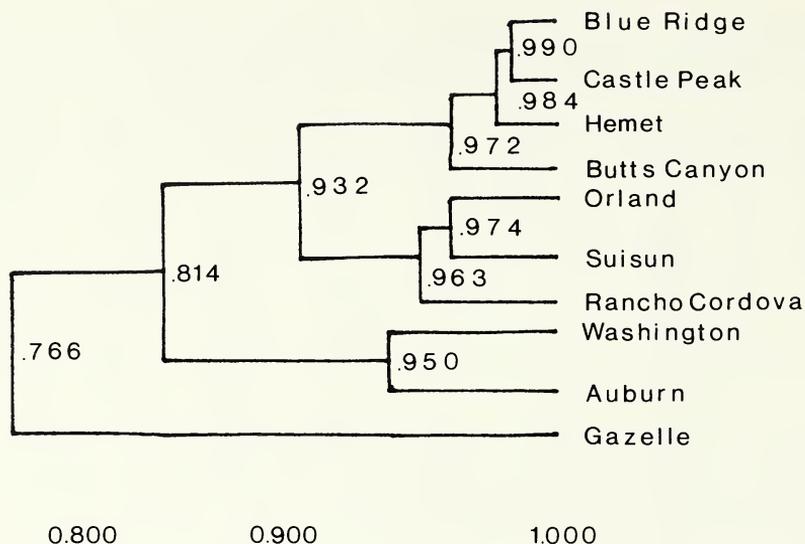
The germinal issue is to what degree populations are reproductively isolated by host-plant selection and physical distance. Certainly, the breeding trials and high I-values suggest that all *zelicæon* populations are potentially intercompatible. However, voltinism may be a genetically heritable trait that divides *zelicæon* into low- and high-elevation ecotypes (Clarke & Sheppard 1970).

Our data support Sims's (1983) contention that *zelicæon* 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 *zelicæon* 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 $n \geq 14$.

Genotype	(Electromorph-electromorph)	Populations					
		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



I-VALUE

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 differ-

entiation 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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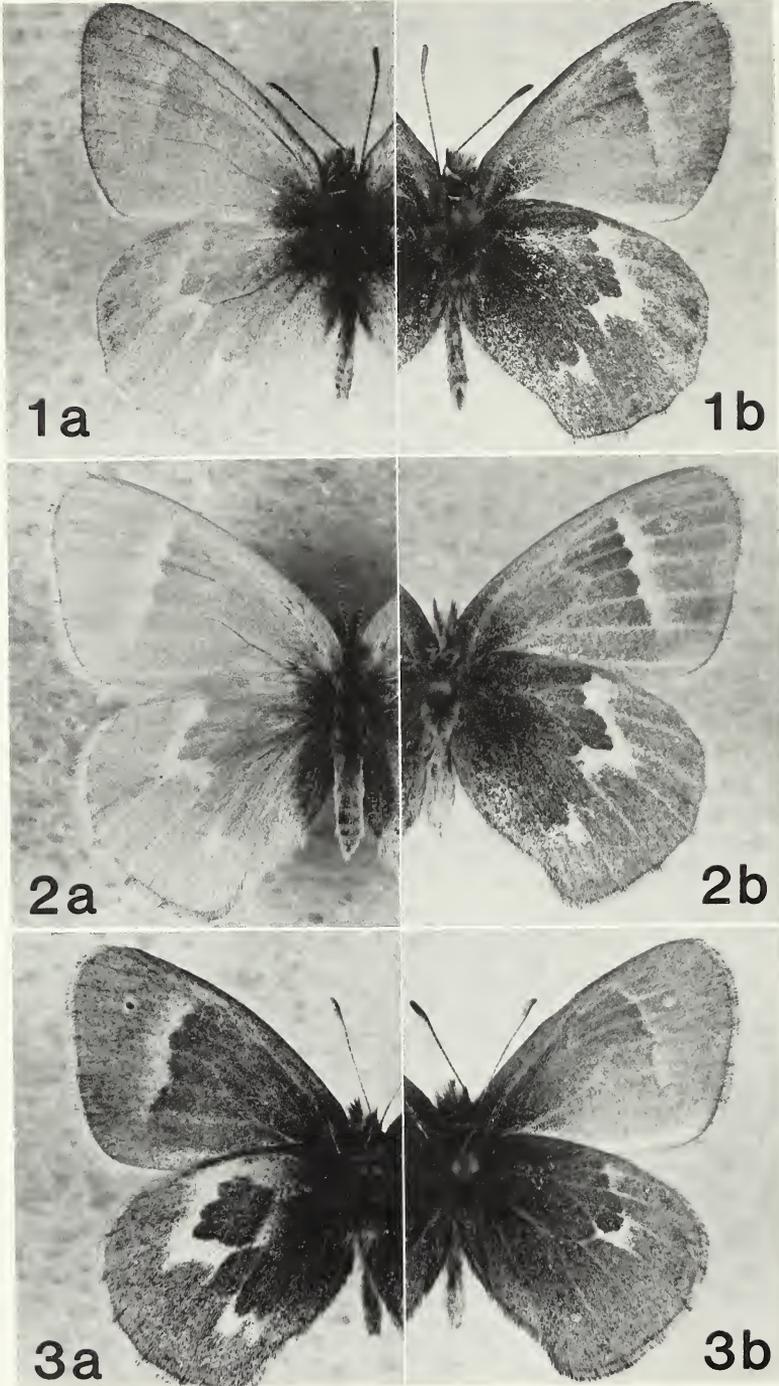
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ABSTRACT. *Coenonympha tullia yontocket* is described from a single known population confined to the coastal sand dunes north of Crescent City, Del Norte County, California. It is most similar in phenotype to *C. tullia eunomia* Dornfield, but may 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 genitally 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.



***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-

←
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.

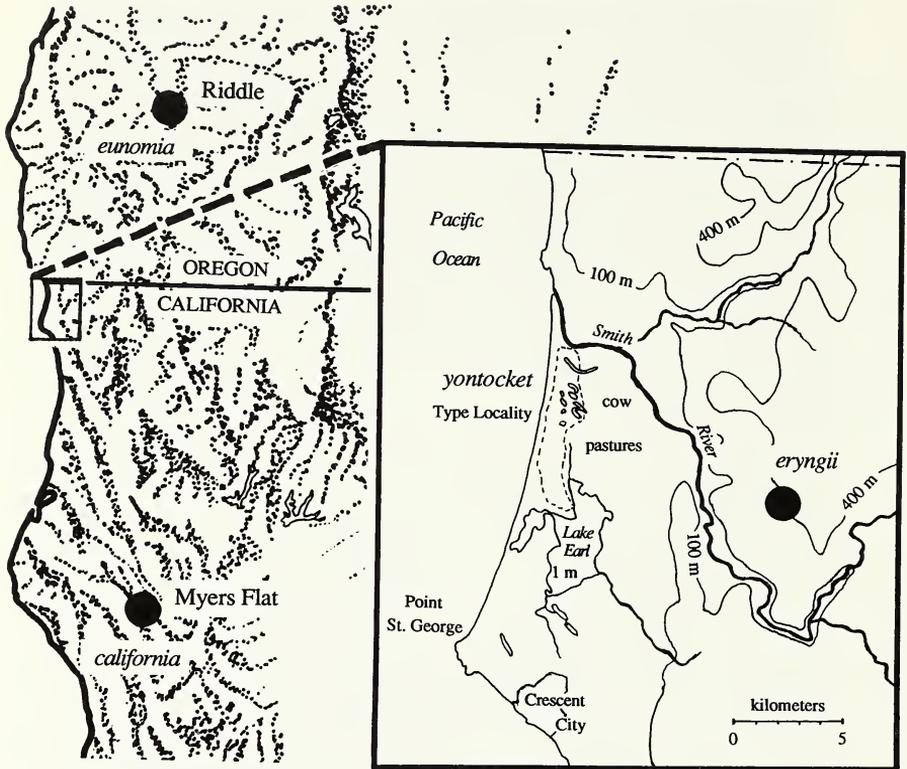


FIG. 4. Map showing localities sampled in northwestern California and southwestern Oregon. Note the close proximity of the *eryngii* population to the type locality of *yontocket* (inset). Neither subspecies occurs in the intervening cow pastures.

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. californica* 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*, *californica*, and *eunomia* are members of a single polytypic species (Porter & Geiger 1988).

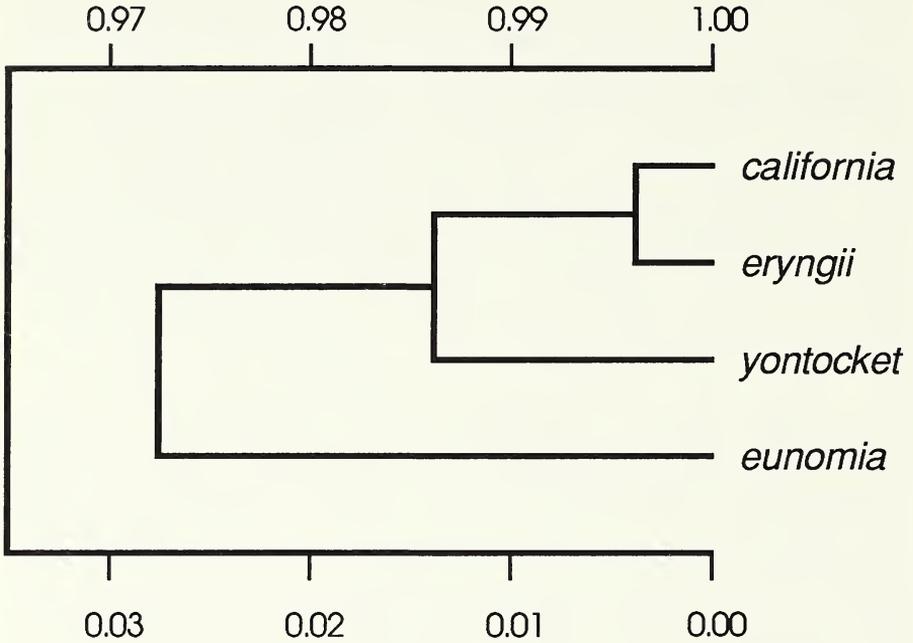
MATERIALS AND METHODS

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), phosphoglucosmutase (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 *californica* 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 &

Nei's (1978) unbiased genetic identity



Nei's (1978) unbiased genetic distance

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			Locus and allele	Taxon		
	<i>california</i> ¹	<i>eryngii</i> ²	<i>yontocket</i> ³		<i>california</i> ¹	<i>eryngii</i> ²	<i>yontocket</i> ³
AK-1				MDH-1			
76	0.056			91	0.028	0.014	
86			0.023	93	0.028		
90	0.361	0.275	0.500	100	0.861	0.986	0.932
100	0.556	0.675	0.432	105	0.028		
102	0.028			110	0.056		0.068
110		0.050	0.045	MDH-2			
ALDO				96	0.028		
100	1.000	1.000	1.000	100	0.972	0.917	0.932
FUM				105		0.069	0.054
100	1.000	1.000	1.000	110		0.014	0.014
GAPDH				PGI			
100	1.000	1.000	1.000	81			0.014
GOT-1				88	0.028		0.014
89	0.028	0.014		94		0.028	
91	0.194	0.111	0.135	97	0.083		
94			0.041	100	0.306	0.333	0.284
100	0.778	0.806	0.730	103	0.056	0.028	
102		0.056		107	0.306	0.389	0.662
108		0.014	0.054	105		0.042	
110			0.041	111	0.028	0.069	
GOT-2				114	0.194	0.056	0.027
100	0.944	0.944	0.973	117		0.014	
112	0.056	0.056	0.027	121		0.042	
α-GPDH				PGM			
75	0.028			90		0.014	
90		0.042		94	0.028	0.042	
96		0.014		97		0.028	0.027
100	0.972	0.931	1.000	100	0.361	0.486	0.662
110		0.014		106	0.528	0.389	0.311
IDH-1				110	0.083	0.028	
90	0.028	0.014		112		0.014	
92	0.028	0.028		SOD-1			
100	0.417	0.583	0.730	89	0.028		
103	0.194	0.208	0.108	100	0.944	1.000	1.000
106	0.306	0.125	0.162	120	0.028		
111	0.028	0.042					

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}
<i>california</i>	3.2 (0.5)	84.6	0.303 (0.090)	0.283 (0.080)
<i>eryngii</i>	3.5 (0.7)	69.2	0.240 (0.078)	0.246 (0.076)
<i>yontocket</i>	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			
	<i>california</i>	<i>eryngii</i>	<i>eunomia</i>	<i>yontocket</i>
<i>california</i>		0.997	0.976	0.982
<i>eryngii</i>	0.003		0.974	0.990
<i>eunomia</i>	0.030	0.035		0.979
<i>yontocket</i>	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 cellulolve (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 Gieson'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 over-staining 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 per-

oxide 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: *Pyr-rhopyge tzotzili*, *Mysoria wilsoni*, *Epargyreus windi*, *Epargyreus brodkorbi* (designated in 1969 paper for Museum of Zoology, Univ. of Michigan), *Astraptus louiseae*, *Astraptus gilberti*, *Polythrix mexicanus*, *Aethilla chiapa*, *Mimia chiapaensis*, *Wandia windi*, *Staphylus veytius*, *Staphylus zuritus*, *Quadrus francesius*, *Enosis matheri*, *Dalla ramirezi*, *Vettius argentus*, *Niconiades comitana*, *Anthoptus macalpinei*, *Cynea nigricola*, *Pher-aeus covadonga*, *Carystoides escalantei*, *Carystoides abrahami*, *Carystoides floresi*, *Carystoides mexicana*, *Atrytone mazai*, *Atrytone potosiensis*, *Mellana montezuma*, *Euphyes chamuli*, and *Tiryntia 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 disentangling 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 acrocneuma* (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)

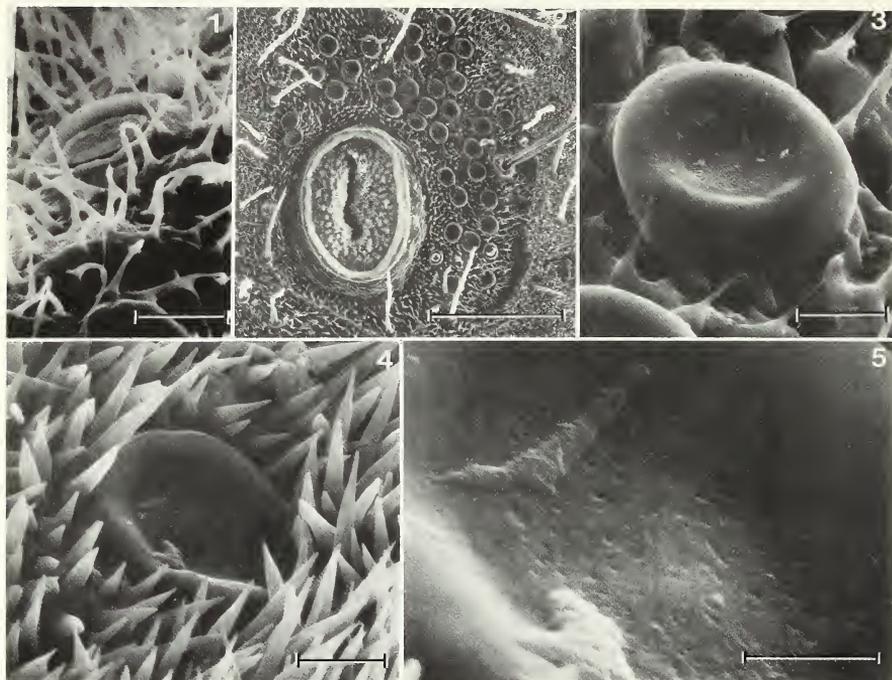
Additional key words: *Euselasia aurantiaca*, *E. mystica*, *Hades noctula*, ultrastructure.

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 μ m); 2, *Hades noctula*, cluster of PCO's around spiracle on A4, left side (scale bar = 200 μ m); 3, *H. noctula*, individual PCO (scale bar = 10 μ m); 4, *E. aurantiaca*, PCO in field of microtrichia, near spiracle on A4, left side (scale bar = 10 μ m); 5, *E. aurantiaca*, sieve plate of PCO showing pores (scale bar = 4 μ m).

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 μ m for *E. mystica* (on prothoracic shield), 27 μ m for *E. aurantiaca* (on A4), and 28 μ m 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 myrmecophilous; ant mutualisms are restricted to the subfamily Riodininae (Harvey, above; Harvey & Gilbert, above).

PCO's of Riodininae differ from those on larvae of the myrmecophilous *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) riordinines, 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 riordinids 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 Riordininae, 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 Riordinidae, 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.

Bridges'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 *Zemerus* 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 indispensable 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, Metar-*

belidae, 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 indispensable for the serious student.

MARC E. EPSTEIN, *Department of Entomology, National Museum of Natural History, NHB 127, Smithsonian Institution, Washington, D.C. 20560.*

Journal of the Lepidopterists' Society
43(3), 1989, 253–255

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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Journal of the Lepidopterists' Society
43(3), 1989, 255-257

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).

BOYCE A. DRUMMOND III, *Natural Perspectives*. P.O. Box 9061, Woodland Park, Colorado 80866.

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.

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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. 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.

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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.

Illustrations: Only half of symmetrical objects such as adults with wings spread should be illustrated, unless whole illustration is crucial. Photographs and drawings should be mounted on stiff, *white* backing, arranged in the desired format, allowing (with particular regard to lettering) for reduction to fit a *Journal* page. Illustrations larger than letter-size are not acceptable and should be reduced photographically to that size or smaller. The author's name and figure numbers as cited in the text should be printed on the *back* of each illustration. Figures, both line drawings and photographs, should be numbered consecutively in Arabic numerals; "plate" should not be employed. Figure legends must be typewritten, double-spaced, on a *separate sheet* (not attached to illustrations), headed EXPLANATION OF FIGURES, with a separate paragraph devoted to each page of illustrations. Color illustrations are encouraged; contact editor for submission requirements and cost.

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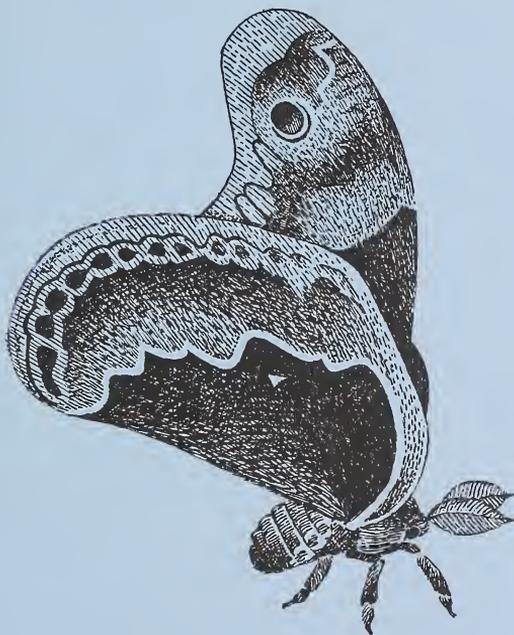
LEPIDOPTERISTS' SOCIETY

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20 December 1989

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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.

Membership in the Society is open to all persons interested in the study of Lepidoptera. All members receive the *Journal* and the *News of the Lepidopterists' Society*. Institutions may subscribe to the *Journal* but may not become members. Prospective members should send to the Treasurer full dues for the current year, together with their full name, address, and special lepidopterological interests. In alternate years a list of members of the Society is issued, with addresses and special interests. There are four numbers in each volume of the *Journal*, scheduled for February, May, August and November, and six numbers of the *News* each year.

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For back issues of the *Journal* and *News*, write the Publications Coordinator at the address below about availability and prices. Prices of *The Lepidopterists' Society commemorative volume 1945-1973* are \$12.00 (\$8.00 to members and subscribers); of *A catalogue/checklist of the butterflies of America north of Mexico*, clothbound, \$19.00 (\$12.00 to members and subscribers), paperbound, \$10.50 (\$7.00 to members and subscribers). Order from the Publications Coordinator, Ronald Leuschner, 1900 John St., Manhattan Beach, California 90266-2608, U.S.A. Make remittance payable to "The Lepidopterists' Society."

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Cover illustration: Male *Promethea* moth (life size), *Callosamia promethea* (Dru.), a subtly shaded member of the Saturniinae (Saturniidae). Submitted by Gerald P. Wykes, 2569 Reinhardt Road, Monroe, Michigan 48161.

JOURNAL OF THE LEPIDOPTERISTS' SOCIETY

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APOSEMATISM OF *URESIPHITA REVERSALIS* LARVAE (PYRALIDAE)

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ABSTRACT. A description is presented of the basic biology of *Uresiphita reversalis* and of the characteristics that indicate that the larvae are truly aposematic. Coloration, position and movements on the plants, feeding activity, and the importance of host plant alkaloids are described and discussed. Field observations and experiments with predators indicate that the larvae are distasteful.

Additional key words: *Cytisus monspessulanus*, quinolizidine alkaloids, predation, host plants, feeding stimulants.

Brightly colored insect larvae conspicuous to humans are often assumed to be aposematic, even in the absence of information about the supposed unpleasant attributes. Such is the case with caterpillars of the pyralid moth *Uresiphita reversalis* (Guenée), which feeds on several plant species in the tribe Genisteae (Papilionaceae), including *Lupinus* spp. and *Cytisus* (= *Genista*) spp. (Munroe 1976). While the adult moth is inconspicuous, with brown forewings and orange-brown hindwings, the larvae (after the first instar) are brightly colored and highly exposed on their host plants. The final (fifth) larval instar has obvious black and yellow markings. It is a multivoltine species, commonly found in coastal California but recorded widely in North America. In the San Francisco Bay area, larvae may be found at any time of year, although growth rate varies greatly, and by the end of winter they are rare. There are four to five generations per year, and populations build up in summer, reaching a peak in the early fall. Generation time varies from about five weeks in summer to as long as 25 weeks in winter. A general description may be found in Munroe (1976).

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This study is a characterization of the particular features of *U. reversalis* that may allow it to be labelled aposematic: description of coloration; description of field behavior and degree of exposure on the plant; feeding patterns on the plants in the field, and laboratory experiments on food selection behavior; chemical protection with host plant chemicals; and levels of predation as determined from field and laboratory experiments.

COLORATION

Eggs are laid in batches of up to 70, and the groups of young larvae, together with the damage they impart to leaves, make them conspicuous to humans, even though first instar individuals are green and somewhat cryptic. The later instars have a dark gold background color, and black head and legs. On the sides of every segment are several black tubercles, each with white patches and long white hairs. In addition there are bright yellow patches laterally on each segment (Fig. 1). The intersegmental membranes of individuals are somewhat transparent so that as ecdysis approaches, dull greenish bands alternate with the golden background. Thus, these larvae appear to have coloration patterns that are conspicuous and consistent with aposematism (Rothschild 1972).

POSITION ON THE HOST PLANTS

The positions of larvae on their host plants in the field is first determined by oviposition site. Egg masses found in the field are usually on the abaxial (lower) surface of leaves 2 to 8 cm from the tips of branches or branchlets. When larvae hatch, they usually feed first on the adaxial (upper) surface of the leaf on which the egg mass was laid. They produce copious amounts of silk, and as the leaf shrivels and curls, its edges are loosely bound together by the silk to make a shelter. Larvae remain together in the shelter, coming out only to feed. In the second instar, larvae begin to disperse, often forming two or more subgroups on adjacent branchlets. Contiguous leaflets or leaves are held together with silk to make shelters, from which foraging occurs. Caterpillars rest and molt in these shelters. By the third instar such shelters are no longer used and groups of larvae feed and rest in groups inside a very loose web of silk threads across branchlets.

On *Cytisus monspessulanus*, larvae of *U. reversalis* are almost invariably found on the upper third of the plants, usually on the distal ends of branches. For example, on 4 September 1985, 57 larval groups of different ages were observed on this plant species. All but five groups were within the distal twenty percent of the length of the branch. The remaining five were on young branchlets more proximally. Thus larvae

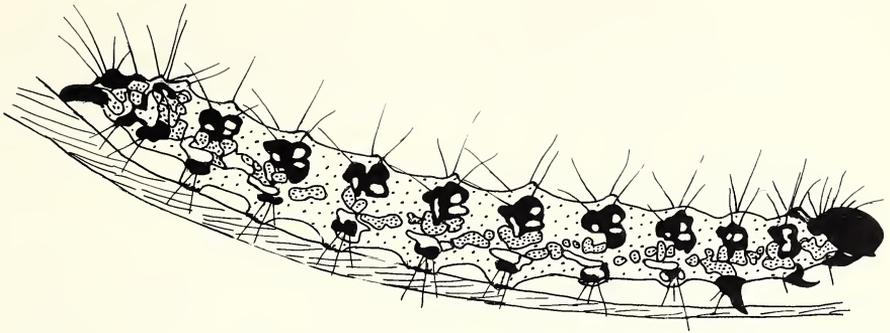


FIG. 1. Drawing of fifth instar larva of *Uresiphita reversalis* to indicate markings. Open areas, white; light dotted area, gold; densely dotted area, bright yellow; black as shown. Hairs are white. Length 25 mm.

rest and feed on the upper periphery of the plant, utilizing the plant's youngest foliage. Populations observed on *Lupinus* spp. appear to have similar relative positions.

There is a tendency for young larvae to move outwards, away from the main stems. Egg masses or groups of newly hatched larvae from a laboratory culture were placed about 15 cm from the tips of branches of *C. monspessulanus* in the field during the summer of 1988 and observed at intervals over the next three weeks. In all ten cases, the first damage was to leaves distal to the placing, and over the first five days all feeding was confined to this region. Only after such foliage was severely damaged was there more proximal movement. Thereafter larvae moved out to the tips of branchlets and across (usually up) to other branches. During observations throughout the day, most movement was associated with feeding, but dispersal bouts to new feeding sites occurred within groups at intervals—usually between 0600 and 1000 h and between 1500 and 2000 h (Fig. 2).

Previous work in our laboratory has shown that larvae are attracted to light and that, in choice tests, young leaves are strongly preferred to old ones (Montllor & Bernays unpubl.). These factors may have a role in determining where larvae are found on plants. An additional factor concerns temperature regulation: larvae will be more exposed to the sun when located on the top and the periphery of the plant, and may be assumed under these circumstances to have body temperatures higher than ambient. This provides an important potential advantage for thermoregulation. In the the San Francisco Bay area, this may be especially important because the daily temperature maxima rarely exceed 25°C (in the years 1984 through 1987, the mean number of days each year on which temperatures rose to this level was only 25). Maximum rates of growth and development of the larvae occur at over 30°C in the

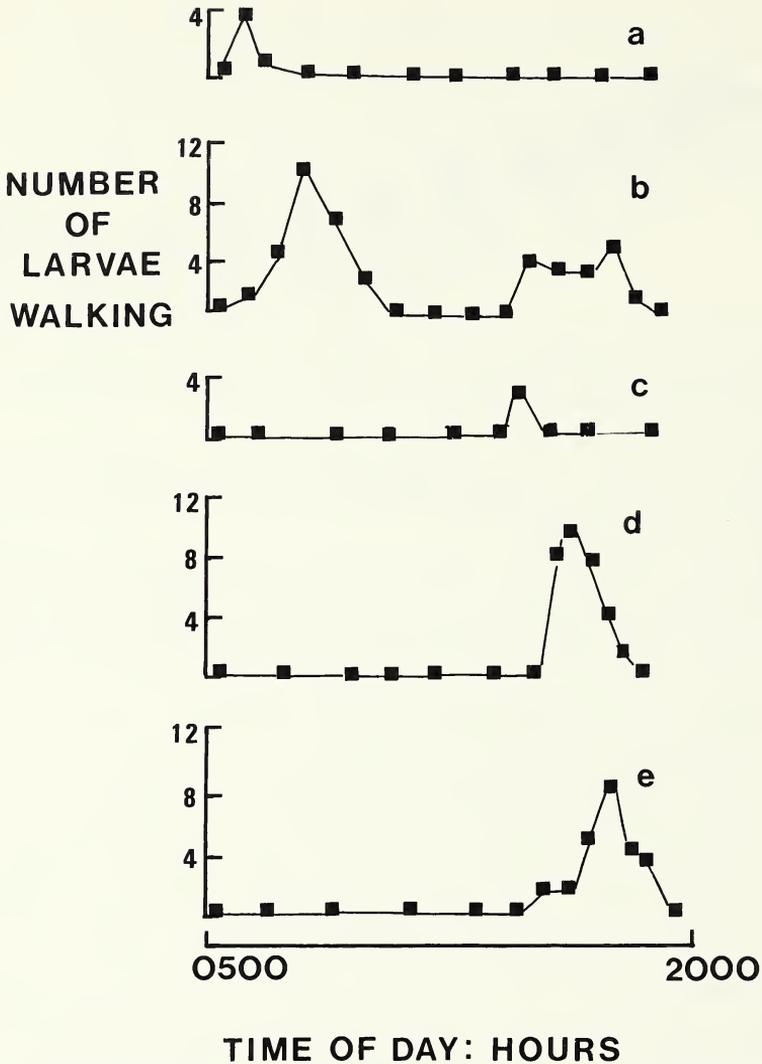


FIG. 2. Patterns of dispersal in five groups (a-e) of larvae (groups composed of 83% third instar and 17% second instar) on 22 June 1988, Berkeley, California.

laboratory (Montllor and Bernays unpubl.) as expected by comparison with other lepidopterans (e.g., Stamp & Bowers 1988).

