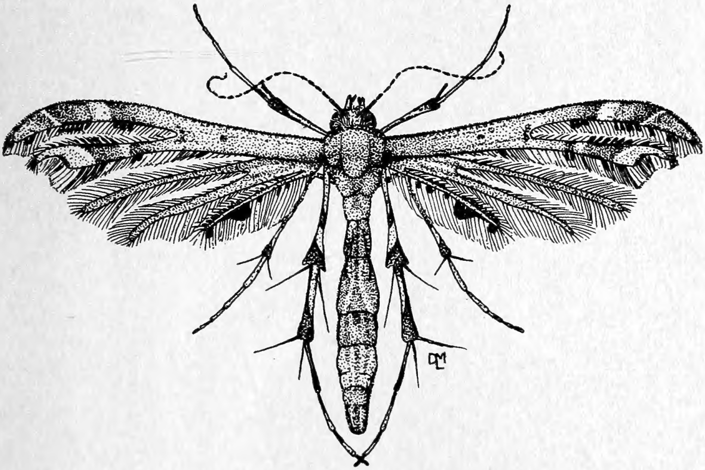
ne 44 1990 Number 2

ISSN 0024-0966

JOURNAL
of the
LEPIDOPTERISTS' SOCIETY

Published quarterly by THE LEPIDOPTERISTS' SOCIETY
Publié par LA SOCIÉTÉ DES LÉPIDOPTÉRISTES
Herausgegeben von DER GESELLSCHAFT DER LEPIDOPTEROLOGEN
Publicado por LA SOCIEDAD DE LOS LEPIDOPTERISTAS



2 November 1990

THE LEPIDOPTERISTS' SOCIETY

EXECUTIVE COUNCIL

EDITORIAL BOARD

HONORARY LIFE MEMBERS OF THE SOCIETY

CHARLES L. REMINGTON (1966), F. MARTIN BROWN (1973), E. G. MUNROE (1973), ZDRAVKO LORKOVIC (1980), J. F. GATES CLARKE (1985), IAN F. B. COMMON (1987), JOHN G. FRANCLEMONT (1988), LINCOLN P. BROWER (1990), DOUGLAS C. FERGUSON (1990)

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.

Active members—annual dues $25.00
Student members—annual dues $15.00
Sustaining members—annual dues $35.00
Life members—single sum $500.00
Institutional subscriptions—annual $40.00

Send remittances, payable to *The Lepidopterists' Society*, to: Fay H. Karpuleon, Treasurer, 1521 Blanchard, Mishawaka, Indiana 46544, U.S.A.; and address changes to: Julian P. Donahue, Natural History Museum, 900 Exposition Blvd., Los Angeles, California 90007-4057 U.S.A. For information about the Society, contact: William D. Winter, Secretary, 257 Common St., Dedham, Massachusetts 02026-4020, U.S.A. To order back issues of the *Journal*, *News*, and *Memoirs*, write for availability and prices to the Publications Coordinator: Ronald Leuschner, 1900 John St., Manhattan Beach, California 90266-2608, U.S.A.

Journal of the Lepidopterists' Society (ISSN 0024-0966) is published quarterly for $40.00 (institutional subscription) and $25.00 (active member rate) by the Lepidopterists' Society, % Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, California 90007-4057. Second-class postage paid at Los Angeles, California and additional mailing offices. POSTMASTER: Send address changes to the Lepidopterists' Society, % Natural History Museum, 900 Exposition Blvd., Los Angeles, California 90007-4057.

Cover illustration: *Sphenarches anisodactylus* (Walker) (Pterophoridae), a pantropical plume moth recently reported from Louisiana and Florida (see p. 92). Submitted by Deborah L. Matthews, Department of Entomology and Nematology, University of Florida, Gainesville, Florida 32611.

JOURNAL OF

THE LEPIDOPTERISTS' SOCIETY

Volume 44 1990 Number 2

Journal of the Lepidopterists' Society
44(2), 1990, 63–76

THE *MITOURA SPINETORUM* COMPLEX IN NEW MEXICO AND THE VALIDITY OF *M. MILLERORUM* (LYCAENIDAE: THECLINAE)

ROBERT K. ROBBINS

Entomology, NHB Stop 127, Smithsonian Institution, Washington, DC 20560

ABSTRACT. *Mitoura millerorum* (Clench) has been considered either a synonym of *M. spinetorum* (Hewitson) or a distinct species that does or does not occur in New Mexico. In a sample of 128 individuals collected in the vicinity of Weed, New Mexico, wing pattern characters previously proposed to distinguish *M. spinetorum* from *M. millerorum* were uncorrelated. Likewise, proposed genitalic [illegible] represented a small portion of continuous unimodal variation. The wing pa [illegible] genitalia of the types of *M. spinetorum* and *M. millerorum* fall within this r [illegible] iation. There is no published evidence supporting the hypothesis that *M. mil* [illegible] distinct species.

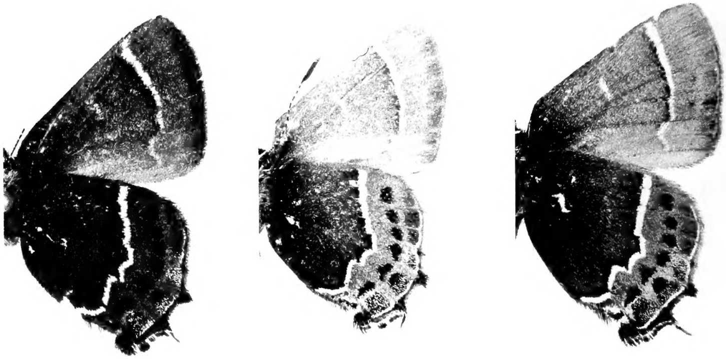
Additional key words: genitalia, wing pattern, continuous genitalic variation, taxonomy.

Specific identity of a female in the *Mitoura spinetorum* (Hewitson) complex from the vicinity of Weed, Otero County, New Mexico, has engendered controversy. There are three published hypotheses concerning its identity, and, more generally, concerning the validity of *M. millerorum* Clench as a distinct species.

Clench (1981) collected the female from Weed and considered it an aberration of *M. spinetorum*. In that paper, he distinguished the Mexican *M. millerorum* from *M. spinetorum* by (1) presence of a ventral hindwing basal line (Fig. 1), lacking in *M. spinetorum* (Fig. 6); and (2) ventral hindwing postmedian line nearly straight from veins Cu2 to 2A (Fig. 1), with a "tooth" in *M. spinetorum* (Fig. 6). He also outlined statistical differences. Although the Weed female has the basal line of *M. millerorum*, it otherwise agrees with *M. spinetorum*.

Johnson (1985) proposed that the Weed female is *M. millerorum*, a new distribution record for the United States. He considered presence of a ventral hindwing basal line "the best overall superficial character for recognizing *millerorum*" and listed seven genitalic differences be-

1 2 3



4 5 6

FIGS. 1–3. Ventral wing surfaces with a hindwing basal line that is well-developed (Fig. 1), faint (Fig. 2), or reduced to a few scales (Fig. 3). Angle of postmedian line between veins Cu2 and 2A is 105.8° (Fig. 1), 87.1° (Fig. 2), 92.9° (Fig. 3).

FIGS. 4–6. Ventral wing surfaces without a hindwing basal line showing variation in angle of postmedian line between veins Cu2 and 2A: 105.3° (Fig. 4), 94.2° (Fig. 5), 82.1° (Fig. 6).

tween *M. spinetorum* and *M. millerorum*. He concluded that shape of the cubital postmedian line did not distinguish the two species.

Scott (1986) treated *M. spinetorum* and *M. millerorum* as conspecific. He noted that specimens from the Sacramento Mountains of New Mexico, such as the Weed area, occasionally have traces of a basal line on the ventral hindwing. Presumably, he considered these populations to be geographically and phenotypically intermediate between *M. spinetorum* and *M. millerorum*. However, he presented no evidence refuting the hypothesis that these species are distinct and sympatric in the Sacramento Mountains.

The purposes of this paper are to determine whether there are one or two species in the *M. spinetorum* complex in the vicinity of Weed, New Mexico, and to determine whether *M. millerorum* is a distinct species. I quantify Clench's ventral hindwing postmedian line character and Johnson's genitalic characters using 128 specimens (some with and some without a ventral hindwing basal line) collected near Weed. If there are two sympatric species distinguished by these characters, then they should have bimodal distributions correlated with the presence or absence of a ventral hindwing basal line. Finally, I compare the types of *M. spinetorum* and *M. millerorum* with variation at this site.

MATERIALS

Steve Cary, Dick Holland, and I collected 44 males and 84 females in the *M. spinetorum* complex on Forest Road 164, 1–4.5 miles from its intersection with State Road 130, in Lincoln National Forest along the Rio Penasco, Otero County, New Mexico, on 16, 21, and 22 June 1986. Clench's Weed female was caught on 12 June 1960 along the Rio Penasco and, if not at the same site, then within two miles of it. Specimens and their genitalia were deposited in the National Museum of Natural History.

METHODS

Distances were measured using a binocular microscope with a drawing tube and a digitizing pad with a puck. To quantify angles, I measured distances among the vertex and one point on each line forming the angle (equivalent to measuring the sides of a triangle) and calculated the angle using the Law of Cosines (Protter & Morrey 1965). To estimate measurement precision, I re-measured each character in 20% of the specimens.

I graphed results and tested them statistically, presenting means, standard deviations, ranges, and medians. Measurements were illustrated as histograms about the mean with quantiles one standard deviation wide. Because the distribution of measured ratios and angles is often skewed, I tested differences between specimens with and without a ventral hindwing basal line using the non-parametric Wilcoxon two-sample test corrected for ties (Sokal & Rohlf 1969).

I quantified shape of the male saccus by assigning a rank to each

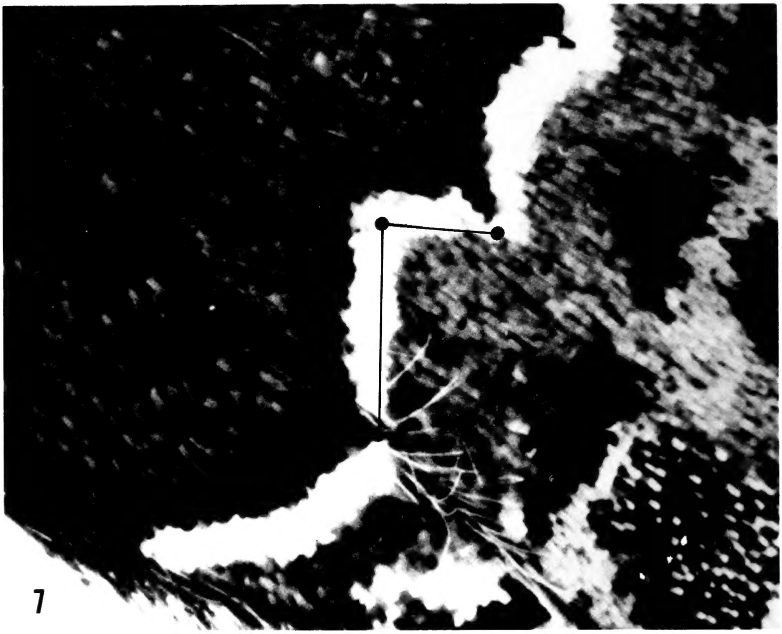


FIG. 7. Points specifying angle formed by the ventral hindwing postmedian line between veins Cu2 and 2A.

specimen. George Venable used the Transform command of Adobe Illustrator '88 software to produce an equally graded series of six shapes that spanned the range of variation in saccus width. Elaine Hodges then assigned each male to a rank by determining to which of the six figures its saccus was most similar. Venable and Hodges are professional entomological illustrators at the Smithsonian Institution and knew nothing about the project except that I was quantifying shape variation. I graphed results by rank and tested differences between specimens with and without a hindwing basal line as described above.

RESULTS

Ventral Hindwing Basal Line

A ventral hindwing basal line is the most important wing pattern character state distinguishing *M. millerorum* from *M. spinetorum* (Clench 1981, Johnson 1985). The line is fuscous, bordered basally with white scales, and not as conspicuous as the postmedian line (Clench 1981). Because specimens in the Weed sample varied from fresh to worn and because expression of the line varied (Figs. 1–3), I examined each individual with a binocular microscope at 24 power to score pres-

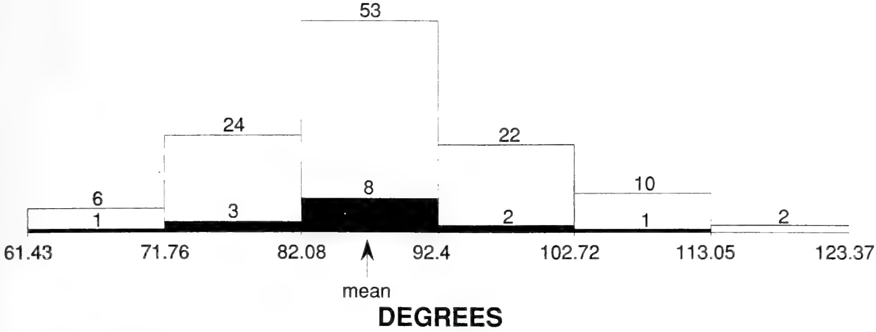


FIG. 8. Distribution of the angle formed by the ventral hindwing postmedian line between veins Cu2 and 2A. White columns represent the complete sample (n = 117), whereas black columns are a subsample of specimens with a basal line (n = 15).

ence or absence. Two specimens had the white portion of the line reduced to 2–3 scales, but in most cases presence was easily scored without a microscope.

Fifteen of 128 specimens (11.7%) had a ventral hindwing basal line (Figs. 1–6). It was present in 2 of 44 males (4.5%) and 13 of 84 females (15.5%). At the study site, either *M. spinetorum* is dimorphic for the ventral hindwing basal line or it is sympatric and synchronic with *M. millerorum*. The original Weed female was not an aberration.

Ventral Hindwing Postmedian Line

The "W" in the ventral hindwing postmedian line of *M. spinetorum* is not recognizable in *M. millerorum* because the line is nearly straight from vein Cu2 to 2A (Clench 1981). I quantified the angle formed by the postmedian line between veins Cu2 and 2A. The three points specifying the angle were: (1) intersection of the postmedian line with vein Cu2; (2) basal-most point of the postmedian line in the cell (vertex); and (3) intersection of the postmedian line with vein 2A (Fig. 7). All were scored in the middle of the postmedian line.

I graphed distribution of postmedian line angles (Fig. 8) and illustrated variation (Figs. 1–6). Eleven specimens were omitted because their hindwings were torn or too worn to be measured. The mean angle was 87.2° (s = 10.32°), ranging from 62.1° to 118.8°, and the median was 85.3°. Second measurements of 23 specimens differed from the first measurements by an average of 4.2° (s = 3.65°). I also graphed the distribution of angles for the 15 specimen subset that had a ventral hindwing basal line (Fig. 8).

The distribution of postmedian line angles was unimodal (Fig. 8), and this angle was not statistically greater in specimens with a basal

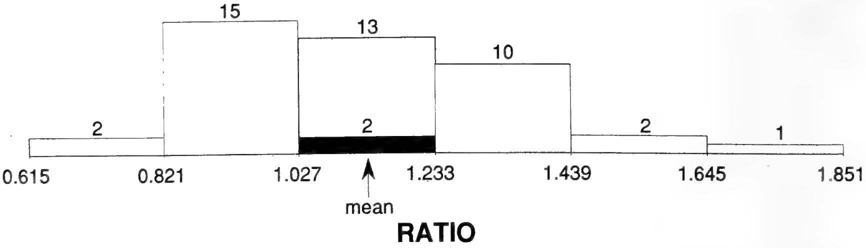
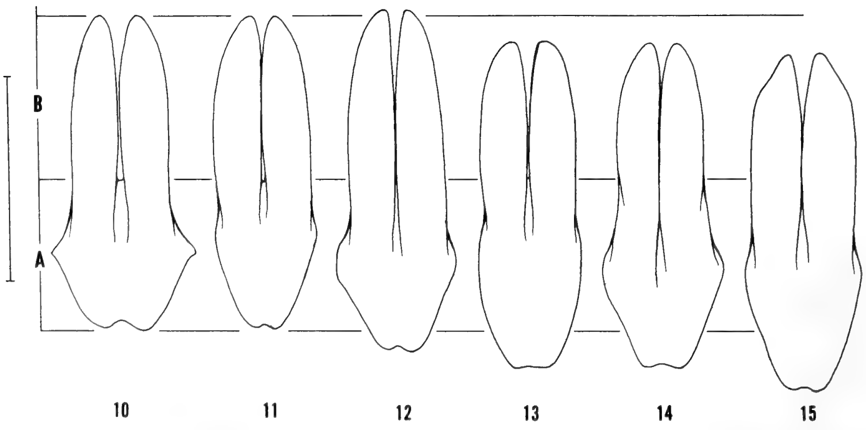


FIG. 9. Ratio of basal to distal length of male genitalia valves. White columns represent the complete sample (n = 43), whereas the black column is a subsample of males with a basal line (n = 2).

line on the ventral hindwing ($t_s = 1.167$). Of those with the basal line, seven had angles above the median and eight below.

Male Genitalia

Valves. The first male genitalic character that Johnson (1985:120) used to distinguish *M. millerorum* from *M. spinetorum* was "bilobed area markedly larger as contrasted to caudal length of valvae." Johnson (1981) figured the "bilobed configuration" as the anterior part of the valves and the "caudal extension" as the posterior part, but did not specify where each begins or ends. I thus measured valve length along the sagittal plane in ventral aspect from the anterior edge of the valves to the point where they separate and then from this point to their distal



FIGS. 10–15. Variation in male genitalia valves (ventral aspect) of specimens without a ventral hindwing basal line. The central horizontal line intersects the point at which the valves are joined medially. The ratio of valve lengths for the specimen in Fig. 10 is distance A divided by distance B. Scale 1 mm.

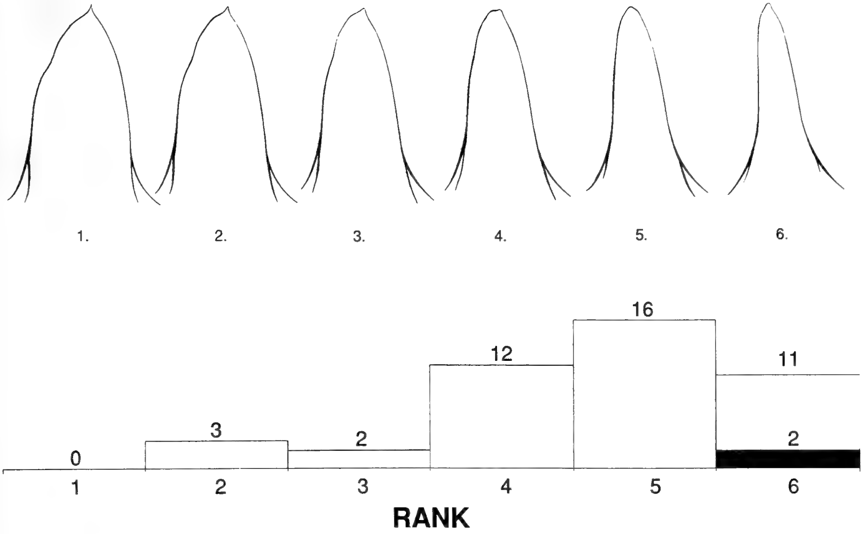


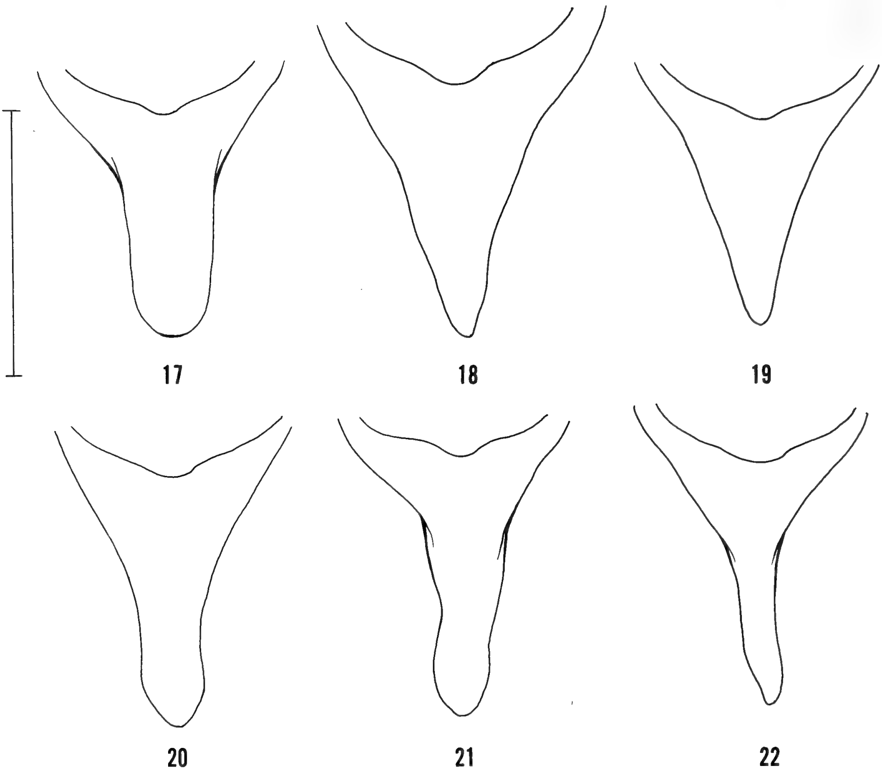
FIG. 16. Model ranks for male genitalia saccus and number of specimens placed in each rank. White columns represent the complete male sample ($n = 44$), whereas the black column is a subsample of males with a basal line ($n = 2$).

tips (Fig. 10) and calculated the ratio of basal to distal lengths. It was not possible to compare absolute lengths because Johnson's illustrations omitted a scale line.

I graphed distribution of valve length ratios for 43 specimens (Fig. 9)—one specimen's valves were damaged during preparation. The mean ratio was 1.13 ($s = 0.206$), ranging from 0.82 to 1.72, and the median was 1.10. Repeated measurements on 9 specimens differed by an average 0.07 ($s = 0.061$). Johnson's (1985) illustration of *M. millerorum* had a ratio of 1.19 and that of *M. spinetorum* was 1.07.

The distribution of valve length ratios was unimodal (Fig. 9) and did not differ significantly between specimens with and without a basal line ($t_s = 0.231$). Males with the line had ratios (1.09, 1.11) just above and below the median. I illustrated valves because length ratios measured only one aspect of variation (Figs. 10–15). Width and length of both the basal and distal parts varied, and the differences between *M. spinetorum* and *M. millerorum* that Johnson illustrated represented a small portion of this variation.

Saccus. Johnson's (1985:120) second distinctive male genitalic character of *M. millerorum* was "saccus widely parabolic" in contrast to the "parabolic" saccus of *M. spinetorum* (Johnson 1976). Although he did not show that saccus shape was parabolic, Johnson (1976:8) defined "parabolic" as "saccus gradually tapering and rounded cephalad" and

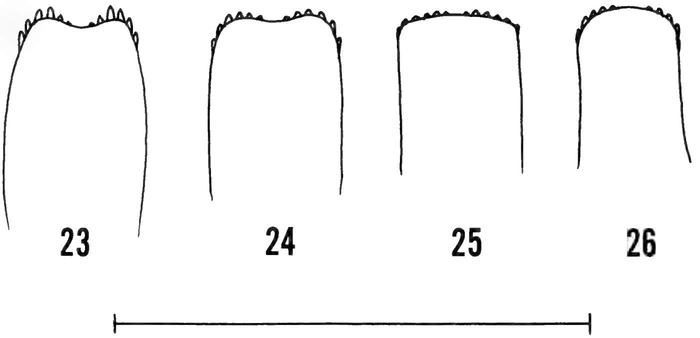


FIGS. 17–22. Variation in shape of male genitalia saccus (ventral aspect) in specimens without a basal line on the ventral hindwing. These specimens were placed in rank 2 (Fig. 17), rank 3 (Fig. 18), rank 4 (Fig. 19), rank 5 (Figs. 20, 21), rank 6 (Fig. 22). Scale 1 mm.

"wide-parabolic" as "saccus parabolic, but tapered less gradually." Thus, male *M. spinetorum* should have a less tapered saccus, as in Johnson's (1985) illustrations.

I graphed the number of specimens that were ranked in each of six graduated saccus shapes (Fig. 16). Mean rank was 4.7 ($s = 1.12$), ranging from rank 2 to rank 6, and the median was rank 5. Johnson's illustration of *M. spinetorum* was placed in rank 3 and that of *M. millerorum* in rank 2.

The distribution of saccus shape ranks was unimodal (Fig. 16) and there was no statistically significant difference ($t_s = 1.747$) between individuals with and without a hindwing basal line. Two males with a line were placed in rank 6, but Johnson's illustration of *M. millerorum* was placed in rank 2.



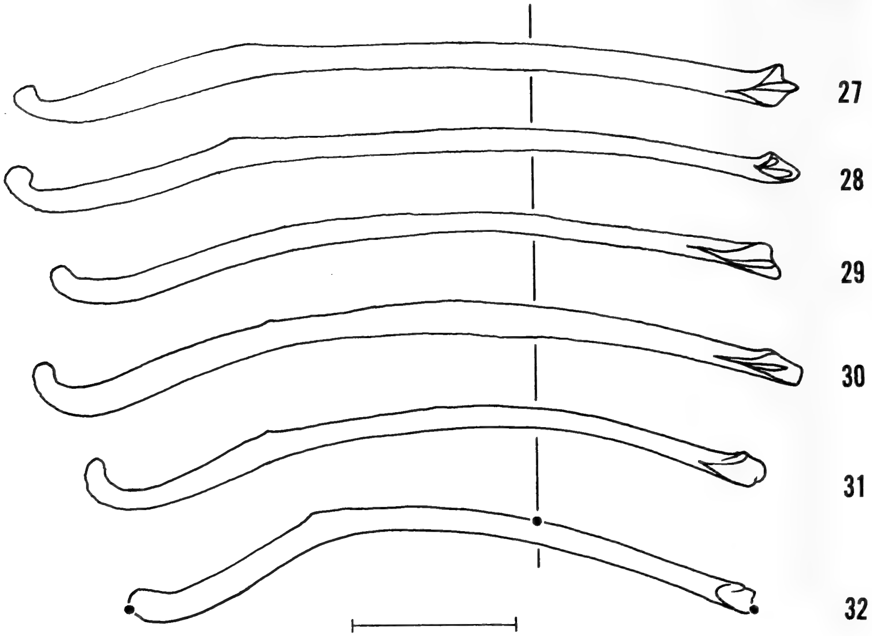
FIGS. 23–26. Variation in shape of the tip of the dorsal cornutus, which was scored as "bifurcate" (Figs. 23, 24) or "not bifurcate" (Figs. 25, 26). Scale 1 mm.

Quantification does not reflect the complexity of saccus shape variability (Figs. 17–22). The saccus can be rounded or triangular (Figs. 17, 18), wide or narrow (Figs. 17, 22), and asymmetrical to the left or right (Figs. 21, 22). Differences in saccus shape between *M. spinetorum* and *M. millerorum*, as illustrated by Johnson, represent a very small portion of intraspecific variability.

Dorsal cornutus. Johnson's (1985:120) third distinctive male genitalic character of *M. millerorum* was "cephalad cornutus at aedeagal terminus bifurcate." The posterior end of the dorsal cornutus is curved upwards a variable amount, is usually twisted, and has teeth on the posterior edge that are sometimes absent or reduced in size in the middle. I oriented the genitalia so that the cornutus tip was at a right angle to the plane of view. If the posterior edge was indented (viewed at 125 power), it was scored as "bifurcate" whereas if it was straight or convex, it was scored as "not bifurcate." Of nine specimens scored a second time, one differed from the original assessment.

Shape of the dorsal cornutus did not distinguish *M. millerorum* from *M. spinetorum*. Twenty of 41 specimens (49%) without a ventral hindwing basal line (*M. spinetorum* phenotype) had a "bifurcate" cornutus as did one of two specimens with a ventral hindwing basal line (*M. millerorum* phenotype). Shape of the posterior edge appeared to vary continuously. I illustrated (Figs. 23–26) examples representing the range of variation in the sample.

Penis. Johnson's (1985:120) fourth male genitalic character for distinguishing *M. millerorum* was "caudal one-third of aedeagus distinctly curved (60°) in known specimen." He did not specify the number of degrees that the penis of *M. spinetorum* curves, but I infer that it is less curved than that of *M. millerorum*.



FIGS. 27–32. Variation in curvature and length of the penis (lateral aspect) of specimens without a ventral hindwing basal line. The vertical line intersects the point one-third of the distance from distal end of each penis. The three points in Fig. 32 specify the angle of curvature that I measured; the middle point was the vertex. Scale 1 mm.

I calculated penis curvature (Figs. 27–32) by measuring the angle specified by (1) the most anterior point of the penis, (2) the ventral tip of the penis, and (3) the penis dorsal surface one-third of the distance from the posterior tip (vertex) (Fig. 32). I used an ocular scale with a perpendicular line to determine the last point.

I graphed distribution of penis curvature for 43 specimens (Fig. 33) and illustrated variation (Figs. 27–32). The mean angle was 158.6° (s = 5.54), ranging from 148.9° to 168.5°, and the median angle was 157.9°. Repeated measurements on 9 specimens differed by an average 3.9° (s = 3.41).

The distribution of angles was slightly bimodal (Fig. 33), but penis curvature of individuals with a ventral hindwing basal line was not significantly different from that of other specimens ($t_s = 1.211$). One male with a line had an angle of 158.6°, the mean for the entire sample, while the other had an angle of 165.9°, a result contrary to the hypothesis that the penis of *M. millerorum* curves more sharply than that of *M. spinetorum*.

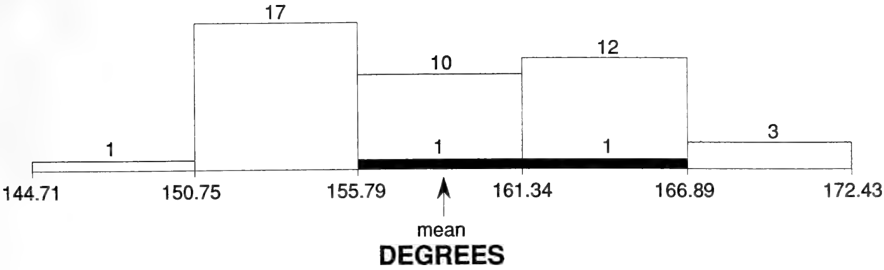


FIG. 33. Penis curvature. White columns represent the complete sample (n = 43), whereas the black column is the subsample of males with a basal line (n = 2).

Female Genitalia

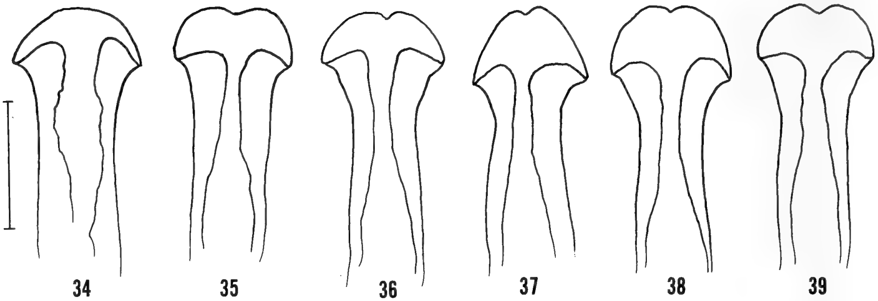
Johnson (1985:120–121) distinguished *M. millerorum* from *M. spinetorum* using shape of the genital plate and ventral ductus bursae. Differences "are most apparent in the nature of the lamellal [sic] lips caudad on the ductus bursae, the nature of the sclerotizations surrounding these lips, and the shape of the sculpturing caudo-ventrad on the ductus bursae." However, shape of the posterior bursa copulatrix in specimens with and without a ventral hindwing basal line varied similarly (Figs. 34–45) and provided no evidence for two species in the Weed sample.

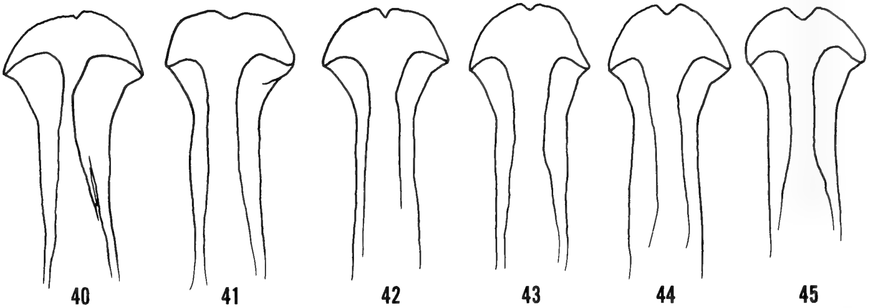
Comparison with Types

The type of *M. spinetorum,* a female housed in the Smithsonian Institution, lacked the ventral hindwing basal line, and the angle formed by the postmedian line between veins Cu2 and 2A was 107.51° (n = 4, s = 2.863). Its genitalia (Fig. 42) and postmedian line angle fall within the range of variation of the Weed population.

The ventral wing pattern and genitalia of the female type of *M. millerorum* were clearly illustrated (by A. C. Allyn, J. Y. Miller) in Clench (1981). It possessed the ventral hindwing basal line, and its postmedian line angle was 112.49° (n = 4, s = 8.810). Its genitalia fall within the range of variation illustrated in this paper (compare Figs. 34–45 with fig. 36 in Clench 1981).

In accord with Scott's (1986) hypothesis, *M. millerorum* Clench is a synonym of *M. spinetorum* (Hewitson). The wing pattern and genitalic characters proposed to distinguish these species (Clench 1981, Johnson 1985) vary continuously in the Weed population and are unimodal. The types of *M. spinetorum* and *M. millerorum* fall within the range of variation of this population. Thus, there is no published evidence





FIGS. 34–39. Posterior bursa copulatrix (ventral aspect) of specimens with a ventral hindwing basal line. Scale 1 mm.

FIGS. 40–45. Posterior bursa copulatrix (ventral aspect) of specimens without a ventral hindwing basal line from the Weed population, except for Fig. 42, which is the type of *M. spinetorum* from California.

supporting the hypothesis that *M. millerorum* is distinct from *M. spinetorum*.

DISCUSSION

Genitalic Differences in *Mitoura*

Johnson (1976, 1978, 1981, 1985) characterized North American *Mitoura* species using genitalic differences, but his results are invalid because he did not assess variation. Brown (1983) examined two male and two female genitalic preparations for each of four Californian *Mitoura* taxa and found greater variation within species than Johnson had reported between species. Johnson listed seven genitalic differences between *M. millerorum* and *M. spinetorum*, but these differences represent a small portion of continuous unimodal intraspecific variation.

TABLE 1. Observed and expected number of specimens of *Mitoura spinetorum* complex from Weed, New Mexico, with and without a ventral hindwing basal line when presence is determined by a sex-linked recessive in Hardy-Weinberg equilibrium (Crow & Kimura 1970). The maximum likelihood estimate for gene frequency is 0.170 and for proportion of males is 0.34.

	Males	Females
With ventral hindwing basal line		
Observed	2	13
Expected	1.3	14.3
No ventral hindwing basal line		
Observed	42	71
Expected	42.7	69.7

Genetic Basis of Ventral Hindwing Basal Line

Two simple genetic mechanisms might account for the greater frequency of ventral hindwing basal line phenotypes in females (15.5%) than in males (4.5%). First, expression of the line may have a quantitative genetic basis with greater prenetrance in females. Wing spots in *Erynnis* Schrank (Burns 1964) are an analogous example. Some spots in *Erynnis* may be present or absent, but are present more frequently in females. Further, spot size varies continuously. The variable expression of the ventral hindwing basal line in *M. spinetorum*, when present, is consistent with this mechanism.

A second possible mechanism is that expression of the line is determined by a sex-linked recessive allele in Hardy-Weinberg equilibrium. Following calculations in Crow and Kimura (1970:41–42) for a sex-linked recessive in which the female is the heterogametic sex, expected frequencies of phenotypes closely match observed frequencies (Table 1, $\chi^2 = 0.57$, df = 1).

These hypotheses on the genetic basis of hindwing basal line expression can be tested by data from rearing. Dimorphic populations are found at different localities in the Sacramento Mountains, and a New Mexican specimen with a hindwing basal line was collected by R. Holland on the crest of the Caballo Mountains (Sierra County).

ACKNOWLEDGMENTS

I thank fellow collectors Steve Cary and Dick Holland for their sharp eyes, companionship, generosity, and encouragement; my brother Gene Robbins and his family for their hospitality during my stay in New Mexico; Cliff Ferris, John Justice, Doug Mullins, and Ray Stanford for information; Adrienne Venables for technical assistance; George Venable and Elaine Hodges for quantifying saccus shape; Greg Ballmer, John Brown, John Burns, Steve Cary, Larry Gall, Dick Holland, John Lane, Paul Opler, Oakley Shields, Adrienne Venables, and Ben Ziegler for commenting on the manuscript.

LITERATURE CITED

BROWN, J. W. 1983. A new species of *Mitoura* Scudder from southern California (Lepidoptera: Lycaenidae). J. Res. Lepid. 21:245–254.

BURNS, J. M. 1964. Evolution in skipper butterflies of the genus *Erynnis*. Univ. Cal. Publ. Entomol. Vol. 37. U. Cal. Press, Berkeley. 214 pp.

CLENCH, H. K. 1981. New *Callophrys* (Lycaenidae) from North and Middle America. Bull. Allyn Mus. 64, 32 pp.

CROW, J. R. & M. KIMURA. 1970. An introduction to population genetics theory. Harper & Row, New York. 591 pp.

JOHNSON, K. 1976. Three new Nearctic species of *Callophrys* (*Mitoura*), with a diagnosis of all Nearctic consubgeners (Lepidoptera: Lycaenidae). Bull. Allyn Mus. 38, 30 pp.

——— 1978. Specificty, geographic distributions, and foodplant diversity in four *Callophrys* (*Mitoura*) (Lycaenidae). J. Lepid. Soc. 32:3–19.

——— 1981. Revision of the Callophryina of the world with phylogenetic and biogeographic analyses (Lepidoptera: Lycaenidae). Dissertation, City University of New York, Univ. Microfilms Int. (#8112361), Ann Arbor, MI. 902 pp.

——— 1985. *Mitoura millerorum* (Clench) and its occurrence in the United States (Lycaenidae). J. Lepid. Soc. 39:119–124.

PROTTER, M. H. & C. B. MORREY JR. 1965. College calculus with analytic geometry. Addison-Wesley Publishing Co., Reading, Massachusetts. 897 pp.

SCOTT, J. A. 1986. The butterflies of North America. A natural history and field guide. Stanford University Press, Stanford, California. 583 pp., 64 pl.

SOKAL, R. R. & F. J. ROHLF. 1969. Biometry. W. H. Freeman & Co., San Francisco. 776 pp.

Received for publication 26 August 1989; revised and accepted 3 May 1990.

Journal of the Lepidopterists' Society
44(2), 1990, 77–87

REDEFINITION OF TRIBE BACTRINI FALKOVITSH AND REVISED STATUS OF GENERA *TANIVA* HEINRICH AND *HULDA* HEINRICH (TORTRICIDAE: OLETHREUTINAE)

P. T. DANG

Forestry Canada, % Biosystematics Research Centre,
Ottawa, Ontario K1A 0C6, Canada

Abstract. The concepts of the tribes Bactrini Falkovitsh and Endotheniini Diakonoff of Falkovitsh (1962), Diakonoff (1973), Kuznetsov and Stekolnikov (1973, 1977, 1984) are reviewed. The tribe Bactrini is redefined on the basis of the morphological structure of the male genitalia, particularly the well-developed, heavily-sclerotized and sharply-recurved uncus, the convex and bent downward tegumen, the near 180° angle formed by the dorsal edge of the basal opening and the basal portion of the costa of the valva, and the absence of coarse setae on the tarsi of the adult of both sexes. The tribe Endotheniini *sensu* Kuznetsov and Stekolnikov, or the subtribe Endotheniina *sensu* Razowski, represented by the genus *Endothenia* Stephens, is removed from the supertribe Gatesclarkeanidii (Kuznetsov & Stekolnikov 1984), from the tribe Gatesclarkeanini (Horak & Brown in press), and from the Olethreutini (Razowski 1989), and assigned to tribe Bactrini. Genera *Taniva* Heinrich and *Hulda* Heinrich are distinguished from *Endothenia*, reassigned to the tribe Olethreutini, and their original generic status is reinstated.

Additional key words: Endotheniini, Gatesclarkeanini, taxonomy, male genitalia, tarsal setae.

Falkovitsh (1962) used secondary sexual structures of the male, including the long hairlike scale tuft on the hind tibia and scent glands on the abdomen or on the hindwing, as morphological criteria in the definitions of a number of tribes in the subfamily Olethreutinae. He defined the tribe Bactrini by the total absence of the tibial hair tuft and the wing scent gland. Although these structures are absent in *Bactra* species, they are also absent in various species of other genera of Olethreutinae. Nevertheless, Diakonoff (1973) used these characters and genital structure to define the subtribe Bactrae, a new status for Bactrini, which includes *Bactra* Stephens, a large genus with numerous species worldwide in distribution, and five genera from the south Asiatic region (*Parabactra* Meyrick, *Syntozyga* Lower, *Bubonoxena* Diakonoff, *Cyclacanthina* Diakonoff, *Henioloba* Diakonoff). Diakonoff also proposed a new subtribe, Endotheniae, consisting of two genera, *Endothenia* Stephens and *Molybdocrates* Diakonoff. *Endothenia* has a moderate number of species and occurs in the Nearctic, Palaearactic, and Oriental regions. *Molybdocrates* is known only from the south Asiatic region with a small number of species. Diakonoff (1973) revised the status of the genus *Endothenia* and synonymized three monotypic genera, *Taniva* Heinrich, *Hulda* Heinrich, and *Tia* Heinrich, under *Endothenia*. This synonymy was accepted in subsequent treatments of the group (Powell 1983, Miller 1987). Kuznetsov (1978) included *Tia* in Olethreutini in the key to genera of Olethreutini in the European part of the

USSR. Although the reason for this transfer was not given, as a result *Tia* was reinstated.

Kuznetsov and Stekolnikov (1984) studied the morphological functions of genital muscles of tortricid males and proposed a classification scheme for the family Tortricidae. In the subfamily Olethreutinae, they recognized three supertribes: Gatesclarkeanidii, consisting of two tribes (Gatesclarkeanini and Endotheniini); Olethreutidii, consisting of three tribes (Microcorsini, Bactrini, and Olethreutini); and Eucosmidii, consisting of three tribes (Enarmoniini, Eucosmini, and Laspeyresiini). They suggested that Bactrini and Microcorsini are related and that Endotheniini differs from Bactrini and other species of Olethreutinae (except species of the tribe Gatesclarkeanini) by the absence of the tergal extensor of the valva, muscle m2. Subsequently, Endotheniini is being synonymized under Gatesclarkeanini by Horak and Brown (in press), also on the basis of the absence of the muscle m2 in the male genitalia of these two tortricid groups. Razowski (1989) recognized five tribes in the subfamily Olethreutinae: Microcorsini, Bactrini, Olethreutini, Eucosmini and Grapholitini. According to this arrangement, Olethreutini includes a number of subtribes as proposed by Diakonoff (1973), of which the Endotheniina and the Gatesclarkeanina are relevant to the present study.

Generic descriptions of the taxa involved in this study were given by Heinrich (1926) (*Taniva, Tia, Hulda, Endothenia,* and *Bactra*), Diakonoff (1956) (*Bactra*), Diakonoff (1973) (*Bactra* and *Endothenia*). Therefore, these descriptions are not repeated here.