Larvae are almost invariably found in groups. Initially, this reflects the fact that eggs are laid in masses on the plant. Of the egg masses found in the field during 1985-87, numbers of eggs varied from 23 to 70 (median 37, $n = 13$). Typically, groups of around 15-20 second and third instar larvae are found, while groups of fourth instars and fifth instars are smaller. It is not clear whether the larvae are actively gre-

garious, or whether the stimuli for movement and direction of movement cause similar displacements. In any case, the exposed positions in which larvae are found, their clumped distribution, and their low rates of movement are consistent with their being aposematic.

FEEDING

Host Plants

Survival and growth of larvae on a range of potential host plants (host records and related plants) in the San Francisco Bay area were tested by giving twenty individual larvae single species diets in small cages in the laboratory and examining survivorship and development rates. These experiments were run simultaneously at laboratory temperatures of 24–26°C and a 12:12 (L:D) cycle. Food was changed daily. There was no feeding and rapid mortality on *Medicago*, *Trifolium*, *Vicia*, and *Pickeringia*. There was limited feeding but no pupation on *Laburnum* and *Ulex*. However, larvae fed extensively on *Cytisus scoparius*, *C. striatus*, *Lupinus arboreus*, and *C. monspessulanus*. These data together with data on rearing from museum collections indicate that the main hosts of *U. reversalis* in California are species of *Lupinus*, with some specimens from *Cytisus*. These plants all contain quinolizidine alkaloids (Kinghorn & Balandrin 1984).

When given a choice in the laboratory of leaves and/or leaflets from *Cytisus monspessulanus* or *Lupinus arboreus*, presented in an alternating array in small cages over two hours, fifth instar larvae collected from either plant in the field significantly preferred the lupine ($n = 20$, Wilcoxon's Signed Rank Test, $P < 0.01$). The basis for host plant preference is not yet known, but is assumed to involve quinolizidine alkaloids, as a wide variety of these occur differentially in the hosts (Johnson et al. 1987, Johnson & Bentley 1988, Kinghorn & Balandrin 1984, Wink 1987); for example, in a single sample of *C. monspessulanus*, 27 different alkaloid structures were identified (Wink pers. comm.).

Individual fourth or fifth instar larvae presented with an alternating array of young trifoliates and more mature single leaflets (with similar areas) of *C. monspessulanus* in Petri dishes in two-hour laboratory tests preferred young leaves over old leaves ($n = 20$, Sign test, $P < 0.001$). The basis for this preference is also not known, but by analogy with other phytophagous insect species it can be expected that the tender young leaves, rich in nitrogen, provide a better diet. Young leaves are also particularly rich in quinolizidine alkaloids (Montllor unpubl.), consistent with the assumption of the importance of these compounds to larval preference.

LARVAE FEEDING: %

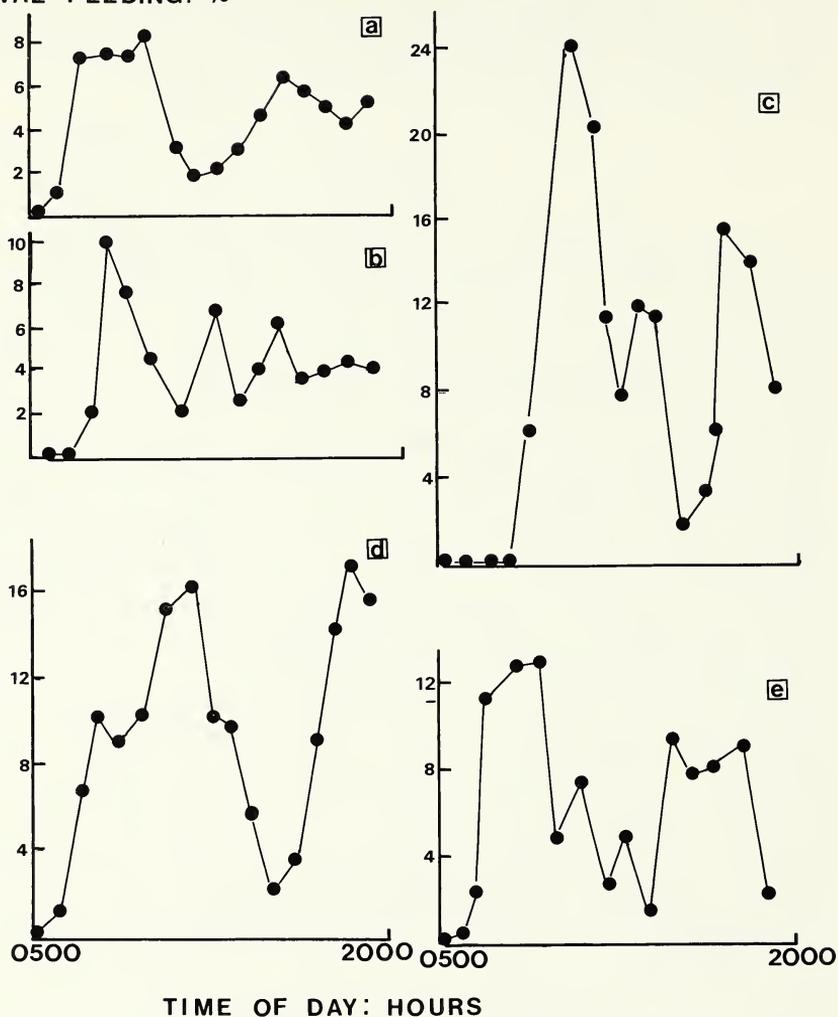


FIG. 3. Patterns of larval feeding throughout the daylight hours on five separate days during summer 1988, Berkeley. a, b = first instar; c, d = second instar and third instar; e = third instar and fourth instar.

Feeding Patterns in the Field

Field observations indicate that larvae of *U. reversalis* feed primarily in the day. In July 1988, five groups were observed from dawn until dusk on three separate days; in June five more groups were similarly observed on two days. The numbers of individuals feeding were monitored at intervals. At first light, young larvae began feeding within 30 minutes on four of the five occasions. On the fifth occasion, early

TABLE 1. Effects of sparteine and cytisine on the palatability of sucrose-impregnated glass fiber filters¹: + = trend but not significant, ++ = significantly preferred at $P < 0.05$, +++ = significantly preferred at $P < 0.01$. At each concentration $n = 14-19$.

	Concentration of alkaloid (% dry weight)				
	0.1	0.5	1.0	2.0	All concs pooled
Sparteine	+	+	+	+	++
Cytisine	+++	++	+++	+++	+++

¹ 5% dry weight of sucrose, larvae presented with a choice of alkaloid-treated (alkaloid plus sucrose) or control discs (sucrose only). Preferences tested using Wilcoxon's Signed Rank Test.

morning temperatures were similar (11–14°C and no direct sun), but the conditions were very foggy and the plants wet; feeding began only after the plant surface dried off at about 0900 h. Although there were morning peaks of feeding, there were no other obvious patterns relating to time, temperature, or sunshine (Fig. 3). Overall, it is clear that, as typical aposematic caterpillars, *U. reversalis* larvae feed actively throughout the day. This could be chemically significant; similar alkaloids are known to vary in concentration throughout the day in *Lupinus albus* (Wink & Witte 1984).

Host Plant Alkaloids

Two host plant alkaloids common to some species of *Cytisus* and *Lupinus*, sparteine and cytisine, were tested as potential phagostimulants for larvae of *U. reversalis*. Individual larvae from a laboratory culture were given a binary choice of glass fiber filters (GF/A) impregnated with sucrose (5% dry weight) and similar glass fiber filters with the sucrose plus sparteine or cytisine at one of several different concentrations. Experiments were at 25°C with the filters in Petri dishes. Amounts eaten were visually estimated after 24 h. The alkaloids were shown to be phagostimulatory (Table 1), but they were not equally effective as feeding stimulants, and it is conceivable that the actual profile of quinolizidine alkaloids influences acceptability.

The host plant alkaloids are bitter to humans and are also known to be poisonous to mammals, including livestock, causing vomiting, convulsions and death (Kinghorn & Balandrin 1984). These compounds are likely to have similar effects on birds. Actively feeding larvae, having a preference for foliage with the highest levels of alkaloids, will contain high doses of the toxins from the gut contents alone. In addition, larvae transfer ingested alkaloids to the cuticle, although pupae contain no detectable alkaloids (Montllor et al. in press). It seems likely that, in common with a number of other species of Lepidoptera feeding on alkaloidal plants, larvae gain protection from the ingested alkaloids. Other cases of protection from predation due to ingestion of host plant

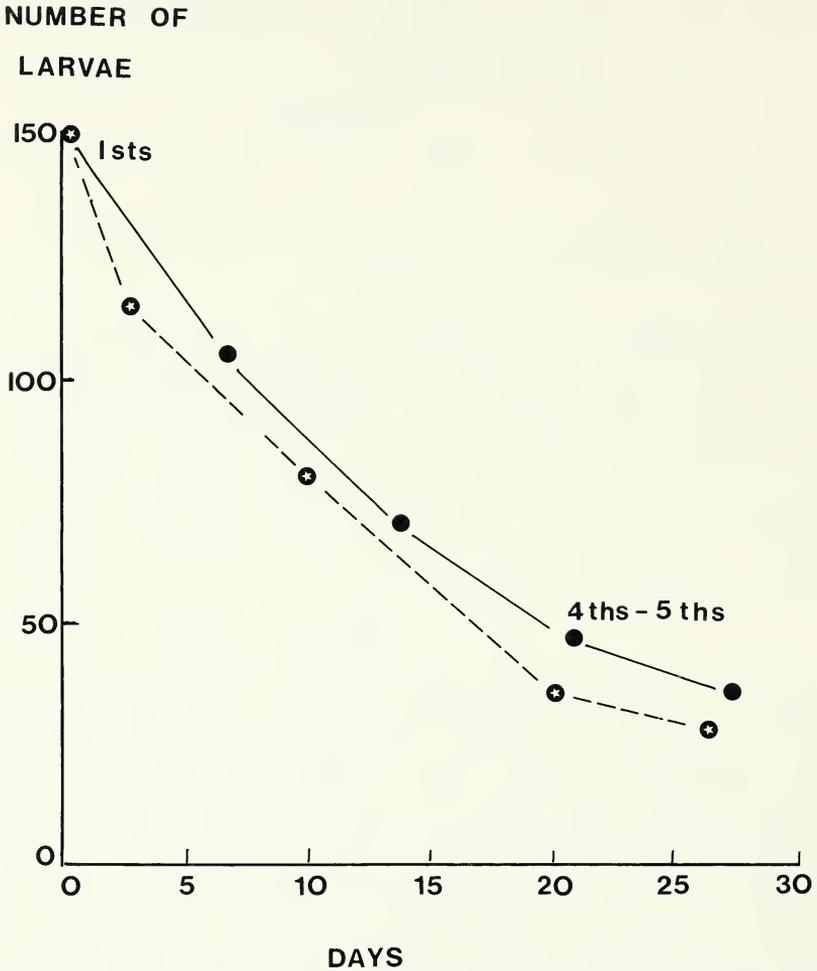


FIG. 4. Survivorship curves of two cohorts of 150 larvae from the time of hatching. Total number of larvae from 5 original egg masses per cohort were counted on each date. Observations were made during the period May-July 1988.

alkaloids involve mainly pyrrolizidine alkaloids (Rothschild 1972, Schneider 1987). This seems to be the first example of the use of quinolizidine alkaloids for protection by caterpillars.

PREDATION

Field Observation in Relation to Invertebrate Predators

In two separate field sites in Berkeley, five groups of newly hatched larvae were placed on appropriate branches of single *C. monspessu-*

NUMBER IN GROUP

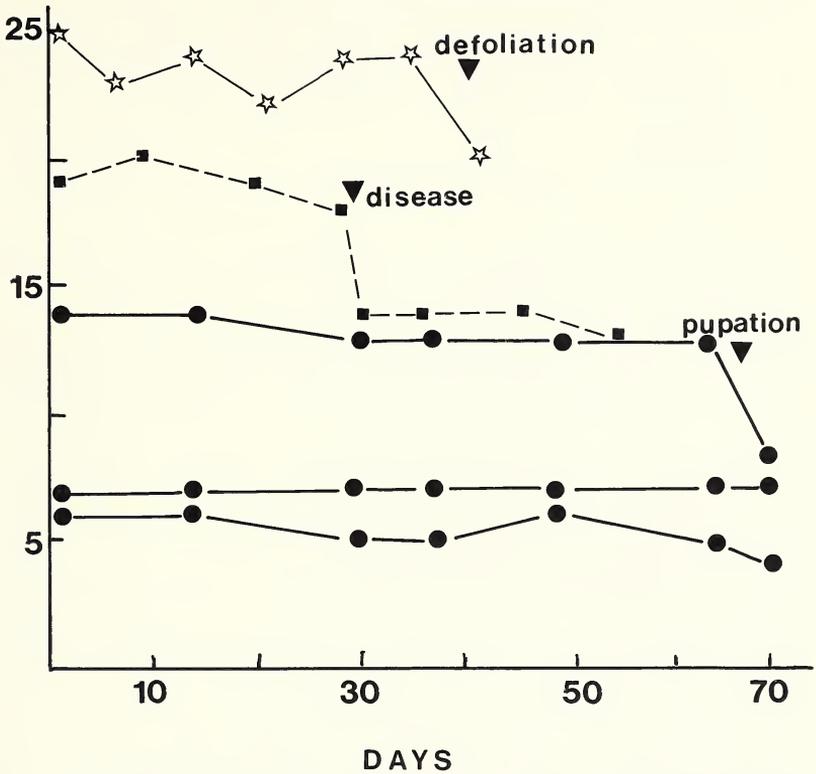


FIG. 5. Survivorship curves of five fifth instar larval groups. Declines in numbers marked with an arrow could be attributed with certainty to defoliation of host plant, virus disease, and pupation as indicated. The otherwise constant numbers imply a lack of predation. Observations were made during the period October–December 1986.

lanus plants in summer 1988. At each site, continuous observations were made from dawn to dusk on activities of the larvae, and any predation attempts on them noted. Similar observations were made on two subsequent occasions during the second and third instars at one site, and on four occasions (during second, fourth, and fifth instars) at the other site. Total counts were made at both sites on four dates during development. Each group had about 30 larvae at the start, and mortality of early instars was high (Fig. 4). This was in marked contrast to the data for fifth instars that was noted in an earlier year (Fig. 5). During the periods of observation, Hemiptera (Anthocoridae) fed on first and second instar caterpillars, and Hymenoptera (Vespididae) removed middle instars. In one of these experiments, 80 larvae (53%) were lost in 17 days, giving an average daily loss of 4.4 larvae. About 40% of the loss

TABLE 2. Numbers of invertebrate predators relevant for *U. reversalis* collected by beating bushes of the host plant, *Cytisus monspessulanus*.

Sample date	Numbers per 60 bushes (6 sites)			
	Salticidae	Thomisidae	Heteroptera	Chrysopidae
18 July 1988	29	13	5	4
27 July 1988	22	6	3	0
18 August 1988	17	4	4	0

could be accounted for by observed predation levels. In the second experiment, 15% of loss could be similarly accounted for.

During the period of field experimentation, censuses of potential predators were made by beating bushes, collecting the arthropods, and testing the predators among them with first and second instar caterpillars of *U. reversalis* as prey. Ants and coccinellid beetles did not attack larvae that they were confined with in small containers in the lab, while neuropterans (*Chrysopa*) and heteropterans (Anthoridae, Nabidae) did. Spiders in the families Salticidae and Thomisidae were deemed relevant predators from daily field observations, and both of these attacked larvae in the lab in no-choice tests. The census data indicate that bushes of *Cytisus* averaged 0.4 to 0.8 relevant predators per bush (Table 2). To test whether invertebrate predation is a significant cause of mortality, we conducted field experiments in which some groups of larvae were protected from predation.

Survivorship of *U. reversalis* larvae placed on branches of *C. monspessulanus*, with or without net bags over the branches, was compared. In April–May 1988 approximately 30 neonate larvae were placed on each of three plants at each of five sites in the San Francisco Bay area. Each plant had a protected and an unprotected group. A similar experiment was done in June–July 1988 on a total of 21 plants at six sites. In all cases, survivorship was considerably higher on bagged branches (Table 3), and although there may be other unknown mortality factors, it is likely that the exclusion of predators was the primary reason for the difference. Fifth instar larvae in five natural groups at three sites in Berkeley were monitored in fall and winter 1986. These represented the last generation of the year and persisted as fifth instars over 5 to 12 weeks because of low temperatures. In all cases the population declines could be attributed to causes other than predation (Fig. 5), in spite of the exposed positions of the larvae and the abundance of birds. Rejection behavior of birds was observed. On two occasions during four all-day observations, a bird was observed to pick up a caterpillar, subsequently drop it, and proceed to rub its beak on the branches of a tree. Aposematism is most commonly associated with protection from

TABLE 3. Survivorship of larvae in the field with or without protection from predators. In all four comparisons, survival was significantly greater in the protected groups (Chi Squared Test, $P < 0.01$).

	Number of groups (total number of larvae)	Mean % surviving (\pm SD)	
		1-2 weeks	3 weeks
Spring 1988			
Protected	15 (482)	76 (15)	36 (15)
Unprotected	15 (499)	39 (4)	9 (8)
Summer 1988			
Protected	21 (530)	61 (18)	37 (23)
Unprotected	21 (503)	38 (17)	18 (14)

predation by birds, and our limited field observations indicate that birds do not prey on larvae of *U. reversalis*.

Predation Experiments

The possible defense against invertebrate predators was tested by comparing the relative acceptability of *U. reversalis* to two invertebrate predators in a situation where food deprivation was clearly not driving indiscriminate predation. In the first case, the vespid wasp *Mischocyttarus flavitarsus* (Saussure), a generalist predator, was employed (Bernays 1988). Naturally hunting wasps from nests in a large greenhouse were allowed to forage in open arenas (1m \times 1m \times 1m) in which caterpillars of *U. reversalis* feeding on *C. monspessulanus* were available at the same time as *Trichoplusia ni* (Hübner) (Noctuidae), *Estigmene acrea* (Drury) (Arctiidae) or *Heliothis virescens* (F.) (Noctuidae), each feeding on its own host plants in close proximity. In each of these three experiments, laboratory-reared larvae of *U. reversalis* and the alternate species were presented at similar sizes and densities. In each case the alternative prey were always attacked early in the experiments.

TABLE 4. Numbers of caterpillars taken by the wasp *Mischocyttarus flavitarsus* (Vespidae) during choice trials. Experiments were terminated after approximately half of either prey species was removed. In each of the three experiments the differences in acceptability are significantly different (Chi Squared Test, $P < 0.001$).

	Numbers of size-matched caterpillars	
	Nos. at start	% taken
1. <i>Estigmene acrea</i> (Arctiidae)	20	50
<i>Uresiphita reversalis</i>	20	0
2. <i>Heliothis zea</i> (Noctuidae)	25	52
<i>Uresiphita reversalis</i>	25	0
3. <i>Trichoplusia ni</i> (Noctuidae)	22	59
<i>Uresiphita reversalis</i>	30	0

Experiments were stopped when approximately half of one species was taken. In no case were any *U. reversalis* larvae taken before half of the alternate species was removed (Table 4).

Experiments on predation by Argentine ants, *Iridomyrmex humilis* (Mayr) (Formicidae: Dolichoderinae), also showed that *U. reversalis* is extremely unacceptable relative to many other species of caterpillars (Bernays & Cornelius 1989).

CONCLUSIONS

Uresiphita reversalis larvae have all the characteristics of aposematic caterpillars. They are brightly colored, relatively inactive, found in groups, and they feed actively during the day. Their favored food is rich in toxic quinolizidine alkaloids, which are phagostimulants. Alkaloids that are not excreted after ingestion are deposited in the cuticle. Larvae are apparently distasteful to at least one avian species, wasps and ants.

Predation data are limited, but on the basis of the observations presented here, it appears that in spite of being chemically defended, *U. reversalis* larvae do suffer extensive predation. Losses to invertebrate predators apparently account for a significant proportion of the mortality in the early instars. Arthropods with piercing and sucking attacks seem to be the dominant predators, perhaps circumventing any protection provided by the alkaloidal cuticle. The early larval instars are much more vulnerable to predation than the last larval instar. Thus, chemically defended aposematic species may nonetheless suffer high mortality from predation.

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BIOGEOGRAPHICAL AFFINITIES OF THE BUTTERFLIES
OF THE SOUTHWEST CARIBBEAN ISLANDS,
SAN ANDRÉS AND PROVIDENCIA

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ABSTRACT. San Andrés and Providencia are small islands east of Nicaragua. N. D. Riley, in his *Field Guide to the Butterflies of the West Indies* (1975), included these islands in his biogeographical definition of the West Indies. Subspecific analyses of butterfly collections made in August 1986, however, show that, of 19 species collected, the 10 that have one or more subspecies in the Antilles are all represented on San Andrés and Providencia by the subspecies occurring on the mainland. Thus, we conclude that this area of the SW Caribbean shows no affinity with Antillean populations, but is clearly an extension of the neighboring populations on the mainland of Central America. Two species are newly recorded for any Caribbean island: *Cybaeus odilia* (Hesperiidae) on San Andrés and *Chlorostymon telega* (Lycaenidae) on Providencia. Based on present, but probably incomplete, sampling, it appears that San Andrés and Providencia maintain discrepant butterfly faunas. These islands are equidistant from a large donor source of immigrants, but differ markedly in geological origin and present vegetation.

Additional key words: island biogeography, subspeciation, dispersal, Nicaragua.

The "West Indies" constitute an area of particular biogeographical interest because they possess components of both the Nearctic (North American) and Neotropical (Central and South American) faunas distributed across a chain of islands, varying greatly in size, topography, and geological history. As a faunistic zone, this region is generally considered to include the Bahamian islands to the north, the Greater Antillean islands of Cuba, Hispaniola, Jamaica (with the small satellite Cayman Islands), and Puerto Rico, and the Lesser Antillean chain from the Virgin Islands east of Puerto Rico south to Grenada, but excluding Trinidad and Tobago, which are insular faunistic extensions of the adjacent continental mainland.

Riley (1975), in the only general account of the butterflies of this area, extended the perimeter to the south and west to include three islands: Swan (in line with the Islas de la Bahía chain off Honduras), Old Providence (Providencia), and St. Andrew (San Andrés). This report is concerned with the biogeographic status of the butterflies of the last

two islands and their supposed affinity with the West Indian (or Antillean) faunistic zone.

San Andrés and Providencia are small isolated islands in the SW Caribbean Sea, situated, respectively, ca. 197 km and 235 km due east of the Central American mainland (Nicaragua) (Fig. 1). Providencia lies ca. 87 km NNE of San Andrés. The latter is situated ca. 365 km due north of the coast of Panamá, while Providencia is ca. 626 km from Jamaica, the nearest neighbor among the Antillean Islands. Despite their proximity, and their relative nearness to the continental landmass, San Andrés and Providencia are thought to have upheaved independently in the early Tertiary and never to have had a land bridge either between them, or between either island and the mainland (Parsons 1956).

The contours of Providencia and San Andrés, with indication of populated areas (and, for Providencia, the altitude of the central peaks) are illustrated in Fig. 1. These maps are based on those in Parsons (1956) and on a Colombian Government publication: "Mapa de la Intendencia Especial de San Andrés y Providencia" (1981). Parsons (1956) has provided a valuable and interesting account of the geology, history, and ecological consequences of colonization, and of the social and cultural geography of San Andrés and Providencia. The following summary is abstracted from that work, with some details obtained from Emmel's (1975) account.

Neither island has a known history of pre-Columbian settlement. Following initial colonization in the early 17th century, much of the islands' original forests were removed for ship building and repair, notably during the 18th century. The two islands differ strikingly in terrain and in their present pattern of vegetation. Providencia is steeply mountainous with igneous peaks (to 360 m) in the interior of the island. Originally, Providencia was densely forested (Parsons 1956); today, the island supports lowland agriculture, the higher areas being dominated by grass and cattle grazing, extending much of the way to the peaks where, in a few areas, the vegetation is described by Proctor (in Parsons 1956) as showing "distinctly Central American" affinities. San Andrés is a slender N-S oriented block of limestone (thought to overlie an igneous base) with a single cliff-bound hill rising to ca. 100 m. Destruction of original forest occurred as on Providencia; a period of cotton planting followed, and in the 1850's the island was thickly planted with coconut palms, a virtual monoculture that dominates much of the island today, although the ancient palm stands are untended and of little economic importance. Abandoned fields and paths through these plantations provide the most ready access to the interior of San Andrés.

Commercial development, primarily for the tourist industry, was

virtually non-existent on either island when Parsons wrote, but was more extensive when Emmel visited the islands (in 1967-68) and clearly continues. On San Andrés (Fig. 1) development is centered primarily around the town. On Providencia, however, other than expansion of the main settlement and some development along the perimeter road, little change has occurred since Parsons' visit in 1953, and little encroachment into the interior has taken place.

BUTTERFLY FAUNAS OF THE ISLANDS

The only published records of the butterflies of these small islands are those of Emmel (1975) who, with coworkers, collected on San Andrés during five visits, and on Providencia during two brief visits, in 1967 and 1968. Work on the former was in February-March and June-July, while Providencia was sampled on one day in June, and two days in July, 1968. Emmel documented 17 species from the two islands. Although of considerable value, these records generally did not include subspecific determinations, and thus afford little information on the affinities of these island faunas to continental America and the Antilles, where subspeciation has been a conspicuous factor (Riley 1975).

The present account is based on an intensive collecting visit by one of us (DSS) to these two islands between 7-23 August 1986, apportioned between San Andrés (9 collecting days) and Providencia (5 collecting days). Several species recorded by Emmel were not found in 1986 and, conversely, a number of species were newly recorded (Table 1). The extent of the discrepancy is noteworthy, and contributory factors may include differing habitat sampling (even on small islands), seasonal fluctuation in adult populations, presence or absence of occasional vagrant species, and recent extinction and/or colonization.

All species collected were determined where appropriate to subspecies, primarily to establish the southwestern limits of the Antillean faunal area and to evaluate the appropriateness of Riley's SW-directed extension of this zone. Taxonomic determination of material collected in 1986 was facilitated by comparison with often extensive series in the Allyn Museum of Entomology, Sarasota, Florida, the Hope Entomological Collections, University of Oxford, and the British Museum (Natural History), London. The sequence of taxa follows that of Miller and Brown (1981). All specimens collected in 1986 are deposited in the Hope Entomological Collections, the University Museum, Oxford, England.