MATERIALS AND METHODS

The following species of tribes Bactrini, Endotheniini s.s., Olethreutini, Gatesclarkeanini, and Microcorsini were examined (information in parentheses indicates geographic regions where specimens were collected):

Bactra lanceolana (Hübner) (N. Amer.), *B. furfurana* (Haworth) (N. Amer.), *B. verutana* Zeller (N. Amer. & Japan), *B. maiorina* Heinrich (N. Amer.), *B. priapeia* Heinrich (N. Amer.), and *B. sinistra* Heinrich (N. Amer.) in the Canadian National Collection (CNC), *B. jansei* Diakonoff (S. Afr.), *B. confusa* Diakonoff (S. Afr.), *B. scrupulosa* Meyrick (S. Afr.), *B. spinosa* Diakonoff (S. Afr.), *B. stagnilicolana* Zeller (S. Afr.), *B. sardonia* (Meyrick) (S. Afr.), *B. pythonia* Meyrick (S. Afr.), *B. aletha* Diakonoff (W. Afr.), *B. tylophora* Diakonoff (Uganda), *B. nea* Diakonoff (Angola), *B. endea* Diakonoff (Gambia), *B. fasciata* Diakonoff (Natal), *B. venosana* Zeller (Pengal), *B. sinassula* Diakonoff, *B. optanias* Meyrick (Ceylon), *B. canopepla* Turner (Ceylon), *B. tornastis* Meyrick (Ceylon), *B. copidotis* Meyrick (Ceylon), *B. metriacma* Meyrick (Ceylon), *B. leucogama* Meyrick (Ceylon), *B. cerata* (Meyrick) (Ceylon), *B. fracta* Diakonoff (India), *B. phaulopa* Meyrick (Palawan), *B. coronata* Diakonoff (Java), *B. clarescens* Meyrick (Jamaica), *B. philocherda* Diakonoff (Jamaica), *B. seria* Meyrick (S. Amer.), *B. erasa* Meyrick (S. Amer.), *B. perisema* Diakonoff (S. Amer.), *B. robustana* (Christoph) (England & Japan), *B. simpliciana* Chrétien (?loc.), *B. hostilis* Diakonoff (Japan), *B. festa* Diakonoff (Japan), *B. honesta* Meyrick (Australia), *B. rhadonoma* Diakonoff (N. Zealand), *B. boschmai* Diakonoff (N. Guinea), *B. difissa* Diakonoff (N. Guinea), and *B. straminea* (Butler) (Hawaii) in the British Museum (Natural History) (BMNH); *Endothenia montanana* (Kearfott) (N. Amer.), *E. heinrichi* McDunnough (N. Amer.), *E. rubipunctana* (Kearfott) (N. Amer.), *E. sordulenta* Heinrich (N. Amer.), *E. melanosticta* (Walsingham) (N. Amer.), *E. affiliana* McDunnough (N. Amer.), *E. hebesana* (Walker) (N. Amer.), *E. infuscata* Heinrich (N. Amer.), *E. nubilana* (Clemens) (N. Amer.), *E. atrata* (Caradja) (Japan), and *E. banausopis* (Meyrick) (Japan) in CNC; *E. gentianeana* (Hübner) (Europe), *E. oblongana* (Haworth) (Europe), *E. sellana* (Gué.) (Europe), and *E. nigricostana* (Haworth) (Europe) in BMNH; *Microcorses marginifasciata* Walsingham (Japan) in the U.S. National Museum of Natural History (USNM), same species (Japan, Nepal) and *M. trigonana* (Walsingham) in BMNH: *Cryptaspasma triopis* Diakonoff (Guam), *C. lugubris* (Felder) (Texas) in USNM, same species (F. Guyana, Brazil, B. Honduras, Colombia) in BMNH; *Gatesclarkeana erotias* (Meyrick) (India), and *G. idia* Diakonoff (Thailand) in BMNH; *Taniva albolineana* (Kearfott) (N. Amer.), *Tia enervana* (Ersch.) (N. Amer.), and *Hulda impudens* (Walsingham) (N. Amer.) in CNC.

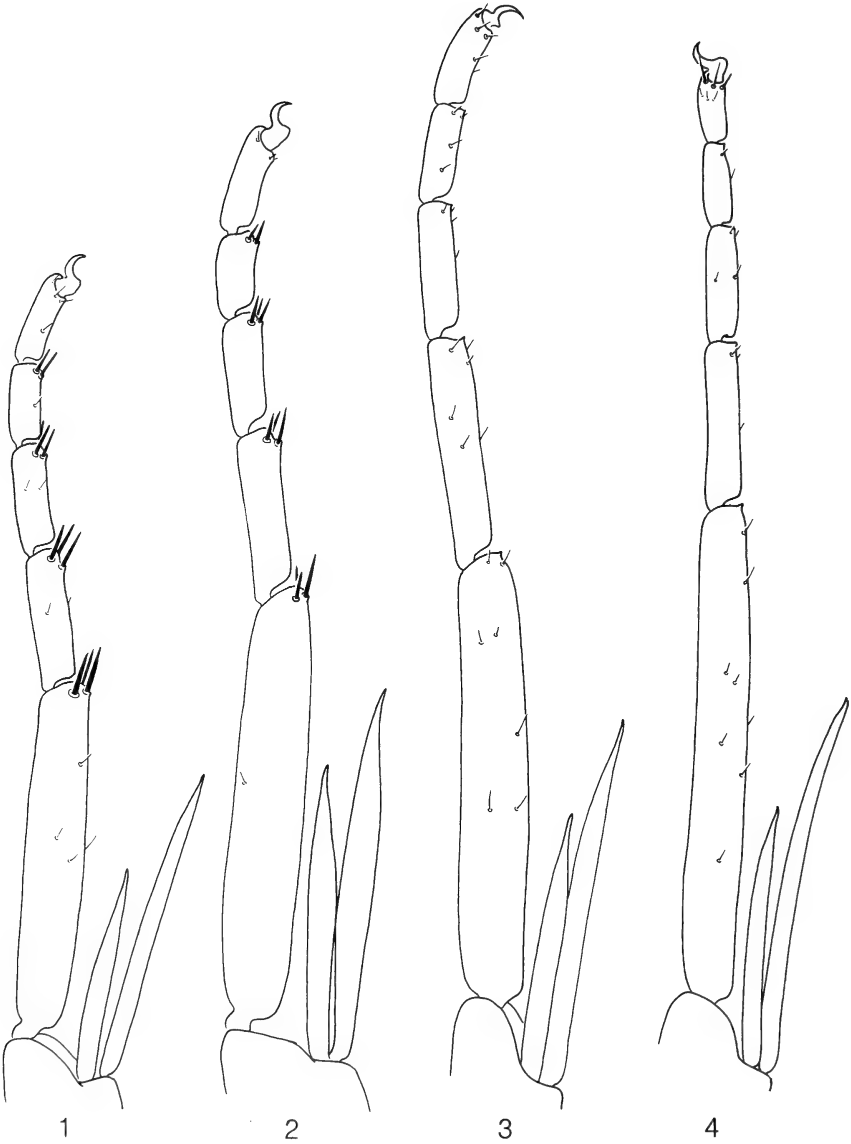
Most North American tortricid species, which are unlisted here, belonging to tribes Cochylini, Sparganothini, Hilarographini, Archipini, Tortricini, Olethreutini, Eucosmini, and Laspeyrasiini were also examined to determine the degree of development of tarsal setation. Additional morphological information on *Bactra* and *Endothenia* species was obtained from the literature (Diakonoff 1956, 1959, 1962, 1963, 1964, 1973, Graaf Bentinck & Diakonoff 1968, Clarke 1958, Kuznetsov 1978, Razowski 1989).

In the majority of cases, leg setae, especially those on the lower margin of the apex of tarsomeres, can be observed directly from pinned specimens (Figs. 1–4). Tarsomeres without developed setae were descaled so that the presence of fine setation could be confirmed; legs were macerated in gently boiling 20% KOH solution for 3–5 min so that scales could be easily removed to reveal setation of tarsomeres. Legs were then mounted permanently in Canada balsam on microscope slides. Genitalia were studied and illustrated while floating in glycerin so that natural shapes of the uncus and other parts of the genitalia could be studied without distortions or deformations due to pressure from a cover slip. Morphological structures of selected specimens were illustrated with the help of a camera lucida and a microprojector. Observations were made at magnifications of 40×, 80× and 200× with dissecting and compound microscopes.

RESULTS AND DISCUSSION

Distributions of morphological characters among selected tortricid genera are given in Table 1.

Examinations of the male genitalia of *Endothenia hebesana* (Walker), *E. melanosticta* (Walsingham), and *E. nubilana* (Clemens) revealed that muscle m2 in the male genitalia of these three Nearctic *Endothenia* species is actually present and developed (Fig. 8A). This finding is contrary to Kuznetsov and Stekolnikov (1977, 1984), who reported that



FIGS. 1–4. Hind tarsi of males of Olethreutinae. **1,** *Taniva albolineana* (Kearfott); **2,** *Tia enervana* (Ersch.); **3,** *Bactra furfurana* (Haworth); **4,** *Endothenia hebesana* (Walker).

TABLE 1. Distribution of morphological characters in various genera of Bactrini, Gatesclarkeanini, Olethreutini, and Microcorsini.

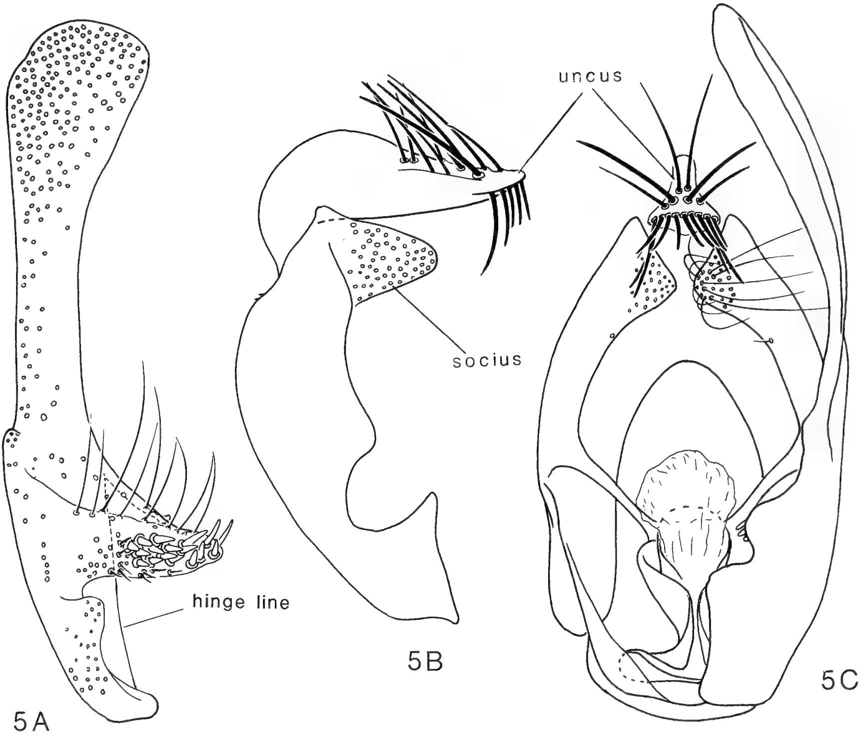
Taxa	Characters						
	1	2	3	4	5	6	7
Bactrini							
Bactra	−	−	+	−	+	+	+
Endothenia	+/−	−	+	−	+	+	+
Gatesclarkeanini							
Gatesclarkeana	+	−	−	−	−	−	−
Olethreutini							
Episimus	−	+	−	−	−	−	(+)
Apotomis	+	+	−	−	−	−	+
Endopiza	+	+	−	−	−	−	(+)
Lobesia	+	+	−	−	−	−	+
Ahmosia	+	+	−	−	−	−	(+)
Eumarozia	−	+	−	−	−	−	(+)
Zomaria	−	+	−	−	−	−	(+)
Pseudosciaphila	−	+	−	−	−	−	(+)
Orthotaenia	+	+	−	−	−	−	+
Olethreutes	+/−	+	−	−	−	−	+
Phaecasiophora	+	+	−	−	−	−	(+)
Hedya	+/−	+	−	−	−	−	(+)
Evora	+	+	−	−	−	−	(+)
Taniva	+	+	−	−	−	−	(+)
Tia	+	+	−	−	−	−	(+)
Hulda	+	+	−	+	−	−	(+)
Microcorsini							
Microcorses	−	+	−	−	−	−	+
Cryptaspasma	−	+	−	−	−	−	+

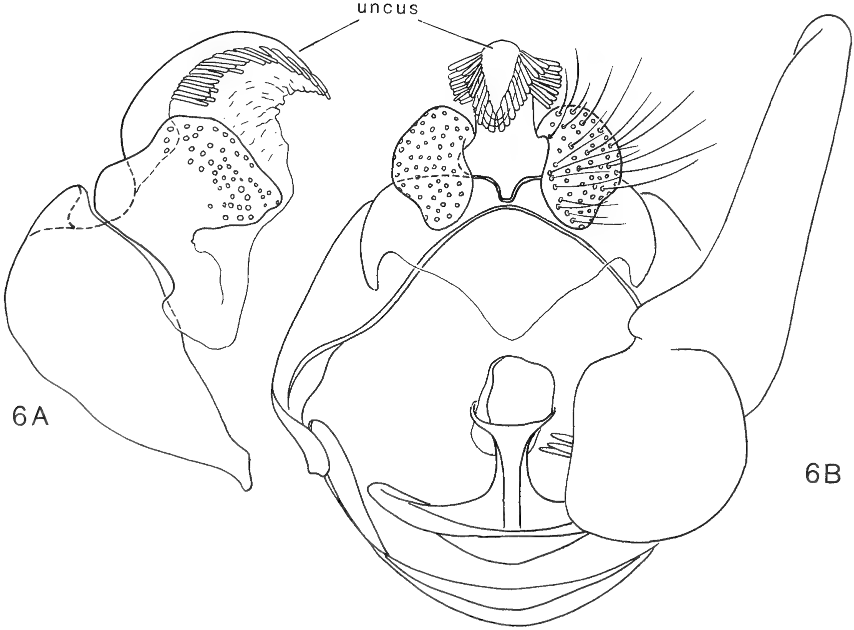
Explanation of characters: 1: Hair tuft on male hind tibia. 2: Setae on distal ends of male and female tarsomeres 1–4 well developed, spinelike. 3: Uncus well developed, heavily sclerotized, strongly recurved forming dorsal fold or pit at base. 4: Socii heavily sclerotized, surface of distal half smooth. 5: Tegumen convex bent downward. 6: Hinge line and basal portion of costa of valva parallel, or forming a straight line; costal hook unpronounced. 7: Tergal extensor of valva of male genitalia, muscle m2 (only ♂ genitalia of *Bactra* and *Endothenia* were examined for this character in the present study, those of others based on data by Kuznetsov & Stekolnikov (1973, 1977, 1984), (+) indicates a theoretical assumption of the presence of m2 based on the above authors' concept of tribe Olethreutini). +/−: Confirmation of above characters: +, affirmative or present; −, negative or absent.

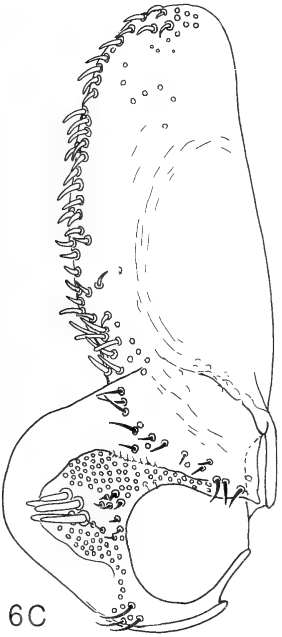
muscle m2 is absent in *E. marginana* (Haworth), leading them to propose the classification scheme outlined above. In light of this new evidence, the placements of Endotheniini in the supertribe Gatesclarkeanidii by Kuznetsov and Stekolnikov (1984) and in the tribe Gatesclarkeanini by Horak and Brown (in press) need to be reassessed and revised.

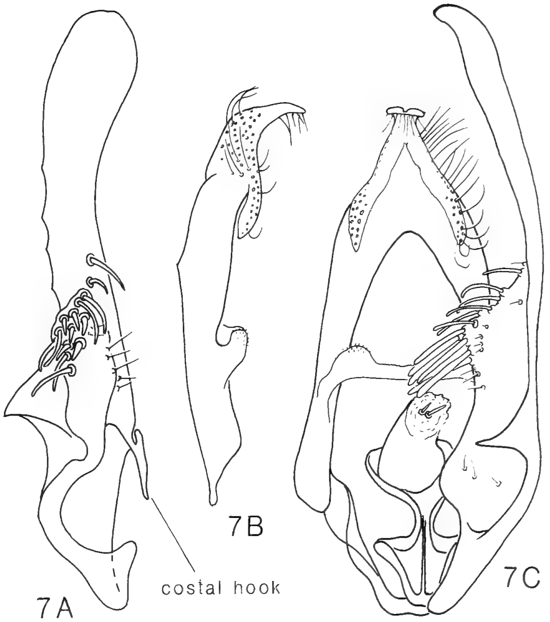
In fact, unlike previously thought, *Endothenia* shows marked similarity to *Bactra* in the following four sets of characters, which can be found nowhere else in the Tortricidae:

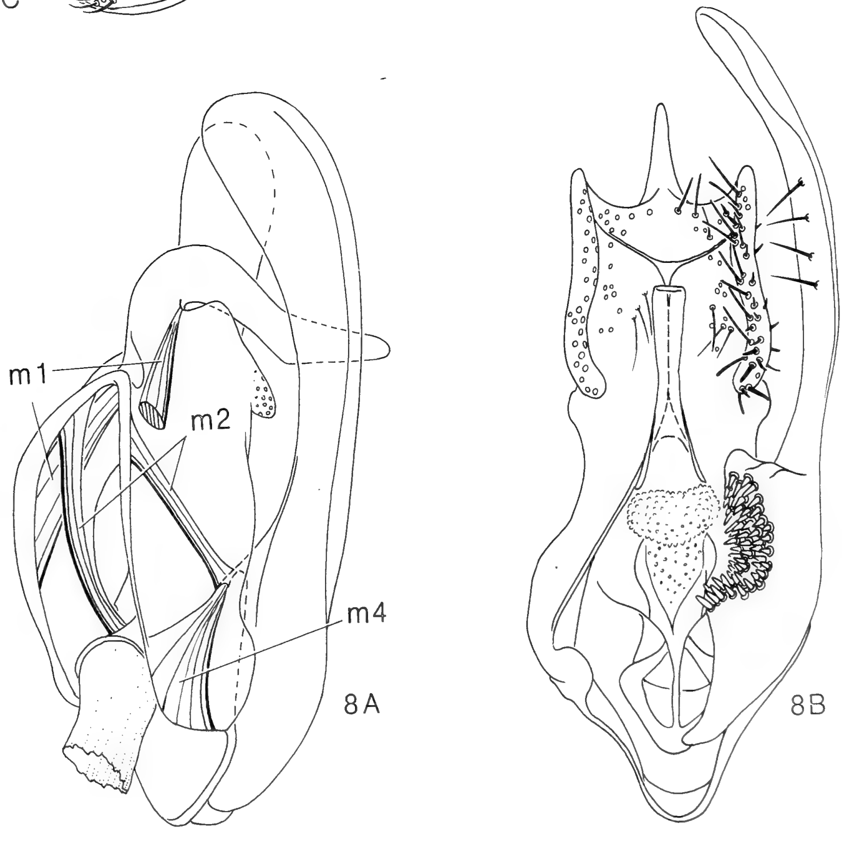
a) The uncus of these two genera is well developed, heavily sclerotized, and sharply recurved with a sharp fold or pit dorsally near the base and with strong, stout, and blunt setae in apical and subapical areas; in *Bactra* species, setae are arranged into a more or less continuous

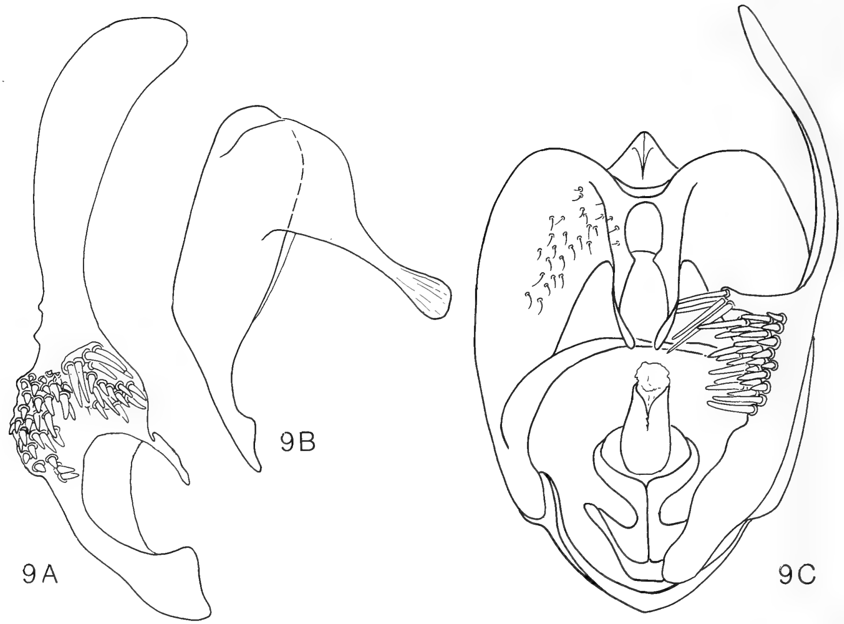

uncus
socius
hinge line
5A
5B
5C


uncus
6A
6B


6C


7A
7B
7C
costal hook


m1
m2
m4
8A
8B



FIGS. 5–9. Male genitalia of species of Olethreutinae. **5,** *Endothenia melanosticta* (Walsingham): A, left valva; B, lateral views of uncus, tegumen, and socius; C, ventral view of genitalia. **6,** *Bactra furfurana* (Haworth): A, lateral views of uncus, tegumen, and socius; B, ventral view of genitalia; C, left valva. **7,** *Taniva albolineana* (Kearfott): A, left valva; B, lateral views of uncus, tegumen, and socius; C, ventral view of genitalia. **8**A, *Endothenia melanosticta* (Walsingham): laterodorsal view of dorsal muscles. **8**B, *Tia enervana* (Ersch.): ventral view of genitalia. **9,** *Hulda impudens* (Walsingham): A, left valva; B, lateral views of uncus, tegumen, and socius; C, ventral view of genitalia.

row fringing the lateral and apical margins (Figs. 6A–B), in *Endothenia* species, setae are arranged into an apical row with a second group not in a row located dorsally (Figs. 5B–C, 6B–C). This strongly-curved and highly-specialized uncus is somewhat similar to that of the Archipini. However, the function of this strong uncus is quite different between these two groups. In the Archipini, both the uncus and the gnathos are well developed, and together they perform like the index finger and the thumb in gripping and holding the female during mating. In *Endothenia* and *Bactra,* however, the gnathos is poorly developed and the uncus alone is unable to grip and hold the female abdomen. Instead, the uncus, because of its hook shape with a distinctly-widened apex, or with a normal apex marginally armed with strong and stout setae, is able to anchor itself securely between the posterior ends of the anal papillae of the female during mating. In other species of the Olethreutinae, the uncus is often fleshy or slightly sclerotized, narrow, fingerlike, straight or gently curved ventrally, and weakly setose (Figs. 7B–C, 8B, 9B–C), or absent. As a result, the uncus of many olethreutine species is much less effective in holding the female during copulation, and that of many others is virtually nonfunctional. With regard to the strong uncus and the classification of these two particular genera, Diakonoff (1956) remarked: "*Bactra* can be placed in *Endothenia* group of genera, with the remarkable spinose, hooked uncus in the males . . . ."

b) The tegumen of the male genitalia of *Endothenia* and *Bactra* is often short and distinctly bent downward, whereas that of other tortricid species is fairly straight, and directed posteriorly.

c) The dorsal side of the sacculus is not developed and expanded. As a result, the hinge line of the valva, i.e., the dorsal edge of the basal opening and the basal portion of the costa of the valva are parallel, or form a relatively straight line. Thus, when the valvae spread out to receive the female, their distal ends move only slightly away from the tegumen. In consequence, they remain virtually in a vertical position while holding onto the female genital segments during mating. Furthermore, in this position, the male would be able to effectively utilize the largely-expanded and strongly-setose sacculi in holding and applying lateral pressure onto the female organs during copulation. The costal hook is small and nonpronounced. In other Olethreutinae, the hinge line and the basal portion of the costa of the valva form an angle of 130 degrees or less, so that, as the valvae spread out to receive the female, their distal ends move away from the tegumen. During mating the pair of valvae stretch out horizontally pressing on along the lateral or ventrolateral sides of the abdomen. There are a few intermediate cases in Olethreutini in which the angle of the hinge line and the basal portion of the valva form nearly a straight line as in Bactrini. In these cases, however, the costal hook is distinctly of the Olethreutini and Eucosmini type, i.e., large, thumb-shaped, and produced from the base of the costa (Fig. 7A).

d) The tarsal setae, particularly those located at the distal end of tarsomeres 1–4 in both sexes, are greatly reduced and are much smaller and finer than surrounding scales in *Bactra, Endothenia, Gatesclarkeana,* and species of the Tortricini (Figs. 3–4). In other tortricid species, these setae are well developed, darkly pigmented and spinelike (Figs. 1–2).