The following list of species includes both Emmel's published records and our records from August 1986; those species recorded by Emmel but not seen during this study are enclosed in parentheses. A compar-

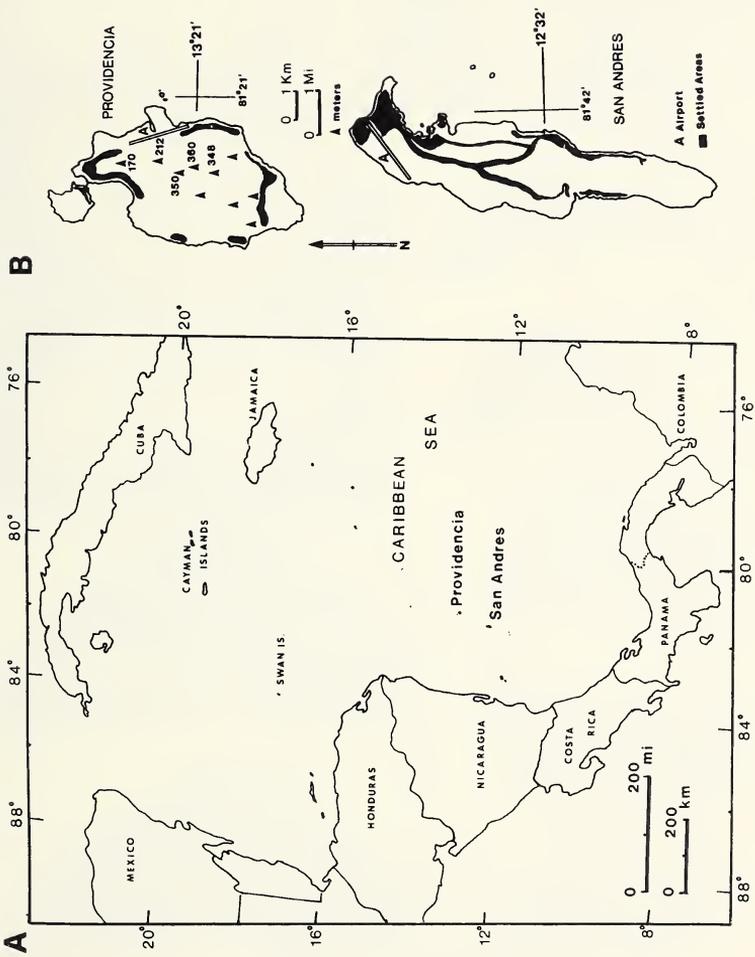


FIG. 1. A. Position of San Andrés and Providencia Islands, in the SW Caribbean Sea. B. Outline maps of Providencia and San Andrés, indicating the main "settled areas" and (Providencia) the principal road around each island is not indicated.

TABLE 1. Butterflies collected in 1986 (this study) and in 1967-68 (Emmel 1975).

San Andrés	Providencia
Hesperiidae	Hesperiidae
++ <i>Urbanus d. dorantes</i> **	++ <i>Urbanus d. dorantes</i> **
++ <i>Urbanus p. proteus</i>	++ <i>Urbanus p. proteus</i> **
++ <i>Cymaenes odilia trebius</i> **	(<i>Hylephila phyleus</i>)
-- <i>Hylephila phyleus</i>	
-- <i>Panoquina sylvicola</i> **	
Papilionidae	
++ <i>Battus p. polydamas</i> **	
Pieridae	Pieridae
++ <i>Ascia m. monuste</i> **	<i>Phoebis sennae</i>
<i>Phoebis sennae</i>	++ <i>P. p. philea</i> **
++ <i>P. p. philea</i> **	-- <i>Abaeis nicippe</i> **
++ <i>Eurema venusta limbica</i> **	(<i>Phoebis statira</i>)
(<i>Eurema daira</i>)	
(<i>E. lisa</i>)	
Lycaenidae	Lycaenidae
++ <i>Leptotes cassius striata</i>	<i>Chlorostrymon telea</i> **
	++ <i>Leptotes cassius striata</i>
	++ <i>Hemiargus hanno zachaeina</i> **
Heliconiidae	Heliconiidae
++ <i>Agraulis v. vanillae</i>	++ <i>Agraulis v. vanillae</i>
(<i>Dryas iulia</i>)	(<i>Dryas iulia</i>)
Nymphalidae	Nymphalidae
-- <i>Vanessa cardui</i> **	++ <i>Anartia jatrophae luteipicta</i> **
-- <i>Junonia genoveva</i> **	(<i>Historis odius</i>)
++ <i>Anartia jatrophae luteipicta</i>	
<i>Historis odius</i>	
(<i>Junonia evarete</i>)	
(<i>Siproeta stelenes</i>)	
Danaidae	Danaidae
(<i>Danaus plexippus</i>)	(<i>Danaus plexippus</i>)

++ Subspecies shared with Central America.

-- Species invariant in the area.

** Newly recorded in 1986.

() Recorded by Emmel (1975) but not seen in 1986.

ative summary of species recorded from both islands is given in Table 1.

Hesperiidae

Urbanus p. proteus Linnaeus (n = 12). Emmel recorded this skipper as common on San Andrés, as it was during the 1986 survey, when a single specimen was also recorded from Providencia. A recent revision of the *proteus* group (Steinhauser 1981) stresses the external similarity of a number of related species occurring in Central and South America, reliably separated only by genitalic characters. All specimens collected in 1986 were dissected and confirmed as *U. p. proteus*: the generally large size of the forewing maculations shows the San Andrés and Providencia populations to represent the Continental

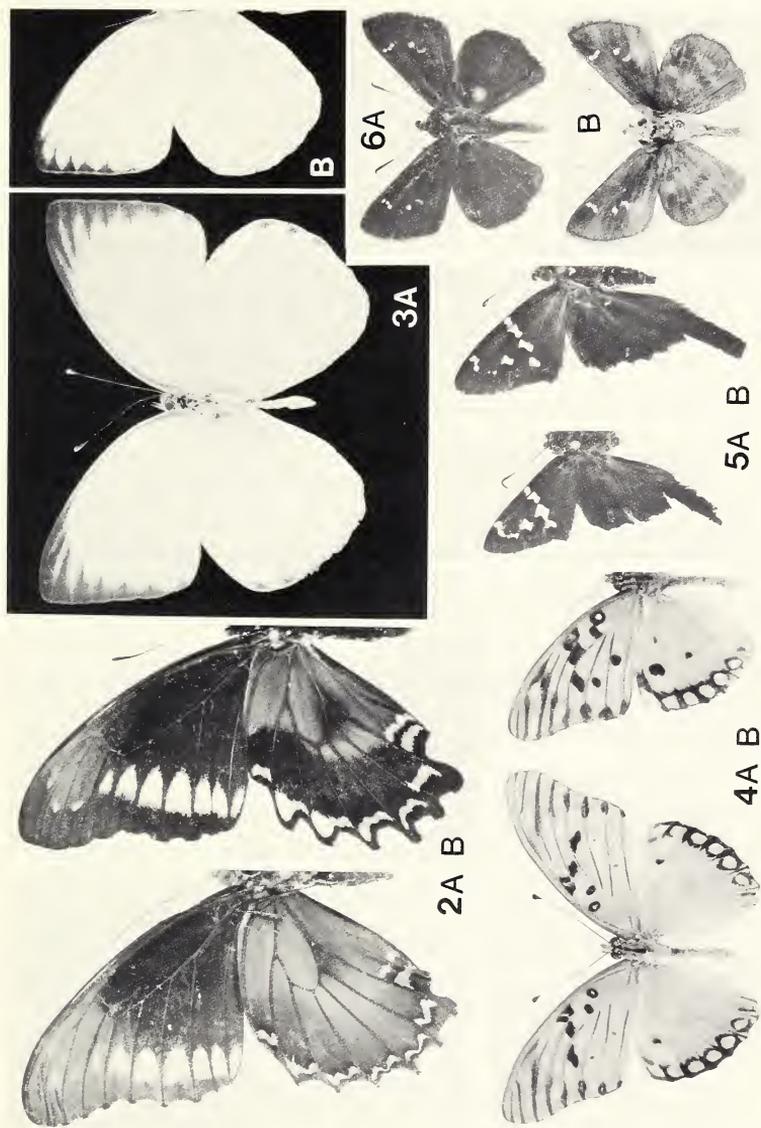


FIG. 2. *Battus polydamas* males, undersides. A: *B. p. polydamas*, San Andrés, August 1986. B: *B. p. polycrates*, Jarabacoa, Dominican Republic, January 1985. ($\times 1.0$). FIG. 3. *Ascia monuste* males, uppersides. A: *A. m. monuste*, San Andrés, August 1986. B: *A. m. eubotea*, Mona Island (Puerto Rico), July 1986. ($\times 1.0$). FIG. 4. *Agraulis vanillae* males, uppersides. A: *A. v. vanillae*, San Andrés, August 1986. B: *A. v. insularis*, Culebra Is. (Puerto Rico), September 1986. ($\times 0.8$). FIG. 5. *Urbanus proteus* males, uppersides. A: *U. p. proteus*, San Andrés, August 1986. B: *U. p. domingo*, Luquillo, Puerto Rico, June 1980. ($\times 0.7$). FIG. 6. *Cymaenes odilia trebbius*, male. A: upperside, B: underside. San Andrés, August 1986. ($\times 1.3$)

nominate subspecies (Fig. 5A), rather than the Antillean *U. proteus domingo* Scudder (Fig. 5B).

U. d. dorantes Stoll (n = 6). This species, absent from Emmel's list, is newly recorded from San Andrés and Providencia, occurring frequently on both islands. All male specimens collected were determined as *U. dorantes*, by comparison with Evans (1952). All are clearly referable to the nominate subspecies occurring on the mainland of the Americas rather than to either of the Antillean subspecies (*U. d. cramptoni* Comstock and *U. d. santiago* Lucas), which differ, respectively, in reduction of forewing maculation (Comstock 1944) and underside markings (Riley 1975).

(*Pyrgus oileus* Linnaeus). This widely distributed skipper, recorded by Emmel as sporadic around Big Pond (San Andrés) in February 1968, was seen on neither island in August 1986.

Cymaenes odilia trebius Mabille (n = 10). This skipper, in flight much resembling *C. tripunctus*, was found commonly, but very locally on San Andrés in August 1986 with a pronounced mid-morning flight period, nectaring at *Stachytarpheta* flowers on an E-W track crossing the island near the southern point. This subspecies (Fig. 6) is recognized primarily by the extent of grey scaling on the forewing underside and by uniformity of the ground color and the distribution and size of the pale spots on the hindwing beneath (Evans 1955). It extends from southern Texas (Howe 1975) through Central America into northern Colombia [Type locality Bogotá]. This species has not previously been recorded from any Caribbean island.

Hylephila phyleus Drury (n = 2). Perhaps the most widely distributed of New World skippers, ranging from Canada to Argentina, *H. phyleus* was noted by Emmel as possibly present on San Andrés, but occurring commonly on Providencia. It was rare on San Andrés in August 1986, and not recorded from Providencia. This skipper has no described insular subspecies in the West Indian region.

Panoquina sylvicola Herrich-Schaeffer (n = 1). Another widely ranging species (from the southern U.S. south to Argentina and through the Antilles), *P. sylvicola* is newly recorded from San Andrés by a single specimen (August 1986).

Papilionidae

Battus p. polydamas Linnaeus (n = 7). This swallowtail is newly recorded from San Andrés, where it was seen, but never common, in August 1986 in scrubby beachside areas, where *Aristolochia* was present. Riley (1975) lists 13 insular subspecific taxa sometimes differentiated on island pairs separated by remarkably short distances. The San Andrés population represents the nominate subspecies (Fig. 2A), which Riley (1975) considered confined to the mainland of Central and South America and not now present on any Antillean island, "... though it seems to have been present earlier on the island of Barbados." A representative Antillean subspecies (*B. polydamas polycrates* Hopffer from Hispaniola and Puerto Rico) is illustrated in Fig. 2B. The island forms are distinguished, one from another, by variations in a number of characters, including the shape, size and tint of the pale upperside spots, and, on the underside, by the uniformity (or otherwise) of the brown ground color of the fore- and hind wings, the size, shape and brightness of the submarginal red markings on the hindwing and, where present, the size and shape of the accompanying silver wedges and distal cream spots (Riley 1975). Each described subspecies is distinctive and the extremes are dramatically different. The nominate subspecies, ranging through Central and much of South America with little variation, cannot be confused with any of the island races. The generally pale brown-grey color of the hindwing beneath, the absence of submarginal pale spots and silver patches associated with the submarginal red markings, and the reduction of the last two pairs of narrow lunules, are diagnostic.

Pieridae

Ascia m. monuste Linnaeus (n = 7). This butterfly was first recorded from San Andrés in August 1986, when it was locally frequent in disturbed coastal waste land and abandoned

fields. Males (all collected) are large, white beneath, with prominent marginal markings (Fig. 3A), and are referable to the continental nominate subspecies which, according to Riley (1975), elsewhere enters the Antillean area from South America *via* Trinidad into the southern Lesser Antilles, possibly occurring further North as an occasional vagrant (Comstock 1944). Despite its migratory proclivity, *A. monuste* has evolved two subspecies in the West Indies: *A. m. eubotea* Latreille (*evonima* Boisduval; see Comstock 1944) is less heavily marked, pale yellow-ochreous on the hindwing beneath, and occurs from Florida and the Bahamas through the Greater Antilles, and *A. m. virginia* Godart, very lightly marked on the upperside, occupying the area between the Virgin Islands and St. Vincent. For comparison with *A. m. monuste*, subspecies *eubotea* is illustrated in Fig. 3B.

***Phoebis sennae* Linnaeus** (n = 35). This widely distributed sulfur was noted by Emmel on each visit to San Andrés and Providencia; in August 1986 it was common on the former and occasional on the latter. Antillean and southern U.S. populations are usually regarded as referable to the nominate subspecies, intergrading with the more northern *P. s. eubule* Linnaeus. The mainland tropical subspecies, *marcellina* Cramer, is described (Howe 1975) as showing a more orange and heavily patterned underside (male) and conspicuous patterning and a ground color of pinkish orange (female) beneath. Klots (1960) regarded this last subspecies as "of dubious worth." Specimens collected in 1986 from San Andrés and Providencia are quite variable and fall within the range of variation of very extensive series examined from the Antilles and the mainland of Central and South America. They do not, therefore, yield reliable information about the affinities of the San Andrés and Providencia populations.

***Phoebis p. philea* Johansson**. This large and (in the male) conspicuously colored species is newly reported from both San Andrés and Providencia (August 1986). Although no specimens were collected, close sightings of males established the identity of the nominate subspecies, which occurs from southern Florida through the mainland south to Brazil (Riley 1975). The two Antillean subspecies, *P. p. huebneri* Fruhstorfer (Cuba) and *P. p. thalestris* Illiger (Hispaniola) are readily distinguished from *p. philea* by a conspicuous large black spot at the end of the forewing cell—certainly absent in specimens seen on San Andrés and Providencia.

***Aphrissa statira* Cramer**. This sulfur was reported by Emmel from two reliable sightings on Providencia in July 1968. The nominate subspecies occurs on the mainland and according to Klots (1960) migrates annually *via* Trinidad into the Lesser Antilles. Two Antillean subspecies have been described, from Cuba and Hispaniola, but until specimens from San Andrés and/or Providencia are examined, the affinity of *statira* in these islands cannot be assessed.

***Eurema daira* Godart**. Emmel recorded this species as "relatively rare" on San Andrés in July, but absent in February, noting that it is widely distributed in the Antilles and the mainland of Central America (and indeed ranges from the SE U.S. to Brazil). It was not found on San Andrés or Providencia in August 1986.

***Eurema venusta limbia* Felder & Felder** (n = 32). Very surprisingly, this "southern" *Eurema* was not encountered by Emmel, yet was one of the most common butterfly species on San Andrés in August 1986, notably in abandoned fields and neglected coconut plantations in the southern part of the island. It was not found on Providencia. *Eurema v. emanoma* Dillon, the Antillean subspecies (Fig. 9B), is found in the Lesser Antilles, from Grenada north to Guadeloupe (Pinchon & Enrico 1969, Riley 1975). Specimens collected on San Andrés represent the more heavily marked continental subspecies *E. v. limbia* occurring in Central America (Fig. 9A). The reported food plant, *Mimosa* (Riley 1975), is present on San Andrés, and the discrepancy between the 1968 and 1986 records may reflect a recent successful colonization of the island from Central America.

***Eurema (Pyrisitia) lisa* Boisduval & Leconte**. As with *E. daira*, this small sulfur was recorded by Emmel as relatively rare on San Andrés in July and absent in February. It was not found on either in August 1986.

***Abaeis (Eurema) nicippe* Cramer** (n = 16). This species was not found on San Andrés in August 1986, yet was one of the most common butterflies on Providencia at a time when few adult butterflies were seen. On Providencia, *nicippe* was generally distributed along the road around the perimeter of the island. No subspecies have been described.

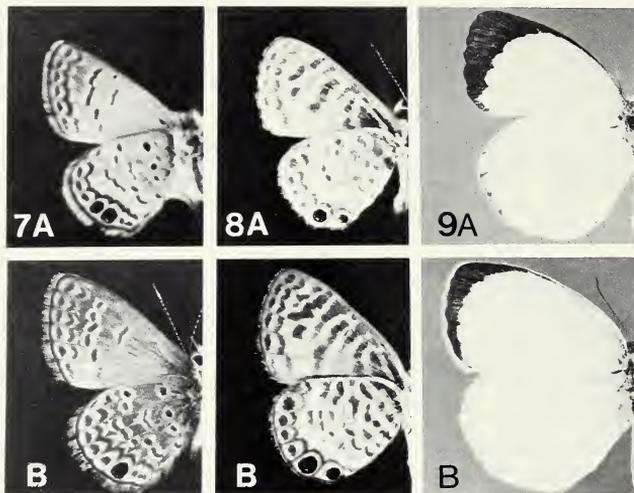


FIG. 7. *Hemiargus hanno* males, undersides. A: *H. h. zachaeina*, Providencia, August 1986. B: *H. h. filenus*, New Providence Is. (Bahamas), July 1980. ($\times 2.0$)

FIG. 8. *Leptotes cassius* males, undersides. A: *L. c. striata*, Providencia, August 1986. B: *L. c. theonus*, Big Pine Key, Florida, September 1984. ($\times 2.0$)

FIG. 9. *Eurema venusta* males, uppersides. A: *E. v. limbia*, San Andrés, August 1986. B: *E. v. emanoma*, Bequia Is. (St. Vincent Grenadines), August 1987. ($\times 1.4$)

Lycaenidae

Hemiargus hanno zachaeina Butler & H. Druce (n = 10). This lycaenid was newly recorded for Providencia in August 1986, where it occurred in the same localities and in comparable numbers with *Leptotes cassius*, discussed below. Comparison between the Providencia material and extensive series in the British Museum (Natural History) establishes the former's grouping with the continental subspecies *H. h. zachaeina* [Type locality Costa Rica]. *Hemiargus h. zachaeina* (Fig. 7A) is readily distinguished from the three described island races (Fig. 7B) by the presence of two well demarcated eye-spots near the anal angle of the hindwing beneath, rather than one.

Leptotes cassius striata W. H. Edwards (n = 12). Emmel noted *L. cassius* as present on Providencia and distinctly colonial on San Andrés. During the 1986 survey, it was widespread and generally common on San Andrés, while on Providencia, at a time when adult butterflies were very scarce, it was the species seen most frequently. Three Caribbean sub-species have been described: *theonus* Lucas from Florida, the Bahamas, and Greater Antilles; and two subspecies from the Lesser Antilles (Riley). Reference to extensive material in the British Museum (Natural History) clearly associates both San Andrés and Providencia specimens with the mainland subspecies *L. c. striata* [Type locality Bogotá], which ranges throughout Central America. Populations of *L. cassius* show considerable variation, but *L. c. striata* (Fig. 8A) is distinguishable from other forms (Fig. 8B) by reduction of the blue suffusion in the upper surface of the female and, in both sexes, in the generally paler brown underside markings, and in the reduced size and more circular shape of the hindwing eye-spots.

Chlorostrymon telea Hewitson (n = 1). A single worn female of this continental hairstreak was collected on Providencia (17 August 1986), representing a new record for a Caribbean island.

Heliconiidae

Agraulis v. vanillae Linnaeus (n = 33). Emmel recorded this species as locally abundant on San Andrés and noted it from Providencia. In August 1986 it was locally common on San Andrés and generally distributed in lowland disturbed areas on Providencia. Emmel described it as resembling "... typical Florida *A. v. nigrior* Michener, although the black forewing spots often form a bar-like continuous row." Material collected in August 1986 does not conform to this description: specimens are much more lightly marked than *nigrior* or the widespread Antillean subspecies *A. v. insularis* Maynard, and correspond to the nominate subspecies, which according to Riley (1975) enters the southern Lesser Antilles from the mainland (Fig. 4).

(*Dryas iulia* Fabricius). Emmel found this widespread species (of which numerous Antillean subspecies have been described) commonly on San Andrés "throughout the year" and also recorded it from Providencia. Surprisingly, *D. iulia* was not seen on either island in August 1986.

Nymphalidae

(*Junonia evarete* Cramer). Emmel reported this species, as *Precis evarete zonalis* (C. & R. Felder), to be relatively rare on San Andrés, from one locality in February and July, and did not report it from Providencia. The proposed reinstatement (Turner and Parnell 1985) of *Junonia evarete* is adopted here for this species, which ranges widely from S Texas and Florida through the West Indies and Central America into South America. It was not seen on San Andrés or Providencia in August 1986.

Junonia genoveva Stoll (n = 25). As for the preceding species, the terminology proposed by Turner and Parnell (1985) is adopted here. It was not recorded by Emmel, but in 1986 it occurred in beach areas and abandoned fields on San Andrés, but was not found on Providencia. Specimens collected correspond well with Turner and Parnell's figures of Jamaican *genoveva*; this species shows considerable general and seasonal variation, but the San Andrés material falls within the range shown by series examined from Hispaniola, Puerto Rico, Trinidad, Guatemala, Costa Rica, and Panama.

Anartia jatrophae luteipicta Fruhstorfer (n = 15). This is another nymphalid exhibiting incompletely documented general and seasonal variation. According to Riley (1975) the nominate subspecies is primarily South American, extending into the Lesser Antilles north to St. Kitts. A number of Antillean subspecies have been described (Munroe 1942, Riley 1975), generally darker than populations on the mainland. Emmel found this species to be fairly common on San Andrés in July, though rare in February. In August 1986, it was locally quite common on San Andrés, especially around ornamental flowers in the town and at the airport, and a single specimen was collected on Providencia. These specimens correspond most closely (particularly in their generally light markings and in displaying a conspicuously yellow distal margin of the hindwing) to the Central American subspecies *A. j. luteipicta* [Type locality Honduras], noted by Munroe (1942) as ranging south from Mexico and merging with the nominate subspecies in Panama.

Vanessa cardui Linnaeus (n = 1). Howe (1975) suggests that this cosmopolitan and invariant species is largely nonresident over much of its range in North and Central America, dispersing widely from a few breeding areas. It has been recorded occasionally from many of the Antillean islands (Riley 1975) and is newly recorded from San Andrés from a single worn specimen collected in August 1986.

(*Siproeta stelenes* Linnaeus). This conspicuous and widely ranging nymphalid was regularly recorded by Emmel at one locality on San Andrés during February 1968, and more rarely in other months, but was not found on either island in August 1986.

Historius odius Fabricius. This species was noted by Emmel from both islands, but rarely on San Andrés (July). In August 1986, it was seen on several occasions, along E-W tracks crossing the southern part of San Andrés, but was not recorded from Providencia. Emmel suggested that the few specimens encountered on San Andrés may have been vagrants from the sister island "or even the mainland," but *Cecropia*, the larval food plant, occurs on San Andrés, and this insect may well be resident there. Because no

specimens were collected in 1986, it was not possible to determine whether the San Andrés population belongs to the nominate subspecies, which occupies the Greater Antilles, or to *H. odius orion* Kaye, which ranges through tropical America to Argentina and (Riley 1975) enters the Lesser Antilles from the mainland.

Danaidae

(*Danaus plexippus* Linnaeus). Emmel recorded "scattered and relatively worn" specimens on all visits to San Andrés (February, March, June, July), and also on Providencia. It was not seen on either island in August 1986, and its resident status is unknown. Emmel found no Asclepiadaceae on San Andrés, but potential larval food plants could be present in the shrubby untended coconut plantation understorey of that island, or in the grasslands and disturbed areas of Providencia.

DISCUSSION

An island's observed fauna and flora may be regarded as the result of a balance between addition by successful colonization from outside and, potentially (in long established populations), by evolution of new species and/or races, countered by extinctions (Munroe 1953, 1957, 1984, MacArthur & Wilson 1967, Williamson 1981). In the West Indian-Caribbean region, evolution of butterfly species and subspecies, frequently endemic to a single island, is a conspicuous feature (Riley 1975), particularly on the large islands of the Greater Antilles (Cuba, Jamaica, Hispaniola, and Puerto Rico). The present butterfly faunas of these islands, together with the Bahamian chain, appear to have drawn primarily from a Central American species pool, while the small islands of the Lesser Antilles show more South American donor input (Fox 1963, Scott 1972, Riley 1975, Munroe 1984).

Scott (1972) has provided a survey of the affinities of Antillean butterflies with respect to individual islands and island groups, and the continental land masses of North, Central, and South America. His analysis makes use of an "index of faunal resemblance" (see also Munroe 1957) defined as "the percentage of species found on the island with the smaller fauna which are the same as those on the island [or continental land mass] with the larger fauna." Although providing a valuable basis for analyzing faunal affinities across the entire West Indian region, Scott's index is of limited value when employed at the specific level to assess short-range affinities, especially between an island pair of greatly disparate area, or between a small island and a nearby continental land mass. In the context of San Andrés and Providencia Islands, Emmel (1975) cites Scott's recognition of the great dispersal ability of many species found in the Antilles, and (of the 17 species he recorded) notes that "All . . . are also found on the adjacent Nicaraguan mainland area, and all represent species that are migratory or are known to be frequent colonisers."

At the level employed, this view is substantially accurate, with only

Chlorostrymon telea (Providencia) and *Cymaenes odilia* (San Andrés) representing new Caribbean island records of continental species without obvious dispersal potential. However, if the "higher resolution" data provided by analysis of subspecies are taken into account, the biogeographical status of Providencia and San Andrés takes on a very different aspect.

In the following discussion, only the 19 species recorded during the 1986 survey are considered, although Emmel's records of species not seen during the present field work raise the total species count for these two islands substantially. Except where noted, the species records from the two islands may be pooled for purposes of discussion of their affinities. The two species noted above (*Chlorostrymon telea* and *Cymaenes odilia*) are clearly derived from continental Central or South America; Scott's index would remain at 1.0 with respect to continental America, and the addition of 2 species (of 19) not present in the Antillean islands would reduce the index with respect to the Caribbean area from 1.0 (as implied by Emmel) to 0.89.

Several species recorded from San Andrés and Providencia (*Hylephila phyleus*, *Panoquina sylvicola*, *Abaeis nicippe*, *Phoebis sennae*, *Vanessa cardui* and *Junonia genoveva*) are considered to be invariant in the area (Antilles and the adjacent tropical American mainland) and thus provide no information on biogeographical origins of the islands' populations. To this group must be added *Historius odius*, given the absence of subspecifically determined material. The remaining 10 taxa, determined to the subspecific level (*Urbanus d. dorantes*, *U. p. proteus*, *Battus p. polydamas*, *Ascia m. monuste*, *Phoebis p. philea*, *Eurema venusta limbia*, *Leptotes cassius striata*, *Hemiargus hanno zachaeina*, *Agraulis v. vanillae*, and *Anartia jatrophae luteipicta*), in each instance possessing one or more Antillean subspecies, are represented on San Andrés and/or Providencia by a subspecies in common with continental tropical America. Thus, while the San Andrés-Providencia butterfly populations remain at 1.0 (Scott index) with respect to Central and South America, this index drops to a *maximum* of 0.39 (7 of 19) with respect to the Antillean islands; the balance being largely accounted for by wide-ranging species that afford no affinity data.

It is now clear that the butterfly faunas of these islands, although presumably much affected by destruction of native habitats, considerable on Providencia and virtually complete on San Andrés, represent extensions of the adjacent Central American mainland with no documented Antillean component.

This not unexpected conclusion exemplifies the value of using subspecific information in approaching the question of affinity determination in island groups such as the Antilles, an approach for comparing

closely related faunas first proposed by Munroe (1957). Another recent application of this approach documented the Puerto Rican, rather than Hispaniolan, contribution to the present butterfly fauna of Mona Island (Smith et al. 1988). In the case of San Andrés and Providencia, their proximity to the continental mainland evidently outweighs potential wind-borne dispersal from the Antilles by predominantly easterly winds (Fox 1963, Calvesbert 1973). In considering records for the two islands, Emmel suggests that "Every species found on San Andrés must occur on Providencia, and with the greatly increased diversity of vegetation [on the latter], one would presume that several additional species of butterflies should occur," a forecast that has received some confirmation here. However, we do not feel that one of a pair of small islands, of approximately equal area and similarly positioned with respect to a large and faunistically rich area, should *necessarily* support a butterfly fauna fully represented on the other.

Even if islands in such a pair are ecologically similar, chance variation in the distribution of incoming vagrant species, reaching one and not the other, could well lead to discrepant faunas. Where the islands differ substantially, as do San Andrés and Providencia, the probability of differences between the two faunas may well be enhanced by different environmental spectra that engender differing probabilities of successful colonization.