On the basis of the present morphological evidence, *Bactra* and *Endothenia* form a distinct monophyletic group that is clearly distinct from other genera in the subfamily Olethreutinae. Therefore, I hereby assign them to the tribe Bactrini. Genera (in Diakonoff 1973) other than *Bactra* in Bactrae and *Endothenia* in Endotheniae, respectively, were not included in the present study. Consequently, tribal placements of these genera (mostly from the south Asiatic region) remain to be investigated and clarified.

The genus *Gatesclarkeana* represents a unique group with extraordinary and unusual genital structure. However, *Gatesclarkeana* does not have well-developed tarsal setae, a character of reduction that has evolved independently a few times in at least three groups in the Tortricidae. Obviously, the shared loss of strong tarsal setae is likely a homoplasy between tribes Tortricini (Tortricinae) and Bactrini (Olethreutinae), or Tortricini and Gatesclarkeanini (Olethreutinae). The tribes in each of the above combinations are distantly related; each belongs to a different subfamily. In *Bactra* and *Endothenia* this tarsal character represents another aspect of affinity between these two genera; perhaps it is useful in strengthening characters a, b, and c above. Razowski (1989) included *Gatesclarkeana* in the subtribe Gatesclarkeanina. However, because of the loss of the strong tarsal setae in species of *Gatesclarkeana,* a condition also found in Tortricini and Bactrini, Gatesclarkeanini should remain as a distinct tribe.

The redefinition of the tribe Bactrini clarifies the taxonomic status of two Nearctic genera: *Taniva* Heinrich and *Hulda* Heinrich. The presence of well-developed apical setae on tarsomeres 1–4 and the lack of a typical bactrine uncus in the male genitalia of *Taniva* and *Hulda* clearly indicate that these genera do not belong to *Endothenia* as thought by Diakonoff (1973). Instead, the morphological evidence presented here confirms that they are best placed in the tribe Olethreutini, in which their generic status, as originally proposed by Heinrich (1926), is reinstated. *Taniva, Hulda,* and *Tia* remain as three monotypic genera: *Taniva albolineana* (Kearfott), *Hulda impudens* (Walsingham) and *Tia enervana* (Ersch.). *Hulda impudens* has male genitalia markably different from all other olethreutine species, in which the tegumen is largely expanded ventrally with fine setae on the ventral surface, the uncus is a low median round wedge arising between two prominent distal lobes of the tegumen, and the socii are heavily sclerotized, flat and entirely bare on the distal half (Fig. 9). *Taniva* differs from *Tia* by the shapes of the socius, the valva, and the uncus (Figs. 7A–C, 8B).

ACKNOWLEDGMENTS

I am grateful to John Huber, J. R. Vockeroth, and A. Mutuura of the Biosystematics Research Center for their constructive suggestions for improving the manuscript. I also thank R. W. Hodges of the U.S. National Museum of Natural History, Washington, D.C., and K. R. Tuck of the British Museum (Natural History), London, for loans of specimens, and T. Yasuda of the University of Osaka for the donation of specimens of *Bactra* and *Endothenia* species from Japan.

LITERATURE CITED

CLARKE, J. F. G. 1958. Catalogue of the type specimens of microlepidoptera in the British Museum (Natural History) described by Edward Meyrick. Volume 3. Tortricidae, Olethreutidae, and Noctuidae. Trustees British Museum, London. 600 pp.

DIAKONOFF, A. 1956. Records and descriptions of microlepidoptera (8). Zool. Verhandl. 29:1–60.

——— 1959. Further records and descriptions of *Bactra* species (Lepidoptera, Tortricidae) chiefly in Dr. H. G. Amsel collection. Bijdragen Tot de Dierkunde 29:175–186.

——— 1962. Preliminary survey of the Palaearctic species of the subgenus *Bactra* Stephens (*Bactra*, Tortricidae, Lepidoptera). Zool. Verhandl. 59:1–48.

——— 1963. African species of the genus *Bactra* Stephens (Lepidoptera, Tortricidae). Tijdsch. Entomol. 106:285–356.

——— 1964 Further records and descriptions of the species of *Bactra* Stephens (Lepidoptera, Tortricidae). Zool. Verhandl. 70:1–81.

——— 1973. The south Asiatic Olethreutini (Lepidoptera: Tortricidae). Zool. Monogr. Rijksmus. Nat. Hist. 1:1–690.

FALKOVITSH, M. I. 1962. Use of secondary sexual characters in the classification of Palearctic Olethreutinae (Lepidoptera, Tortricidae). Entomol. Rev. 41:546–549.

GRAAF BENTINCK, G. A. & A. DIAKONOFF. 1968. De Nederlandse Bladrollers (Tortricidae). Een Geillustreerd Overzicht. Monogr. Nederland. Entomol. Vereen. 3:1–201.

HEINRICH, C. 1926. Revision of the North American moths of the subfamilies Laspeyrasiinae and Olethreutinae. U.S. Natl. Mus. Bull. 132:1–207.

HORAK, M. & R. L. BROWN. (in press). Taxonomy and phylogeny. *In* van der Geest, L. P. S. (ed.), World crop pests. Tortricoid pests, their biology, natural enemies, and control.

KUZNETSOV, V. I. 1978. Family Tortricidae (Olethreutidae, Cochylidae)—Tortricid moths, pp. 297-967. *In* Medvedev, G. S. (ed.), Keys to the insects of the European Part of the USSR. Vol. IV Lepidoptera-Part 1. Acad. Nauk SSSR Zool. Inst. Leningrad 1978. Translated from Russian, U.S. Dept. Agric. & Natl. Sci. Foundation, Washington, D.C. 1987. 991 pp.

KUZNETSOV, V. I. & A. A. STEKOLNIKOV. 1973. Phylogenetic relationships in the family Tortricidae (Lepidoptera) based on studies of the functional morphology of the genitalia. Trudy Vses. Entomol. Obshch. 56:18–43. [English translation, pp. 20–56, *in*Davis, D. R. (ed.). 1989. Lepidopterous fauna of the USSR, a collection of papers dedicated to Professor A. S. Danilevskii. E. J. Brill, New York.]

——— 1977. Functional morphology of the male genitalia and phylogenetic relationships of some tribes in the family Tortricidae (Lepidoptera, Tortricidae) of the fauna of the far east. Trudy Zool. Inst. Leningrad 70:65–97.

——— 1984. The evolution and system of higher taxa of tortricid moths (Lepidoptera: Tortricidae) of the world fauna with reference to the comparative morphology of genitalia. Acad. Nauk SSSR, Union Entomological Society, 36th Annual N. A. Holodkovskovo Memorial Lecture, 1 April 1983, Nauka, Leningrad, 1984:51–91.

MILLER, W. E. 1987. Guide to the olethreutine moths of Midland North America (Tortricidae). U.S.D.A. For. Serv., Agric. Handbook 660:1--104.

POWELL, J. A. 1983. Tortricoidea. *In* Hodges, R. W. (ed.), Check list of the Lepidoptera of America north of Mexico. E. W. Classey Ltd. and The Wedge Entomological Research Foundation, London. 284 pp.

RAZOWSKI, J. 1989. The genera of Tortricidae (Lepidoptera). Part II: Palaearctic Olethreutinae. Acta Zool. Cracov. 32(7):107–328.

Received for publication 13 April 1989; revised and accepted 28 February 1990.

Journal of the Lepidopterists' Society
44(2), 1990, 88–90

A NEW SPECIES OF *SONIA* FROM EASTERN NORTH AMERICA (TORTRICIDAE)

William E. Miller

Department of Entomology, University of Minnesota, St. Paul, Minnesota 55108

ABSTRACT. *Sonia divaricata* is described from three male and one female specimens captured in Missouri and Kentucky. It differs from its six known congeners by various combinations of small body, bifid male uncus, nearly square female sterigma, and scant constriction of the medial dark forewing band.

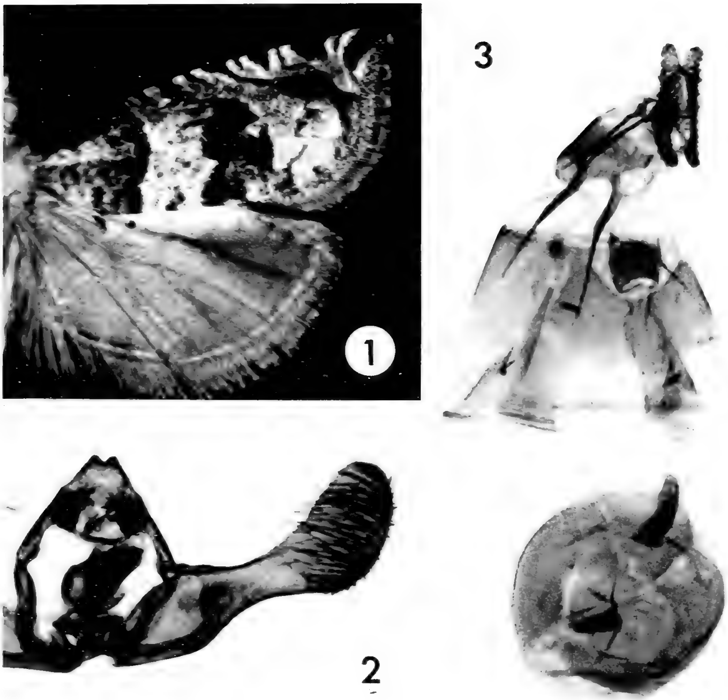
Additional key words: *Sonia divaricata*, Olethreutinae, taxonomy, Missouri, Kentucky.

Heinrich (1923) proposed the olethreutine genus *Sonia* for three Nearctic species. Three more Nearctic *Sonia* species have been described since, bringing the total for the genus to six (Blanchard 1979, Powell 1983). The six species occur in various parts of eastern and western North America (Blanchard 1979, Clarke 1952, Heinrich 1923, Miller 1987, Powell 1975). Biological information is available for *S. canadana* McDunnough, *S. comstocki* Clarke, *S. filiana* (Busck), and *S. vovana* (Kearfott), all of whose larvae bore in roots of Asteraceae (Čapek 1971, Hetz & Werner 1979, Powell 1975). Larvae of the first and third species above have been taxonomically described (Hetz & Werner 1980, MacKay 1959).

The present species is being named to facilitate faunistic works in progress as well as to augment knowledge of this small genus. In the description that follows, italicized character states identify *Sonia* and justify the generic placement of the new species (Heinrich 1923). The letter n preceded by a numeral denotes number of specimens underlying a statement; published wingspans are converted to forewing lengths with a proportionality constant derived by Miller (1977); and wing venation terminology follows Common (1970).

Sonia divaricata, new species
(Figs. 1–3)

Male. Forewing 7.5–8.0 mm long (3n). **Head.** Labial palpus off-white for most of its length, brown on outsides and at apex, vestiture lengthening apically, 2nd segment subequal in length to eye diameter, 3rd segment ¼ length of 2nd. Vertex off-white or pale brown. **Thorax.** Vestiture brownish dorsally, shiny white ventrally. Upper side of forewing white, silver, and shades of brown interlaced as in Fig. 1, underside dark brown, *veins R_4 and R_5 united,* upper internal vein arising between R_1 and R_2, R_2 arising from before middle of discal cell, termen faintly concave, veins M_2, M_3, and CuA_1 approximate at termen, costal fold present on basal ¼ of wing. Upper side of hindwing grayish brown, *veins CuA_1 and M_3 stalked, Rs and M_1 anastomosing toward their bases.* **Abdomen.** Genitalia (3n) (Fig. 2). Valva with rudimentary clasper, valval neck constricted to ½ or more maximum parallel dimensions of sacculus and cucullus; uncus bifid; socii finger- or



FIGS. 1–3. *Sonia divaricata*. **1,** Wings of holotype male (negative reversed). **2,** Genitalia of holotype. **3,** Genitalia of female, with corpus bursae darkened by spermatophore (negative reversed).

ribbonlike; aedeagus a sheath open on one side for much of its length, vesica with 25–30 closely packed deciduous cornuti.

Female. As described for male except as follows. Forewing 6.5 mm long (1n). Genitalia (1n) (Fig. 3). Anterior and posterior apophyses subequal in length; sterigma approximately square in outline, consisting entirely of lamella postvaginalis; ductus bursae with a partial sclerotized ring at middle; corpus bursae with two similar finlike signa.

Etymology. The name *divaricata* refers to the bifid or divaricate uncus.

Types. Holotype male (Fig. 1), Prairie State Park, Barton Co., Missouri, 10 June 1980, J. R. Heitzman, genit. prep. WEM 243893 (Fig. 2), in American Museum of Natural History, New York. Two male paratypes same data except genit. preps. DH 225811 and DH 303821, and one female paratype Red River Gorge, Powell Co., Kentucky, 14 May 1988, L. Gibson, genit. prep. WEM 243894. The paratypes, respectively, are in the University of Minnesota Entomology Museum, St. Paul; J. R. Heitzman Collection, Independence, Missouri; and L. D. Gibson Collection, Florence, Kentucky.

Differentiation. *Sonia divaricata* differs from all known congeners except *comstocki* by its bifid uncus (Fig. 2); other congeners have less developed, rounded unci (Blanchard 1979, Heinrich 1923, McDunnough 1925). From *comstocki* it differs by its smaller body and its more distinct wing pattern; forewing length is 6.5–8.0 mm (4n) compared with 9.0–11.0 mm (8n) in *comstocki,* ranges which represent two- to threefold differences in body weight (Miller 1977). In *divaricata,* the forewing basal patch and medial crossband, both brown, are sharply demarcated (Fig. 1) while in the overall tan *comstocki* they are obscure (Clarke 1952). *Sonia divaricata* differs from its eastern congeners, *constrictana* (Zeller), *paraplesiana* Blanchard, and *canadana,* by its nearly square sterigma (Fig. 3) and by its unconstricted or slightly constricted medial dark crossband (Fig. 1), which contrast with the oblong, rounded, or emarginate sterigmata and greatly or completely constricted medial crossbands in the other species (Blanchard 1979, Miller 1987). Scant constriction of the medial crossband readily separates *divaricata* from the sympatric *constrictana* and *paraplesiana* without dissection.

Biology. *Sonia divaricata* capture dates range from 14 May to 10 June (4n). The larva probably bores in roots of Asteraceae, but the food plant is unknown.

ACKNOWLEDGMENTS

I thank J. R. Heitzman, L. D. Gibson, and C. V. Covell Jr. for specimen loans and other assistance.

LITERATURE CITED

BLANCHARD, A. 1979. New status for *Epiblema minutana* (Kearfott) and new species of *Epiblema* Hübner and *Sonia* Heinrich (Tortricidae). J. Lepid. Soc. 33:179–188.

ČAPEK, M. 1971. The possibility of biological control of imported weeds of the genus *Solidago* L. in Europe. Acta Inst. Forest. Zvolenensis 1971:429–441.

CLARKE, J. F. G. 1952. Two new species of Olethreutidae from California (Lepidoptera). Bull. South Calif. Acad. Sci. 51: 60–62.

COMMON, I. F. B. 1970. Lepidoptera, pp. 765–866. *In* Waterhouse, D. F. (ed.), The insects of Australia. Melbourne Univ. Press, Carlton, Victoria, Australia. 1029 pp.

HEINRICH, C. 1923. Revision of the North American moths of the subfamily Eucosminae of the family Olethreutidae. U.S. Natl. Mus. Bull. 123, 298 pp.

HETZ, M. W. & F. G. WERNER. 1979. Insects associated with roots of some rangeland Compositae in southern Arizona. Southwest. Entomol. 4:285–288.

——— 1980. Descriptions of the larvae of two olethreutine moths reared from roots of woody Compositae. Ann. Entomol. Soc. Am. 73:536–540.

MACKAY, M. R. 1959. Larvae of the North American Olethreutidae (Lepidoptera). Can. Entomol. 91, Suppl. 10, 338 pp.

MCDUNNOUGH, J. H. 1925. New Canadian Eucosminae (Lepidoptera). Can. Entomol. 57:115–116.

MILLER, W. E. 1977. Wing measure as a size index in Lepidoptera: the family Olethreutidae. Ann. Entomol. Soc. Am. 70:253–256.

——— 1987. Guide to the olethreutine moths of Midland North America (Tortricidae). U.S. Dept. Agr. Agr. Handb. 660, 104 pp.

POWELL, J. A. 1975. Biological records and descriptions of some little known *Epiblema* in the southwestern United States (Lepidoptera: Tortricidae). Pan-Pacif. Entomol. 51:99–112.

——— 1983. Tortricidae, pp. 31–41. *In* Hodges, R. W. (ed.), Check list of the Lepidoptera of America north of Mexico. E. W. Classey & Wedge Entomological Research Foundation, London. 284 pp.

Received for publication 19 July 1989; revised and accepted 5 March 1990.

GENERAL NOTES

Journal of the Lepidopterists' Society
44(2), 1990, 91

RECORDS OF A PALEARCTIC TORTRICID IN BOREAL COLORADO: *TRACHYSMIA VULNERATANA* EVIDENTLY IS HOLARCTIC

Additional key words: Cochylinae, Alaska.

Trachysmia vulneratana (Zetterstedt) (Tortricidae: Cochylinae) was described from Altai (Mongolia); subsequently it has been recorded widely across the Palearctic, from Japan, Siberia, the Swiss and Italian Alps, and Scandinavian countries (Razowski, J. 1970, *in* H. G. Amsel et al. (eds.), Microlep. Palaear. 3:99). The species lives in Arctic-Alpine habitats, where the adults fly during June, July, or August; but the biology otherwise is unknown, according to Razowski.

Nomenclatural confusion, which was occasioned by an overlooked designation of the type species of *Trachysmia* Guenée, resulted in the transfer of its concept from Cnephasiini to Cochylinae and the subjective synonymy of *Hysterosia* Stephens, to which *T. vulneratana* was formerly assigned (Leraut, P. 1978, Alexanor 10:339). Whether the cochylids should be recognized as a taxon at the level of the Family, Subfamily, Tribe within Tortricinae, or Subtribe within Archipini has been debated without convincing consensus.

I discovered *T. vulneratana* in Colorado, at Loveland Pass in August, 1973, and subsequently identified older records from unsorted material at the American Museum of Natural History (AMNH). The adults from Colorado closely resemble the typical phenotype and male genitalia (2 examined) illustrated by Razowski (*op. cit.*, plates 3, 37) and are of the same size range (forewing length 10.8–12.4 mm).

Probably populations of *T. vulneratana* are scattered across boreal Canada, although I did not find specimens at the Canadian National Collection in 1986. I failed to encounter any in Alaska during brief visits to tundra country around Fairbanks in 1979, but there are specimens of an aberrant population of this species or a closely related one from the Endicott Mts., northern Alaska (Anaktuvuk Pass, 2200 ft [670 m], VII-8/11-70, K. W. Phillip, AMNH). These moths are smaller (FW 7.4–8.0 mm), with relatively broader, paler forewing bands. The male genitalia (n = 1) differ from Colorado examples by having relatively smaller valvae that have broader costal sclerotization basally and a rounded apical flange on the sacculus. However, this morphological variation falls within the range illustrated by Razowski.

Colorado data: "Bullion [?] Peak, Col.", 1 ♂, VII-25-1898 (no collector given) Kearfott Coll. Acc. 4667 (AMNH). [There is a Bullion Peak in northern La Plata County.] Berthoud Pass-Vasquez Peak, 11,314–12,927 ft [3460–3950 m], Clear Creek-Grand counties, 1 ♂ VII-29-67 (F., P. & M. Rindge, AMNH). Loveland Pass, 11,700–12,000 ft [3580–3670 m], Summit County, 3 ♂ VIII-9-73, 2 ♂ VIII-10-73 (J. Powell).

J. A. POWELL, *Department Entomological Sciences, University of California, Berkeley, California 94720.*

Received 12 June 1989; revised and accepted 17 March 1990.

Journal of the Lepidopterists' Society
44(2), 1990, 92

SPHENARCHES ANISODACTYLUS (WALKER) (PTEROPHORIDAE), NEW TO NORTH AMERICA

Additional key words: Louisiana, Florida, Texas, pantropical distribution, long-distance dispersal.

During a visit to the American Museum of Natural History (AMNH) in New York City, I sorted from the miscellaneous Pterophoridae collection all specimens that I thought would be either *Sphenarches ontario* (McDunnough), *Geina periscelidactyla* (Fitch), or *Geina* sp. Of the series of specimens sorted, there were only three for which I could not provide an immediate determination. After dissection, one of those specimens proved to be a male of *Sphenarches anisodactylus* (Walker) when compared with a photograph of the male genitalia of the type provided by S. Adamczewski (1951, Bull. B.M. (N.H.) Ent. 1:303–387). This rather worn specimen from Louisiana had been collected by A. H. & S. K. Rindge in New Orleans, on 29 September 1953. No more information could be obtained from the collectors. It is pale yellowish-brown with a wingspan of 15 mm. It has the same wingspan as an average-sized *Sphenarches ontario* (McDunnough) but does not show the contrasting dark brown markings on the forewings. Moreover, the dark brown scales in the fringe of the third hindwing lobe are subapical in this species instead of apical as in *S. ontario* and the similar (although larger) *Geina periscelidactyla* (Fitch).

After this paper had been submitted for publication, D. L. Matthews, Florida State University, kindly sent me a manuscript reporting this species from Florida and describing its life-history (Cassani, J. R., D. H. Habeck & D. L. Matthews, Life history and immature stages of a plume moth *Sphenarches anisodactylus* (Lepidoptera: Pterophoridae) in Florida, Florida Entomol. 73:257–266). In addition, Matthews informed me that a series of "about" 12 specimens had been collected in October and November 1983, October 1984, and December 1984 in Bellaire (Harris Co.), Texas, by E. C. Knudson. These specimens are in the United States National Museum, Washington, D.C. (D. L. Matthews, pers. comm. 1990).

Sphenarches anisodactylus (Walker) is widely polyphagous and has a pantropical distribution. K. Yano (1963, Pac. Ins. 5:849–871) reported it from Japan, India, Ceylon (the type locality), Thailand, New Guinea, Bismark Archipelago, Solomon Islands, New Hebrides, New Caledonia, Fiji, Samoa, Australia, West Indies, South America, North Africa, and Madagascar. Its broad distribution has been explained by cyclones (Fletcher, T. B. 1910, Trans. Linn. Soc. Lond. Zool. 13:265–323) and human activity (Fletcher, T. B. 1921, Mem. Dep. Agric. India Ent. 6:1–9) which favor long distance dispersal. It is possible that the species was introduced into the United States with one of the following host-plants (listed by Adamczewski, *op. cit.*): *Hibiscus mutabilis* L. (Malvaceae); *Lagenaria vulgaris* Ser. = *siceraria* (Mol.) Standl. (Cucurbitaceae); *Dolichos lablab* L., *Cajanus indicus* K. Spreng. = *C. Cajan* (L.) Huth, *Mimosa pudica* L., *Phaseolus vulgaris* L. (Fabaceae); *Averrhoa bilimbi* L. (Oxalidaceae). These are all tropical plant species that have been imported into the United States to be cultivated mostly for ornament (Bailey, L. H. & E. Z. Bailey, 1949, Hortus Second, MacMillan Co., New York). It is interesting to note that Cassani et al. (*op. cit.*) found *S. anisodactylus* feeding on an indigenous plant species unrelated to those mentioned above.

My visit to the AMNH was made possible through a Collection Study Grant provided by that institution. I thank Dr. F. H. Rindge of the AMNH for his help during my stay in New York and Dr. J.-F. Landry, Dr. J. D. Lafontaine, and two anonymous reviewers for commenting on the manuscript.

B. LANDRY, *Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada.*

Received for publication 3 June 1989; revised 3 March 1990; accepted 2 June 1990.

Journal of the Lepidopterists' Society
44(2), 1990, 93–94

LARVAL MANDIBLE OF *CARGIDA PYRRHA* (NOTODONTIDAE)

Additional key words: morphology, retinaculum, Costa Rica.

The mandible of *Cargida pyrrha* (Druce) was characterized as having three large, truncated retinacula based on last-instar larvae collected near the end of their feeding phase (Godfrey, G. L. 1984, J. Lepid. Soc. 32:88–91). The mandibular specimens appeared to be worn, but the absence of other collections of larval *C. pyrrha* prevented further study. D. H. Janzen (pers. comm.) suggested that the truncated retinacula of *C. pyrrha* may be used to crush excised leaf tissue. A refined picture of the mandible's functional morphology became possible with the collection of a third-instar larva of *C. pyrrha* in Cañon del Tigre, Santa Rosa National Park, now part of Guanacaste National Park, Guanacaste Province, Costa Rica, on 10 June 1986. The sharpness of the edges on the retinacula and distal teeth indicated that the mandibles were unworn. As expected, the distal teeth are more angulate than earlier described. Especially noteworthy is a very distinct, dorsally directed, angular extension of the dorsalmost retinaculum (Fig. 1). When the mandible is fully closed, this extension is directed posteriorad. This suggests that, in addition to having a possible crushing function, the dorsalmost retinaculum may also help move food material toward the pharynx during mandibular adduction. In an unworn state, the last-instar mandible should be morphologically and functionally similar. This assumption partially is supported by the larval mandible of *Crinodes besckei* Hübner, which also has distinct retinacula that are similar morphologically from the third through fifth (=final) instars (Godfrey, G. L., J. S. Miller & D. J. Carter 1990, J. New York Entomol.

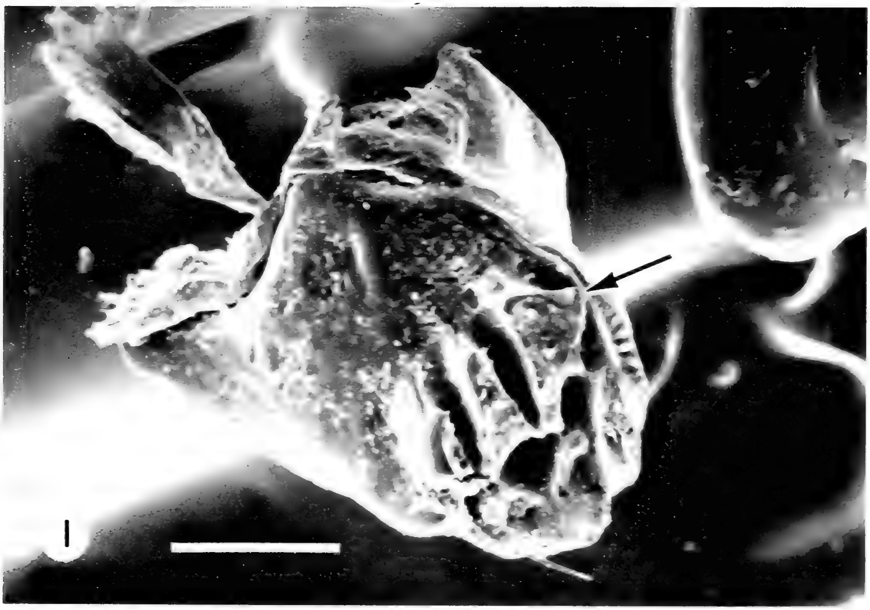


FIG. 1. Scanning electron micrograph showing medial view of third-instar larval mandible of *Cargida pyrrha* (scale bar = 0.25 mm). Pointer shows dorsalmost retinaculum.

Soc. 97:172–197). The observed third-instar larva of *Cargida pyrrha* was found clinging to a rock in the middle of a steep, eroded jeep trail, apparently having been disloged or washed there from its host by torrential rains that recently had ended. Attempts to locate feeding larvae of *C. pyrrha* in the area were futile, so no additional specimens or hostplant information were gathered.

Gratitude is owed the Servicio de Parques Nacionales de Costa Rica for permission to work at Santa Rosa National Park. D. E. Dockter assisted with the scanning electron microscopy. Financial support came from the University of Illinois Research Board, Herbert Holdsworth Ross Memorial Fund and Illinois Agricultural Experiment Station Project 12-361 (Biosystematics Insects).

G. L. GODFREY, *Center for Biodiversity, Illinois Natural History Survey, 607 E. Peabody Drive, Champaign, Illinois 61820.*

Received for publication 26 December 1989; revised and accepted 21 February 1990.

Journal of the Lepidopterists' Society
44(2), 1990, 94–95

DIETARY BREADTH IN *EUPHYDRYAS GILLETTII* (NYMPHALIDAE)

Additional key words: *Lonicera, Pedicularis, Valeriana, Veronica,* hostplants.

Ever since J. A. Comstock (1940, Bull. S. Calif. Acad. Sci. 39:111–113) reported its hostplant to be *Lonicera involucrata* (Rich.) Banks (Caprifoliaceae), *Euphydryas gillettii* (Barnes) has been thought to be monophagous. My observations over the past decade, however, have revealed oviposition by *E. gillettii* on several additional plant species. Here I report these observations, along with an evaluation of dietary breadth of this butterfly in light of hostplant choice in other *Euphydryas.*

These reports are based on observed oviposition or discovery of egg masses on the plants, not simply on larval feeding; thus, they differ from other reported hostplant records for *E. gillettii,* such as those in J. A. Scott (1986, The butterflies of North America, Stanford Univ. Press, 583 pp.), which include records of feeding by wandering post-diapause larvae. Although the following new hostplants differ in growth form (shrub or perennial), all are in families that possess iridoid glycosides (M. D. Bowers, pers. comm.). These compounds are sequestered, producing unpalatability (Bowers, M. D. 1981, Evolution 35:367–375; Gardner, D. R. & F. R. Stermitz 1988, J. Chem. Ecol. 14:2147–2168), and also may function as feeding and ovipositional stimulants. The additional records are the following. E. H. Williams and M. D. Bowers (1987, Am. Midl. Nat. 118:153–161) reported infrequent oviposition (1–4% of all egg masses) in a Wyoming population on *Valeriana occidentalis* Heller (Valerianaceae). A field survey of *E. gillettii* populations (Williams, E. H. 1988, J. Lepid. Soc. 42:37–45) revealed extensive use in an Idaho population of *Pedicularis groenlandica* Retz. (Scrophulariaceae) and *Lonicera caerulea* L., in addition to *L. involucrata.* Furthermore, an alpine population of *E. gillettii* oviposits on *Veronica wormskjoldii* Roem. & Schult. (Scrophulariaceae) (letter, C. F. Gillette, 14 Feb 1985).

Feeding experiments have shown that larvae survive and grow well on the additional hostplants. Williams and Bowers (*op. cit.*) found no significant difference in survivorship and growth of larvae on *V. occidentalis* and the usual host *L. involucrata.* Similar experiments showed no difference among *L. involucrata, L. caerulea,* and *P. groenlandica* as hostplants for larvae from the population that uses all three (Table 1). The use of alternative hostplants is therefore not simply ovipositional error.

Although individual populations are locally specialized, all other *Euphydryas* species whose basic ecology is known, including Eurasian as well as North American species, oviposit on several plant species each. The *minimum* number of plant genera (species)

TABLE 1. Growth of *E. gillettii* larvae from a single population on alternative hostplants. Second instar larvae were raised on each of the 3 possible hostplants, with 9 replicates per plant and 5 larvae per replicate, for 6 days. Methods follow those of Williams and Bowers (*op. cit.*). Analysis by one-factor ANOVA.

Hostplant	*Lonicera involucrata*	*Lonicera caerulea*	*Pedicularis groenlandica*	F	P
Survivorship (%)	97.8	93.3	97.8	0.615	>0.50
Relative consumption rate (mg food/[mg larva·day])	1.81	1.67	1.94	0.429	>0.50
Relative growth rate (mg larva/[mg larva·day])	0.104	0.106	0.094	0.248	>0.50

used by each *Euphydryas* species is as follows (references: Higgins, L. G. 1950, Trans. Roy. Ent. Soc. Lond. 101:435–499; Higgins, L. G. & N. D. Riley 1970, A field guide to the butterflies of Britain and Europe; White, R. R. & M. C. Singer 1974, J. Lepid. Soc. 28:103–107; Howe, W. H. 1975, The butterflies of North America): *E. anicia* (Doubleday)—2(5), *E. aurinia* Rottemburg—7(7), *E. chalcedona* (Doubleday)—4(7), *E. colon* (Edwards)—1(3), *E. cynthia* Schiffermuller—2(2), *E. desfontainii* Godart—3(3), *E. editha* (Boisduval)—5(13), *E. maturna* L.—3(3), and *E. phaeton* (Drury)—3(3). Other Eurasian species appear too little known to evaluate their dietary breadth.

I suggest that *E. gillettii* is like other members of its genus in hostplant choice; more than one plant species is a potential host, but host specificity and host rank order (Singer, M. C. 1982, Oecologia 52:224–229) vary among species and among populations within a single species. In spite of its past reputation, *E. gillettii* is oligophagous, though it may have greater host specificity than most other *Euphydryas* (i.e., a larger gap in preference between the first and second host choices). As a result, there are populations, though infrequent, in which plant species other than *L. involucrata* are used. I expect that additional hostplants will be reported for *E. gillettii* as more populations are studied. The above evidence also provides support for Singer's (*op. cit.*) model of hostplant preference.

Meredith Lane kindly identified *Lonicera caerulea* and deposited voucher specimens at the Rocky Mountain Herbarium, University of Wyoming. Deane Bowers made helpful comments on a draft of the manuscript.

ERNEST H. WILLIAMS, *Department of Biology, Hamilton College, Clinton, New York 13323.*

Received for publication 12 June 1989; revised and accepted 27 February 1990.

Journal of the Lepidopterists' Society
44(2), 1990, 95–96

NATURAL INTERGENERIC MATING IN LYCAENIDAE

Additional key words: *Fixsenia favonius, Calycopis cecrops*, Florida.

Documented natural matings between distantly related species of butterflies are rare. Most published reports of intergeneric and interfamilial matings involve species of Lycaenidae and Nymphalidae (e.g., Downey, J. C. 1962, J. Lepid. Soc. 16:235–237; Frechin, D. 1969, J. Lepid. Soc. 23:115; Jae, R. J. 1972, J. Lepid. Soc. 26:28; Arnold, R. A. 1986,

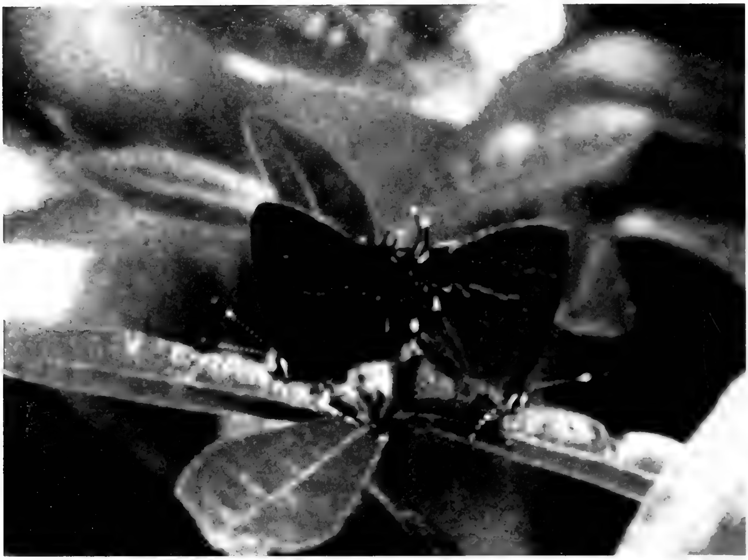


FIG. 1. Intergeneric mating between *Fixsenia favonius* (left) and *Calycopis cecrops*.

J. Lepid. Soc. 40:238–239). I observed an additional intergeneric mating between species of Lycaenidae in central Florida.

On 17 April 1990, a male *Fixsenia favonius* (J. E. Smith) and a female *Calycopis cecrops* (Fabricius) were observed in copula at McKethan Lake, Hernando County, Florida. The pair (Fig. 1) was flushed into flight and ultimately came to rest approximately 0.5 m above the ground on the sunlit leaves of a nearby laurel oak (*Quercus laurifolia* Michx., Fagaceae). The habitat consisted of a narrow powerline easement that bisected an ecotone between turkey oak (*Quercus laevis* Walt., Fagaceae)-wiregrass (*Aristida stricta* Michx., Poaceae) scrub and mesic hardwood hammock. The pair was first encountered at about 1430 h EDT and was observed for several minutes. The female *C. cecrops* was more worn than the male *F. favonius*. While I was adjusting my camera, the pair flew away and was not relocated.

This report is particularly interesting because a similar pairing involving a male *F. favonius* and a female *C. cecrops* was observed at the same location on 25 April 1982 (H. D. Baggett, pers. comm.). Baggett also witnessed the bobbing courtship flight of the male *F. favonius* prior to coupling. Arnold (*op. cit.*) proposed that such pairings may be the result of a breakdown in a premating reproductive isolating mechanism.

The observation of two matings between *F. favonius* and *C. cecrops* at the same location suggests that such intergeneric matings may be more frequent than previously believed (at least locally).

JOHN V. CALHOUN, *3524 Old Village Way, Oldsmar, Florida 34677.*

Received for publication 2 May 1990; accepted 29 June 1990.

TECHNICAL COMMENT

Journal of the Lepidopterists' Society
44(2), 1990, 97

HORMESIS IN LEPIDOPTERA?

Hormesis (from the Greek verb to set in motion) has come to mean the stimulating effect of small doses of any substance that in larger doses is inhibitory.

In a recent paper, P. A. Parsons (1989, Biol. J. Linn. Soc. 37:183–189) describes experiments in *Drosophila* that show conclusively that, as measured by longevity, acetaldehyde is beneficial at low and lethal at high concentrations. Others have demonstrated the same phenomenon with ethanol, where the reproductive span has also been increased. There has been much discussion about the possible favorable effects of natural background radiation.

I had never heard of hormesis until I read Parson's paper, but having done so, and being medical, I first speculated on therapeutic aspects and in particular on the old saying "A little of what you fancy does you good"—especially with regard to alcohol.

I next came across a paper by W. E. Miller (1989, J. Lepid. Soc. 43:167–177) on the effects of honeydew imbibed by adults in enhancing reproductive performance of the spruce budworm, compared with water. There was no mention, however, of the effect of excess honeydew, and hormesis was not referred to.

I wrote to Dr. Miller and he confirmed that a number of alcohols occur in fresh honeydew (Auclair, J. L. 1963, Ann. Rev. Entomol. 8:439–490 and refs. cited therein). Miller: "I was certainly intrigued by the possibility that alcohol hormesis is involved in budworm response to imbibed honeydew. Your suggestion brought to mind a couple of things. One, the news story here after the recent London storm in which adult lepidopterans escaped, and then were recaptured at beer, after which they oviposited liberally. Two, the use of rotting fruits as feeding sites by many tropical lepidopterans, and the traditional use of alcohol baits by collectors."

The purpose of this comment is to enquire whether lepidopterists have views or experience concerning hormesis with respect to their specialty (or hobby). If so, they might consider launching experiments to explore further the phenomenon.

The principal difficulty as I see it is to establish the two end-points of the substance in question, and the methodology.

Cyril A. Clarke, *Department of Genetics, University of Liverpool, P.O. Box 147, Liverpool L69 3BX, England.*

Received 1 February 1990; revised and accepted 17 May 1990 (William E. Miller served as Special Journal Editor for this manuscript).

Journal of the Lepidopterists' Society
44(2), 1990, 98–100

BOOK REVIEWS

LOCAL LISTS OF LEPIDOPTERA; OR, A BIBLIOGRAPHICAL CATALOGUE OF LOCAL LISTS AND REGIONAL ACCOUNTS OF THE BUTTERFLIES AND MOTHS OF THE BRITISH ISLES, by J. M. Chalmers-Hunt. 1989. Hedera Press, Uffington, Oxfordshire, U.K. iii + 247 pp. Hard cover, 22 × 14 cm, ISBN-0-86096-023-4, Pounds Sterling 22 (about $48).

In the early 1970's, I compiled a detailed list of the butterflies I had encountered along the High Line Canal in Colorado over the previous fifteen years of studying its fauna. Much inspired by the local lists and associated commentaries published by other lepidopterists in the 1950's and 1960's, I was eager to add my own experience to the genre. But when it came time to seek publication, I was nonplussed; it seemed that the local list had gone out of style. Having come to be considered merely anecdotal and seldom rigorous enough to justify serious attention, such local and regional tabulations went largely into eclipse.

About the same time, as a student of John Heath's in England, I was exposed to many of the active British lepidopterists and their list-making, in conjunction with the mapping activities of the Biological Records Centre. One field trip found us on the Essex marshes, seeking to confirm the recent first British record of *Gortyna borrellii* (Noctuidae). John Heath had arrayed his Heath Trap near the mercury vapor light belonging to Michael Chalmers-Hunt, then at work on supplements to his great work on the butterflies and moths of Kent. I remember the keen excitement of both men when the beautiful orange noctuid appeared in the ultraviolet field, insuring a new dot on John's maps and a new entry for the most intensely scrutinized local list of all, the British.

Mr. Chalmers-Hunt's enthusiasm for faunistic inventory has now been translated into a monumental compilation of all known lists of British Lepidoptera. To my knowledge, this kind of fastidious bibliography of local studies is extremely rare. The only other work that approaches its scale, on a national level, is the wonderfully useful catalog of American sources prepared by William D. Field, Cyril F. Dos Passos, and John H. Masters (*A Bibliography of the Catalogs, Lists, Faunal and Other Papers on the Butterflies of North America North of Mexico Arranged by State and Province (Lepidoptera: Rhopalocera).* Smithsonian Contributions to Zoology Number 157, Washington, 1974. 104 pp.).

With admirable brevity, Chalmers-Hunt introduces the catalog with a single page of text. The thirty years of reference-collecting that went into the task resulted in 3161 entries. They include "all county and regional lists and local accounts of British Isles' lepidoptera known to me," omitting only "lists with relatively few species." Chalmers-Hunt defines "local lists" circularly but effectively as "covering all the items in this work." He justifies the effort by explaining that such items "often contain information of considerable interest to be found nowhere else, particularly in regard to distribution." He goes on to note that, while such lists are often rare and difficult to find, this book should render their location relatively simple. That it will.