Present documentation of the butterfly faunas of San Andrés and Providencia is undoubtedly very incomplete, relying only on brief periods of sampling in 1967–68 and 1986. However, of the nine species recorded in August 1986 on Providencia, three were not seen on San Andrés, of which *Abaeis nicippe* is widely ranging, while *Chlorostrymon telea* is not obviously dispersive. *Hemiargus hanno*, at the specific level, is one of the widest-ranging lycaenids in the American tropics, yet a continental subspecies is noted on only one island (Providencia). Of the 16 species found during the same period on San Andrés, eight were not noted on Providencia (although sampling followed a prolonged rainless period on that island). Of these, *Vanessa cardui* is a well known wanderer, occasionally recorded as a vagrant on many Caribbean islands: *Panoquina sylvicola* and *Junonia genoveva* are widely dispersed residents in the area and beyond, as is *Hylephila phyleus*, found by Emmel on both islands in 1967–68, but only on San Andrés in 1986. The remaining four butterflies (*Cymaenes odilia trebius*, *Eurema venusta limbia*, *Battus p. polydamas*, *Ascia m. monuste*), at the subspecific level noted, show either limited or no dispersive colonization of the Antillean islands. Yet the last three, at the specific level, are amongst the most widely distributed of the Antillean butterflies. While it is, of course, possible that their absence from the Providencia list merely

reflects our incomplete documentation, it seems as possible that this reflects a real disparity between the butterfly faunas of Providencia and San Andrés.

The position of these ecologically dissimilar islands—about 87 km apart, separated by long distances from a windward potential source of immigrants (the Antilles), but approximately equidistant from a much closer continental land mass—may be regarded as a “natural experiment” from which further data pertinent to questions of general biogeographical interest may be expected. Further field work on these islands would be of great value, not only adding to our knowledge of their butterflies, but in providing data which may refute, modify, or substantiate the biogeographical hypotheses outlined above.

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AN INEXPENSIVE PORTABLE TRAP FOR MONITORING BUTTERFLY MIGRATION

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ABSTRACT. Seven types of low-cost flight traps for monitoring migrating butterflies were designed, built, and tested. The most efficient type caught ca. 7-55% of the migrants crossing a 3- or 6-m line perpendicular to the direction of migration. Traps of polyester mosquito netting, monofilament shrimp netting, or a combination of the two did not differ significantly in capturing spring migrating *Precis coenia*. Trios of 3-m traps yielded consistent estimates of variation in numbers of *P. coenia* migrating during spring. Portable traps can be used in mark-and-release studies of migrating butterflies and for quantifying distribution of migrants in time and space. Instructions for building the most efficient type of portable trap are given in the Appendix.

Additional key words: *Precis coenia*, *Phoebis sennae*, phenology, Florida, trap efficiency.

Migrating butterflies generally fly in a straight line within a few meters of the ground. When they encounter an obstacle, their response is to fly up and over rather than around (Williams 1930). This behavior can be exploited in devising traps that intercept and capture migrants (Walker 1978, 1985a, Gytoku et al. 1987).

Early traps were inefficient and expensive to maintain; later ones were elaborate, permanent structures costing ca. \$500 each for materials (Walker 1985a). Our long-term goal in the present study was to develop an inexpensive, portable trap that would encourage and facilitate studies of butterfly migration. For the short term, we needed traps to quantify the phenology of butterfly migration at numerous stations on transects along and across the Florida peninsula and to enable high school science classes to catch migrants for marking and release.

Our study compared five variations of the most promising of two prototype portable traps (Part I) and tested three fabric coverings of the most promising variation (Part II).

I. PROTOTYPES AND PILOT TESTS

During spring 1987, we built and tested two prototype traps that contrasted in complexity and cost but that proved similar in efficiency. That fall we tried five variations of the less expensive design.

Materials and Methods

All traps were of gray polyester mosquito netting supported by end frames largely of thin-wall metal electrical conduit. Cross members and guys were braided nylon rope. Cages that retained the trapped but-

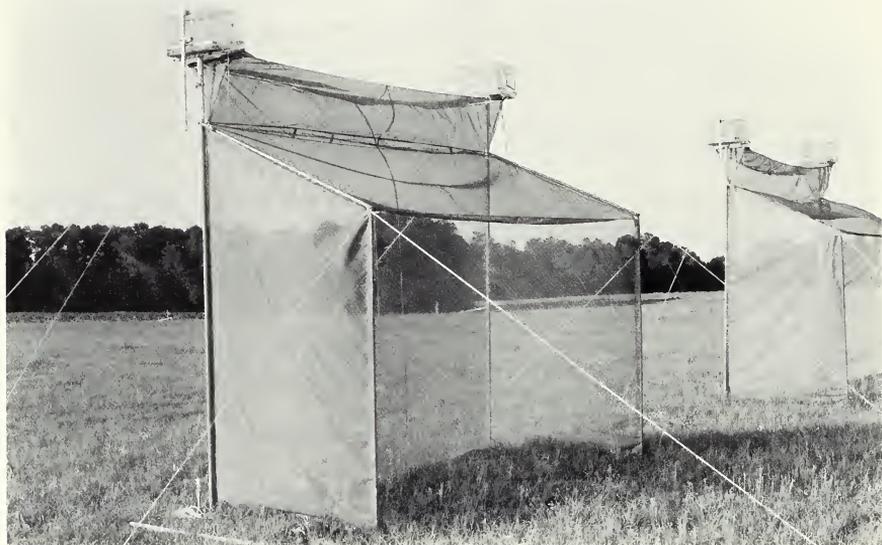


FIG. 1. Standard traps. Trap in foreground is of polyester mosquito netting; the other has the main wall and back of duct of monofilament shrimp net.

terflies were made of 6.4 mm ($\frac{1}{4}$ ") hardware cloth held together by pop rivets. Traps were generally 3 m long with openings 2 m tall.

During the 1987 fall migration, we tested these five variants of the simpler prototype trap:

(1) **Standard trap.** This variant (Fig. 1) was most similar to the prototype and is described in detail in the Appendix. It was designed to catch butterflies coming from one direction.

(2) **Two-way trap.** This trap was two standard traps on opposite sides of a shared main wall. The duct and cages were partitioned to segregate butterflies entering the trap from opposite directions, thus permitting calculation of net movement in the migratory direction (as in earlier traps; e.g., Walker 1985a).

(3) **Six-meter trap.** This trap was identical to the standard trap except it was 6 m instead of 3 m wide.

(4) **Taller-opening trap.** The roof of the standard trap sloped from 2.6 m to an opening 2.0 m tall. The roof of the taller-opening trap was horizontal, producing a 2.6 m opening.

(5) **Deeper trap.** This trap had roof and side walls twice as deep as in the standard design (3 m vs. 1.5 m for the roof). The opening was still 2.0 m tall, reducing the slope of the roof to half that of standard.

In early October 1987, traps were erected randomly along an ENE-WSW line in an 8-ha open field at the University of Florida's Green

TABLE 1. Relative trapping efficiencies of portable traps for *Phoebis sennae*: fall migration, 1987.

Trap	Days ^a	Relative efficiency ^b n = 555 ^c (501)
Standard	38	0.66 ^d
Standard	30	0.83
Two-way	29	0.72
6-meter	31	0.95
Taller-opening	21	0.4
Deeper	11	(0.4) ^e
1st four combined	128	0.78

^a Portable traps were in service for various periods during 1 Oct to 8 Nov.

^b (Number caught flying southward per meter by portable trap)/(number caught flying southward per meter by permanent trap).

^c Total caught in north-facing portable traps. Value in () is total for first four traps listed.

^d Efficiencies with no () are for >40 individuals caught in the portable trap.

^e Efficiency based on 12 individuals caught in the portable trap.

Acres Farm (29°41'N, 32°20'W) near Gainesville. Two standard traps, the two-way trap, and the 6-meter trap were run simultaneously for 29 days or more; the taller-opening and deeper traps were run sequentially (Table 1). All traps faced NNW, into the migratory stream (Walker 1985b). Captures were recorded daily for all traps: after 1600 h or before 1000 h of the next day. For the standard traps, captives were marked on the wings with a silver marking pen and returned to the trap cages except on Mondays and Thursdays, when they were permanently removed. Captives were removed daily from the remaining traps. The marked captives were used to estimate the rate at which butterflies disappeared from the cages by predation or escape. This was an important consideration in evaluating the effects of reducing the trap service interval to twice weekly.

Two permanent traps, Walker's (1985a) model #3 and a minor modification of it, continuously monitored the migration across 12 m of ENE-WSW line at a site 4.4 km ESE of the portable traps. For species that cannot pass through 1.3 cm mesh hardware cloth, these traps catch 22 to 70% of migrants.

Results and Discussion

Numbers of fall migrants per meter caught by the various portable traps were compared to the numbers caught per meter by the two permanent traps (Table 1). This method of expressing results in terms of relative trapping efficiency was used for two reasons. First, the absolute trapping efficiencies of the model #3 trap had been estimated through direct observations (Walker 1985a), making possible estimations of the absolute efficiencies of the portable traps. Second, direct comparisons among portable traps were complicated by small catches and by different durations of service. The permanent traps ran contin-

uously and sampled more of the migratory front than any single type of portable trap.

Phoebis sennae (L.) (Pieridae) was the only migrant caught by the portable traps in substantial numbers. The taller-opening and deeper traps ranked lowest in catching this species, and the 6-m trap ranked highest (Table 1). When results from the four traps that were standard in height of opening and depth of walls and roof were combined, the estimate of relative efficiency became 0.78. If the rates of migration at the portable and permanent traps are assumed to be the same, the estimated absolute efficiency of standard portable traps in catching *P. sennae* becomes 38 to 55%. (The permanent traps caught 49 to 70% of *P. sennae*: Walker 1985a.)

The two-way trap caught 81 *P. sennae* flying south and 3 flying north, for a southward consistency of 96%, not significantly different from the consistency of 98% (447 south and 9 north) for the permanent traps during the same 29-day period.

Marked butterflies disappeared from the cages of the standard traps at an average rate of 12% per day ($n = 147$ butterflies and 284 butterfly-cage-days). The rates of disappearance for the two traps were similar (chi square: $P > 0.50$). Rates of disappearance between day 0 (=day of marking) and day 1, between days 1 and 2, and between days 2 and 3 were similar (chi square: $P > 0.95$).

The standard trap equaled or exceeded the performance of its variants in the the fall 1987 tests—with the possible exception of the 6-m trap, which caught 28% more *P. sennae* per meter than the mean of the two standard traps.

II. REPLICATED TESTS OF TRAP FABRICS

During the spring of 1988, we tested standard traps made of different fabrics. This was prompted by two problems noted the previous fall: polyester netting tore easily after a few months of exposure to sunlight, and migrating butterflies seemed to detect and avoid portable traps made of polyester more frequently than permanent traps made of 1.3 cm mesh hardware cloth.

Materials and Methods

The fabrics tested were polyester mosquito netting; shrimp net (9.5 mm square mesh made of knotted 0.28 mm diameter nylon monofilament); and a combination of polyester netting and shrimp net. The polyester traps were from the previous fall; the shrimp net traps were made by stretching the monofilament netting on a frame and gluing edges together with silicon caulking; the combination traps were made

TABLE 2. Number of *Precis coenia* captured by standard portable traps of three fabric types, Green Acres Farms: spring migration, 1988.^a

Date	Block	Type of fabric			Mean
		Polyester	Combination	Shrimp net	
6-22 April					
	(Blocks in sequence: west to east)				
	I	7	19	20	15
	II	2	7	12	7
	III	31	9	17	19
	Mean	13	12	16	14
23 Apr-31 May					
	(Block I moved to east end of array)				
	I	18	19	13	17
	II	4 ^b	28	9	17
	III	30 ^b	25	11	19
	Mean	17	24	11	17
6 Apr-31 May					
	Mean (n)	30.7	35.7	27.3	31.2
	Mean (n/m)	9.7	11.3	8.7	9.9

^a Analysis of variance for effect of fabric type showed no significance. (F value = 0.77, P = 0.46; model degrees of freedom = 3 fabrics - 1 = 2; error degrees of freedom = 504 trap-days - 1 = 503.)

^b These numbers are for the traps, which were exchanged in position 11 May. The numbers for the trap positions are 14 and 20.

by cutting out the main wall and the back of the duct of polyester traps and gluing shrimp net in their places.

Three traps of each material were erected along a 67-m ENE-WNW line in the field at Green Acres Farm. The traps were assigned to three randomized blocks with the constraint that the first trap in one block could not be of the same material as the last trap in the previous block. Traps were separated by 5 m, and the mouth of each trap was made 3.15 m wide.

Traps were serviced daily starting 6 April 1988. After 17 days, traps in Block II had caught fewer than half the numbers of migrants caught in the outside blocks, and the eastmost trap (Polyester III) had caught $>1\frac{1}{2} \times$ as many migrants as any other trap. On 23 April, to test for possible effects of relative or absolute trap position, we removed the three traps of Block I from the west end of the array and erected them east of Block III, thereby making Block II an end block and Block III the middle block. By 10 May, Polyester II and Polyester III, which had caught 2 and 31 butterflies, respectively, before Block I was moved, had caught 3 and 19 more, indicating that relative position of blocks had not caused the discrepancy. To distinguish between an individual trap effect and an absolute position effect we exchanged the two traps.

% of Total Number

Northward

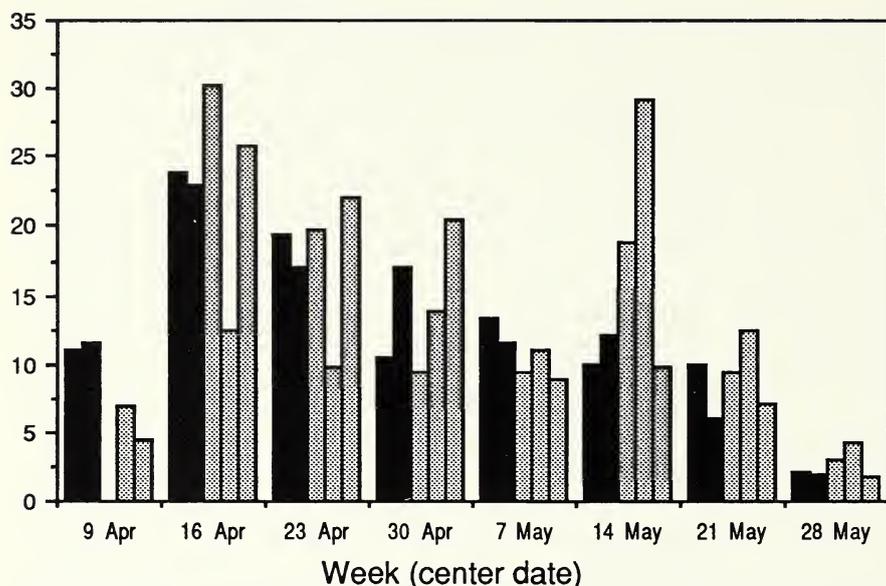


FIG. 2. Seasonal course of migration of *Precis coenia*, spring 1988, as recorded by two permanent traps (black bars) and by three trios of portable traps (stippled bars, representing traps of Blocks I, II, and III).

We concluded the test 31 May, when spring migration had ended. As before, two permanent traps were operated continuously.

Results

As expected from previous studies (e.g., Walker 1985a), *Precis coenia* (Hübner) (Nymphalidae) was the only spring migrant numerous enough to yield data useful in comparing trapping efficiency. Analysis of variance revealed no significant differences among fabric types (Table 2).

During 11–31 May, the Polyester II trap (moved to Block III) caught 1 migrant; Polyester III (moved to Block II) caught 11. These numbers are similar in ratio to the total catches of 5 and 50 prior to swapping, indicating that the trap rather than the position caused the variation.

The mean number of *P. coenia* caught per portable trap 6 April to 31 May was equivalent to 9.9 individuals flying south across each monitored meter (mean no. caught per trap/meters per trap = 31.2/3.15). During this time, the permanent traps caught 381 *P. coenia* or 31.8 per monitored meter. If the migration rate was the same at the two sites, the portable traps were 31% as efficient as the permanent traps. For the three most numerous migrant species, the permanent traps are

22 to 70% efficient (Walker 1985a). Applying these figures to the present data, the estimated absolute efficiency of the portable traps in catching *P. coenia* is 7 to 22%.

The three trios of portable traps and the two permanent traps produced similar estimates of weekly changes in numbers of migrating *P. coenia*. A chi square test of the weekly total catches for the five estimators (Fig. 2) did not refute the hypothesis that all had come from the same distribution (chi square = 19.2, df = 28, $P > 0.75$).

Discussion

Shrimp net did not result in a significant increase in the standard trap's ability to catch *P. coenia*, but it lasted longer outdoors and had less wind resistance.

An unexpected result of the tests was that supposedly identical traps of polyester differed greatly in numbers of migrating *P. coenia* caught: 6, 25, 61. The totals for the other traps were much more uniform—viz., 34, 35, 38 for combination traps and 21, 28, 33 for shrimp net traps. Inspection of the poorly performing polyester trap revealed that its throat was narrowed at one end and that its catching cages fitted loosely into the holding trays. Loose fitting catching cages were evident on other traps, and on three occasions we watched a *P. coenia* escape through a crack rather than enter a catching cage. Polyester III ($n = 61$) had a uniform throat and snug fitting cages.

The efficiency of the traps for smaller migrants (such as *P. coenia*) could probably be increased and the variance in catches reduced by redesigning the trays and building the cages to closer tolerances. A substantial improvement might also be obtained by experimenting with the width and uniformity of the throat. Traps of greater width, such as the 6-meter trap, offer a cost-effective means of increasing the catch.

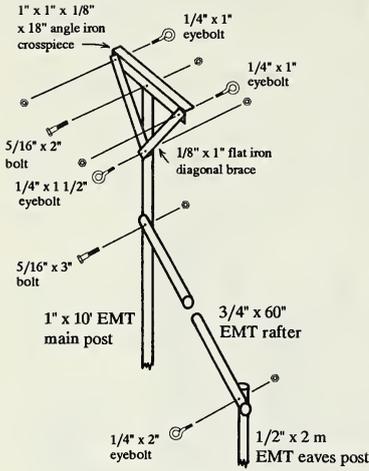
Unless the variance in catch among traps is reduced, groups of about 5 traps are needed to achieve a 95% chance of detecting a twofold difference in numbers of migrants at two sites (Snedecor & Cochran 1980: 102; formula adjusted for variance being an estimate).

Standard portable traps have been used to capture fall migrants for marking and release at four high schools in southern Georgia (J. J. Whitesell pers. comm.) and to quantify fall migration at five stations along a north-south transect from Valdosta, Georgia, to Lake Placid, Florida (B. Lenczewski pers. comm.).

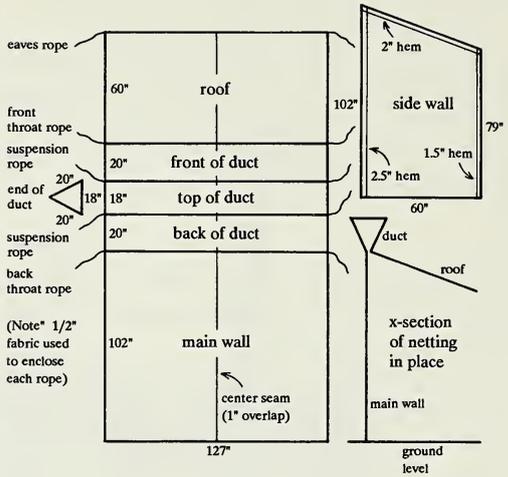
ACKNOWLEDGMENTS

We thank J. J. Whitesell for help with construction of the combination and monofilament traps and R. C. Littell and G. S. Wheeler for help with statistical analysis. The suggestions of S. Malcolm, J. J. Whitesell, and Oakley Shields substantially improved the manuscript. Florida Agric. Exp. Sta. Journal Series No. 9481.

3A FRAME



3B NETTING



3C COLLECTOR

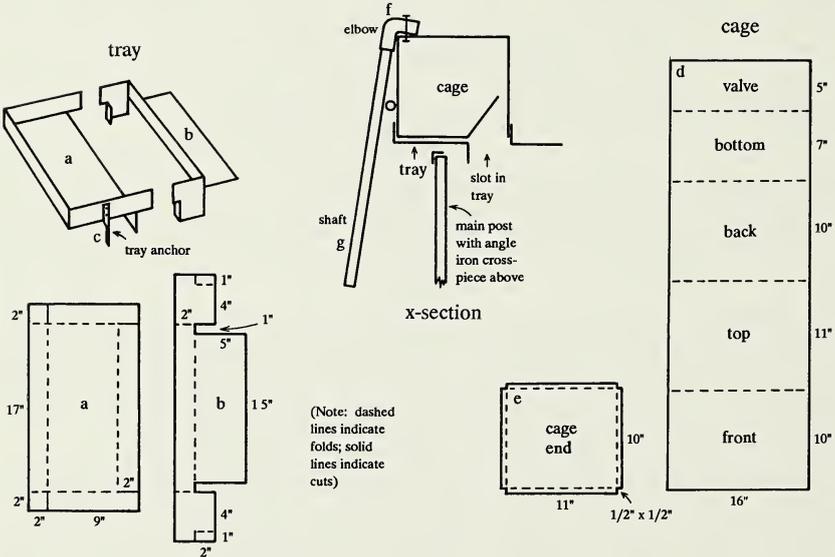


FIG. 3. Construction details of standard trap. (Dimensions are in inches: 1" = 2.54 cm.)

APPENDIX: BUILDING A TRAP

The standard portable trap (Fig. 1) consists of a frame, netting, and collectors that are built separately and then assembled (Fig. 3). Total cost of materials (1988) is ca. \$68 per trap. (Most measurements are in inches: 1" = 2.54 cm.)

Frame (ca. \$23 for materials). Each end of the trap is supported by a 120" main post (1" thin-walled metal electrical conduit = EMT), a 2 m eaves post ($\frac{1}{2}$ " EMT), and a 60" rafter ($\frac{3}{4}$ " EMT) (Fig. 3A). Attach 18" crosspiece of $1 \times 1 \times \frac{1}{8}$ " angle iron to top of each main post with $\frac{5}{16} \times 2$ " bolt. Strengthen crosspiece with diagonal braces (Fig. 3A) or with a welded 8" length of $1 \times \frac{1}{8}$ " flat iron (Fig. 1). Secure bottom of braces to main post with $\frac{1}{4} \times 1\frac{1}{2}$ " eyebolt. At each end of each cross piece attach $\frac{1}{4} \times 1$ " eyebolt. Attach rafters to main posts at 102" with $\frac{5}{16} \times 3$ " bolts and to top of eaves posts with $\frac{1}{4} \times 3$ " eyebolts. Make eight guys (4 @ 120" and 4 @ 144") of $\frac{1}{8}$ " braided nylon rope. Make eight 15" guy stakes of $\frac{1}{2}$ " EMT; to keep rope from slipping off, put a $\frac{1}{4}$ " bolt through each stake at 2" from top. Optional: Prepare four "feet" for the posts by cutting short pieces of $\frac{3}{4}$ " EMT that can be driven into the ground or welded to $\frac{3}{32} \times 2 \times \frac{1}{2}$ " pieces of flat iron. The posts fit over or into the $\frac{3}{4}$ " EMT.

Netting (ca. \$33). (We used 653" of 64" wide "silvergray polyester mosquito netting".) The main wall, duct (except ends), and roof are two 222.5" lengths of fabric joined lengthwise by sewing with nylon thread. At the indicated intervals (Fig. 3B), sew the fabric around five 130" lengths of $\frac{1}{8}$ " braided nylon rope. Cut two pieces for side walls from 185" of netting (81" short side, 104" tall side) (Fig. 3B). In each, sew 1.5"-wide front hem (for eaves post), 2.5" rear hem (for main post), and 2" top hem (for rafter). Cut two $20 \times 20 \times 18$ " triangles. Sew top hems of side walls to roof, triangles to ends of duct, and wide hems of side walls to main wall. (The trap can be made wider by using more than two 222.5" lengths of netting and longer ropes.)

Collectors (ca. \$12). Each collector consists of a $10 \times 11 \times 16$ " cage resting in a $2 \times 12 \times 17$ " tray (Fig. 3C). To make the tray, join two pieces of $\frac{1}{4}$ "-mesh hardware cloth, cut and bent as shown (Fig. 3C: a + b), to leave a 4×17 " opening in the bottom with flaps of hardware cloth projecting downward for attachment of the netting. Make tray anchors (c) of $\frac{1}{16} \times \frac{1}{2} \times 3$ " aluminum pieces and rivet to each end of tray at center. Drill $\frac{1}{4}$ " holes in tray anchors for attachment to frame. To make the cage, fold a 16×43 " piece of $\frac{1}{4}$ "-mesh hardware cloth as shown (d) and use pop rivets with backup washers to attach ends (e) made of two 11×12 " pieces. If desired, cut 4×5 " access in one end and fit piece of hardware cloth to serve as closure. (Cages can be emptied through the bottoms.) Longitudinally folded 1" strips of sheet metal may be crimped over principal edges of the cages and trays for strength and safety. All other rough edges should be taped with 1" pressure sensitive tape. Bolt to each cage 1" PVC elbow (f) with downward projecting 30" shaft of 1" PVC pipe (g) to permit removing and replacing the cage from the ground (Fig. 1). Make tool for servicing cages from 36" of 1" PVC pipe with female fitting on one end, from which projects 4" of 1×8 " dowel (not figured).

Erecting the trap. (Two persons recommended.) Determine the orientation and position of the trap; place feet or markers at the four corners. Set stakes for guys in approximate positions. Insert main posts, rafters, and eaves posts into appropriate hems. Attach rafters to posts. Tie guy ropes to appropriate eye bolts. Tie suspension ropes to 1" eye bolts. Erect one end of trap and temporarily guy; then erect other end. Tie ends of front and back throat ropes around each main post. Tie ends of eaves rope to 2" eyebolts. Adjust ropes, guys, and stakes until trap is trim. Make three $\frac{1}{4} \times \frac{3}{4} \times 2$ " wooden spacers with $\frac{1}{16}$ " holes at each end. Sew across the throat at even intervals.

Once trap is up, install collectors from a tall step ladder. Cut fabric in top of duct and insert flaps that surround slot in tray bottom. Insert shank ends of 1" eye bolts (Fig. 3A) into tray anchors and secure tray to main post crosspiece with two $\frac{1}{4}$ " nuts. Sew fabric to flaps. Position cage in tray, making sure it fits snugly but is loose enough to service from ground.

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BIOLOGY AND IMMATURE STAGES OF
POLIA LATEX (GUENÉE) (NOCTUIDAE)

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ABSTRACT. *Polia latex* was studied from 1984-86 at Cooper's Rock State Forest in northern West Virginia as well as under laboratory conditions. Adult flight period was from 24 May to 29 August and larvae were collected from 21 June to 2 October. Thirteen host plants and 14 species of parasites were recorded for *P. latex* larvae. The egg and seven larval instars are described. Larval duration averaged 45.3 days at 24°C.

Additional key words: hardwood defoliator, West Virginia, parasites, Hadeninae.

Polia latex (Guenée) is a common hadenine (Noctuidae, Hadeninae), the adults of which are well known and easily recognized. The adults fly from May to August with melanics being common (Covell 1984). The immature stages are less well known.

Larvae are found from early June to mid-August with a peak in early August (Prentice 1962). Brief descriptions of larvae were given by Crumb (1956) and Godfrey (1972). Godfrey figured the head, hypopharyngeal complex, and mandible and illustrated habitus of the mature larva.

According to Crumb (1956), the distribution of *P. latex* is restricted to the northeast United States and adjoining Canada. Smith (1893) recorded it from the northern, eastern, and middle states.

During 1984-86 *P. latex* was studied at Cooper's Rock State Forest in northern West Virginia, just west of the leading edge of the infestation of the gypsy moth, *Lymantria dispar* (L.) (Lymantriidae). The objective of the study was to obtain baseline data for native lepidopterous defoliators and their parasites before the build-up of gypsy moth to enable evaluation of changes in native defoliator populations later as the gypsy moth population increases. During this study, *Polia latex* was one of the more abundant defoliators, but was producing no significant defoliation. Since little information is available on the biology of *P. latex*, we recorded duration of larval development, host plants, and parasites of this species. Voucher specimens are in the West Virginia University Arthropod Collection.

MATERIALS AND METHODS

The West Virginia University Forest at Cooper's Rock State Forest is located in Preston and Monongalia counties about 32 km east of Morgantown, West Virginia. The area consists of 50- to 60-year-old even-aged mixed mesophytic forest and has a mean elevation of 561 m (Carvell 1983). The most abundant tree species in the study area are red maple (*Acer rubrum* L., Aceraceae), white and red oak (*Quercus alba* L., *Q. rubra* L., Fagaceae), black cherry (*Prunus serotina* Ehrh., Rosaceae) and black birch (*Betula lenta* L., Betulaceae).

The flight period of *Polia latex* was determined by blacklight trapping throughout the 1984 and 1985 seasons. A single gravid *P. latex* female was live-trapped at a blacklight trap and caged with foliage of maple, cherry, birch and oak on which to oviposit; the adult was provided with water and black cherry blossoms as a nectar source.

Larvae were reared in 150 × 25 ml plastic petri dishes. Fresh red maple foliage was placed in clean petri dishes every other day. Larvae were observed daily, and at each instar some larvae were killed in KAAD and preserved in 80% ethanol for head measurements. Pupation was in a layer of moist vermiculite 5 cm deep in quart canning jars. All rearing was conducted at 24°C and 12L:12D photoperiod.

Larval descriptions were based on laboratory reared specimens only. The terminology used is that of Godfrey (1972). Eggs and larval head capsule measurements were made with an ocular micrometer.

Field sampling of *P. latex* larvae was conducted in 1984 and 1985 by pruning foliage samples once each week during the growing season. Foliage sampled was primarily *Acer rubrum*, *A. saccharum* Marsh., *A. saccharinum* L. and *A. nigrum* Michx. f., *Prunus serotina*, *Betula lenta*, *Quercus alba*, *Q. rubra*, *Q. prinus* L. and *Q. velutina* Lam. Some additional host trees were observed during field sampling. During 1986, larvae were sampled by burlap banding black cherry, black birch, red maple, and mixed oaks (45 trees total). All field collected larvae were reared in the laboratory on the appropriate host plants to isolate parasites.

RESULTS

Phenology, Host Plants, and Parasites

Seasonal flight period of *P. latex* during 1984 was from 25 May–29 August; 128 specimens were trapped. In 1985, 79 specimens were collected between 24 May–13 August. Peak trap numbers were on 6 July 1984 and 12 June 1985. Despite the long adult flight period, field collections of larvae indicate that *P. latex* is univoltine.

In 1984, 91 larvae were collected on foliage in the field between 21

June and 13 September; in 1985, 52 larvae were collected between 3 July and 12 September. In 1986, 255 *P. latex* larvae were taken between 11 July and 2 October from burlap bands placed on 45 trees. Thirty-nine percent of the larvae were on birch (7 trees), 24% on black cherry (12 trees), 19% on red maple (13 trees), and 18% on mixed oaks (13 trees). *Polia latex* made up 86% of all lepidopterous larvae found under burlap bands during that time period.

The larvae of *P. latex* are general feeders on deciduous broad-leaved trees; the 13 host species found during this study were: *Acer nigrum*, *A. rubrum*, *A. saccharinum*, *A. saccharum* (Aceraceae); *Betula lenta* (Betulaceae); *Nyssa sylvatica* Marsh. (Nyssaceae); *Magnolia acuminata* L. (Magnoliaceae); *Prunus serotina* (Rosaceae); *Quercus alba*, *Q. prinus*, *Q. rubra*, *Q. velutina* (Fagaceae); and *Sassafras albidum* Nees (Lauraceae). Additional host plants given by other authors include: *Betula nigra* L. (Crumb 1956), *B. lutea* Michx. f. and *B. papyrifera* Marsh. (Betulaceae) (Prentice 1962); *Fagus grandifolia* Ehrh. (Fagaceae) (Covell 1984); and *Ulmus americana* L. (Ulmaceae) (Covell 1984).

Larval instar durations as determined from laboratory rearing are summarized in Table 1; the larval period averaged 45.3 days at 24°C.

Parasites reared from field-collected *P. latex* larvae were: *Hyphantriphaga virilis* (Aldrich & Webber) and *Lespesia stonei* Sabrosky (Diptera: Tachinidae); *Alloplasta suberba* (Provancher), *Eutanyacra improvisa* (Cresson), *Hyposoter fugitivus* (Say), and *Mesochorus pictilis* Holmgren (hyperparasite) (Hymenoptera: Ichneumonidae); *Perilampus* sp. (hyperparasite) (Hymenoptera: Perilampidae); *Eulophus nebulosus* (Provancher), *Euplectrus* sp. and *Enplectrus maculiventris* (Westwood) (Hymenoptera: Eulophidae); *Diolcogaster facetosa* (Weed), *Microplitis hyphantriae* (Ashmead), *Microplitis* sp. and *Meteorus bakeri* C. & D. (Hymenoptera: Braconidae).

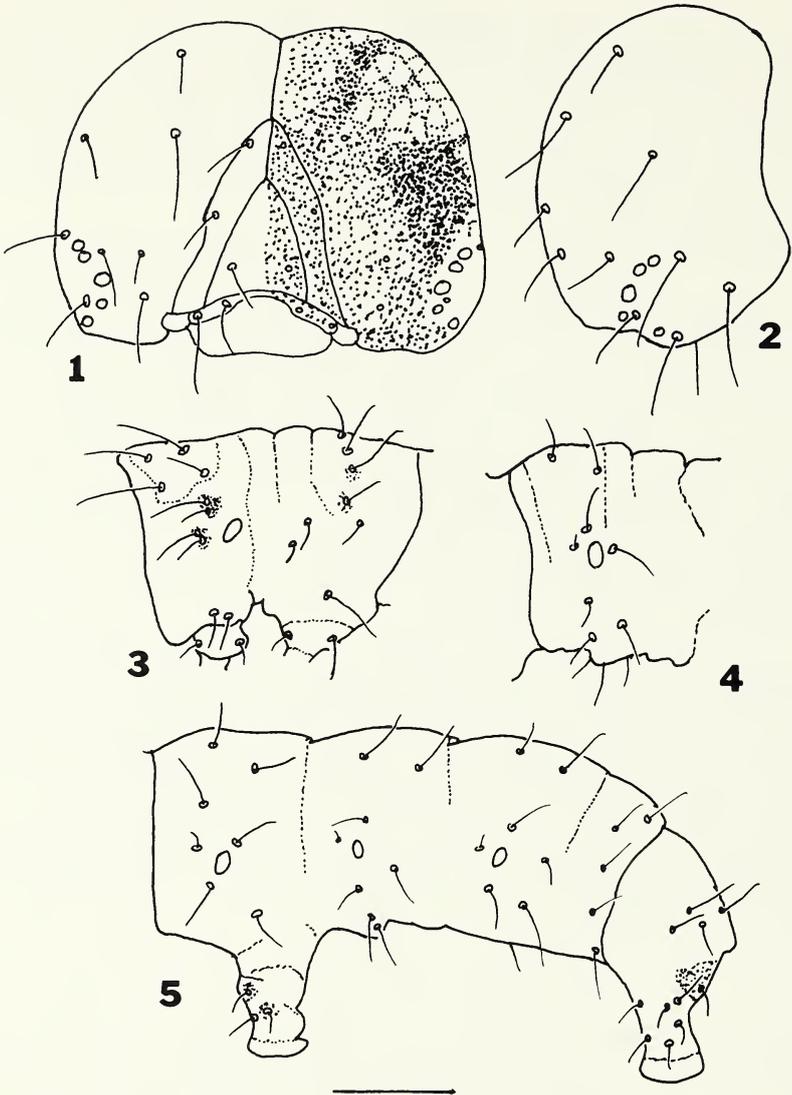
Description of Immature Stages

Eggs: In the laboratory, the caged female oviposited, producing a one-layered egg mass (129 eggs) and a three-layered egg mass (217 eggs). The eggs were spherical in shape, 0.66 mm ($n = 50$) in diameter. One egg observed by scanning electron microscope at 130 \times was sculptured with 37 ridges and paralleled by transverse cross-striae forming hexagons toward the anterior pole and more quadrate shapes toward the posterior; at 650 \times , 16 micropyles were observed at the anterior pole.

Larvae: Instar 1 ($n = 13$): Head capsule 0.36 mm (range 0.33–0.36), light tan. Body ground color transparent to yellowish with gut contents giving a basic green color; pinacula black and prominent. Prolegs on abdominal segments 3 and 4 reduced with the greatest reduction on abdominal segment 3. Prothoracic shield light tan and difficult to distinguish from general body surface; lateral shields of anal prolegs tan and prominent.

Instar 2 ($n = 14$): Head capsule 0.58 mm (range 0.50–0.60), tan. Body ground color yellowish-green. Pinacula prominent.

Instar 3 ($n = 14$): Head capsule 0.97 mm (range 0.90–1.00), tan with black reticulations. Body color variable (olive green, light brown, grey, yellow); dorsal (D), subdorsal (SD),



FIGS. 1-5. *Polia latex*, mature larva: 1, head capsule, frontal view; 2, head capsule, lateral view; 3, prothorax and mesothorax, lateral view; 4, abdominal segment 2, lateral view; 5, abdominal segments 6-10, lateral view. Scale line = 1 mm for Figs. 1-2, 2 mm for Figs. 3-5.

and lateral (L) lines white with the D line being most prominent; the body region between the D and SD lines much darker than the body ground color.

Instar 4 ($n = 16$): Head capsule 1.49 mm (range 1.29-1.72), tan. A black pinaculum around the D1 seta on each segment; abdominal segments 8 and 9 olive green to black, the white D line ending on the anterior half of the 8th abdominal segment.

Instar 5 ($n = 15$): Head capsule 2.24 mm (range 2.00-2.57), with extensive reticulations

TABLE 1. Larval duration of *P. latex* reared on leaves of red maple at 24°C (n = 14).

Instar	Mean time \pm SD (days)
1	5.6 \pm 0.5
2	4.2 \pm 0.6
3	4.5 \pm 1.3
4	5.9 \pm 1.8
5	5.9 \pm 1.5
6	7.0 \pm 3.6
7	10.5 \pm 3.8
Prepupal	3.8 \pm 1.0
Total	47.4 \pm 4.4

and submedial arcs. Body mostly dark green; lateral band creamy yellowish-white and surrounding the lower half of black abdominal spiracles; venter pale green. White D and SD lines still present; area between D and SD lines mottled green and white; area between white SD and L lines dark olive, slightly lighter olive green just below SD line; dorsal dark wedge-shaped markings on abdominal segments and black dorsal bars evident on the 8th abdominal segment.

Instar 6 (n = 14): Head capsule 3.01 mm (range 2.86–3.29); reticulation and submedial arcs similar to those of instar 5. Body dark with D, SD, and L lines mottled white and green; the L line most distinct. Black dorsal bars more evident than in previous instar.

Instar 7 (n = 13): Head capsule 3.65 mm (range 3.29–4.15), dark brown with reticulations covering the entire head. Lateral line consisting of a brown supraspiracular line and a pinkish-peach subspiracular line; prothoracic and abdominal 8 spiracle set completely within supraspiracular line; abdominal spiracles 1–4 and 7 located between the supraspiracular and subspiracular lines and spiracles 5 and 6 completely within subspiracular line.

GENERAL: Body of mature larva 33 mm long and 4 mm wide; prolegs present on abdominal segments 3–6, size increasing caudad; crochets uniordinal, 25–28 per third abdominal proleg, 28 per fourth, 29–31 per fifth, 29–32 per sixth. All setae simple. Chaetotaxy illustrated in Figs. 1–5.

DIAGNOSIS: *Polia latex* larvae may be distinguished from larvae of other *Polia* spp. common in the study area on the basis of color pattern (Crumb 1956, Godfrey 1972). *Polia purpurissata* (Grote) is larger and also differs in being yellow grey or violet grey with obscure markings. The cervical shield, which is shiny brown in *P. purpurissata*, lacks contrast in *P. latex*. *Polia imbrifera* (Guenée) is similar in size but is greyish with distinct black oblique lines from D2 to SD1 on abdominal segments 1–8; these lines are lacking in *P. latex*. *Polia nimbosea* (Guenée) also possesses distinct black oblique lines on abdominal segments as well as a prominent segmental series of black, diamond-shaped middorsal spots. *Polia detracta* (Walker) is smaller with head reticulation darker than that of *P. latex*. The body of *P. detracta* is more reddish and has darker cervical and anal plates than *P. latex*.

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FOOD PLANT SPECIFICITY AND BIOLOGY OF
ITAME VARADARIA (WALKER) (GEOMETRIDAE),
A NORTH AMERICAN MOTH INTRODUCED INTO
AUSTRALIA TO CONTROL THE WEED
BACCHARIS HALIMIFOLIA L.

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ABSTRACT. *Itame varadaria* (Walker) is an infrequently encountered ectophagous, foliage feeding geometrid that occurs from South Carolina to Texas on *Baccharis halimifolia* L. Laboratory studies indicated that the moth completes its development in about 28 days, that there are five larval instars, and that females have an average potential fecundity of 165 eggs. In Texas there are at least three generations per year and there was no evidence of diapause. The moth was reared through a number of generations in the laboratory using cut foliage as a food source. Food plant specificity studies were conducted both in Texas and Australia. Moths were not specific in their oviposition preference under cage conditions but larvae developed only on four species of *Baccharis*. *Itame varadaria* is therefore sufficiently stenophagous for use as a biocontrol agent and approval was granted for its release in Australia.

Additional key words: Texas, Queensland, Asteraceae, fecundity.

The woody shrub *Baccharis halimifolia* L. (Asteraceae: Astereae: Baccharinae), introduced from North America, is a serious weed in Queensland, Australia (Stanley & Ross 1986, Palmer 1987). The Queensland Department of Lands, through the Alan Fletcher Research Station (AFRS), therefore initiated a long-range research program in 1962 to find biological control agents in the New World for release in Australia. This ultimately led to the establishment of the North American Field Station (NAFS) at Temple, Texas, in 1982.

The insect fauna on *B. halimifolia* has been described by Palmer (1987) and Palmer & Bennett (1988). A rather rare geometrid, *Itame varadaria* (Walker) was listed in both these studies and was identified as a possibly monophagous insect that should be investigated further as a biological control agent.

This paper describes the experimental and field observations undertaken to investigate the biology, phenology, and food plant specificity of this moth prior to its release in Australia.

LIFE HISTORY

Eggs were green with a slightly flattened ovoid shape and sculptured exochorion. Mean length and width of the eggs were 0.74 mm (SE = ± 0.02 ; n = 6) and 0.40 mm (± 0.02 ; n = 6) respectively. They were attached to the leaf margin along the longitudinal axis of the egg and

TABLE 1. Life history of *I. varadaria* when reared at 28°C.

Stage	Head capsule width mm (\pm SE; No. obs.)	Larval length range in mm	Development time days	Feeding damage
Egg	—	—	4	—
1st Instar	0.25 (0.01; 11)	2.2–3.3	3	pinholes
2nd Instar	0.44 (0.01; 12)	3.0–6.0	3	pinholes
3rd Instar	0.71 (0.03; 5)	7.0–8.5	1	from margin
4th Instar	1.1 (0.01; 24)	6.0–12.0	3	from margin
5th Instar	1.76 (0.04; 22)	10.0–21.0	6	whole leaf
Pupa	—	—	8	—

were usually oviposited singly or in groups of two or three, rarely in larger clusters.

Larvae developed through five instars before pupation. A cohort of larvae was kept at 28°C in the laboratory and observed daily. First and second instars chewed tiny holes 0.5–1.0 mm in diameter through the epidermis to feed on underlying parenchyma tissue. Later instars fed from the leaf margin inwards. Fifth instars consumed about a leaf a day. Measurements of head capsule width and larval length were made daily on a selection of 4–6 larvae from the cohort and these are given in Table 1 together with the time spent in each development stage. The insect completed its life cycle in approximately 28 days.

The mean head capsule widths for the five instars were consistent with the "Brooks-Dyar" rule (cf. Daly 1985). Relatively constant growth ratios of 0.57, 0.62, 0.65 and 0.63 can be calculated to describe the width of head capsules as a proportion of the width of the following instar.

Pupae were very difficult to sex and it was found more reliable to wait for the emergence of the adult to determine sex. Mean weights were 40 mg (\pm 2; n = 6) and 55 mg (\pm 2; n = 10), for male and female pupae respectively.

Four single pair matings were made by confining pairs of moths in 10 oz. paper cups with moistened raisins. After the death of the female, the eggs in the container were counted, the female dissected and eggs remaining in the abdomen counted. The two counts were added to give an estimate of the total potential fecundity. Mean total potential fecundity was 165 eggs (\pm 20; n = 4). Some 31% of the total egg count remained in the insects' abdomens.

PHENOLOGY AND RANGE

I. varadaria occurs from South Carolina (Ferguson 1973) to Florida (Palmer & Bennett 1988) and along the Gulf Coast to Houston, Texas (Palmer 1987). Its only known larval food plant is *B. halimifolia*. Fer-

guson (1973) noted at least two broods a year with the moths of the spring generation being slightly larger, darker, and less brightly marked than the summer ones.

An area to the west of Beaumont, Texas, was periodically surveyed throughout 1986 and 1987 by sweeping the bushes with a heavy duty net to recover larvae. Larvae were recovered as early as March and were also seen as late as early December. It therefore appeared that there could be up to 6 or 8 generations a year and certainly at least 3 generations per year.

Larvae were never very abundant and numbers showed little variation with season; an hour's sweeping rarely resulted in the capture of more than half a dozen larvae. At such low densities the insect was not adversely affecting the plant.

Because only a few larvae were captured and these by sweeping, no natural enemies were observed nor parasites reared from the immatures.

REARING

A colony was maintained in a laboratory kept at 25–28°C and 40–60% RH for more than four generations with the following procedure. Batches of 10–15 unsexed pupae were placed in 10 oz. paper cups. Emerging moths were offered soaked raisins (or a sugar-water wick) and a piece of fine polyester netting (approx. 20–30 cm²). Moths successfully mated in the cups and then laid most eggs on the netting but some on the cup itself.

Neonate larvae were transferred to bouquets of foliage held in 1 oz. soufflé cups. The foliage of both *B. halimifolia* and *B. neglecta* Britton (a species growing near the NAFS) were equally acceptable. The larvae were transferred to fresh bouquets of foliage twice a week. On completing their growth, fifth instars usually wandered from the foliage before becoming prepupae. Naked pupae were collected from the cage floor and sometimes from the foliage.

An alternative method of rearing was also successful. Moths were released into large cages containing potted plants held in an airconditioned greenhouse. Providing care was taken to replace plants if they were defoliated, this system required little work and pupae or adults could be recovered from the cage regularly.

FOOD PLANT SPECIFICITY TESTING

Oviposition preference. In an experiment with two replicates, mesh cages (62 × 45 × 45 cm) were set up, each containing ten asteraceous species in gallon pots. Three sugar-water wicks were placed in each cage before the release of twelve unsexed moths from the laboratory

TABLE 2. Mean number of eggs oviposited by moths on various species of plants in a multiple choice experiment replicated twice.

Plant species	Eggs (\pm SE)
<i>Baccharis neglecta</i> Britton	20.0 (\pm 8)
<i>Ageratum houstonianum</i> Mill.	0.0
<i>Aster novae-angliae</i> L.	3.0 (\pm 1)
<i>Bellis perennis</i> L.	1.0 (\pm 1)
<i>Callistephus chinensis</i> (L.)	0.0
<i>Chrysanthemum morifolium</i> Rem.	0.0
<i>Conyza canadensis</i> L.	0.0
<i>Dahlia pinnata</i> Cav.	0.0
<i>Parthenium hysterophorus</i> L.	11.0 (\pm 10)
<i>Solidago altissima</i> L.	0.5 (\pm 0.5)
Cage walls	many ($>$ 10)

colony. Four and seven days later, all plants and the cages were very carefully examined using a lighted magnifier and any eggs counted.

Although most eggs were laid on *B. neglecta*, some were also found on other species and on the wire netting of the cages (Table 2). Under these laboratory conditions the insect was not specific in its oviposition behavior. This is not an uncommon finding when Lepidoptera are held in close confinement.

Survival of neonate larvae on cut foliage. These tests, which constituted the most comprehensive component of the food plant testing, were conducted at both the NAFS in Texas and at the AFRS in Australia because many of the plant species were available on only one continent. However, the same procedure was used at both locations. The insect was tested against 6 species of *Baccharis*, 13 genera in the Astereae tribe, 26 genera in 10 other tribes of the Asteraceae and a further 24 genera in 18 other plant families. In all, a total of 72 plant species (Table 3) was tested. Not all plants could be tested simultaneously so they were tested in batches of about 20 plants. *B. halimifolia* was always included as a control with each batch. The plants were randomly selected for each batch but eventually each species was tested at least three times by the following method. Except for a few cases, foliage was taken from different potted plants for each replication.

Five unfed, neonate, laboratory reared larvae were placed in a glass vial with a leaf of one plant species. The vials were observed daily and wilted leaves replaced. Survival was assessed after 72 h and again after 144 h.

Larvae survived for 144 h only on 4 species of *Baccharis*. Mean survival on *B. halimifolia*, *B. neglecta*, *B. pilularis* D.C., and *B. sarothroides* Gray were 70%, 80%, 100% and 50%, respectively, and significant feeding was observed in each case. Almost all larvae on plants

TABLE 3. The plant list against which neonate larvae were tested in a cut foliage, no-choice experiment. Species selected for additional experiments are also indicated (*†).

Anacardiaceae: *Mangifera indica* L.
 Apiaceae: *Apium graveolens* L.
 Asteraceae: **Tribe Astereae:** *Aster novae-angliae* L.*†, *A. novi-belgii* L., *Baccharis bigelovii* Gray, *B. glutinosa* Pers., *B. halimifolia* L.*†, *B. neglecta* Britton†, *B. pilularis* D.C., *B. sarothroides* Gray, *Bellis perennis* L.†, *Brachyscome multifida* D.C.*†, *Calistephus chinensis* (L.) Nees*†, *Calotis cuneata* (F. Muell. ex Benth.) G. L. Davis*†, *Chrysothamnus nauseosus* (Pall.) Britt., *Conyza canadensis* L.†, *C. sumatrensis* (Retz.) E. H. Walker*, *Gutierrezia microcephala* (D.C.) Gray, *Isocoma wrightii* (Gray) Rydb., *Olearia subspicata* (Hook.) Benth.*†, *Solidago altissima* L.†, *Vittadinia sulcata* N. T. Burbidge*†. **Tribe Heliantheae:** *Cosmos bipinnatus* Cav.*†, *Dahlia pinnata* Cav., *D. variabilis* Desf.†, *Eclipta prostrata* (L.) L.*†, *Gaillardia aristata* Pursh†, *Glossogyne tenuifolium* (Labill.) Cass.†, *Helianthus annuus* L.†, *Iva frutescens* L., *Wedelia spilanthis* F. Muell.†, *Zinnia angustifolia* H.B.K.*†. **Tribe Inuleae:** *Cassinia laevis* R. Br.*†, *Gnaphalium sphaericum* Willd.†, *Helichrysum bracteatum* (Vent.) Andr.*†. **Tribe Senecioneae:** *Emilia sonchifolia* (L.) D.C.†, *Flaveria australasica* Hook†, *Senecio laetus* G. Foster ex Willd†. **Tribe Anthemideae:** *Artemisia frigida* Willd., *Chrysanthemum carinatum* Schousb.†, *C. morifolium* Remat, *Cotula australis* (Spreng.) Hook. F.*†. **Tribe Eupatorieae:** *Adenostemma lavenia* (L.) Kuntze†. **Tribe Vernoniae:** *Vernonia cinerea* (L.) Less*†. **Tribe Lactuceae:** *Cichorium intybus* L., *Lactuca sativa* L. **Tribe Cynareae:** *Carthamus tinctorius* L.†, *Cynara scolymus* L.†. **Tribe Calenduleae:** *Calendula officinalis* L.†. **Tribe Tageteae:** *Tagetes lucida* Cav.
 Brassicaceae: *Brassica oleracea* L.
 Caricaceae: *Carica papaya* L.
 Chenopodiaceae: *Beta vulgaris* L.
 Cucurbitaceae: *Cucurbita maxima* Duch.*
 Fabaceae: *Arachis hypogaea* L.*, *Medicago sativa* L., *Phaseolus vulgaris* L.
 Liliaceae: *Allium cepa* L.*
 Malvaceae: *Gossypium hirsutum* L.*
 Myrtaceae: *Eucalyptus* sp.
 Passifloraceae: *Passiflora edulis* Sims.
 Poaceae: *Triticum aestivum* L., *Saccharum officinarum* L., *Sorghum vulgare* L., *Zea mays* L.
 Proteaceae: *Macadamia integrifolia* Maid & Betche.
 Rosaceae: *Fragaria vesca* L.
 Rubiaceae: *Coffea arabica* L.
 Rutaceae: *Citrus sinensis* (L.)
 Solanaceae: *Solanum tuberosum* L., *Lycopersicon lycopersicum* L.
 Vitaceae: *Vitis vinifera* L.

* Potted plants tested against neonate larvae.

† Cut foliage tested against third instar larvae.

other than these four species were dead after 72 h and little evidence of feeding was observed. The exceptions were two larvae on *Cassinia laevis* R. Br. where a little feeding was seen, and one larva each on *Calotis cuneata* (F. Muell. ex Benth.) and *Olearia subspicata* (Hook) Benth. where no evidence of feeding was present.

Survival of neonate larvae on potted plants. To ascertain whether larvae responded similarly on growing plants as they did on cut foliage, neonate larvae were exposed to twenty plant species (Table 3). Two potted plants of each selected species were available and these were

placed in an air-conditioned glasshouse. Ten neonate larvae were placed on the foliage of each plant and a fine mesh bag placed over them to confine them to a limited portion of the plant so that they could be more easily observed and protected from marauding ants. The plants were examined after 4 days and surviving larvae noted.

After 4 days 100% survival and substantial feeding were noted on both *B. halimifolia* plants but no live larvae were found on any other plant. Feeding marks were noted only on one *Cassinia laevis* plant.

Late instar survival on cut foliage. This experiment was conducted to determine if late instar larvae have a wider food plant range than neonate larvae. Neonate larvae were reared on *B. halimifolia* foliage for 10 days at 22°C at which time they were third instars. Five larvae were transferred to foliage of each of 25 species of Asteraceae (Table 3), cuttings of which had been placed in small bottles of water. These cuttings were replaced after three and six days. The experiment was evaluated on the 7th day and live larvae noted.

Survival of larvae on *B. halimifolia* and *B. neglecta* averaged 80% and 100% respectively and extensive feeding occurred. No feeding occurred on any other plant. Soon after their placement on the cuttings, most larvae on plants other than *Baccharis* left the foliage and were subsequently found on the bottom of the containers; most larvae had died by the fifth day and all were dead by the seventh.

DISCUSSION

Itame varadaria was tested very comprehensively against a wide range of plant species with particular emphasis being given to closely related species in the Asteraceae. It was evident that the larval food plant range of this insect is confined to certain species of *Baccharis*. The four species on which *I. varadaria* could be reared (viz., *B. halimifolia*, *B. neglecta*, *B. pilularis*, and *B. sarothroides*) must be phytochemically very similar as other highly stenophagous species tested at the NAFS have had the same host range [e.g., *Prochoerodes truxaliata* (Guenee) reported by Palmer and Tilden (1987)]. *Itame varadaria* is considered to pose no threat to existing flora in Australia.

Of the four plant species acceptable to *I. varadaria* larvae in the laboratory, only *B. halimifolia* grows within the geographic range of this moth. Therefore, environmental factors unsuitable to *I. varadaria* probably explain why *B. neglecta*, *B. sarothroides*, and *B. pilularis* are not natural larval food plants. However, two other species, *B. glomeruliflora* Pers. and *B. angustifolia* Michx., which are closely related to *B. halimifolia* and *B. neglecta*, respectively, do occur within the insect's range and it would not be surprising if they are someday reported as food plants.

There was good agreement between the three feeding tests. Cut foliage experiments are the simplest in design and have the advantage that the insects are kept under maximum supervision. However the question is sometimes raised that the insects may respond differently on growing plants than on cut foliage. Similarly, while the insect can not become established on a plant species if neonate larvae cannot feed on it, there is sometimes concern, particularly with mobile species, that late instar larvae might move onto non-target plants. In this case there was no evidence that late instars had a broader food plant range. The technique of using neonate larvae exposed to cut foliage accurately determined the food plant range for this insect.

Although *I. varadaria* is not abundant in its native habitat, it has a number of useful characteristics that might make it an effective agent. It has a relatively short life cycle, is quite fecund, is easily reared in the laboratory, occurs in areas with similar climates to southeastern Queensland, and apparently has no diapause mechanism. Its success will probably depend on the predation rate in its new environment.