The book is sturdy and functional, with no frills. It may seem costly for an unillustrated book of modest proportions, but the profit margin cannot have been high. Eric Classey, the dean of British Lepidoptera booksellers and publisher in his own right, deserves our gratitude for bringing such a book to print. The new imprint, Hedera Press, was erected to honor the publisher's late wife, Ivy Classey. A well-designed volume, the book does her memory justice. I found no typos, and if the author hadn't pointed out that several serial numbers were deleted from the sequence, I would have noticed no errors at all.

Chalmers-Hunt combed many sources, beginning with "that great treasure house of knowledge, The General Library, British Museum (Natural History);" running through many other libraries, private and public; and finishing with his own extensive files. He checked all the usual journals as well as a fascinating array of lesser known serials, from the august to the arcane, from *Science Gossip* and *Journal of the Manx Museum* to proceedings of the natural history societies of Eton and Rugby Schools. He has brought together not only published and easily accessible references, but also typescripts, private unpublished lists, and real rarities such as John Heath's "The Lepidoptera of Devon" from 1946, only two copies of which exist. Wherever possible, he indicates the present location of all lists not generally available and of obvious provenance. He examined the great majority of the sources personally.

The catalog entries are arranged alphabetically by author. Each entry consists of a four-digit serial number; the name of the author(s); date of publication or compilation; title or description; journal or other source of publication, if published, and date of serial if different from actual publication date; abbreviated notation of county or counties covered or referred to; occasional notes specifying vicinity, quoting reviews, annotating contents, or drawing attention to items of special significance; and location of manuscripts or rare published items. Little more could be desired, short of full annotations, which would have made the product unwieldy and the task unmanageable.

The lists themselves vary from the quaint through the highly personal and anecdotal to the strictly scientific: "Entomological scraps from a lepidopterist's notebook during a month's sojourn in the north of Scotland in the summer of 1905," "Captures in Epping Forest," "An entomological ramble among the rocks of Chudleigh, Devon," and "A survey of the lepidoptera of a small oak-beech wood on the midland kuyper marl with ecological notes on the species and two appendices." The lists include the truly local ("The lepidoptera of a Birmingham garden"), the rather local ("The macro-lepidoptera of Sherwood Forest"), and the more broadly regional ("The lepidoptera of Jersey"). Some cover the whole order, others treat either butterflies or moths, still others list families or genera. They range from brief ("The moths of Widdop, 1896") to long (Christ's Hospital School's lists for 1903 to 1927). This great range underscores the enormous array of origins of our basic zoological knowledge.

While "A day's collecting near Dorking" may be less meaningful than "An ecological survey of the insects of the Farne Islands," all of the lists add up to a picture of the British fauna. Collectively, they reveal the astonishing effort that has gone into documenting this small insular fauna that yet yields surprises.

The book concludes with a cross-referenced tabulation of entries-per-county, by serial number. This useful feature reveals the disproportionate attention given populous counties at the expense of the hinterlands. Kent, the author's own bailiwick, scores 200 lists; Peeblesshire, Scotland, has only one. This fact alone should inspire young collectors to redress the balance over the next century. In doing so, they are bound to make valuable contributions, as every record of a species' occurrence is a fresh quantum of knowledge.

In the end, one must ask whether listing is just a trivial game, or whether Chalmers-Hunt is merely engaging in compulsive list-listing, having run out of leps to list in Kent. I think not; not, at least, for anyone concerned with building a detailed picture of our fauna, and of how it changes over time. My list of "The Butterflies of the High Line Canal of Colorado" was published (in 1971) by John Masters in his *Mid-Continent Series on the Lepidoptera* (Volume 2, Number 24; 19 pp.). Since then, I have been able to document that some forty per cent of the species listed have become locally extinct or seriously reduced. This knowledge, combined with updates from the ongoing Xerces Society Fourth of July Butterfly Counts, has influenced management policy for the remaining habitats along the canal.

So the importance of local lists is to be found in their usefulness to efforts to conserve biological diversity, in filling out our understanding of biogeographical patterns and processes, and in providing stimuli for future studies. In addition, the compilation and refinement of local lists, intelligently approached, is an immensely enjoyable enterprise for many naturalists.

For the past ten years I have been rambling in the ravaged land of the Willapa Hills of Washington State, and listing the local butterfly fauna as I go. From an initial impression that very few species occupy the region, my list has now grown to forty-some species. This modest fauna is beginning to tell us things about forestry, climate, and ourselves that we might otherwise miss.

Field et al. wrote that bibliography is the handmaiden of all research. It may be added that the local list is the midwife of faunistic and ecological understanding. How can one hope to decipher a system without knowing its components? Those of us who engage in making local lists, and who know it for more than the pleasant game it no doubt is, can appreciate the great effort and service rendered by Michael Chalmers-Hunt in preparing this simple but remarkable list of lists. It should inspire interest in making more lists, and help bring them back into fashion, from Fourth of July counts to full faunal inventories. One hopes that future list-makers will apply modern tools to make their lists more analytical than merely rambling, although there should always be room for rambles as well. At least, if lists must pass, this comprehensive work will keep us from forgetting the important contribution they have made to the literature.

ROBERT MICHAEL PYLE, *369 Loop Road, Gray's River, Washington 98621.*

Journal of the Lepidopterists' Society
44(2), 1990, 100–101

THE CHARAXINAE BUTTERFLIES OF AFRICA, by Stephen Frank Henning (foreward by C. G. C. Dickson). 1989. Aloe Books, Johannesburg. Distributed by Aloe Book Agency, P.O. Box 4349, Johannesburg, South Africa 2000 and Bioquip, Inc., 17083 LaSalle Avenue, Gardena, CA 90248. 457 pp., over 750 color illustrations, 114 text figs. Hard cover, 25 × 34 cm, ISBN 0-620-12811-9 (Standard Edition), $240.00; 0-620-12812-9 (Collectors' Edition), $500.00.

First of all, it must be said that this is a monumental work, one that covers a significant part of Africa's lepidopteran fauna. The author is to be congratulated on compiling such a significant book, and the publishers for having published it. This is not a field guide, measuring more than 9½ by 13 inches and printed on heavy coated paper. It is beautifully presented enough to stand on its own as a "coffee table" book, even if it did not possess its obvious scientific merit.

There are seven introductory sections. In the first two, the author characterizes the subfamily and gives succinct discussions of morphology and terminology employed, including those of the early stages. The section on behavior discusses the effects of temperature on flight, feeding, foodplant preference, hilltopping, and mating behavior. The discussion of evolution, including speciation, species concepts, cladistics, mimicry, and polymorphism, is well done. The zoogeography section only concerns distribution within Africa and perhaps should have been labelled "geographic distribution": it is by no means theoretical but clearly delineates major habitat types and subregions. Concluding the introductory material are short sections on collecting methods and conservation, the latter stressing the degradation of the environment and its effects on charaxine populations.

In the taxonomic section (most of the book), each tribe and genus is carefully described. The individual species are covered in much detail, with descriptions of adults, geographical distribution, and the locations of types (where known to Henning) provided for all taxa. Additionally, where known, immature stages, life histories, larval foodplants, habits, and the degree of polymorphism of each species are described. Two keys to species groups, one based on adult characters and one on final instar larval characters, precede the species accounts, which are arranged by species group. Color illustrations are given of all 162 species and most subspecies, as well as of their larvae and pupae, when available, and of many habitats. Henning has had the cooperation of most of the active workers on African Charaxinae, and descriptions of 19 new taxa (3 species and 16 subspecies) by a number of these workers are included, often in French (in the case of Plantrou), more frequently in English (Henning, Canu, Collins), but occasionally interspersed French and English (Turlin).

The illustrations of individual insects are true to color and accurately represent the distinguishing features of the taxa. They should prove very useful to those who wish to identify their African charaxines without resorting to genitalic dissections. In those cases where the genitalia are the only means of certain identification, line drawings of the salient features are presented. Illustrations of eggs, larvae, and pupae are likewise very well done and suggest that when more such data become available, the preparatory stages could provide independent characters to falsify the existing phylogeny.

Another useful attribute of this book is the documentation for and citation of statements made in it. Opinions of the author are clearly labelled as such, and others' opinions are scrupulously referenced. Such citing of sources should be a requirement for any major work but, sadly, is not always done.

The last few pages are devoted to detailed lists of the species recorded from each African country and the islands off its coast, a synonymic checklist of the African Charaxinae, foodplant lists for those species for which the life history is known, an addendum of taxa described too recently for inclusion in the main body of the book, a glossary of terms, an extensive bibliography, and an index.

There are very few, but slightly disturbing, typographical errors in the volume, but they in no way detract from the usefulness of the book. Perhaps the most serious is the identification of *Charaxes barnsi* Joicey and Talbot (named for the collector, T. A. Barns) on page 156 as *Charaxes "barnesi"* consistently in the text, though the figure caption and the mention in the checklist (p. 424) are correct. On page 211, the repository of the type-specimen of *Charaxes lydiae* Holland is given as "Carnegie Museum, Pittsburg, USA," rather than "Pittsburgh." Elsewhere, Henning simply gives the name as "Carnegie Museum, USA." Finally, the subspecific name of *Charaxes baumanni tenuis* van Someren is given in the heading as *"tenius,"* though it is correct elsewhere.

A much more distressing set of errors surely cannot be laid at Mr. Henning's doorstep. On the interleaf a list of sponsors of the publication is given, and at least this seems to be correct, but below this is given a list of subscribers to the very expensive Collectors' Edition, in which there appear to be several grievous errors. The late A. C. Allyn's name came out "Allen"; the author's father, W. H. (Bill) Henning, is listed as "B. Henning"; and D. M. Kroon's name had the initials reversed as "M. D. Kroon." It would seem to be a vital part of public relations that one cites major benefactors correctly: this seems to have been a rather sloppy job of proof-reading on a third party's part.

None of these complaints, niggling as they are, diminish the satisfaction that the author should feel on having produced a significant book on the African Charaxinae that is destined to be the definitive work on these insects for many years to come. Mr. Henning has succeeded in all of his objectives beyond most lepidopterists' dreams. Although the price may preclude many interested readers from obtaining *The Charaxinae Butterflies of Africa,* it is a must for all museums and anyone with a sincere interest in these fascinating butterflies. I strongly recommend that such afficionados buy a copy now, before it goes out of print. (The Standard Edition is limited to 1200 numbered copies; the leather-bound, signed Collectors' Edition to 100 copies.)

LEE D. MILLER, *Allyn Museum of Entomology, Florida Museum of Natural History, 3621 Bay Shore Road, Sarasota, Florida 34234.*

Journal of the Lepidopterists' Society
44(2), 1990, 101–102

MARIPOSAS MEXICANAS, by Roberto de la Maza Ramírez (with technical assistance from Javier de la Maza E.; in Spanish). 1987. Fondo de Cultura Económica, S. A. de C. V. México, D.F. Distributed by Bioquip, Inc., 17803 LaSalle Avenue, Gardena, CA 90248. 9 + 302 pp., 58 text figs., 67 color plates. Hard cover, 21 × 27.5 cm, ISBN-968-16-2316-9, $60.00 (U.S.).

Roberto de la Maza R., assisted by his sons, has written a very fine book on the butterflies of his country. He is to be congratulated for this accomplishment: it is emphatically not just another rather amateurish Mexican butterfly book.

Only 651 of nearly 1500 Mexican butterfly species are included in this volume. As might be expected, the coverage is not uniform: most of the species of Papilionidae, Pieridae and Nymphalidae (*s.l.*) are illustrated and discussed in some detail, whereas species of Riodinidae, Lycaenidae and Hesperiidae are given much more cursory and incomplete treatment. The species accounts are somewhat reminiscent of the annotations given by Hoffmann in his catalogues 50 years ago, but the data are updated considerably and augmented by new ecological and distributional findings.

The color illustrations are usually of high quality, though disconcerting shadows are found on some plates (e.g., 2, 4, 18, 24, 39, 60, etc.) that could have been avoided by using a light box to illuminate the subjects evenly from several sides. The backgrounds are also uneven, but seldom disconcertingly so. The illustrated butterflies are more or less true to color and readily serve to identify the species.

The nomenclature is mostly up to date, and there are relatively few typographical errors. To cite a few examples: *Neophasia* is misspelled "*Neopasia*" on Plate 2, but correctly on page 83; *huascama* is misspelled as "*huascuma*" on page 103; *Ganyra howarthi* (Dixey) is misidentified as *G. josephina kuschei* (Schaus); the generic name for *Pareuptychia ocirrhoe* (Fabricius) is misspelled as "*Paraeuptychia*" and the species is identified as "*hesione*" (Sulzer), a name rejected as a homonym. The generic treatment of the Theclinae (Lycaenidae) does not always follow the most recent revisionary studies.

The general topics covered at the beginning of the book (pages 13–70) are well presented, especially those sections on the uses of butterflies in ancient art and the discussions of life zones inhabited by Mexican butterflies. Excellent photographs of each life zone are presented, which supplement the text by giving the reader a "feel" for where the various species fly.

The few criticisms that I have in no way diminish the accomplishment by Sr. de la Maza in producing a book that will remain the standard Mexican text for many years. It is vastly better than most books on the Mexican fauna. The entire de la Maza family stands in the forefront of Mexican lepidopterology, and this book only strengthens this assessment. Anyone with an interest in the butterflies of Mexico must have *Mariposas Mexicanas*; those who simply are interested in beautiful butterflies should have it to enjoy the plates.

LEE D. MILLER, *Allyn Museum of Entomology, Florida Museum of Natural History, 3621 Bay Shore Road, Sarasota, Florida 34234.*

Journal of the Lepidopterists' Society
44(2), 1990, 102–103

LAS MARIPOSAS ENTRE LOS ANTIGUOS MEXICANOS, by Carlos R. Beutelspacher (prolog by Rafael Martín del Campo). 1988. Fondo de Cultura Económica, Avenida de la Universidad, 975; 03100 México, D.F., México. 103 pp., 308 color and b&w figures. Hard cover, 22 × 28 cm, ISBN 968-16-3042-4, $27.69. In Spanish.

Cultural entomology, the influence of insects in the humanities, has been recognized in recent years as a singular and provocative field of insect study (Hogue, C. 1987, Cultural Entomology, Ann. Rev. Entomol. 32:181–199). This copiously illustrated book is a significant contribution to the field. It brings together, in an aesthetic way, a collection of images and information, demonstrating and documenting the multifarious and significant ways that butterflies and moths were woven into ancient Mexican cultures. These range from transient and simple uses of the lepidopteran form for adornment of pottery and in featherwork to deeply religious symbolisms hewn in stone.

The deification of at least two species is known with certainty, evidence for which receives major treatment in the book. Xochiquetzal, who was represented by the common papilionid *Papilio multicaudatus*, was the wide-serving god of beauty, love, and flowers, patron of domestic labor and the courtesans, and symbol of the soul and the dead (Chapter

VI). The "flint moth," *Rothschildia*, signified Itzpapalotl, a mother diety and god of human sacrifice, war, and travelers, as well as the personification of the earth and moon (Chapter VII).

In these and accompanying chapters the author discusses and figures lepidopterans in the history (including place names-Chapter IV), art, mythology, folklore, and poetry (Chapter V), of the Teotihuacanan, Aztecan, Mixtecan, and other ancient Mexican cultures. A particularly beautiful poem contrived on the occasion of the death of the prince Tlacahuepan, 1493–1498, is quoted:

Life after Death

Golden butterfly now sipping:
The flower that has opened is my heart,
O my friends, it is a fragrant flower,
I now spread abroad upon the rain.

(p. 37, translated from Nahuatl to Spanish by Garikay; thence to English by the reviewer.)

The book also contains diverse representations of butterflies in human culture in general (Chapter IX, Appendix) as well as summaries of the pertinent literature (Chapter I) and the relation of other organisms to butterflies among ancient Mexicans (Chapter II). The author pays special attention (in Chapter X) to the interpretation of references to lepidopterans in 16th Century chronicler Sahagún's book 11 of *Historia General de las Cosas de Nueva España* and accompanying *Codex Florentino*.

The Appendix contains an essay on butterflies in the folklore of other peoples and a taxonomic index of species treated in the book.

The book is nicely laid out and beautifully illustrated, mostly by the author's own hand. Although not in English, the figures and captions will be understandable to the educated lepidopterist armed with a Spanish dictionary. A rudimentary knowledge of Mexican archaeology and history will aid greatly both Spanish-speaking and non-Spanish-speaking readers in assimilating the text.

Errors are rare; I note only the following: Robelo 1940 on p. 21 should be 1904; Cortés 1976 cited on p. 18 is not listed in the bibliography.

CHARLES L. HOGUE, *Curator of Entomology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.*

Journal of the Lepidopterists' Society
44(2), 1990, 103–105

THE BUTTERFLIES OF HISPANIOLA, by Albert Schwartz. 1989. University of Florida Press, Gainesville. xiv + 580 pp., 2 general maps and distribution maps throughout text, 1 color and 15 black & white plates. Hard cover, 23.5 × 16 cm, ISBN 0-8130-0902-2, $35.00.

The history and quality of books on the butterflies of the "West Indies" has been patchy. The recent work on the fauna of Cuba (Alayo, D. & L. R. Hernandez 1987, Atlas de las mariposas diurnas de Cuba [Lepidoptera: Rhopalocera], Editorial Cientifico-Técnica, La Habana, 148 pp.) is difficult to obtain; R. Pinchon and P. Enrico's treatment of the Lesser Antilles (1969, Faune des Antilles Français, Les Papillons, Forte-de-France, 258 pp.) came and went with scarcely a notice outside the francophone world and only F. M. Brown and B. Heineman's excellent work on Jamaica (1972, Jamaica and its butterflies, E. W. Classey, London, 478 pp.) is still readily available. Even N. D. Riley's field guide (1975, A field guide to the butterflies of the West Indies, Collins, London, 224 pp.), valuable though it is, is out of print. A general and up-to-date work on the butterflies of Hispaniola (Haiti and the Dominican Republic) has been conspicuously absent, and it is this void that Dr. Schwartz's book is designed to fill.

Dr. Schwartz's book is a remarkable contribution. He knows Hispaniola uniquely well from numerous extended visits to both its countries over some ten years and, very importantly, covering most months and with wide sampling of the very diverse habitat types that the island affords. In recent years, research publications by Dr. Schwartz and a dedicated group of colleagues, and by independent workers, have greatly added to our knowledge of this fauna, with its noteworthy incidence of endemism, and this book is designed as a synthesis of available information. Of the 196 species considered in the book, 30 have been described in the years following Riley's field guide. This list includes 19 species of the evolutionary jewel in Hispaniola's crown, the genus *Calisto,* and a most interesting group of hesperiids and lycaenids described by Johnson, Matusik and others from, and in some instances apparently endemic to, a remote and until recently largely pristine area in SW Dominican Republic. The list is rounded off by Dr. Schwartz's capture of the long-awaited Hispaniolan representative of the endemic Greater Antillean genus *Atlantea,* and by the recognition of *Memphis johnsoni* and *Adelpha lapitha* as residents of the island. But the value of the book lies not only in documenting species richness, but in clarifying patterns of distribution, essential for any rational conservation effort which, although probably a lost cause in Haiti, is still feasible in principle in some areas of the Dominican Republic. It is particularly heartening to learn that several taxa, formerly thought to be extremely rare, are, in the right place and at the right time, quite common or even abundant. These include, for example, *Pyrgus crisia, Oarisma stillmani, Hesperia nabokovi, Eurema dina mayobanex, Myscelia aracynthia, Doxocopa thoe, Heraclides aristor, Battus zetides* and numerous others. The hesperiids *Epargyreus spanna* and *Rhinthon bushi,* known to Riley only from the holotypes collected many years ago, have been given a new lease on life. On the other side of the coin, no trace has been found of either *Phaereus unia* or *Polythrix octomaculata decussata,* the latter with questionable claim to Hispaniolan status in the first place.

The book is enlivened by a wealth of first-hand details of flight behavior, nectaring predilections, and habitat structure, but some features of the work restrict its appeal. Although the key (in English and Spanish) appears to be well constructed, it only partially makes up for the absence of figures and of formal text descriptions of each taxon. Illustrations in color of at least some of the newly added species would have been a notable feature. While bibliographic citations are clearly presented, full use of the book requires access to a library with good journal coverage. It seems a pity that a reader less than very familiar with the Hispaniolan fauna will need a second reference to put together a mental image of many of the butterflies in their field settings.

This is an idiosyncratic and very "personal" book: equipped with admirably extensive field notes, the author has elected to present these substantially in their entirety, leaving distillation to the reader. Although perfectly valid, this is a somewhat unusual approach. One cannot fault Dr. Schwartz's insistence on full collecting data, though I confess to being irritated by elevations given to the nearest meter. Maybe it is the limitation of my qualitative mind at work, but to read that *Hemiargus hanno* has been taken in Haiti at the higher elevation of 1891 m *versus* the 1617 m for *H. ceraunus* simply does not engage the memory as effectively as 1900 *versus* 1600 meters, and little information would have been lost by such an approximation. After a while, I found myself wondering whether all records were made with altimeter held at chest height, or whether some had been obtained from a prone position, while the author was enjoying a well earned bottle of *Presidente*!

The listing of detailed locality records after each taxon is of obvious value for new and little known species, and where substantially new information on distribution is provided, but these lists occupy the equivalent of 70 pages of the book, and a solid page of records of *Eurema lisa* or *Phoebis sennae,* in small type, is formidable. Altitude ranges are, however, presented in more assimilable form in Table 1, which also summarizes temperature data and species noted from preliminary work on the satellite islands ranged around Hispaniola. It is not easy to select black and white photographs that convey the "feeling" of a locality, but those included here (28 on 14 pages) are certainly adequate in this respect. The tabulation of habitat types for those species with a demonstrable preference is an excellent ecological aid, and the discussion following the taxonomic and general text considers the incidence of endemism on present-day Hispaniola in the context of the original North and South palaeo-islands, with particular reference to the genus *Calisto*. An original description of *Tmolus victoria* (K. Johnson and D. Matusik) is appended, for the holotype collected in the Dominican Republic in 1984; this includes a half-tone plate that reminds one what a help even black and white figures would have been.