RELEASE IN AUSTRALIA

Permission to release *I. varadaria* in Queensland was granted in December 1988 by the Australian Quarantine and Inspection Service and the Australian National Parks and Wildlife Service, which administer the Quarantine Act of 1908 and the Wildlife Protection Act of 1982, respectively. The insect was then moved out of quarantine facilities at the AFRS and a mass rearing program commenced.

It is anticipated that the first field releases will be made in spring of 1989. Moths will be released at a number of sites in southeast Queensland over the following twelve months. In some situations the moths will be released into cages covering *B. halimifolia* bushes to give some measure of protection against predators to the establishing colony.

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GENERIC REASSIGNMENTS FOR NEOTROPICAL TORTRICID MOTHS (TORTRICIDAE)

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ABSTRACT. Based on current studies of neotropical tortricine moths, I propose generic reassignments for 20 species, comprising 18 Euliini (Tortricinae), 1 Chlidanotini (Chlidanotinae), and 1 Eucosmini (Olethreutinae), and identify characters that support the new combinations.

Additional key words: Tortricinae, Euliini, Chlidanotini, Eucosmini, hairpencil.

Although nearly all species of Holarctic Tortricinae can be placed confidently within our current generic and tribal framework (Powell 1983, Razowski 1987a), a comparable system for the neotropical fauna has not yet been realized. The most significant contribution toward this goal is Powell's (1986) synopsis of the classification of the Neotropical Tortricinae, in which all described genera are assigned to tribal categories compatible with those of the Nearctic and Palearctic faunas. However, nearly 30% of neotropical species lack meaningful generic assignments, and a large portion of the fauna is still undescribed. Through the efforts of Razowski (1982, 1986a, 1987b, 1987c, 1988) and Powell (1986), a generic framework is emerging, providing categories to which previously "unplaced" species can be assigned. The purpose of this paper is to transfer 20 neotropical species described prior to 1930 in broadly defined, polyphyletic genera, such as *Eulia* Hübner and *Tortrix* Linnaeus, into well-defined, monophyletic genera. This will provide appropriate generic combinations, and rationalizations for such, for a forthcoming checklist of the Neotropical Tortricinae (Powell & Razowski 1989).

Depositories abbreviated in the text are as follows: BMNH, British Museum (Natural History), London, England; CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; NHMV, Naturhistorisches Museum Vienna, Austria; UCB, Essig Museum of Entomology, University of California, Berkeley; USNM, United States National Museum of Natural History, Washington, DC.

TORTRICINAE: EULIINI

Seticosta Razowski

Seticosta was described by Razowski (1986a) to accommodate *Eulia archnogramma* Meyrick, *Eulia tholeraula* Meyrick, and *Eulia homo-sacta* Meyrick. Males are characterized by elongate antennal cilia (1.5-2.0 × segment diameter), a foreleg hairpencil (Brown 1989), narrow

or subbasally constricted valvae, and a dense patch of long, spine-like setae on the subbasal region of the costa of the valva. The latter character appears to provide the most convincing synapomorphy for the genus. Females have long, narrow apophyses, slender papillae anales, an elongate, slender ductus bursae, and an accessory bursa arising from the ductus bursae, unassociated with the ductus seminalis that usually arises from the corpus bursae.

***Seticosta aeolozona* (Meyrick), new combination**

Eulia aeolozona Meyrick, 1926, Exotic Microlepidoptera 3:252; Clarke, 1958, Cat. Type Spec. Microlep. Brit. Mus. Descr. Meyrick 3:116.

The male holotype (BMNH) lacks the abdomen, prohibiting genitalic comparison. However, *aeolozona* is extremely similar to several undescribed species of *Seticosta* (BMNH, USNM) in forewing shape, size, and pattern. The holotype possesses a foreleg hairpencil consistent with other species in the genus.

***Seticosta hypsithrona* (Meyrick), new combination**

Eulia hypsithrona Meyrick, 1926, Exotic Microlepidoptera 3:251; Clarke, 1958, Cat. Type Spec. Microlep. Brit. Mus. Descr. Meyrick 3:128.

The holotype male (BMNH) can be assigned to *Seticosta* on the basis of the long, spine-like setae on the subbasal portion of the costa of the valva, the narrow valva, the elongate labial palpi, and the long (1.5× segment diameter) antennal cilia.

***Seticosta mirana* (Felder and Rogenhofer), new combination**

Tortrix mirana Felder and Rogenhofer, 1875, Reisse Novara, pl. 139:24.

The holotype (BMNH), reported to be a male from Venezuela, is a female. In the genitalic preparation (BMNH slide no. 7811), the corpus bursae has a pair of small triangular signa, indicating that this species should be assigned to the Laspeyresiini (Olethreutinae). However, I dissected an identical female (Venezuela, Aragua, Colonia Tovar, 6000–7000', Holt C. M. Exped.; CMNH) and found the genitalia to be consistent with other species of *Seticosta*, i.e., long, slender apophyses and narrow papillae anales, and the presence of an accessory bursa unassociated with the ductus seminalis. The female genitalia on BMNH slide no. 7811 evidently are associated incorrectly with the holotype of *mirana*. *Seticosta mirana* is superficially similar to other large species in the genus (e.g., *arachnogramma* and several undescribed species [USNM]). A male from Rio de Janeiro (BMNH) has elongate labial palpi, long antennal cilia, and a foreleg hairpencil. It lacks the abdomen, prohibiting genitalic comparison.

***Seticosta multifidana* (Zeller), new combination**

Teras multifidana Zeller, 1877, Exotische Microlepid., Hot. Soc. Entomol. Ross. 13:47, fig. 29.

This species is represented only by the holotype female (BMNH) collected in Bogotá. Although the genitalia (BMNH slide no. 8588) are fairly divergent from other species in the genus, particularly the sparsely setose, crescent-shaped papillae anales and the sclerotized patch of the corpus bursae, *multifidana* is similar to other species of *Seticosta* in the general configuration of the female genitalia and in superficial facies. Three males from Carabaya and Cuzco, Peru, are associated with the holotype (BMNH); although similar, they probably are not conspecific with *multifidana*. The males possess several features typical of *Seticosta*, namely elongate labial palpi, long antennal cilia, foreleg hairpencil, and the unusual patch of spine-like setae on the costa of the valva (BMNH slide no. 8767).

***Seticosta sagmatica* (Meyrick), new combination**

Eulia sagmatica Meyrick, 1912, Trans. Entomol. Soc. London 1911:680; Clarke, 1958, Cat. Type Spec. Microlep. Brit. Mus. Descr. Meyrick 3:136.

The holotype male (BMNH) from Colombia can be unambiguously assigned to *Seticosta* on the basis of the spine-like setae on the subbasal region of the costa of the valva (JFGC slide no. 6217). Other features are consistent with this association, including elongate labial palpi, long antennal cilia, and male foreleg hairpencil.

***Seticosta versabilis* (Meyrick), new combination**

Eulia versabilis Meyrick, 1926, Exotic Microlepidoptera 3:251; Clarke, 1958, Cat. Type Spec. Microlep. Brit. Mus. Descr. Meyrick 3:143; Razowski, 1986, Bull. Polish Acad. Sci., Biol. Sci. 35:70.

Although superficially similar to some Chlidanotini (Razowski 1986b), the female genitalia of *versabilis* are consistent with those of other species of *Seticosta*. The apophyses are long and slender, the papillae anales are narrow, the ductus bursae is long and slender and bears an accessory bursa from the ductus bursae unassociated with the ductus seminalis. In addition to the female holotype from Bolivia (BMNH), there are two females and a male from Carabaya, Peru (BMNH), that are almost certainly conspecific with *versabilis*.

Inape Razowski

Inape was described by Razowski (1988) to accommodate *Eulia birem* Meyrick and the type species, *Inape penai* Razowski. Synapomorphies include a pair of blunt, digitate processes submedially from

the transtilla in the male, and complex signa in the female with a longitudinally arranged, strongly spined signum and a large, marginally dentate, more caudal signum. In some species one of the two signa is reduced. Males of all species have a well developed foreleg hairpencil (Brown 1989).

***Inape auxoplaca* (Meyrick), new combination**

Eulia auxoplaca Meyrick, 1926, Exotic Microlepidoptera 3:255; Clarke, 1958, Cat. Type Spec. Microlep. Brit. Mus. Descr. Meyrick 3:119.

I. auxoplaca is represented by the holotype male only (BMNH). The unique modification of the transtilla (JFGC slide no. 6348) provides evidence for its inclusion in *Inape*. In addition, the genitalia share many symplesiomorphies with other species in the genus, e.g., large upturned valvae with broadly rounded apex, short, stout aedeagus with two stout cornuti, and unmodified uncus, gnathos and socius. *I. auxoplaca* also is similar to other species in the genus in superficial facies. Given the sexual dimorphism exhibited by several species of *Inape*, it is possible that *auxoplaca* represents the male of *I. biremis*; both were collected at Mt. Tolima, Colombia, in October 1920.

***Inape iantha* (Meyrick), new combination**

Cnephasia iantha Meyrick, 1912, Trans. Entomol. Soc. London 1911:684.

Eulia iantha; Clarke, 1958, Cat. Type Spec. Microlep. Brit. Mus. Descr. Meyrick 3:131.

I. iantha is represented by the holotype female (BMNH) and a second female (USNM; same data as holotype). The characteristic longitudinal signum with elongate spines confirms its membership in *Inape*. The second signum is reduced to a patch of slender, parallel spines.

***Inape xerophanes* (Meyrick), new combination**

Tortrix xerophanes Meyrick, 1909, Trans. Entomol. Soc. London 1909:15.

Eulia xerophanes; Clarke, 1958, Cat. Type Spec. Microlep. Brit. Mus. Descr. Meyrick 3:143.

I. xerophanes was described from a single male taken in Aqualani, Peru (BMNH). It is assigned to *Inape* on the basis of the digitate submedial processes from the transtilla, the most convincing male synapomorphy for the genus. It also shares many symplesiomorphies with its congeners, including the upturned valva with broadly rounded apex, stout aedeagus with two slender cornuti, and unmodified uncus, gnathos and socius. A female specimen (BMNH) from Santo Domingo, Peru, appears to be conspecific with the holotype. The genitalia of the female (BMNH slide no. 8857) are typical of the genus.

***Inape zelotypa* (Meyrick), new combination**

Eulia zelotypa Meyrick, 1912, Trans. Entomol. Soc. London 1911:679; Clarke, 1958, Cat. Type Spec. Microlep. Brit. Mus. Descr. Meyrick 3:143.

I. zelotypa was described from 15 specimens that appear to represent at least three species (BMNH), all of which can be referred to *Inape*. The two new species will be described in a revision of the genus (Brown, in prep.). In *I. zelotypa* the digitate submedial processes of the transtilla are extremely elongate, but other features of the genitalia (viz., valvae, uncus, gnathos, socii, aedeagus) are consistent with other species of *Inape*. In addition to the foreleg hairpencil, males of *I. zelotypa* have an additional hairpencil arranged longitudinally along the costa of the hindwing, densely covered by black scales. Three males (BMNH) of a closely related undescribed species, included in the type series, have both the foreleg and hindwing hairpencil, but lack the patch of black scales on the hindwing.

***Clarkenia* Razowski**

Clarkenia was described by Razowski (1988) to accommodate *C. superba* Razowski and *C. miramunda* Razowski. Adults are large, brightly colored, somewhat checkered moths. Males have large valvae, short, oval socii, a long, narrow uncus, and two patches of distinctly different types of cornuti in the vesica of the aedeagus; they lack the foreleg hairpencil. Females have narrow, nearly parallel-sided papillae anales, a short, slender ductus bursae, and an elongate corpus bursae.

***Clarkenia lacertana* (Zeller), new combination**

Sciaphila lacertana Zeller, 1866, Stett. Entomol. Z. 27:151.

Eulia lacertana; Meyrick, 1926, Exotic Microlepidoptera 3:249; Clarke, 1958, Cat. Type Spec. Microlep. Brit. Mus. Descr. Meyrick 3:140.

Although the holotype is apparently lost, two males, one from Colombia and one from Venezuela, match the description of *lacertana*, and are identified as such in the collection of the BMNH. The specimens are similar to other species of *Clarkenia* in superficial facies and characters of the genitalia.

***Clarkenia nivescens* (Meyrick), new combination**

Eulia nivescens Meyrick, 1926, Exotic Microlepidoptera 3:250; Clarke, 1958, Cat. Type Spec. Microlep. Brit. Mus. Descr. Meyrick 3:132.

C. nivescens is represented by the holotype male (BMNH) collected on Mt. Tolima, Colombia. The species is transferred to *Clarkenia* on the basis of the similarity of the valvae, socii, uncus, and cornuti, to those of *C. superba*. The two species also are superficially similar. *C.*

nivescens differs from *superba* in its uniquely modified gnathos with elongate lateral processes.

***Clarkenia trilobopa* (Meyrick), new combination**

Eulia trilobopa Meyrick, 1926, Exotic Microlepidoptera 3:249.

Eulia triloba (misspelling) Clarke, 1958, Cat. Type Spec. Microlep. Brit. Mus. Descr. Meyrick 3:140.

C. trilobopa was described from a single male (BMNH) from Rio Grande do Sul, Brazil. The holotype is lacking the abdomen. Although slightly smaller in forewing length, *C. trilobopa* is extremely similar in superficial facies to other species in the genus. The holotype lacks the foreleg hairpencil. In his description of *Eulia trilobopa*, Meyrick (1926) indicated that it was "allied" to *lacertana*; both species herein are transferred to *Clarkenia*. Razowski (1988) recognized the similarity of *trilobopa* to *Clarkenia superba*, but incorrectly interpreted the figure of *trilobopa* in Clarke (1958, pl. 70) as that of *Eulia trapezoides* Meyrick. Consequently, he did not include *trilobopa* in *Clarkenia* because the genitalia of *trapezoides* (which he believed belong to *trilobopa*) were dissimilar to other species of *Clarkenia*.

Ernocornutia Razowski

Ernocornutia was described by Razowski (1988) to accommodate *E. catopta* Razowski and *E. capronata* Razowski. Males are characterized by the strong, slender sacculus reaching about three-fourths the distance from the base to the apex of the valva, capitate uncus, and a small funnel-shaped cornutus; all known species possess the male foreleg hairpencil (Brown 1989).

***Ernocornutia carycodes* (Meyrick), new combination**

Eulia carycodes Meyrick, 1926, Exotic Microlepidoptera 3:256; Clarke, 1958, Cat. Type Spec. Microlep. Brit. Mus. Descr. Meyrick 3:120.

E. carycodes is represented by the holotype male (BMNH) from Mt. Tolima, Colombia. It is similar to *E. catopta*, also from Colombia, in several features, namely the narrow portion of the valva extending beyond the sacculus, widely separated, distal processes from the gnathos, and the general configuration of the aedeagus. *E. carycodes* can be distinguished from *E. catopta* by the broad dorsal portion of the tegumen and by the presence of slender teeth-like cornuti in the distal portion of the vesica.

Silenis Razowski

Razowski (1987) described *Silenis* for the single Bolivian species *S. senilis* Razowski, known only from the male holotype (USNM). Several

undescribed congeners are represented in the collections of the BMNH, USNM, and UCB.

***Silenis eurydice* (Butler), new combination**

Sericoris eurydice Butler, 1883, Trans. Entomol. Soc. London 1883:72.

The holotype male (BMNH) from Chile lacks the abdomen preventing genitalic comparison. However, in superficial facies, *S. eurydice* is nearly identical to several undescribed species (BMNH, USNM) that are clearly congeneric with *Silenis senilis*.

***Proeulia* Clarke**

Prior to the description of *Proeulia boliviae* (Razowski 1988), the genus was considered restricted to Chile and its offshore islands. Clarke (1962) described the genus for two species from Juan Fernandez Islands, Obraztsov (1964) added nine species from central Chile, and Clarke (1980) described two additional species from San Ambrosio Island. Males have broad valvae with an upturned costa and a narrow sacculus, short antennal cilia, a short, stout aedeagus with several large cornuti, and a foreleg hairpencil. Females are characterized primarily by sympletiomorphies, except for the short, broad ductus bursae, and the unusual signum consisting of a nearly circular sclerotized patch bearing a short, blunt thorn.

***Proeulia hypochloris* (Meyrick), new combination**

Eulia hypochloris Meyrick, 1932, Exotic Microlepidoptera 4:256; Razowski, 1964, Polska Akad. Nauk, Ann. Zool. 22:459.

Eulia hypochloris (holotype NHMV), which occurs from Costa Rica to Brazil (USNM), is almost certainly congeneric with *Proeulia boliviae*, to which the male genitalia are extremely similar. The female of *hypochloris* lacks the signum and the male lacks the foreleg hairpencil. The inclusion of *hypochloris* and *boliviae* in *Proeulia* significantly broadens previous concepts of the genus both morphologically and biogeographically; hence, it is possible that *hypochloris* and *boliviae* represent an undescribed genus closely related to *Proeulia*. Consequently, the assignment of these species to *Proeulia* may represent only an interim solution.

***Proeulia dives* (Butler), new combination**

Oenectra dives Butler, 1883, Trans. Entomol. Soc. London 1883:68.

The name *dives* is listed as a synonym of *Cnephasia fulvaria* Blanchard in the collection of both the BMNH and USNM. I examined the

holotype of *dives* (BMNH), but I have been unable to locate the holotype of *C. fulvaria* to confirm the synonymy. Powell and Razowski (1989) assign *fulvaria* to *Proeulia*. The holotype of *dives* from Chile was reported to be male; it is a female. The genitalia of the holotype and two additional females (BMNH slides no. 7806, 8766, 8702) are similar to other species of *Proeulia*. Although the single male from Valparaiso, Chile (BMNH), matches the holotype in superficial facies, the genitalia differ from other species of *Proeulia* in the spined transtilla, weakly dentate gnathos, and absence of cornuti; the specimen lacks the foreleg hairpencil. These characters are fairly divergent from other *Proeulia* and either represent autapomorphies for the species, or evidence that a new genus may be required for *dives*. Consequently, the transfer of *dives* (and possibly *fulvaria*) to *Proeulia* is provisional.

Bonagota Razowski

Bonagota was described by Razowski (1986a) for *Sciaphila bogotana* Zeller (Colombia), *Ptherochroa cranaodes* Meyrick (Argentina), *Eulia melanecta* Meyrick (Ecuador), *Cryptolechia penthinella* Zeller (Colombia), and *Eulia salubricola* Meyrick (Argentina). The genus is remarkably homogenous in superficial facies, and extremely similar to *Apotomops* Powell. *Bonagota* and *Apotomops* appear to be sister taxa on the basis of the unique, slightly attenuate, accessory pouch from the ductus bursae, and the similarity in wing venation (Powell 1986). The male genitalia of both genera are characterized primarily by sympleiomorphies. The valvae are large, weakly deflexed medially in the distal third (inconspicuous in slide mounted preparations), and usually with a distinctly sclerotized, strongly-arched costa. In *Bonagota* the male antennal cilia and the uncus are unmodified, and the socii are moderately digitate. In *Apotomops* the antennal cilia are extremely short, the uncus is broadly capitate with a large basal expansion, and the socii are greatly reduced and nearly entirely fused to the gnathos.

Bonagota wilkinsonii (Butler), new combination

Sericoris wilkinsonii Butler, 1883, Trans. Entomol. Soc. London 1883:41.

The holotype of *B. wilkinsonii* (BMNH) lacks the abdomen, but is superficially similar to other species of *Bonagota*. A specimen matching the holotype (BMNH) has genitalia that share many sympleiomorphies with other species of *Bonagota*. They are also similar to "*Acleris*" *crocoptycha* (Meyrick) from Argentina, and "*A.*" *acmanthes* (Meyrick) from Chile, which appear to be congeneric with each other, and unrelated to the genus *Acleris* (Tortricini).

CHLIDANOTINAE: CHLIDANOTINI

Monortha Razowski and Becker

Monortha was described in the Polyorthini for the species *M. funesta* Razowski and Becker and *M. corusca* (Meyrick), known only from males (Razowski and Becker 1981). Razowski (1986b) transferred the genus to the Chlidanotini on the basis of the female genitalia, which share several uniquely derived characters with other Chlidanotini, viz., strong setae on the sterigma, ductus seminalis from near the junction of the corpus and ductus bursae, a unique accessory bursa from near the middle of the corpus, and the unusual "asteroid" signum of long spines. *Monortha* is distinguished from other chlidanotines by the following male genitalic characters: socii and hami fused, with stout, spine-like setae, and similar spine-like setae from the venter of the uncus.

***Monortha illaqueata* (Meyrick), new combination**

Capua illaqueata Meyrick, 1917, Trans. Entomol. Soc. London 1917:6.

Capua illaqueata (misspelling) Clarke, 1958, Cat. Type Spec. Microlep. Brit. Mus. Descr. Meyrick 3:71.

This species is represented only by the holotype female from French Guiana (BMNH). The heart-shaped configuration of the papillae anales, strong setae on the posterior edge of the sterigma, position of the ductus seminalis, and putative possession of an accessory bursa, indicate that *illaqueata* should be assigned to *Monortha*. The signum is greatly reduced to a patch of concentric, dimple-like sclerites, and the accessory bursa is lacking in the genitalic slide (JFGC 6289), hence its position in the Chlidanotini has not been recognized previously. Vestiges of the ductus of the accessory bursa are present, and the dimple-like modification of the signum is seen to a lesser degree in other Chlidanotini. In superficial facies *illaqueata* is most similar to *M. corusca* (holotype BMNH).

OLETHREUTINAE: EUCOSMINI

***Eucosma torrens* Meyrick, revised status**

Eucosma torrens Meyrick, 1927, Exotic Microlepidoptera 3:334.

Eulia torrens; Clarke, 1958, Cat. Type Spec. Microlep. Brit. Mus. Descr. Meyrick 3:140.

The holotype of *torrens* (BMNH) lacks the abdomen. Clarke (1958) transferred the species to *Eulia* on the basis of its superficial similarity to other Neotropical species assigned to this large, polyphyletic genus. However, the genitalia of an undescribed species (USNM) superficially nearly identical to *torrens* indicate that the two are obviously olethreutines, probably referable to the Eucosmini.

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NEOEROMENE LUTEA
(LEPIDOPTERA: PYRALIDAE; CRAMBINAE),
A NEW SPECIES FROM BRAZIL

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ABSTRACT. *Neoeromene lutea*, a new species of diptychophorine Crambinae, is described from three specimens from southern Brazil, raising the number of known species in this genus to seven. *Neoeromene lutea* shares juxtal apomorphies with *N. straminella* (Zeller), also of Brazil, but has less development in the costal region of the valva and in the apical sclerotization of the aedeagus.

Additional key words: *Neoeromene straminella*, Santa Catarina.

The neotropical Crambinae assigned to *Pareromene* Osthelder by Błeszyński (1967) were recently transferred to new genera, one of them *Neoeromene* (Gaskin 1986). To prove the well-known unwritten rule that a tidy revision of a taxonomic group is by far the best way to stimulate discovery of all that other material the author missed, Julian Donahue contacted me immediately and drew my attention to three specimens from Brazil, taken by E. D. Jones, in the collection of the Natural History Museum of Los Angeles County. This paper describes these, which are conspecific and represent the only known specimens of a hitherto unrecognized species of *Neoeromene*. The name *lutea* is applied, with reference to the brilliant yellow-orange ground color of the forewings. In the description, decimals indicate the position of a feature, as a proportion of the total length of a structure or organ. In the forewing, measurements along the costa are from the base, on the termen from the apex, and along fascia from the costa. In the male genitalia they are from the base of each structure.

Neoeromene lutea, new species

(Fig. 1)

Description. Forewing length 7.5 mm (N = 3). Head and thorax bright yellow, latter with a black ring of scales anteriorly, patagia with a few scattered, large dark spots. Labial and maxillary palpi pale yellow with blackish apices. Abdomen pale brown with some scattered yellow scales, legs pale yellow banded with brown. Antennae with small bipectinations and no macroscopic sexual differences. Male frenulum single, female double. Ground color of forewings bright yellow, including apical and subterminal regions. Basal region with three blackish brown spots in an oblique line towards base of antemedial fascia which is at 0.4 from base, dark brown, narrow and tridentate in the form of a crude Greek letter ξ . There is a small brown streak on the costa at 0.5 and some variable dark streaks of scales in the reniform region of the disc. Postmedial fascia double, a pair of brown waved lines with a few lustrous silvery scales between them from costa to about 0.3, fascia then diverging towards dorsum, proximal line dentate at 0.8 from costa. There are three brown spots on the termen from 0.5-0.8. Apical zone contains a narrow, elongate,



FIG. 1. *Neeromene lutea* n.sp. Male paratype from Santa Catarina, Brazil, and below, female paratype, unlabelled but from the same series in the Natural History Museum of Los Angeles County.

oblique silvery white streak from the costa, not reaching the termen. Subapical indentation present at 0.3 from apex, and a secondary indentation at 0.5, with some silvery scaling not quite reaching postmedial fascia. Ventral surfaces brownish, with apical and termen markings repeated from dorsal surface. Hindwings lustrous off-white in both sexes, with

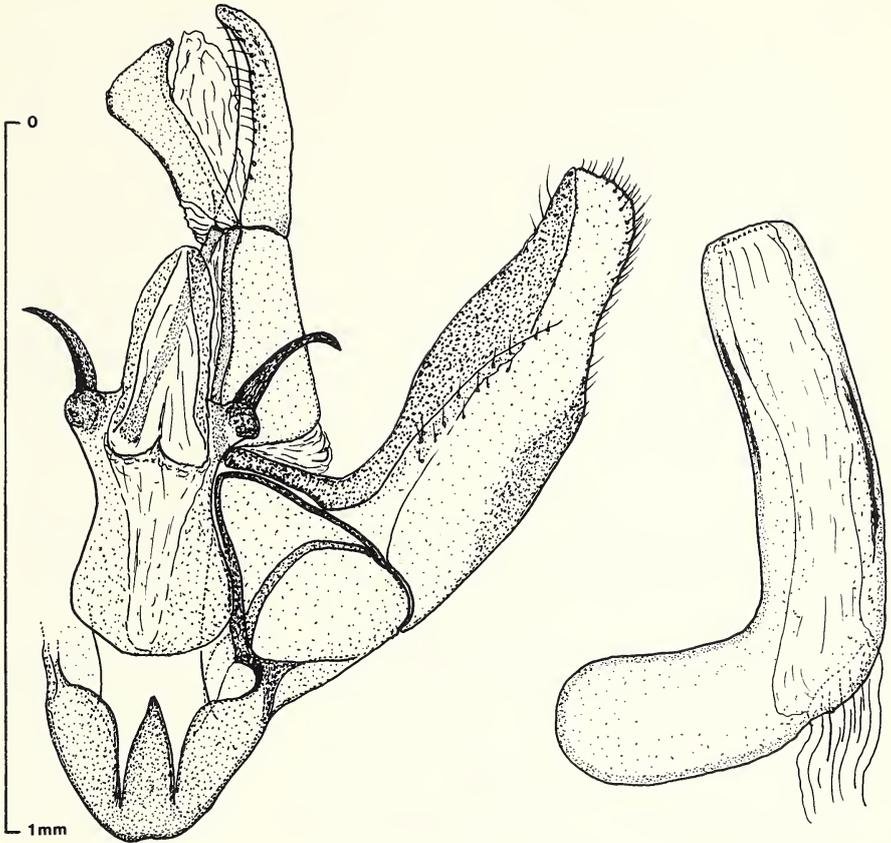


FIG. 2. *Neeromene lutea*. Male holotype. Genitalia in posterior aspect, with left valva not shown (left) and aedeagus (right).

white cilia with brown bases, giving the appearance of a double brown marginal line. The cilia of the forewings are lustrous gray-brown.

Male genitalia (Fig. 2) ($N = 1$). Uncus curved, with blunt apex; gnathos slightly shorter than uncus, curved dorsad with apical region significantly swollen, bluntly pointed; tegumen squat with strong posterior margins; saccus broadly rounded, vinculum broadly triangular. Juxta a large complex structure, with a spatulate apex equal in length to uncus, and a broadly rounded basal region, the whole about $2 \times$ uncus; below apical area a pair of lateral swellings each have a sharp prong, about $0.5 \times$ uncus, curved extrorse. Valva about $2-2.5 \times$ uncus [depending how measured, basally or along costa] with a sclerotized costal region reaching the bluntly rounded apex. Aedeagus about $1.3 \times$ length of valva, sharply curved ventrad in proximal third, with a pair of elongate lateral striations and some minute apical spines.