The author stresses the need for continuing work on the island, and particularly on its satellites. This reviewer was greatly encouraged to find that four brief visits to the Dominican Republic yielded two "new" Province records and even a species (*Appias punctifera*) (Smith, D. S., E. R. Classey & S. J. Ramos 1989, J. Lepid. Soc. 43:332–336) that had, as it were, slipped through Dr. Schwartz's net! This is unquestionably an important work, and clearly a labor of love, invaluable to the biologist concerned with the evolution of Antillean butterflies, if limited in its value to the more casual visitor. While wishing that both might have been catered for, one cannot but applaud the author's comment that publication of the mass of information included in this book is indeed timely.

DAVID SPENCER SMITH, *Department of Zoology and Hope Entomological Collections, The University Museum, Oxford OX1 3PW, England.*

Journal of the Lepidopterists' Society
44(2), 1990, 105–106

BUTTERFLIES OF BORNEO, Volume 1, by Kazuhisa Otsuka. 1988. Tobishima Corporation, 2, Sanban-cho, Chiyoda-ku, Tokyo 102, Japan. xx + 61 pp. in Japanese, xix + 62 pp. in English, 80 color plates, plus text figures. Hard cover, 19 × 27 cm. No ISBN number. Price unknown.

A remarkably active group of Japanese lepidopterists continues to publish new books documenting the butterfly faunas of many South East Asian countries. Now, Kazuhisa Otsuka, a member of the Lepidopterological Society of Japan and a teacher in Mushino City, Tokyo, has undertaken the task of publishing the first book on the butterflies of Borneo, and has done a capable job.

During more than ten years of extensive field work, Otsuka compiled photographs and identification notes for his own use. The stimulus to prepare this present field guide came from an official who reviewed his album at Sabah National Parks headquarters and requested that Otsuka publish his notes and photographs. As Otsuka points out, the current rate of destruction of the natural forest of Borneo is horrific, and the beauty and interest of Borneo's butterflies may play an important role in alerting the world to this serious danger. Thus the author has published this book with the help of the Tobishima Corporation in the hope that many young entomologists in Japan and Malaysia will be stimulated to study the butterflies of Borneo and other island portions of South East Asia, thereby contributing to the preservation of the remaining natural areas.

The book covers 327 species in seven families: Papilionidae, Pieridae, Danaidae, Satyridae (including the subfamily Amathusiinae), Libytheidae, Nymphalidae, and Riodinidae. The author plans to follow this first volume with a second volume in December 1990 that will cover the remaining 600 species of Lycaenidae and Hesperiidae.

The main purpose of the book is identification, which, as the author indicates, is the most difficult task facing lepidopterists in these areas of the world. Although the author records some life history descriptions (eggs, larvae, pupae, and foodplants), they are far from complete.

This book also briefly describes a number of the many habitat types found in Borneo. The author discusses the role of historical biogeography, climate, glacial periods and speciation, and mountain masses as well as national parks in influencing present-day butterfly distributions. A fascinating summary of the flora of Mt. Kinabalu in the center of Kinabalu National Park is included. This 4101 m mountain has distinct climates at different elevations and consequently has a remarkable diversity of butterflies. The author calls it "a dreamland for butterfly lovers."

Otsuka believes that Borneo's present highly diverse fauna of butterflies is due to the historical biogeography of this large island, which is believed to have been warm during all the northern glacial periods of the past 60 million years, with continuous presence of tropical rain forests that preserved many of the older forms of plant and animal life. Great diversification is seen in certain genera, such as *Euthalia, Tanaecia, Arhopala,* and *Potanthus.* With about 1000 species of butterflies known from the Malay Peninsula as a whole, the author states that his checklist totals about 910 species living in all of Borneo (and about 850 in Sabah). Most of the butterflies in Borneo are represented by the same species as those found on the Malay Peninsula. Only a few are shared with the butterfly faunas of the Philippines and Palawan. About 50 species are endemic to Borneo, and most of these live in the Mt. Kinabalu region.

Under the respective family names, each species account consists of the scientific name, the author and date of description, wing radius size for male and female, and a very brief (telegraphic) description of the adults of both sexes. This is followed by a generalized distribution comment (i.e., "West Malaysia," "Sumatra," "New Guinea to Australia," and even "Oriental Region"). Thus the reader will not find any guide to habitat distribution or even specific geographic localities.

The color plates are outstanding, with a reduced figure included for the upperside and underside of most species. The colors are crisp and well reproduced. The species name, sex, and a letter code for the location where the specimen of that species was caught, are given immediately below each color figure, a most useful feature usually not found in butterfly books. Very brief introductions to the structure of scientific names, nomenclature of wing venation and pattern areas, etc., are given at the front of the book, and a list of references for the butterflies of South East Asia is included. Unfortunately, these references are given in incomplete form, omitting the publisher (for books) and the journal title (for papers). In contrast, the Acknowledgments section is extraordinarily detailed and continues on for three pages.

Perhaps the best way to summarize this book is to say that the beautiful color cover illustration (of Mt. Kinabalu) conveys the extraordinary richness of habitat diversity in Borneo in one picture, portraying steaming lowland rain forest stretching up to an alpine zone on the highest mountaintop, while the 80 color plates of the 327 species of the families of butterflies covered in this first volume convey most of the information needed for ready identification. After the publication of Volume Two in late 1990, *Butterflies of Borneo* will represent an important contribution to the zoogeographic coverage of the fauna of the South East Asian islands and adjacent continental areas. The author is to be commended for his efforts to make the butterfly fauna of Borneo better known, particularly by his inclusion of a complete English translation of the Japanese text. Because of the small number printed and the high demand for this work, Volume One is already to be out-of-print. Perhaps we will be fortunate enough to see a reprint edition of Volume One at the time Volume Two is published. These two volumes will form a valuable addition to the working library of anyone interested in the butterflies of South East Asia, and in the ecology and zoogeography of tropical butterflies in general.

THOMAS C. EMMEL, *Division of Lepidoptera Research, Department of Zoology, University of Florida, Gainesville, Florida 32611.*

Journal of the Lepidopterists' Society
44(2), 1990, 107–110

BUTTERFLIES OF THE SOUTH EAST ASIAN ISLANDS (in 6 Volumes), edited by Etsuzo Tsukada (Volumes 1 and 2 translated into English by Kazuhiko Morishita and Hideyuki Chiba, Volumes 3 to 6 in Japanese only). Plapac Co., Ltd., Noge 3-4-6, Setagaya-ku, Tokyo 158, Japan. Volumes are hard cover, 24 × 30.5 cm. Currently available are Volumes 1, 2, 3, and 4 (Part 1). Length and price vary by volume (see below).

Butterflies of the South East Asian Islands is an excellent set of volumes for those interested in thorough coverage of the butterflies of this region. It is the first attempt to account for all known species and most subspecies in an area unparalleled for its geographically isolated populations and concomitant great diversity. The various authors have pooled information from the literature, and, more importantly, have included experiences of many current collectors. Detailed maps and information on species and subspecies distributions are provided for the region for the first time. The color photography is superb and the text coverage is complete and current for most species. For those seeking to identify specimens, these volumes are unmatched. For those planning trips to the region for general collecting or for scientific research, each volume is full of useful information. Although these volumes may seem expensive, when compared to several books on the market that provide color photographs with little or no text, they are well worth the money. The lay-out and design are artistically done, and the dust jackets (particularly the slip cases for the Japanese editions) are beautiful. This set of volumes would be a worthy addition to any lepidopterist's library.

The geographic area of coverage includes the Andamon and Nicobar Islands, the Malay Peninsula, Sumatra and Islands of West Sumatra, Java, Borneo, Islands of the Philippines and Natunas, the Celebes, the Lesser Sunda Islands, Tanimbar and all the islands west of Weber's line. Species occurring in the Malay Peninsula, but not in other areas covered, as given above, are not included. At the front of each volume is a series of maps of the area, along with a "Place Names Index" to aid in locating on maps important localities given in the text.

With very few exceptions, all butterfly species known to occur within the area defined above are included and illustrated in life-size color photographs. Both sexes are illustrated, along with a majority of the subspecies, forms, and major aberrations known at the time of publication. Also, ventral surfaces are illustrated when they are markedly different from the dorsal. Detailed range maps are provided for each species and subspecies. There are line drawings of male genitalia (with superuncus omitted) for each species, with few exceptions. References to original descriptions of species and subspecies are provided in the species accounts. Superb color habitat photos are interspersed throughout the plates.

Each volume is divided into 2 parts, Plates followed by Text. Before the plates, a Contents section gives plate and page numbers for each species illustrated, providing convenient and quick reference when identifying specimens in collections. The rather extensive Text section is arranged by headings as follows: Scientific name of the species followed by 1. *Author(s)*, 2. *Original Description*, 3. *Notes*, 4. *Range*, 5. *Plates*. These are followed by the range maps and drawings of male genitalia. Below is a brief description of each heading.

Original Description: Taxa are listed in order of year of publication with the name of species and subspecies, author, journal, volume number, page and publication year. Locations of type specimens, where known and verified by the authors, are given in parentheses.

Notes: These give general information about each species. Notes may include hints on species identification or recognition of sexes, comments on endemism, general biology and life histories (including larval foodplants if known). Information on habitat preference (often including adult nectar sources), seasonal flight periods, daily flight times, specific information on good collecting locations and detailed information on access to these locations is given. Key differences between some subspecies are enumerated. Frequently included are anecdotes on interesting collecting expeditions and observations on species behavior. The authors describe the various islands, their characteristic habitats, and the enormous habitat losses, especially in lowlands.

Range: Ranges of all subspecies are given, including those of a few subspecies occurring outside the coverage area when this serves the author's purpose.

Plates: The collecting date and locality of all figured specimens are listed in this section and plate numbers guide the reader to the color illustrations in the plates. For easily confused species, figures (drawings) are included that provide distinguishing characteristics or keys or both to facilitate identification. An index of scientific names concludes each volume.

Volume 1—PAPILIONIDAE, by E. Tsukada and Yasusuke Nishiyama. English edition 1982, 457 pp., 79 figs., 166 full page color plates. Dust jacket. 25,000 Yen (about $170.00).

For lovers of papilionids, this book is required reading. The thorough text and excellent color plates cover 121 species in 12 genera, and 349 out of a total of 401 subspecies. The authors name, describe, and figure 18 new subspecies. About 1300 specimens are figured in color, including several rare species and subspecies, some illustrated for the first time. For example, since its discovery and naming in 1935, *Atrophaneura luchti* was known only from a single male specimen; in this volume 6 specimens (3 of each sex) are illustrated for the first time—life-size and in color. Photographs of other rare species seldom found in books include *Papilio jordani* (male and female), *P. mayo* (male and female), spring and summer forms of both sexes of *P. chikae, Losaria rhodifer, Chilasa osmana, Graphium dorcus*; males and females of the four races of *Papilio karna*; and aberrant *Graphium androcles*.

Highly variable species are well illustrated. For example, there are 45 color illustrations of female *Papilio memnon*! Text and illustrations are provided for separating the sympatric and sometimes confusingly similar *Triodes cuneifera* and *T. amphrysus*; the *Haliphron* subgroup of the birdwing butterflies; the 8 species of Philippine *Pachliopta*; all of the *Helenus*-like species; the 3 similar species *Graphium euphrates, decolor, antiphates*; and the similar species in the *Macareus* group (*Paranticopsis*). A diagram of the phylogeny of South East Asian Papilionidae is given on pages 436–444.

The English translation is good and the few very minor errors in grammar do not detract from the clear and readable text. Given the large amount of text, the translators must be commended. There are also some minor errors in the plates. These include wrong subspecific names for figured specimens (two) and minor spelling errors of subspecific names in plates or dorsal/ventral designation errors for figured specimens (five). A corrigenda is included for these errors.

The only shortcomings I find for this volume are in the plates. Latin species names are given at the top of each plate and the various numbered figures give only the subspecific names. When two or more species are on the same plate it is sometimes confusing (at least for very similar species) to know where the subspecies of one species end and those of another begin. Use of the initial of the species name with the numbered figures would have been helpful. Also helpful, for quick reference between plates and text, would have been the inclusion of the text page next to the species names on the plates. These minor shortcomings are corrected in the remaining volumes.

Volume 2—PIERIDAE AND DANAIDAE, by Osamu Yata and Kazuhiko Morishita. English edition 1985, 623 pp., text divided into 2 parts: Part I—Pieridae (pages 206–438) by Yata, and Part II—Danaidae (pages 439–598) by Morishita, 87 figures (plus standard line drawings of wing venation for each genus and male genitalia for each species), 172 full page color plates and 16 black and white photographs. Dust jacket. 35,000 Yen (about $237.00).

This volume covers the Pieridae and Danaidae of the region in greater detail than I have seen in any other book. For the pierids, 45 holotypes and paratypes and 152 of 155 species are illustrated and all are discussed. (The three pierid species not illustrated are known only from their type specimens from unknown locations.) Tsukada states that a prior check-list for this area contained approximately 133 species, which he says may indicate that the area had been somewhat neglected by systematists. Forty-six species of the popular and large genus *Delias* are discussed and illustrated in color. Rare *Delias* species seldom illustrated in books include, *singhapura, kuehni,* the recently (1981) discovered *ganymede* (originally described as a ssp. of *D. georgina*), *lemoulti, shirozui, benasu, eumolpe, melusina, sambawana, fasciata,* and *mitisi*. A diagram of the phylogeny of Pieridae is included.

All 80 species of Danaidae known to occur within the area are illustrated and discussed, and 35 holotypes and paratypes are illustrated, including the recently discovered (1981) and very rare Celebesian *Idea tambusisiana,* here pictured life-size in color for the first time. There are 3000 color photographs, which, with the text, greatly facilitate the identification of species, subspecies and forms. Above the scientific names in the plates are page numbers to guide the reader to the appropriate text. Beautiful habitat photographs are interspersed throughout the plates section.

The authors discuss the taxonomy of each family and introduce each genus in detail (including figures of wing venation and shape) before discussing the species in that genus, a practice continued in subsequent volumes. Each genus introduction includes diagnostic characteristics of adults, eggs, and larvae (when known), and general information, such as world distribution and typical habits. Both authors have changed the arrangements (groupings) of some genera, but they give reasons and appropriate literature citations for all changes. When known, chromosome numbers are given.

Yata has raised several races to species status, especially in *Delias*. This splitting has resulted in an increase in the number of species on the check-list of Pieridae. Morishita has done likewise in his treatment of the Danaidae, but to a lesser extent.

The authors provide informative overviews of biological aspects of the species in these two families. They also disclose good collecting locations and identify best collecting seasons for many of the species. Citations to the literature are thorough. For lepidopterists interested in either the Pieridae or the Danaidae, this volume is a must, as no other book covers the South East Asian islands in such detail. Whether or not one agrees with the taxonomy, the editor and authors have done an admirable job.

Volume 3—SATYRIDAE AND LIBYTHEIDAE, by Toshiaki Aoki, Shuhei Yamaguchi, and Yoshinobu Uémura. Japanese edition 1982, 500 pp., 72 figures (plus illustrations of male genitalia and wing venation), 120 full page color plates and 8 black and white photos. Slip case. 28,000 Yen (about $190.00).

Although Volume 3 is in Japanese (except for scientific names), a non-reader will still glean a wealth of information from this book, which covers the 165 species of Satyridae, 45 species of Amathusiinae, and 3 species of Libytheidae that occur within the region. A total of 2000 illustrated specimens (including 137 holotypes and paratypes) shows all species and a majority of the subspecies. Thirty-one species of the popular and often colorful *Elymnias* are illustrated, including rare species such as the recently described (1982) *E. detanii*. There are eight beautiful close-up color photographs of live butterflies, and several full page habitat photos.

Before the index of scientific names at the back of the book the authors add "A LIST OF NEW COMBINATIONS, NEW STATUS, REVIEW STATUS, NEW SYNONYMS AND NEW DISTRIBUTIONS," which guides the reader directly to newly revised taxonomy and range extensions found in this volume. For *Lohora*, for example, there are 10 species under "new combinations," 20 species and subspecies under "new status," 3 species under "review status," 11 species and subspecies under "new synonyms," and 43 species and subspecies under "new distributions."

Those who need to identify species from this region will find the extensive illustrations superb; no other single source has color illustrations of all species and of so many subspecies in these families. This alone makes the book an important addition to the butterfly literature. For the serious lepidopterist with world-wide interests, or for those mainly interested in the South Pacific, this is a "must have" volume.

Volume 4—NYMPHALIDAE (part 1), by Etsuzo Tsukada (with assistance from Yasasuke Nishiyama and Misao Kaneko). Japanese edition 1985, 558 pp., 16 figs., 157 full page color plates and 9 black and white photographs. Slip case. 39,000 Yen (about $264.00).

This volume covers 194 species and many of their subspecies. It encompasses 29 genera (from *Acraea* to *Athyma*), with the remainder of the Nymphalidae to be completed in Volume 4, part 2. Two of the species, *Ariadne proximus* and *Chirrochroa eremita*, are newly described and pictured for the first time. Eighty-six new subspecies are also newly described and illustrated in color photographs. Conveniently, these 88 new taxa are described in the first part of the text. All species and subspecies (up to *Athyma*) are well illustrated with life-size color photos of 3317 specimens. Over 200 of these are holotypes and paratypes, and 7 are types. This volume includes the beautiful and often sought after *Cethosia* (12 sp.), *Hypolimnas* (9 sp.), *Kallima* (4 species), and *Cyrestis* (16 sp.). Rare species illustrated include *Cethosia leschnault*, *Hypolymnas saundersi*, *H. sumbawana*, and *Kallima albofasciata*. Although this volume, like Volume 3, is in Japanese, there is still a wealth of information available to the non-reader.

Future volumes to complete the set are Volume 4 (part 2—Nymphalidae concluded, expected in 1990), Volume 5 (Lycaenidae and Riodinidae) and Volume 6 (Hesperidae). A Volume 7 (supplement) will be published as needed. These remaining volumes will be in Japanese.

WAYNE H. WHALEY, *Dept. of Zoology, 574 WIDB, Brigham Young University, Provo, Utah 84602.*

Journal of the Lepidopterists' Society
44(2), 1990, 111

ANNOUNCEMENT

JOURNAL COVER ILLUSTRATIONS AND FEATURE PHOTOGRAPHS

The *Journal* is an excellent outlet for artistic expression. COVER ILLUSTRATIONS and FEATURE PHOTOGRAPHS are two recently established submission categories that provide opportunities to publish drawings and photographs (black and white or color) in an international publication devoted to Lepidoptera. Submissions in both categories may deal with any aspect of Lepidoptera study but must be accompanied by brief captions that include scientific names.

COVER ILLUSTRATIONS now change with each issue of the *Journal*. Recent covers serve as good examples, but the range of potential subject matter is much greater than the adults or larvae usually depicted. Submissions should be no larger than letter size (21 by 28 cm), with the caption for the inside front cover on a separate sheet. Drawings are usually more suitable than photographs because drawings better withstand the coarse reproduction necessitated by the textured surface of the *Journal*'s cover stock. Submitted drawings or crisp photographs will be selected for artistry, novelty, and general appeal. There is no limit to the number of submissions per person; no author page charges are assessed for cover illustrations.

FEATURE PHOTOGRAPHS have been published in the first three issues of Volume 43 (1989) of the *Journal* and in an expanded format in the first issue of Volume 44 (1990), which included both black and white and color illustrations. Submissions in this category might show unusual behaviors, unusual habitats, type localities, specimens in nature illustrating identifying marks, unusual collecting conditions or techniques, or other subjects. Photographic submissions should be mounted on white cardboard no larger than letter size, with a brief caption on a separate sheet. The caption should include details of the photographic equipment and exposure used as well as information on the subject portrayed. Feature photographs must be suitable for reduction to either a half or full *Journal* page (8.5 cm high by 11 cm wide, or 17 cm high by 11 cm wide, caption included). Submissions will be selected for photographic quality, scientific merit, and general appeal. Regular page charges will apply to accepted feature photographs. Color photographs are welcome and should be submitted as mounted color prints, not as transparencies (for submission details, contact the editor).

Submissions in both of these artistic categories should be sent to the *Journal* Editor.

BOYCE A. DRUMMOND, Editor

NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of Lepidoptera study. Categories are Articles, General Notes, Technical Comments, Book Reviews, Obituaries, Feature Photographs, and Cover Illustrations. Reviews should treat books published within the past two years. Obituaries must be authorized by the President of the Society. Requirements for Feature Photographs and Cover Illustrations are stated on page 111 in Volume 44(2). *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 submit manuscripts in *triplicate*, typewritten, *entirely double-spaced*, with wide margins, on one side only of white, letter-sized paper. Prepare manuscripts according to the following instructions, and submit them flat, not folded.

Abstract: An informative abstract should precede the text of Articles.

Key Words: Up to five key words or terms not in the title should accompany Articles, General Notes, and Technical Comments.

Text: Contributors should write with precision, clarity, and economy, and should use the active voice and first person whenever appropriate. Titles should be explicit, descriptive, and as short as possible. The first mention of a plant or animal in the text should include the *full scientific name* with *author*, and *family*. Measurements should be given in metric units; times in terms of the 24-hour clock (0930 h, not 9:30 AM). Underline only where *italics* are intended.

Literature Cited: References in the text of Articles should be given as Sheppard (1959) or (Sheppard 1959, 1961a, 1961b) and listed alphabetically under the heading LITERATURE CITED, in the following format without underlining:

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

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

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

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.

Tables: Tables should be numbered consecutively in Arabic numerals. Headings for tables should not be capitalized. Tabular material must be typed *on separate sheets*, and placed following the main text, with the approximate desired position indicated in the text. Vertical lines as well as vertical writing should be avoided.

Voucher specimens: When appropriate, manuscripts must name a public repository where specimens documenting identity of organisms can be found. Kinds of reports that require vouchering include life histories, host associations, immature morphology, and experimental enquiries.

Proofs: The edited manuscript and galley proofs will be mailed to the author for correction of printer's errors. Excessive author's changes at this time will be charged to authors at the rate of $2 per line. A purchase order for reprints will accompany proofs.

Page charges: For authors affiliated with institutions, page charges are $20 per *Journal* page. For unaffiliated authors, page charges are $10 per *Journal* page with a $50 maximum. Authors of Book Reviews and Obituaries are exempt from page charges. Authors unable to pay page charges for reasons such as difficulties with foreign exchange should apply to the editor for free publication.