Types: Holotype δ ; without label but probably same as for paratype male. Paratypes: 1 δ , BRAZIL, Santa Catarina, -4.1922, E. D. Jones; 1 ♀ without label. Both paratypes lack their abdomen. Consequently, the only specimen with an abdomen has been designated as holotype, even though it has no locality label.

Discussion. *Neoeromene lutea* resembles *N. straminella* (Zeller) in most major forewing characters, but the yellow-orange ground colour and the dark, strongly marked fascia immediately distinguish the former species. There is little variation between the three specimens examined. Like *N. straminella*, *N. lutea* has a proportionately huge, apically bicornuate juxta. The form of the valva in both species is almost identical except that *N. straminella* has a basal prong. Both differ from all other species in the genus except *N. felix* (Meyrick) in having virtually no sclerotization in the sacculus of the valva. *Neoeromene lutea* has the least apical sclerotization of the aedeagus in the genus, represented only by a row of microscopic prongs. The apically swollen gnathos and the blunt, setulose uncus closely resemble those of *N. parvipuncta* Gaskin, also of Brazil. The early stages, food plants and duration of the flight period (which included April), are unknown.

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I thank Julian P. Donahue, Natural History Museum of Los Angeles County, for bringing this material to my attention and arranging the loan, and two anonymous reviewers for constructive criticism.

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GENERAL NOTES

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DISCOVERY OF THE CARPENTER MOTH *MORPHEIS CLENCHI* (COSSIDAE) IN MEXICO

Additional key words: Zeuzerinae, Sierra Madre Occidental.

When I described *Morpheus clenchi* (Cossidae: Zeuzerinae) from southern Arizona (Donahue, J. P. 1980, *J. Lepid. Soc.* 34(2):173-181), I predicted that this large, striking, sphingid-like carpenter moth would undoubtedly be found in adjacent México. This prediction has been confirmed as a result of field work by members of the Sonoran Lepidoptera Survey, in cooperation with Sonoran Arthropod Studies, Inc. (SASI) of Tuscon, Arizona, and by Terry A. Sears et al., whose extensive moth collections from the Barrancas del Cobre ("Copper Canyon") region of the Sierra Tarahumara, Sierra Madre Occidental, are deposited in the Bohart Museum of Entomology, University of California, Davis (UCD). I thank Steve Prchal of SASI and R. O. Schuster and Adam Porter of UCD for loaning the specimens reported on here.

I have now examined 11 adult male specimens of *Morpheus clenchi* from the Mexican states of Sonora, Sinaloa, and Chihuahua, and which have been deposited in the following institutions: SASI, UCD, Natural History Museum of Los Angeles County (LACM), and Instituto de Biología, Universidad Nacional Autónoma de México, México, D.F., México (UNAM). Seven localities are represented, all west of the continental divide in the Sierra Madre Occidental; they are listed from north to south. Localities not readily found on road maps are annotated. The female and the larval food plant of this species remain unknown.

SONORA: ¼ mi (0.4 km) E of Rancho El Encino, elev. 3600 ft (1097 m), 29 July 1983, Steve Prchal (1 ♂ SASI, 1 ♂ LACM). [This locality is in the Sierra La Madera between Moctezuma and Huasabas, approx. 29°50'N, 109°20'W.]

SONORA: 17 mi (27 km) W of Moctezuma, to U.V. [light], 20 July 1984, Doug Mullins (1 ♂ LACM).

SONORA: 13 mi (21 km) E of El Novillo, Study Canyon, elev. 3600 ft (1097 m), 3-4 Aug. 1983, Steve Prchal (1 ♂ SASI, 1 ♂ UNAM). [This locality is in the Sierra La Campanera between Mazatán and Bacanora, approx. 29°00'N, 109°30'W.]

SONORA: Trinidad Mine Canyon, at house, elev. 3425 ft (1044 m), 30 July 1984, Steve Prchal (1 ♂ SASI); same locality and collector, 11-12 Aug. 1983 (1 ♂ SASI, 1 ♂ LACM). [This locality is ca. 5 road mi (8 km) E of Santa Rosa, between Santa Rosa and Yécora, approx. 28°27'N, 109°00'W.]

CHIHUAHUA: 3 mi (4.8 km) S Témoris, elev. 4700 ft (1433 m), 29 Aug. 1969, T. A. Sears, R. C. Gardner, C. S. Glaser (1 ♂ UCD). [Témoris and nearby Témoris Station, where the elevation is 3365 ft (1026 m), are at km 708 on the Chihuahua al Pacifico Railroad, approx. 27°15'N, 108°15'W.]

CHIHUAHUA: Santo Niño, 9 Aug. 1969, T. A. Sears, R. C. Gardner, C. S. Glaser (1 ♂ UCD). [Approx. elev. 1800 ft (550 m), very near the Sinaloa state line at km 737 on the Chihuahua al Pacifico Railroad, approx. 27°00'N, 108°22'W.]

SINALOA: 5.5 mi (8.9 km) NW Choix, 15 July 1968, T. A. Sears, R. C. Gardner, C. S. Glaser (1 ♂ UCD).

All of these localities, and the known localities for this moth in Arizona, are in the biotic community described as Madrean Evergreen Woodland, a mild winter/wet summer community characterized by evergreen oaks (*Quercus*) or a mixture of oaks, juniper (*Juniperus*) and Mexican pinyon (*Pinus cembroides*) (Brown, D. E., ed. 1982, *Biotic communities of the American Southwest—United States and Mexico*, Desert Plants 4(1-4):342 pp., and accompanying map by Brown, D. E. and C. H. Lowe 1980, *Biotic*

communities of the Southwest, Gen. Tech. Report RM-78, Rocky Mountain For. & Range Exp. Sta., Forest Service, U.S. Dept. Agric.).

Besides documenting the first, but not surprising, records of *Morpheis clenchi* from México, this note illustrates a distributional phenomenon that will be observed more commonly as surveys of the Lepidoptera fauna of northwestern México are intensified, namely that species presently known only from the southwestern United States may actually be widespread and common in adjacent northwestern México. Similarly, with more intensive faunal studies in the southwestern United States we may expect to find species presently known only from northwestern México, although perhaps only in isolated, relict populations or as strays. I urge lepidopterists from the United States and México to pool their talents and efforts to conduct a joint survey of this intriguing border-straddling region.

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A DESCRIPTION OF TOPOTYPICAL MALE *HEMILEUCA DIANA* (SATURNIIDAE)

Additional key words: Colorado, type locality, *Hemileuca grotei*, sister species.

Hemileuca diana Packard (Saturniidae) was first described in 1874 from a single female, collected in 1873; the locality was cited only as "Plum Creek" in Colorado (Packard, A. S. in Hayden, F. V. 1874, Annual Report of the United States Geological and Geographical Survey of the Territories embracing Colorado, being a report of progress of the exploration for the year 1873, Government Printing Office, Washington, D.C., 718 pp.). Prior to F. M. Brown (1972, J. Lepid. Soc. 26:245-247) a more precise location of the type locality of *H. diana* was largely in question because there are many streams in Colorado named "Plum Creek." According to the historical records of Hayden and A. C. Peale (in Hayden *op. cit.*), the most probable Plum Creek would be the northward flowing tributary of the segment of the South Platte River that flows through what is now Douglas County. The most likely *H. diana* type locality on this tributary is along the headwaters of Plum Creek in the area between Larkspur and Palmer Lake (Brown *op. cit.*). This location is slightly southwest of Castle Rock south of Denver, near present Interstate Highway 25. The study area where this research was conducted is along Plum Creek about 12 km W of Castle Rock at the junction of Douglas County roads 46 and 105 (Wolfensberger and Perry Park roads, respectively) very near or in the Christy Ridge housing development. This is about 8 km N of the probable location cited by Brown and well within the presumed type locality area.

Hemileuca diana is recorded from Colorado, Arizona, and Mexico (Ferguson, D. C. 1971, Bombycoidea, Saturniidae (in part), in Dominick, R. B., et al. (eds.), The moths of America north of Mexico, fasc. 20.2A:1-153, col. pls. 1-11, E. W. Classey, London; Tuskes, P. M. 1986, J. Lepid. Soc. 40:27-35), but until quite recently no other specimens were known to have been collected from the type locality. The biology of Arizona *H. diana* has been described (Tuskes *op. cit.*), although comparison of southern Arizona males to topotypical males was not made because such topotypical material was unknown at that time. Topotypical *H. diana* males are now known. At the Christy Ridge housing devel-

opment, between the dates of 28 September and 4 October 1987, 72 *H. diana* males were collected by the authors and R. S. Peigler.

Hemileuca grotei Grote & Robinson is recorded from the Edwards Plateau in central Texas and from New Mexico (Ferguson *op. cit.*; Kendall, R. O. & R. S. Peigler 1981, J. Lepid. Soc. 35:41–50; and Tuskes *op. cit.*). Through comparison of topotypical *H. diana* to Arizona and Mexico *H. diana* and to *H. grotei* populations found in Texas and New Mexico, it is clear the two taxa are closely related, quite possibly sister species, and form the closely knit *H. diana* complex (Tuskes, P. M. 1984, J. Lepid. Soc. 38:281–308, Table 1). Morphological differences of material sampled from various localities seem to indicate that some populations of what are now called *H. grotei* and *H. diana* may be misidentified or even undescribed taxa (see Tuskes 1986 *op. cit.*: p. 28, figs. 2c and 2d). An investigation of the *H. grotei* complex is currently underway.

Topotypical *H. diana* males have been deposited in the Museum of Comparative Zoology, Harvard University, in association with the holotype female; Natural History Museum of Los Angeles County and San Diego Natural History Museum, California; Denver Museum of Natural History, Colorado; National Museum of Natural History, Smithsonian Institution, Washington, D.C.; American Museum of Natural History, New York; and in the personal collections of R. S. Peigler, Colorado; K. L. Wolfe, M. J. Smith, P. M. Tuskes, California; W. A. Nässig, West Germany; C. Lemaire, France; and the authors.

The following description of a topotypical *H. diana* male is based on a specimen (Fig. 1a) collected 4 October 1987 by the senior author and R. S. Peigler very near the presumed type locality.

HEAD: Eyes dark brown near black. All hairs black. Labial palps absent. Antennae black, bipectinate, 7 mm long, with 36 segments. **THORAX:** Collar off-white, thoracic tufts light gray with black bases, pronotum clothed with short, light rust-red hairs with mixed black to light gray bases, meso- and metathorax clothed with rust-red tufts. **LEGS:** Femur covered with very long dark rust and white hairs, tibia with shorter black and white hairs, tarsi black and sparsely covered with short black hairs, claws brown. **ABDOMEN:** Abdominal segments I–VII covered dorsally with black hairs, longer sparser hairs white. Caudal segments covered with long burnt orange hairs. Ventrally segments I–IX covered with shorter black and white hairs. Intersegmental spaces black. **FOREWING:** Elongated, length 23 mm, ground color dark brown with dark brown veins, antemedian band absent; yellow, bare, crescentic bar in center of black discal spot, postmedian band white, originating at base of R5, 3 mm wide at R5, intersected proximally by discal spot; discal spot completely interrupting postmedian band transforming it to two profound dashes, band terminating at anal vein. Band 1–2 mm wider ventrally than dorsally. Postmedian area moderately suffused with silver-gray scales. **HINDWING:** Length 18 mm, ground color light black with light black veins, antemedian band absent, black discal spot partially obscured by ground color and fading into postmedian band, postmedian band white, 3 mm wide at R, tapering sharply to tornus, and terminating at anal vein. Dorsal and ventral postmedian band with the same. Postmedian band originating at Sc. Proximal margin of postmedian band not sharply defined but grading from ground color to white. Distal margin of postmedian band sharply defined. Anal margin heavily clothed in long, light black hairs

Material examined ($n = 50$) demonstrates remarkably uniform morphological characteristics; differences occur only in wing length, the amount of development of the fore- and hindwing postmedian bands, and the suffusion of silver-gray scales in the forewing postmedian area. The forewing is always elongated as in *H. magnifica* (Rotger) and *H. hera hera* (Harris). The ground color of the fore- and hindwings remains constant while forewing length varies between 21.0 mm and 24.5 mm ($\bar{x} = 23.3$ mm), hindwing length varies from 16.0 mm to 20.0 mm ($\bar{x} = 18.0$ mm). Although the forewing postmedian band is rarely reduced to two slight dashes, it is always conspicuously developed, varies

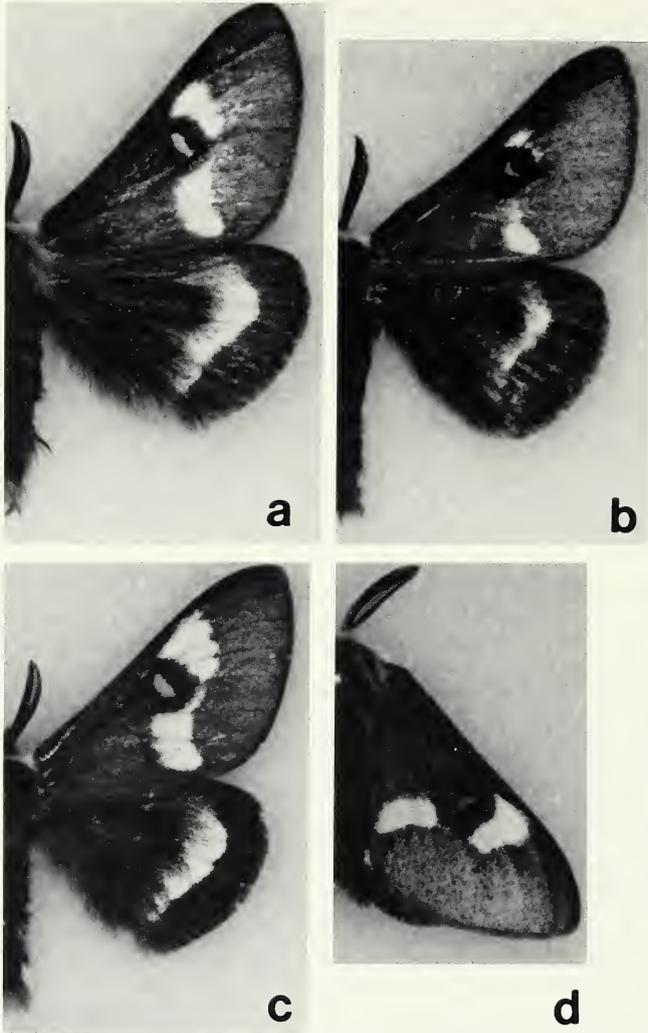


FIG. 1. a-d. Topotypical *Hemileuca diana* males, showing wing pattern variation. All specimens from Plum Creek, Douglas County, Colorado; collected by S. E. Stone, D. E. Bowman, and R. S. Peigler, 28 September-4 October 1987.

in width from 2 to 6 mm at R5, and is completely disrupted by the discal spot in 37 (74%) of the males examined (Fig. 1b). In 13 (26%) of the males examined, the discal spot penetrates the postmedian band but fails to disrupt it entirely; the band remains connected distally by a thin (<1 mm) portion of the band (Fig. 1c). The postmedian area is suffused with silver-gray scales in 40 (80%) of the males examined; the amount of suffusion varies from slight to very pronounced (Fig. 1d). The hindwing postmedian band is always present. It is well developed in 46 (92%), but reduced to a dash or dot in 4 (8%) of the males examined.

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DIURNAL NECTARING BY A *CATOCALA* MOTH (NOCTUIDAE)

Additional key words: Manitoba, Canada, *Catocala briseis*, *Cirsium arvense*.

At about 1200 h on 4 August 1988, I was surprised to see a *Catocala* moth (Noctuidae) nectaring on Canada thistle (*Cirsium arvense* (L.) Scop.; Asteraceae) at the Whiteshell Nuclear Research Establishment, 8 km south of Lac du Bonnet, Manitoba. The temperature was about 21°C, with a slightly hazy sun and a light north wind. After feeding for a few minutes, the moth flew to rest on the trunk of a cultivated poplar (*Populus* sp.; Salicaceae).

I identified the moth as *C. briseis* W. H. Edwards, based on illustrations in texts by C. V. Covell, Jr. (1984, A field guide to the moths of eastern North America, Houghton Mifflin, Boston, 496 pp.), W. J. Holland (1903, The moth book, 1968 reprint by Dover Publications, New York, 479 pp.), and T. D. Sargent (1976, Legion of night: The underwing moths, Univ. of Massachusetts Press, Amherst, 222 pp.). The most distinctive features were an irregular whitish band between the postmedian and subterminal lines on the dorsal surface of the mainly blackish forewing, and a smaller whitish patch between this band and the body. The hindwing was boldly banded with black and scarlet above, and more subdued below. The only similar species, *C. grotiana* Bailey, is apparently unknown in Manitoba (D. C. Hawks and R. R. Hooper pers. comm.).

Catocala moths are largely nocturnal, and are usually observed by day only if disturbed (Sargent *op. cit.*). It is possible that this individual had been flushed by a predator, and was subsequently attracted to the thistle flower before finding a new resting place. It may well, however, have initiated feeding behavior without such stimulus. Diurnal feeding has previously been observed in several *Catocala* species at "sugar" patches left over from prior baiting trips (T. D. Sargent pers. comm.).

Although adults of many *Catocala* species visit bait readily (Sargent *op. cit.*), little is known about their natural feeding habits. Sargent cites two species taken while nectaring at night, both by M. C. Nielson in Michigan: *C. unijuga* Walker at milkweed (*Asclepias* sp.; Asclepiadaceae) and joe-pye-weed (*Eupatorium* sp.; Asteraceae), and *C. mira* Grote at wild bergamot (*Monarda* sp.; Lamiaceae). In Manitoba and elsewhere, Canada thistle is a favored nectar source for several butterflies (Opler, P. A. & G. O. Krizek 1984, Butterflies east of the Great Plains, Johns Hopkins Univ. Press, Baltimore, 294 pp.).

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MYRMECOPHILY AND LARVAL FOOD PLANTS OF
BREPHIDIUM ISOPHTHALMA PSEUDOFEA (LYCAENIDAE)
IN THE FLORIDA KEYS

Additional key words: *Batis maritima*, oviposition behavior, *Salicornia virginica*, *Tapinoma sessile*, pupal stridulation.

G. W. Rawson (1961, J. N.Y. Entomol. Soc. 69:88-91) described and illustrated the life history of *Brephidium isophthalma pseudofea* (Morrison) (Lycaenidae: Polyommatainae) from a population near New Smyrna Beach, Florida. During a visit to the lower Florida Keys, we made additional observations on the biology of this species.

On 23 June 1979, at the N end of Sugarloaf Key, Monroe Co., we found adults of *B. i. pseudofea* in a semitidal flat where *Salicornia bigelovii* Torr., *S. virginica* L. (Chenopodiaceae), and *Batis maritima* L. (Batidaceae) grew. Fifteen larvae of *B. i. pseudofea* were found on two adjacent plants of *S. virginica* and *B. maritima*. Between the bases of the two plants was a nest of an ant, *Tapinoma sessile* (Say) (Formicidae: Dolichoderinae). These ants patrolled the stems of both plants, and avidly tended larvae of *B. i. pseudofea*, stroking them with their antennae and feeding on secretions from the dorsal nectary organ on abdominal segment (A)7. One pupa was found attached to a stem of *B. maritima*. The ants also showed interest in this pupa, running over it and stroking it with their antennae. We could not verify if they actually fed on any secretions from the pupa, but later examination revealed a conspicuous scar on A7 corresponding to the dorsal nectary organ on the larva. We placed a living pupa in a small glass vial, and, upon tapping, the pupa stridulated, as has been reported for many lycaenids (Downey, J. C. 1966, J. Lepid. Soc. 20:129-155).

Several adults were seen near the plants with larvae. At ca. 1100 h, one female was observed alternately flying around and walking over the plants for several minutes, in the presence of the ants. We observed no aggressive behavior by the ants toward the female. She eventually deposited a single egg on the tip of a leaf of *B. maritima* and then flew away.

Rawson (*op. cit.*) raised *B. i. pseudofea* on *Salicornia bigelovii*, and suggested that *Batis* may also be a larval food plant. We raised larvae from both *S. virginica* and *B. maritima* to adults, thus confirming these species as larval food plants. Rawson made no observations of ants associated with larvae or pupae.

A dorsal nectary organ on A7 and paired tentacle organs on A8 (terminology of Cottrell, C. B. 1984, Zool. J. Linn. Soc. 79:1-57) are present in this species and many other members of Polyommatainae. Myrmecophily has been reported for *Brephidium exilis* Boisduval (Coolidge, K. 1924, Entomol. News 33:305-309), and for the African *B. metophis* (Wallengren) (Clark, G. C. & C. B. C. Dickson 1971, Life histories of South African butterflies, Purnell & Sons, Capetown, South Africa, 272 pp.). Ant association in *B. i. pseudofea*, although previously unreported, is therefore not surprising.

The clumped distribution of immatures of *B. i. pseudofea* raises the possibility of ant dependent oviposition. Although larvae and eggs were abundant on the two plants patrolled by the ants, a search of nearby plants that appeared identical in general aspect, but which lacked patrolling ants, yielded no larvae. This suggests that females may preferentially oviposit on plants with ants (review in Cottrell *op. cit.*). The distribution of ants may be a significant factor in the biology of *B. i. pseudofea*, which is extremely sporadic in its appearance despite ubiquitous larval food plants in coastal habitats.

Preserved immatures are deposited in the Allyn Museum of Entomology, Florida State Museum, Sarasota, Florida. We thank two anonymous reviewers for comments on this manuscript.

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APPIAS PUNCTIFERA D'ALMEIDA (PIERIDAE) IN
THE DOMINICAN REPUBLIC AND PUERTO RICO

Additional key words: island biogeography, seasonal dimorphism, Greater Antilles, Virgin Islands, *Appias drusilla*.

Appias punctifera is perhaps the least known and most elusive of endemic Antillean pierids. It much resembles the familiar "Florida White" (*A. drusilla* Cramer) and most obviously differs in possessing a black spot at the distal end of the forewing (FW) cell in both sexes, more prominently in the female. It is rare in collections, and N. D. Riley (1975, A field guide to the butterflies of the West Indies, Collins, London, 224 pp.) mentioned that he had not seen a specimen.

The taxon *punctifera* was first proposed by R. F. D'Almeida (1939, Bol. Biologico, São Paulo, 4(NS):50-66) as a subspecies of *Appias drusilla*, reducing to synonymy *Tachyris molpadia* Dewitz, *Tachyris margarita* Dewitz, and *Appias drusilla* f. *molpadia* Röber. *Appias punctifera* was raised to specific status by W. P. Comstock (1943, Amer. Mus. Novitates No. 1238, 1-6). D'Almeida based his description on four "all white" females collected in Puerto Rico, the type locality. Both sexes were available to Comstock who illustrated substantial differences between male genitalia of *A. drusilla* and *A. punctifera*, notably in the shape of the valvae and aedeagus. He recorded from Puerto Rico one female (Barros [sic], June), three females and one male (Coamo Springs, April) and one female (Lajas, June). The known range of *A. punctifera* was extended eastwards (Comstock 1944, Ann. N.Y. Acad. Sci. 12 Pt. 4: Lepidoptera, 527-528) to include the American Virgin Islands, by five males and one female (St. John, March) and one female (St. Thomas, June). More recently, one of us (SJR) found *A. punctifera* to be rare but occurring consistently in the Guánica xeric forest region of SW Puerto Rico, where it flies with the common *A. drusilla*, from which it is indistinguishable on the wing. Additional records (SJR) comprise one male (Toro Negro, October 1974), another male (Coamo, November 1974), and three males and two females (Ponce, Rt. 139, km 9.0, January 1987).

A. punctifera was first recorded from Hispaniola in a list of the butterflies of the Dominican Republic published by O. Cucurullo (1959, Lista de Mariposas (Rhopalocera) de Santo Domingo, published by the author, Santo Domingo, 1-13) without locality or collecting data. Subsequently, it was mentioned by L. Marion (1975, Helios 3:42-49) but, again, with no details. A. Schwartz (1983, Haitian butterflies, Editora R. Taller, Santo Domingo, Dominican Republic, 69 pp.) does not list this species from western Hispaniola. Here we report field observations on a population of *A. punctifera* in eastern Dominican Republic, with comparative comments on this species in western Puerto Rico.

Puerto Rican specimens are housed in the Department of Biology, University of Puerto Rico, Mayagüez; all specimens collected by us from the Dominican Republic are deposited in the Hope Entomological Collections, the University Museum, Oxford, England; the

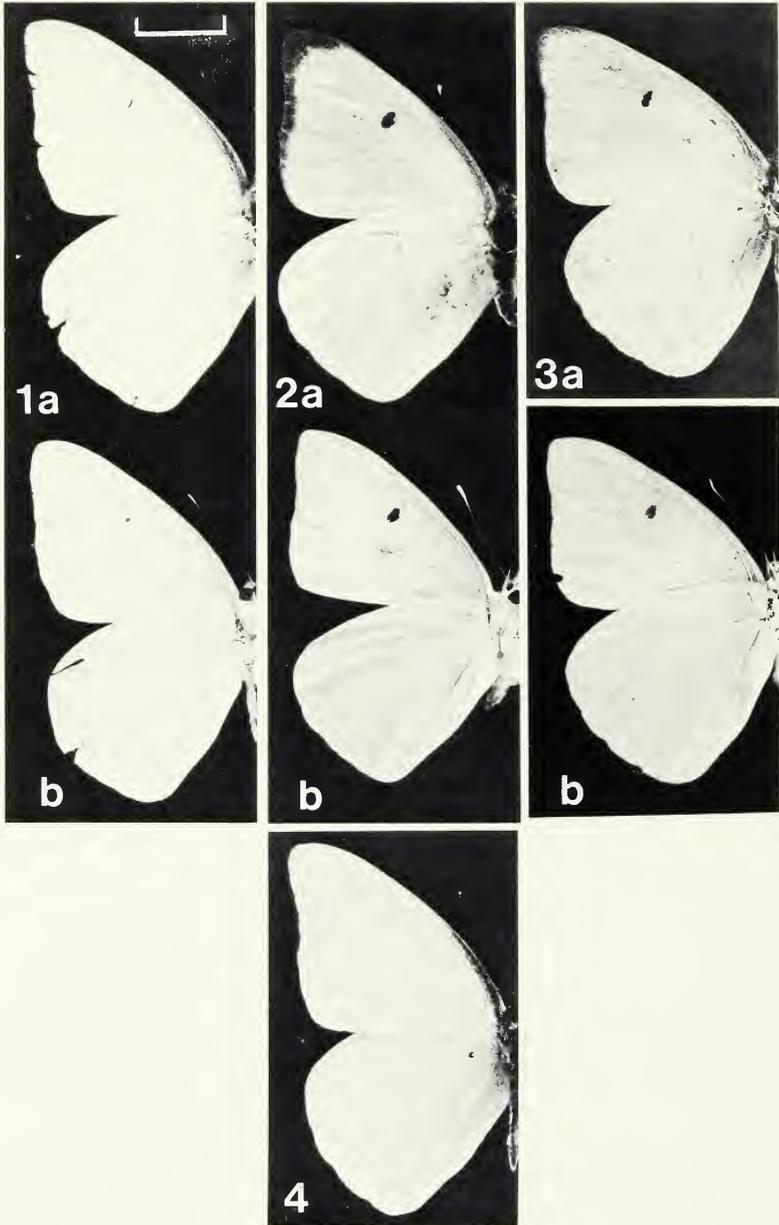


FIG. 1. *Appias punctifera* male from Boca de Yuma, Dominican Republic: a, upperside; b, underside. Scale line = 1 cm.

FIG. 2. *Appias punctifera* female from Boca de Yuma, Dominican Republic: a, upperside; b, underside.

FIG. 3. *Appias punctifera* female from Ponce, Puerto Rico: a, upperside; b, underside.

FIG. 4. *Appias drusilla boydi* male from Boca de Yuma, Dominican Republic: upperside.

male collected by L. D. and J. Y. Miller is in the Allyn Museum of Entomology, Sarasota, Florida.

Between 4–10 January 1987, two of us (DSS, EWC) visited the Dominican Republic and worked primarily near Boca de Yuma Dominican Republic (Altagracia Province). The limestone surface of the plateau in this region is substantially under cultivation or pasture, but with residual areas of xeric forest much resembling that of the Guánica region of SW Puerto Rico. We found *A. drusilla boydi* Comstock in, and apparently confined to, the forest patches, while in the cleared areas, *A. punctifera* was found. After a chance capture of a worn male of *A. punctifera*, we particularly sought this species and its relative *A. drusilla* and collected four further males and two females of the former, all in fairly fresh condition. An additional male was collected by L. D. Miller and J. Y. Miller, who revisited the site shortly after. All *Appias* collected in the fields and cleared areas proved to be *punctifera*: most seen were flying out of reach (above 5 m) around *Ficus*, *lignumvitae* (*Guaiacum*), and other isolated trees, occasionally making excursions to nearby ground scrub (where most specimens were collected), nectaring on *Eupatorium*, *Lantana*, and other plants. We saw perhaps five specimens for each one collected, and frequency of sightings did not appear to vary from early morning to late afternoon through each day of observation. We cannot be certain that *A. punctifera* does not fly with *A. drusilla* in the forest scrub, but all *Appias* collected there were of the latter species.

Riley (*op. cit.*) did not illustrate *A. punctifera*, and male and female specimens from Boca de Yuma are illustrated here (Figs. 1–2) with a male of *A. drusilla boydi* from the same region (Fig. 4). Our specimens conform closely to Comstock's (1943 & 1944 *op. cit.*) descriptions, notably in the cell spot size and the conspicuous bright lemon-yellow suffusion that occupies the basal third of the FW cell on the underside, and half or more of the cell area in the female. The "glistening" or silky appearance of the underside ground color in both sexes is striking. However, our material diverges slightly from Comstock's accounts in that we note the female upperside ground color as pale cream on the forewing and deeper cream-yellow on the hindwing (rather than "white" and "distinctly cream") and, in fresh males, the upperside ground color is not "white" but very pale eggshell green-blue, a tint that soon fades in dried specimens.

The original four males described by D'Almeida were "white" (with only a limited black suffusion at the FW apex, as illustrated by H. Dewitz (1877, Entomol. Z. Stettin. 38:233–245) while Comstock (1944 *op. cit.*) described this sex as "white, with or without a fuscous border," but did not mention any seasonal distribution of the two forms in his very small sample. The two female specimens in our Boca de Yuma sample both show broad fuscous-black borders (Fig. 2), but sampling of the population over an extended period is required to establish whether this dimorphism reflects seasonality, as has been proposed (e.g., Riley *op. cit.*) for comparable variation in female markings in *A. drusilla poeyi* Butler (Bahamas, Cuba and Cayman Is.) and *A. drusilla boydi* (Hispaniola, Puerto Rico, the Virgin Is., and the northern Lesser Antilles), in which the more heavily marked females have been associated with the wet season. Both females collected near Ponce (Puerto Rico) at the time of our visit to the Dominican Republic represented the "white" morph (Dewitz *op. cit.*) and one of these is illustrated in Fig. 3. In these specimens, the fuscous FW border above is very reduced in width, to only ca. 1 mm at the apex. In addition, the FW end-cell spot above is slightly narrower than in the more heavily marked morph, although in each instance this spot occupies about two thirds of the distal end of the cell. A male collected near Ponce is indistinguishable from specimens taken at the same time in the Dominican Republic.

Unless future work in Hispaniola points to the contrary, it seems that the center of the range of *A. punctifera* is Puerto Rico. Although present in W Puerto Rico and E Hispaniola, it has not been noted in the remarkably rich butterfly fauna of Mona Island, almost equidistant from the two documented localities on either side of the Mona Passage. On this small island (23 mi²/62 km²), largely covered with xeric forest, its congener *A. drusilla boydi* is present in a very restricted area (Smith, D. S. et al. 1988, Bull. Allyn Museum, No. 121, 1–35).

The larval food plant(s) and immature stages of *A. punctifera* are unknown. It is hoped

that this note will stimulate further documentation of the range, significance of female dimorphism, and developmental biology of this species. Awareness of its possible presence is important: except for the serendipitous recognition of a minute cell-end spot on a worn male *Appias* we might well have overlooked a substantial population of *punctifera*.

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BOOK REVIEWS

FLORIDA BUTTERFLIES, by Eugene J. Gerberg and Ross H. Arnett, Jr. 1989. Natural Science Publications, Inc., Baltimore, Maryland. v + 90 pp., 105 color figs. Soft cover, 14 × 21.5 cm, ISBN 0-89140-031-1, \$9.95.

FLORIDA'S BUTTERFLIES AND OTHER INSECTS, by Peter D. Stiling. 1989. Pineapple Press, Sarasota, Florida. 95 pp., 155 color figs. Hard cover, 22 × 28.5 cm, ISBN 0-910923-54-X, \$24.95.

Florida has always occupied a special place in the minds of most North American lepidopterists. Its subtropical southern counties and habitats, especially the Florida Keys, serve as a breeding ground and landing place for exotic butterflies and moths not generally encountered elsewhere in the eastern United States. The resulting attractiveness to travelling collectors every year is almost paradoxical when one realizes that Florida has only 164 butterfly and skipper species, less than many central and most western states, and approximately *half* the fauna of Texas, which has extensive subtropical areas adjacent to the rich Mexican faunal regions.

The reasons for this exotic but relatively depauperate fauna are rooted in Florida's biogeographic history and in the current floral and climatic differences between the northern and southern halves of the state. Most of Florida's tropical species have, in fact, arrived over water from the Caribbean islands and not (as in the case of Texas) via a rich continental connection directly from Mexico. And the northern temperate species that reach Florida are at the southern limits of their ranges when they hit subtropical conditions and their northern plant hosts disappear.

But perhaps even more surprising is that this unique and attractive state of Florida has received little attention in terms of books describing its lepidopteran fauna. The collector has had to use Klots (1951, *A field guide to the butterflies of North America, east of the Great Plains*, Houghton Mifflin Co., Boston, 349 pp.) or the poorly-illustrated monograph by C. P. Kimball (1965, *Lepidoptera of Florida. Arthropods of Florida and neighboring land areas*, Vol. 1, Division of Plant Industry, Florida Department of Agriculture, Gainesville, 363 pp.) to identify his catch and learn a little about Florida butterflies and their ecology. Now in quick succession, two new popular books have appeared in 1989 to partially remedy the situation for the casual naturalist and lepidopterist.

Florida Butterflies by Eugene Gerberg and Ross Arnett provides a color illustration and a half-page or so of text on each of 97 butterfly species found in Florida. The illustrations are 6.5 cm square, two at the top of each page, and show normally only the dorsal surface, occasionally both dorsal and ventral surfaces, of a pinned specimen on black background. The brief species account includes forewing size (helpful, as the color illustrations are not reproduced to relative scale) and a brief color description, and a little, rather generalized information on known hosts, habitat, flight period, and distribution. The skippers (species 98-164, representing an amazingly large proportion of the state's fauna) are given cursory telegraphic attention (e.g., "All of Florida. Larvae on various grasses.") and only 8 skipper species are illustrated. A checklist of Florida butterflies (with common name as well as scientific name) and a complete index to the butterfly names are included. At the end of the text are sections on rearing butterflies and making a collection. The introductory part of the book includes short sections on butterfly biology, butterfly gardening, the butterfly families, and butterfly conservation. This attempt to summarize the lives of butterflies is laudable, but, unfortunately, contains several misleading statements, ranging from pointless (e.g., "their lives are free") to erroneous (e.g., "the simple brain is without memory"). The brief descriptions of ten Florida life zones, with five color illustrations, provide the first-time visitor with an idea of what to expect and where most butterfly species may be found. In addition to the 164 breeding species, 25 stray species found in Florida are listed (but not described or illustrated). While some glaring errors will be noted (e.g., butterfly eggs do not have an average size of "2-4 mm

in diameter," most are less than 1 mm, and eggs of only a few neotropical satyrids and Australasian *Ornithoptera* reach 2–5 mm in diameter), this pocket-sized field guide provides a concise, color-illustrated guide to most of the butterflies that the visitor or beginning student will encounter in Florida.

Florida's Butterflies and Other Insects, by Peter D. Stiling, opts to present a cross-section of Florida's butterfly and skipper fauna with color photographs of "wild" specimens (the great majority are posed dead or pinched specimens). Forty butterflies are illustrated; each has an accompanying paragraph of text on that species. More information on Florida food plants is usually included here than in Gerberg and Arnett's book, and reference to the original literature is often made following behavioral and ecological notations. In addition to the butterflies, 22 photographs and species accounts of Florida moths (8 Saturniidae, 10 Sphingidae, 2 Arctiidae, and 2 Noctuidae) are included. Finally for the lepidopterist, an interesting section of 17 photographs and species accounts covers butterfly and moth caterpillars. The remainder of the book's main text (pp. 50–84) covers other insect groups. The author provides a valuable page on butterfly gardening, and three pages listing nectar sources and larval food plants used in Florida. A brief section on commercial butterfly gardens and state insect collections completes the text. An excellent index to insects and plants, along with an extensive literature cited section, are included. This book, published in 8½ × 11" size, with a full-color hardbound cover depicting a live *Eumaeus atala*, is not intended for field identification but is an attractive book for the home library.

In summary, the intricacies of Florida butterfly biology, distribution, and ecology are not covered by either of these two new books. For a thorough treatment of Florida's butterflies and skippers, we must await the publication of other, more-detailed books currently being prepared by H. David Baggett, Marc C. Minno, John B. Heppner, and others. However, the Gerberg and Arnett field guide will serve as a good introduction to Florida's fauna, and the Stiling book will interest the general beginner in other Florida insects as well as in some of the state's fascinating tropical Lepidoptera.

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LEPIDOPTERAN ANATOMY, by John L. Eaton. 1988. Wiley-Interscience Series in Insect Morphology, John Wiley & Sons, New York. 257 pp., 194 text figs. Hard cover, 17 × 24 cm, ISBN 0-471-05862-9, \$49.95.

Here, finally, is a book dedicated solely to the somewhat disjointed subject of lepidopteran anatomy. The author has amassed a general collection of anatomical information on the tobacco hornworm moth, *Manduca sexta*; information previously difficult to locate amidst the scatterings of textbook chapters and original scientific articles, some of which are difficult to obtain or are not available in English. Considering the growing number of scientists using lepidopterans as experimental models, in addition to the multitude of professional and amateur lepidopterists, there is potentially a large audience that would appreciate a single source on lepidopteran anatomy.

The book is divided into eleven chapters. Each of the first four provides a general description of one of the developmental stages. The chapters on the egg and pupa are scant, consisting of fewer than three pages each, including drawings, while the two chapters on the larva and adult are much more detailed, treating the complex subjects of the exoskeleton and musculature. Each of chapters five through ten focuses on a particular system: the nervous system and endocrine glands; the circulatory system; the

respiratory system; the alimentary canal, salivary glands, and excretory system; the internal organs of reproduction; and the exocrine glands. Of these five, the chapter on the nervous system and endocrine glands and the chapter on the adult exoskeleton and muscles receive most attention, possibly because J. L. Eaton has published some worthy articles on these topics himself. The last chapter of the book very briefly describes the organs of sound production and hearing. As this is my own area of specialty, I must admit that I find the author's treatment of this subject to be somewhat cursory and outdated. Whether this reflects the accuracy of other sections of the book, which I am unable to review with such a critical eye, I cannot say.

The book concludes with two appendices and an index. Appendix 1 briefly describes Eaton's methods. I feel that this section would be more useful to the general reader if the author had included formulae for the solutions used in dissections and an explanation of the derivations of the nomenclature employed in the drawings. Appendix 2 defines, in alphabetical order, the mnemonic abbreviations used in the book. The index contains surprisingly few entries for a book on anatomy and includes only a fraction of the structures treated in the text.

The book is exclusively devoted to descriptive anatomy. There are plenty of drawings (although some were surprisingly simplistic) to guide the reader through each system. I used the book as a dissection guide to the adult musculature and nervous system and felt satisfied, as the book did not force me to consult other references to locate and identify any particular structure. The book does not, however, go much beyond strict anatomical description, and thus will disappoint those who are seeking a book that provides information on the functional properties of a particular structure (as some morphology books will do).

Personally, my main disappointment in this book stems from the expectations I had after reading the title, *Lepidopteran Anatomy*. Since the Order Lepidoptera is extremely rich in behavioral and morphological diversity, I expected a book that approached the topic from a comparative standpoint. The author, in a sense, acknowledges this aspect of his book in the preface, saying that he used *Manduca sexta* as a model for all Lepidoptera and that "users of this book should be readily able to apply it to the anatomy of other lepidopterans." I agree with this only partially. For instance, there is considerable variation in larval form, color, and ornamentation; in egg morphology; and in adult antennae and feeding parts, which unfortunately receive no (or very little) mention. Perhaps the title "*Anatomy of Manduca sexta*" would have been more appropriate. However, readers interested in comparative morphology are not left entirely empty handed. At the end of each chapter is a list of 'selected references' that covers at least some of the key references to the anatomy of other lepidopteran species.

Despite these few shortcomings, the book is, in general, a good one, and, to my knowledge, the only one of its kind. I recommend it as a useful addition to university libraries and to the personal collections of lepidopterists or other scientists who have an interest in morphology.

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OBITUARY

GORDON BURGESS SMALL, JR. (1934-1989)

Sometime during the evening of 22-23 January 1989, Gordon Small, a Life Member of the Lepidopterists' Society, passed away in his sleep in his apartment in San Francisco where he had been residing for the past two years. His sudden death at a relatively young age has left many of us in a state of shock. Indeed, the Society has lost one of its most ardent collectors and accomplished lepidopterists.



Gordon Small in Panama, 1970

Gordon was born in Cambridge, Massachusetts, on 19 April 1934. He is survived by two younger brothers, Chip and Peter. After graduation from Glenridge High School in Cambridge in 1951, he entered Bowdoin College in Brunswick, Maine, graduating with his B.A. in Mathematics in 1955. He obtained his Masters Degree in Mathematics at Brown University in Providence, Rhode Island, in 1956 and began work toward a Ph.D. He had completed most of the requirements for his doctorate except the dissertation when he accepted a position with the Panama Canal Company as an instructor in their Department of Education in the Panama Canal Zone in 1962.

Gordon's interest in insects and natural history in general began at the age of 10. His brother recalls an early photograph in which Gordon is chasing a bird in order to put salt on its tail. His oldest spread butterfly specimen is a Compton Tortoiseshell taken in Glen Ridge in 1950. Like many of us, he dreamed for years of collecting in the tropics.

And suddenly, as if in answer to his prayers, the offer from the Panama Canal Company provided an opportunity not only to collect in the tropics, but to live there and get paid for it! It is not surprising then, that when the opportunity arose, Gordon took advantage of it.

Gordon and I first corresponded in 1960. He wanted to know the exact whereabouts of *Problema bulenta* (Hesperiidae), reported to be in or near Wilmington, North Carolina, and knew through correspondence with others that I had collected it there. We eventually met, collected a few times together prior to his departure for Panamá, and began a correspondence that continued for 28 years. We briefly discussed getting together for some tropical collecting after he became settled in the Canal Zone. Both of us were very interested in the Lycaenidae, particularly the genus *Thecla*, so it was exciting to think of my getting some military leave to join him in Panamá. Thus, after Gordon had spent some 6 months in Panamá, our day-dream became reality when we made our first collecting trip together in February of 1963—a memorable event indeed, and one that was to be repeated time and time again for the next 20 years.

Collecting with Gordon was an excursion fortified with the highest expectation, punctuated with surprises at every turn and with the never-to-be-forgotten exhilaration of a new "find." In those early years, when much of the territory was still unexplored, each trip produced a number of species not taken previously. Gordon would spend weekends searching out new places to collect, write long letters detailing his catch, and plan strategy for our next joint venture. Our trips were taken in his beloved tomato-red VW Beetle. In retrospect it proved to be one of the best vehicles for the purpose; few of the roads we traveled in those early years were impassable, and the car's light weight and maneuverability proved invaluable. In the tropics, passable roads do not necessarily mean good roads; the Pan-American Highway between the Canal Zone and Chiriquí Province was incredibly rough—passable, but just barely. But, bad road or not, we made the trip many, many times.

The 1960's were probably the most productive for Gordon because there was a seemingly endless array of new localities to collect, each producing species that had not been taken on previous trips or in other localities. It was during this period that he decided to concentrate only on the butterfly fauna of Panamá and to abandon the study of species from other localities in the Neotropics. His original intent had been to concentrate on the Lycaenidae and Riodinidae of the entire Neotropics, trading material with collectors in other countries. But as he became more familiar and fascinated with all the Panamanian fauna, it became clear that a choice between the two goals had to be made. His decision resulted in the finest collection of butterflies from a single Neotropical country that has ever been made. It is doubtful that such a feat will be duplicated.

Gordon's initial assignment in the Canal Zone was as a mathematics teacher in the Balboa High School. Eventually, he moved to the Balboa Junior College. With the exception of his teaching position, which, over time, he was able to arrange to better accommodate a good field collecting schedule, there were no other responsibilities or demands on his time. Gordon was not married. It is safe to say that, in reality, he devoted most of his free time (and there was lots of it) to his collection. He was a wonderfully meticulous technician, which is apparent to anyone who views his collection of superbly spread and curated specimens. He often voiced regret over the lack of opportunity to attend concerts or similar artistic endeavors. Panamá is not a part of the world where the arts flourish. To fill this void he purchased a beautiful baby grand piano that took up a large section of his living room. He was an excellent pianist with a passion for the music of J. S. Bach and he followed a rigorous practice schedule.

Gordon's address in the Canal Zone became the focus of attention for collectors from both North and South America. His unique location provided an ideal stopover for visitors going north or south and he received a great many written requests for butterflies from the Canal Zone. For more than 20 years he provided logistical support, transportation, and a place to stay for a steady stream of visitors. Both professional and casual lepidopterists sought information, help in collecting, or just a visit with this kind, knowledgeable young man who lived where he could collect tropical butterflies virtually at his back door.

The decade of the 1970's brought continuing challenges and new interest in families

other than his beloved Riodinids and Lycaenids. He became fascinated with the Ithomiinae and other Nymphalidae. By the end of the decade, his collection of Panamanian butterflies was unsurpassed. After it became increasingly difficult for him to find species new to his collection, he purchased a four-wheel-drive vehicle to reach areas that were inaccessible to his VW, which by this time was showing signs of distress and hard use. The new vehicle provided Gordon with the opportunity to venture into remote areas recently penetrated by new roads, as yet uncompleted and not yet open to normal traffic, the road into the Darién being the most desirable. His summer vacations were now being spent in Costa Rica and the areas adjacent to it in Chiriquí Province, collecting in the very high country of the Volcan de Chiriquí.

By early 1980, Gordon was already beginning to see the end of life in Panamá as he had known it for nearly 20 years; he began to make plans to collect the final "unreachable" collecting area in Panamá—the Darién. In the first week of July 1981, Gordon hired a small plane at considerable expense to take him, with some necessary supplies (rice, sugar, salt, etc.) plus collecting equipment, to a small mining camp at the foot of a mountain range far into the Darién Peninsula. Using a small building at the mine as a base of operations, Gordon climbed some 1200 meters to the summit of a small mountain, where, over a period of time, he cleared the top with a machete, creating his own "hilltop."

His original intent was to stay only a few weeks, but collecting was so good he extended his stay, spending 7 weeks in virtual isolation, climbing the 1200 meters to his mountain top each day that weather conditions permitted. Due to the confusion following President Torrijo's death in August, the airplane that Gordon expected to take him back to civilization never arrived. Accompanied by his young Indian guide, he had to carry out all his gear and specimens on foot, walking over 40 kilometers through hilly jungle terrain and swamp just to reach the bare edges of human habitation. In spite of the difficulties, hardship, and personal expense, Gordon made four more collecting trips to his abandoned mining camp during the next two years. The fourth trip was to be his last serious collecting effort in Panamá.

It is difficult to point out a single event that could be called more memorable than many others, for so much of his collecting was into new and remote areas and each could be called a memorable event. But the one incident that stays in my mind above all others was Gordon's encounter with a very large bushmaster snake in July 1969. The snake struck him just above the knee; luckily he was near his car and, after identifying the snake and making a brief effort to kill it, he drove as rapidly as possible to Gorgas Hospital, which, fortunately, was only 30 minutes away. After intensive treatment, he was released within a week. The experience never quelled his enthusiastic and determined efforts to collect every remote area that he could reach. The Darién experience provides ample testimony to his indomitable courage and dedication, for an encounter with a bushmaster there would probably have been fatal.

It was during his work in the Darién that Gordon became interested in the study of butterfly life histories. Encouraged by Annette Aiello of the Smithsonian Tropical Research Institute, Gordon devoted most of his time and effort during his last three years of residence in the Republic of Panamá to the rearing of butterflies, especially the genus *Anaea* (Nymphalidae). He reared about 150 species in all, mostly Nymphalidae, Pieridae, and Papilionidae, but also Hesperidae, Lycaenidae, and Riodinidae. His detailed rearing notes, preserved immatures, and reared adults were added to his superb collection of over 50,000 specimens, all of which were sent to the Smithsonian Institution (Robbins, R. K. & J. F. Gates Clarke 1986, *J. Lepid. Soc.* 40:106) just before he retired and moved his residence from the Canal Zone to Panamá City. Gordon moved from Panamá to the United States in 1986, spending most of that year on the east coast near his old home while working on the Smithsonian butterfly collection. In the fall of 1986 he moved to San Francisco, something he had dreamed about for many years. Here, surrounded by the artistic and music community he had missed so much in Panamá, and, enjoying the mild climate, he lived the few remaining years of his life.

Gordon Small has left a rich legacy—a unique butterfly collection of over 50,000 specimens, extensive notes accompanying his reared material, volumes of personal correspondence, and the meaningful way he touched the lives of all who knew him. These

will remain forever a tribute to this intelligent, generous, wonderfully kind, and gentle man.

Bibliography

Gordon was most reluctant to publish or become involved with it. He felt that he was not well enough trained technically and that he could contribute more by concentrating on his field work. A list of publications follows:

1. 1962. Notes on *Eurystrymon ontario ontario* and *Satyrrium caryaevorus* (Lycaenidae). *J. Lepid. Soc.* 16:195–196.
2. 1969. A new subspecies of *Pyrrhopyge creon* (Hesperiidae) from Panama. *J. Lepid. Soc.* 23:127–130 (with S. S. Nicolay).
3. 1981. Illustrations and descriptions of some species of Pyrrhopyginae from Costa Rica, Panama and Colombia (Hesperiidae). *J. Res. Lepid.* 19:230–239 (with S. S. Nicolay).
4. 1981. Wind dispersal of Panamanian hairstreak butterflies (Lepidoptera: Lycaenidae) and its evolutionary significance. *Biotropica* 13:308–315 (with R. K. Robbins).
5. In press. Catalog of the Nymphalinae (Lepidoptera: Nymphalidae) of Panama. In Quintero D., and A. Aiello (eds.), *Insects of Panama and Mesoamerica: Selected studies*. Oxford Univ. Press, London (with Gerardo Lamas).

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I Remember Gordon

I remember a bus ride in 1976 bound from San Jose, Costa Rica, to Panamá to meet a man that several people had told me knew a lot about butterflies. Perhaps he could help me identify the Costa Rican butterflies I had been working on was how my thoughts ran at the time. Feeling as one can only feel after 28 hours on a bus, beyond weariness, I eventually found myself in front of one of the Canal Zone houses, rapped on a door, and found the face of Gordon B. Small smiling down the stairs at me.

I remember being filled with wonder when walking into his apartment for the first time. Picture, if you will, a room furnished on one end with two chairs, a sofa with a long, low table between, and two lamps. Only two other things were in that room, both of which were of great importance to Gordon: long rows of insect cabinets and boxes filled to capacity with what I have come to know as the finest collection of Central American butterflies ever made, and a baby grand piano. The chair, lamps, and table were obviously there to make looking at butterflies easier; the piano had its own seat and lamp.

I remember that within a matter of hours Gordon and his collection profoundly changed my life. Here was someone who knew, absolutely, the Central American butterfly fauna. Over the course of a week he taught me not only the names of the species, but where and how they flew, the problems with the revisions done by “experts,” and gave me snippets of wisdom I still am puzzling over today. Gordon’s initial gift to me was that he showed an unflagging interest in my meager observations on butterflies, and encouraged me to keep working on this lunatic idea I had of doing a treatment of the Costa Rican butterfly fauna. No matter that he was clearly the consummate master, and I the complete novice.

I remember Gordon playing the piano. His sense of ordering complex patterns found affinity within the music of J. S. Bach; for him, other composers apparently did not come up to snuff. After playing some of “The Inventions,” Gordon made self-deprecating remarks about his ability. When pressed, he reluctantly admitted his one-time desire to

be a concert pianist, but felt he lacked the discipline to make it. I remember standing next to that piano transfixed by what was clearly a magnificent performance—me a hardened jazz fanatic. The man was a gifted player.

After a week of studying his collection in Panamá, Gordon offered to drive me back to Costa Rica where we could do some collecting enroute (and I could happily omit the ordeal of another bus ride). I was struck by two things on that trip: the man's knowledge of butterflies in the field (he knew everything), and his patience with my repeated, naive questions about how to distinguish the species of satyrines, charaxines, and ithomiines. On the drive back to Costa Rica, I remember his wild-eyed excitement if I unwittingly stumbled upon something interesting. After completely exhausting my recollection of what the insect was doing, Gordon then worked relentlessly until he had found the species and collected it. As comes natural to any great teacher, Gordon kindled a fanatical interest in me by his example.

Some days later on a mud track through the forest in Costa Rica, I remember being introduced to the quintessential Gordon Small. In the midst of conversation he suddenly exclaimed, "Hey, there's *Napeogenes hemisticta*!", jumped out of the jeep, opened the back, attached several poles to his net, and caught a butterfly flying at a subcanopy level. He was right, of course. It was *hemisticta*, and no matter that neither one of us had ever been to this locality or seen the butterfly alive before, let alone pick it out of the other mimetic species flying there at the time. This type of feat was commonplace with Gordon and similar scenes were to be repeated virtually every time I was in the field with him. Over the years Gordon would periodically visit me in Costa Rica to check on what I had turned up and to talk butterflies, and we'd go off collecting together. Somehow he always found new things, even at localities I had been pounding away at for years. Quintessential Gordon Small.

When I left permanent residence in Costa Rica in 1980 to go to graduate school, Gordon and I kept up a steady flow of letters concerned with all aspects of butterflies. My education on butterflies continued through these letters. While I was at the British Museum writing the text for my Costa Rican butterfly book Gordon was one of my most constant correspondents. In letters he would query about the types of this or that species, inform me about his work in the Darién and to proudly tell me that he had finally begun to rear caterpillars and that he could see their importance to systematics. He provided a sounding board for my many questions about certain species, and he often made sound suggestions about the names of certain troublesome species, even though he had never seen the types. Even from afar, sight unseen, Gordon was usually correct about the identity of the specimens that sat in front of me. In fact, I remember Gordon being correct about most things concerned with butterflies throughout the twelve years of our friendship. He had a gift for this type of thing.

Gordon was a fanatically meticulous person who never relaxed his critical standards for anyone or anything when it involved butterflies. I remember the last time I saw Gordon. Standing around between sessions at the Lepidopterists' Society meetings at University of California, Berkeley, I saw him enter the building and make his way over to me. Delighted to see him and keen to hear his response to my then just published book (1987, *The butterflies of Costa Rica and their natural history*, Princeton University Press, Princeton, New Jersey, 327 pp.) I immediately introduced him to someone near me as the person who taught me everything I knew about butterflies. Gordon was cheerful and shook off the compliment, but I knew him well enough to know something was up. When I asked what was wrong he said, "Phil, you misrepresented me in your book." Feeling the bottom drop out of my stomach, I asked him falteringly, "I'm terribly sorry. How?" Gordon stated in dead earnestness, "In your species account of *Haematera pyramus*. I collected the species by clapping my net down over individuals visiting wet sand. Those individuals never flew. The person who was collecting with me chased his down, and the observation that they flew like *Diaethria* was his, not mine."

I remember Gordon as a consummate butterfly biologist. Quite simply, Gordon B. Small, Jr. knew more about butterflies than any person I have ever met, corresponded with, or have heard about. Many of the places where he worked have vanished into the oblivion of human "progress." All that remains of those Panamanian habitats are the

mute testimonies to tropical butterfly diversity now found in his collection, currently housed at the Smithsonian Institution. We and future generations owe him a profound debt of gratitude for singlehandedly learning the butterfly fauna of an entire country and for making such a thorough and masterful collection. Death has silenced a truly great naturalist, teacher, and extraordinary human being. After losing such a friend and source of inspiration, some of us may feel left behind. But, as in so many things, I remember that Gordon always was way ahead of the rest of us.

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