Correspondence: Address all matters relating to the *Journal* to the editor.

PRINTED BY THE ALLEN PRESS, INC., LAWRENCE, KANSAS 66044 U.S.A.

CONTENTS

GENERAL NOTES

TECHNICAL COMMENT

BOOK REVIEWS

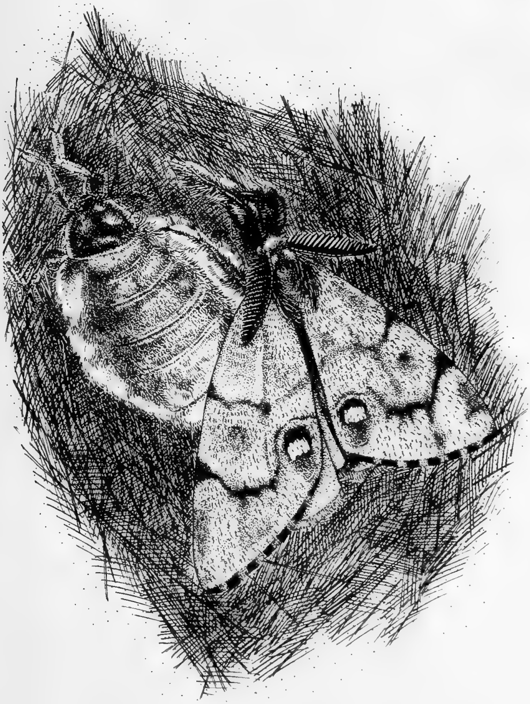
ANNOUNCEMENT

Volu 4 1990 Number 3

ISSN 0024-0966

JOURNAL
of the
LEPIDOPTERISTS' SOCIETY

Published quarterly by THE LEPIDOPTERISTS' SOCIETY
Publié par LA SOCIÉTÉ DES LÉPIDOPTÉRISTES
Herausgegeben von DER GESELLSCHAFT DER LEPIDOPTEROLOGEN
Publicado por LA SOCIEDAD DE LOS LEPIDOPTERISTAS



6 December 1990

THE LEPIDOPTERISTS' SOCIETY

EXECUTIVE COUNCIL

EDITORIAL BOARD

HONORARY LIFE MEMBERS OF THE SOCIETY

CHARLES L. REMINGTON (1966), F. MARTIN BROWN (1973), E. G. MUNROE (1973),
ZDRAVKO LORKOVIC (1980), J. F. GATES CLARKE (1985), IAN F. B. COMMON (1987),
JOHN G. FRANCLEMONT (1988), LINCOLN P. BROWER (1990),
DOUGLAS C. FERGUSON (1990)

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.

Active members—annual dues $25.00
Student members—annual dues $15.00
Sustaining members—annual dues $35.00
Life members—single sum $500.00
Institutional subscriptions—annual $40.00

Send remittances, payable to *The Lepidopterists' Society*, to: Fay H. Karpuleon, Treasurer, 1521 Blanchard, Mishawaka, Indiana 46544, U.S.A.; and address changes to: Julian P. Donahue, Natural History Museum, 900 Exposition Blvd., Los Angeles, California 90007-4057 U.S.A. For information about the Society, contact: William D. Winter, Secretary, 257 Common St., Dedham, Massachusetts 02026-4020, U.S.A. To order back issues of the *Journal*, *News*, and *Memoirs*, write for availability and prices to the Publications Coordinator: Ronald Leuschner, 1900 John St., Manhattan Beach, California 90266-2608, U.S.A.

Journal of the Lepidopterists' Society (ISSN 0024-0966) is published quarterly for $40.00 (institutional subscription) and $25.00 (active member rate) by the Lepidopterists' Society, % Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, California 90007-4057. Second-class postage paid at Los Angeles, California and additional mailing offices. POSTMASTER: Send address changes to the Lepidopterists' Society, % Natural History Museum, 900 Exposition Blvd., Los Angeles, California 90007-4057.

Cover illustration: Wingless female (left) and male of the Vaporer Moth, *Orgyia antiqua* L. (Lymantriidae) in copula on the female's cocoon. This species is distributed throughout China, Japan, the USSR, and Europe despite the fact that the flightless females never leave the cocoon from which they emerge. Original drawing by Xu Xiangming, No. 31, Qian Men Wai Zhu Bao Shi, Beijing, China.

JOURNAL OF
THE LEPIDOPTERISTS' SOCIETY

Volume 44 1990 Number 3

Journal of the Lepidopterists' Society
44(3), 1990, 113–142

BODY SIZE AND DIET QUALITY IN THE GENUS *CYDIA* (TORTRICIDAE)

WILLIAM E. MILLER

Department of Entomology, University of Minnesota,
St. Paul, Minnesota 55108

ABSTRACT. I examine forewing length, a body-size index, relative to three quality classes of larval diet for more than 75 *Cydia* species. Quality of diet refers to protein concentration in the part of the food plant consumed. Mean crude protein percentages are near 25 in the high class, near 12 in the medium, and near 6 in the low. All data are from published sources. Forewings range in length from 4.0 to 10.5 mm among study taxa, and are longest in the high food-quality class, intermediate in the medium, and shortest in the low. The high food-quality class consists entirely of seed predators whose body sizes correlate positively with food-plant seed sizes. Medium and low food-quality classes consist mostly of nonseed feeders. Results imply that as *Cydia* colonize new food plants and plant parts of differing diet quality, body sizes evolve to those for which larvae can obtain sufficient nourishment. This interpretation withstands cladistic testing against an independent *Cydia* phylogeny.

Additional key words: Olethreutinae, evolution, cladistics, seed predation, food plants.

For organisms generally, body size is thought to be a quantitative adaptive trait (Bonner 1965, Calder 1984, Roff 1981). Much interest in body size derives from consequences of allometric relations among body components (Peters 1983). Body-size physiology and ecology are more tractable and better understood than body-size evolution, one facet of which is genesis of body-size diversity. Body size usually varies somewhat within species, but it does so around a genetically controlled norm. The norm represents an adaptive and fitness compromise in a given environment; analysis of norms and environments can yield evolutionary insights (Fisher 1930, Ridley 1983, Williams 1966).

Lepidopteran body-size diversity has just begun to be studied. Dietary factors are natural choices for independent variables: food quantity and quality are potent determinants. Among examined lepidopteran families, individual and population biomass correlate with density, size, and diet quality of food plants (Mattson 1977, 1980, Mattson & Scriber

1987, Niemelä et al. 1981). Within examined lepidopteran genera, subfamilies, and families, body size correlates also with breadth of diet (Niemelä et al. 1981, Wasserman & Mitter 1978). Within lepidopteran families that mine leaves of *Quercus* (Fagaceae), body size correlates with leaf persistence, smaller-bodied species occurring on deciduous species (Opler 1978). If body size is viewed as an effect, then in evolutionary time it would seem to shift positively with diet breadth, food-plant size, and leaf persistence, and negatively with diet quality, although diet quality and plant size themselves correlate positively. Information is still too scant to yield well integrated generalizations about the genesis of lepidopteran body size diversity.

In this paper I examine body-size diversity relative to quality of larval diet in a large, worldwide sample of *Cydia* species (Tortricidae, Olethreutinae), defining food quality as protein concentration and testing analytical results cladistically.

For species of the subfamily Olethreutinae, a commonly available measure of body size is forewing length (L), values of which range from 4 to 20 mm (Miller 1987). Single genera cover large portions of this range. *Cydia* occupies more than half of it. Forewing length closely estimates dry body weight (W) of olethreutines by a power function summarized as $W = 0.0085L^3$ (Miller 1977). This function reveals that small differences in forewing length denote larger differences in body mass. The low standard error of estimate of this function justifies using forewing length as an index of body size.

Cydia in the strict sense consists of ca. 250 species. Many species are important economically, a fact responsible for much information about the genus. The most famous species is the codling moth, *C. pomonella* (L.). The generic name is in flux; I follow Brown (1979) in using *Cydia*, but others argue for using *Laspeyresia* (Kuznetsov & Kerzhner 1984).

MATERIALS AND METHODS

I devise three larval food-quality classes based on concentration of crude protein in the part of the food plant eaten, place each *Cydia* in an appropriate food-quality class, analyze inter- and intraclass differences in forewing length, and compare results with an existing phylogeny.

I include only taxa conforming to the strict *Cydia* concepts of Obraztsov (1959) and Danilevsky and Kuznetsov (1968). Using broader generic concepts, some authors refer species to *Cydia* that are more strictly referable to *Grapholita*, *Pammene*, and other genera. Strict interpretation focuses and simplifies the study by limiting genetic heterogeneity to that of *Cydia* monophyly. In classification and nomenclature of *Cydia* subgenera, sections, species, and subspecies, I follow

Danilevsky and Kuznetsov (1968) for taxa treated by them; for other taxa I apply their classification as far as I can do so confidently.

Wing measure of *Cydia* species is usually published as a range. I therefore use midrange, a statistic approximating the mean. Wingspan (S), the maximum distance between tips of spread wings, more often appears in the literature than forewing length (L). I convert span to length by the proportionality constant L = 0.458S (Miller 1977). All midranges are from published sources, mostly detailed faunal works (Appendix). Where forewing-length sample sizes are small, and a best source unavailable, I combine data from several sources. When midrange could not be based on at least two individuals, I excluded the taxon. Using standard approximate methods, I estimate standard deviation (SD) of the midrange for all taxa where explicit sample sizes are nine or more individuals. I work with midranges expressed to three decimal places, but record them here to only one place (Appendix and elsewhere).

Food-plant parts eaten by *Cydia* larvae differ in food quality. Protein is a major component of food quality (Mattson 1980, Mattson & Scriber 1987, Scriber & Slansky 1981). "Crude protein", a standard food-science term, refers to the mathematical product of Kjeldahl nitrogen percentage and a multiplier, usually 6.25 (Crisan & Sands 1978, Williams 1984, and others). Crude protein percentage of food-plant parts used by *Cydia* forms a continuum. Below, I divide this continuum for study purposes into three food-quality classes: high, medium, and low. The letter n (or N) denotes number of analyses in this section of the text, number of observations in later sections.

High (mean near 25%)—seeds of Leguminosae; *Pinus*, *Picea*, *Abies* (Pinaceae); *Malus* and *Pyrus* (Rosaceae). Nutritional superiority of seeds for seed eaters over other plant parts is evident in the survey by Mattson (1980). It may be further documented with Leguminosae, one of the two plant families most used by *Cydia*: in forage species (6n), mean percentage crude protein is 24 in seeds, 16 in foliage, and 7 in pod husks (Skerman 1977). In other surveys, percentage crude protein in seeds ranges from 4 to 62 in Leguminosae (>1000n), 6 to 38 in *Pinus* and *Picea* (21n), and 18 to 49 in *Malus* and *Pyrus* (6n) (Barclay & Earle 1974, Dickmann & Kozlowski 1969, Earle & Jones 1962, Haut 1938, Jones & Earle 1966, Katsuta & Satoo 1964, McCarthy & Matthews 1984, NAS 1979, Pulliainen & Lajunen 1984, Räder-Roitzsch 1957, Short & Epps 1976, Skerman 1977, Winton & Winton 1932, 1935, Yoon et al. 1983).

Medium (mean near 12%)—inner bark, fungus-infected woody parts, photosynthesizing bark, foliage, flowers; seeds of *Acer* (Aceraceae), *Corylus* (Betulaceae), *Cryptomeria* (Taxodiaceae), and *Quercus*. Fungi are equally as proteinaceous as the seeds comprising the high food-quality class (Crisan & Sands 1978, Mattson 1980), but fungi only supplement *Cydia* underbark diets. Photosynthesizing bark occurs in the food-plant genus *Populus* (Salicaceae) (Shepard 1975). Percentage crude protein in seeds is 7 to 32 for *Acer* (11n), 4 to 32 for *Quercus* (21n), and 11 to 26 for *Corylus* (5n) and *Cryptomeria* (1n) (Anderson & Kulp 1921, Barclay & Earle 1974, Earle & Jones 1962, Jones & Earle 1966, McCarthy & Meredith 1988, Schmidt-Hebbel & Pennacciotti M. 1979, Short & Epps 1976, Wainio 1941, Winton & Winton 1932).

Low (mean near 6%)—habitations of other insects, fruits or other seed-containing parts, sapwood, outer bark; seeds of *Araucaria* (Araucariaceae), *Castanea, Fagus* (Fagaceae), and Palmae. Wood and seed-containing parts are among the plant parts lowest in protein (Mattson 1980, Skerman 1977). Percentage crude protein in seeds is 4 to 16 in *Araucaria* (2n), *Castanea* (8n), *Fagus* (3n), and Palmae (20n) (Barclay & Earle 1974, Cardemil & Reinero 1982, Earle & Jones 1962, Jones & Earle 1966, McCarthy & Meredith 1988, Schmidt-Hebbel & Pennacciotti M. 1979, Wainio 1941, Winton & Winton 1932).

In intraclass analyses, I examine *Cydia* forewing length relative to food-plant seed size measured as weight of one seed. Mean seed weights for a given plant species do not vary much (Harper et al. 1970). I take most seed weights from published sources (Appendix, Table 2), using sample means and midranges in that order of preference. Where reported weights are few, I combine data from several sources if available. For seeds also consumed by man, I use seed weights of wild-type food plants if known. For other domesticated seeds, I use the smallest values reported. Because such plants have long been cultivated or bred for large seeds (Smartt 1980), the lowest weights are probably nearer to wild-type values. For those few species for which only seed dimensions are available, I estimate weights from one or more relatives of known seed weight and similar seed dimensions. Where one main food-plant species is not apparent, I use the mean of available seed weights for the appropriate number of food-plant species. In botanical nomenclature, I give only original authors (Appendix), following Schopmeyer (1974) and Krüssmann (1978) in that order for food plants treated by them, and following source authors for others. I work with seed weights expressed to four significant figures, but report them here to three figures (Appendix, Table 2).

I use both nonparametric and parametric statistics because sample sizes are sometimes unequal, and distributions are sometimes more important than parametric values. Nonparametric methods treat data by ranks rather than by values. Hence differences between means may actually refer to differences between underlying rank distributions.

Because forewing-length equations involve dimensions, I use nonlinear power functions for them (Peters 1983) solved by ordinary least squares.

For one-third of *Cydia* taxa, the part of the food plant eaten is known, thus enabling estimation of the quality of larval diet. This fraction of the genus comprises the study sample. There are 82 observations in all, one each for 78 species, 2 other than nominotypical subspecies, and 2 additional populations that behave like separate taxa in using food plants different from those of allopatric sister populations. Observations are grouped into high, medium, and low food-quality classes within which they appear alphabetically by *Cydia* species-level taxon in the Appendix. The 34 taxa and populations in the high food-quality class, all of which are seed predators, are from six continents; the 34 in the medium class feed mostly on nonseed parts, and are from three continents; and the 14 in the low class feed mostly on nonseed parts, and are from five continents. Corresponding numbers of food-plant families are 3, 12, and 9, respectively. Food-plant families and percentages of *Cydia* study species using them are, for the high class: Pinaceae—47%, Leguminosae—47%, Rosaceae—6%; for the medium class: Pinaceae—35%, Fagaceae—16%, Aceraceae—10%, Leguminosae—9%, Salicaceae—9%, others—21%; for the low class: Pinaceae—21%, Salicaceae—21%, Fagaceae—14%, others—44%.

I provisionally include five *Cydia* species whose strict generic affinities are unconfirmed: *araucariae* (Pastrana), *palmetum* (Heinrich), *staphiditis* (Meyrick), *stirpicola* (Meyrick), and *tonosticha* (Meyrick). Some species whose strict generic affinities require exclusion are *Fulcrifera torostoma* (Clarke), *F. tricentra* (Meyrick), *Grapholita deshaisiana* (Lucas), *Leguminivora glycinivorella* (Matsumura), *L. ptychora* (Meyrick), *Matsumuraeses critica* (Meyrick), and *M. fabivora* (Meyrick).

RESULTS

Forewing lengths range from 4.0 to 10.5 mm (Appendix, Table 1). The main assumption in this study is that body-size diversity really exists in this sample range. If such diversity is present, variance (SD^2) in forewing length among taxa should exceed that within taxa; if it is absent, the two variances should not differ. Comparison shows that variance among taxa (1.611, 82n) exceeds weighted average variance within taxa (0.156, 38n) ($1.611/0.156 = 10.3$, $P < 0.001$, variance ratio test), thus confirming the presence of diversity.

Body-size and Food Quality

Forewings are longest in the high food-quality class (6.8 mm), intermediate in the medium class (6.4 mm), and shortest in the low class

TABLE 1. Body size of *Cydia* taxa and populations relative to quality of larval diet.

Food-quality class	N	Forewing-length midrange (F) (mm) Mean ± SD[a]	Forewing-length midrange (F) (mm) Range	Estimated mean dry wt. (W) (mg)[b]
High	34	6.8 ± 1.4	4.0–10.5	2.6
Medium	34	6.4 ± 0.9	4.8–8.2	2.2
Low	14	5.8 ± 1.3	4.4–8.5	1.7

[a] Means differ statistically (F-test, $P < 0.05$); their rank distributions differ in all possible comparisons (Kruskal-Wallis and Mann-Whitney tests, $P < 0.001$).
[b] $W = 0.0085\ F^3$.

(5.8 mm) (Table 1). Estimates of body weight (Table 1) differ more markedly among the classes because forewing length is being multiplied by a power function. On average, members of the high class are 1.16 times heavier than those of the medium class, and 1.57 times heavier than those of the low; members of the medium class are 1.35 times heavier than those of the low.

Members of the high food-quality class have the greatest range and variability in forewing length (Table 1). Further scrutiny and analysis of this group reveals a major source of intraclass body-size variation. In this class, forewing length correlates with food-plant seed size; the larger the seeds, the longer the forewings in both the pinaceous and leguminous subsets (Fig. 1). In a control analysis of nonseed-feeders from the medium and low food-quality classes, no such correlation appears between forewing length and food-plant seed size (Fig. 2: line A).

Size is only part of the seed factor accounting for body-size variation in the high class. Food-plant seed weight in this class traverses three orders of magnitude; the smaller the seed, the greater the number required to nourish a larva, the number increasing from 2 to more than 30 in taxa for which such data are available (Fig. 3, Table 2). Thus the product of seed size and number required underlies the correlation of forewing length and seed size shown in Fig. 1.

In the medium and low food-quality classes, range and variability of forewing length are narrower than in the high class (Table 1), and sources of intraclass body-size variation are less evident. In pooled medium and low classes, mean forewing length of seed predators (7.2 mm) is greater than that of nonseed feeders (5.9 mm) ($P < 0.001$, Student *t*- and Mann-Whitney tests). Forewing length of seed predators in these classes also correlates with seed size (Fig. 2: line B). Secondary plant chemistry could be a factor in intraclass variation in the medium and low food-quality classes because a greater diversity of food plants is involved: 12 and 9 food-plant families, respectively, compared with 3 in the high class.

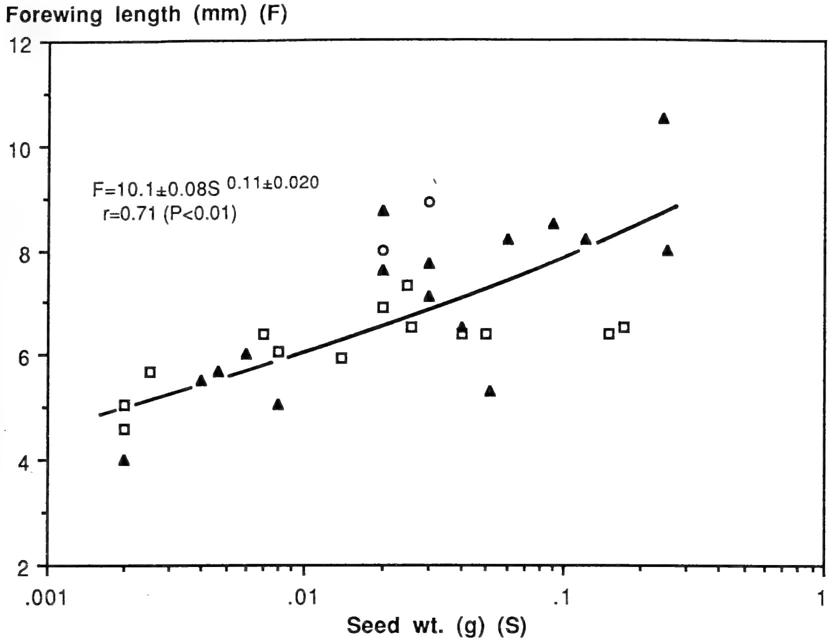


FIG. 1. *Cydia* body size as related to food-plant seed size in the high food-quality class. Each point represents a *Cydia* taxon or population enumerated in the Appendix. Solid triangles depict the pinaceous subset; open squares, the leguminous subset; open circles, others. The symbol ± denotes standard error.

TABLE 2. Number of seeds eaten or destroyed per *Cydia* larva in the high food-quality class. (Ditto is abbreviated do.)

Species of *Cydia*	Food plant	Mean seed wt. (g)[a]	Mean no. seeds/ larva	References
anaranjada	*Pinus elliottii*	0.0314	6	Merkel 1967
conicolana	*P. sylvestris*	0.00605	7	Gibb in Betts 1958
ingens	*P. elliottii*	0.0314	12	Coyne 1968
do.	*P. palustris*	0.0926	4	do.
montezuma	*P. montezumae*	0.0198	9	Cibrián-Tovar et al. 1986
n. nigricana	*Pisum sativum*	[0.178]	2.6	Stenmark 1971
piperana	*Pinus p. ponderosa*	0.0589	4	Hedlin 1967
do.	*P. p. scopulorum* Engelm.	[0.0346]	5	Kinzer et al. 1972
pomonella	*Malus pumila*	0.0227	8	Crandall 1917, Denno & Harwood 1973, Heriot & Waddel 1942
toreuta	*Pinus banksiana*	[0.00346]	10	Kraft 1968
do.	*P. resinosa*	[0.00872]	7	Lyons 1957
strobilella	*Picea abies*	0.00709	17	Andersson 1965, Györfi 1956
do.	*P. glauca*	0.00201	31	Tripp & Hedlin 1956

[a] Brackets denote weights absent or different in the Appendix. Bracketed weights for *Pinus* from Krugman & Jenkinson (1974).

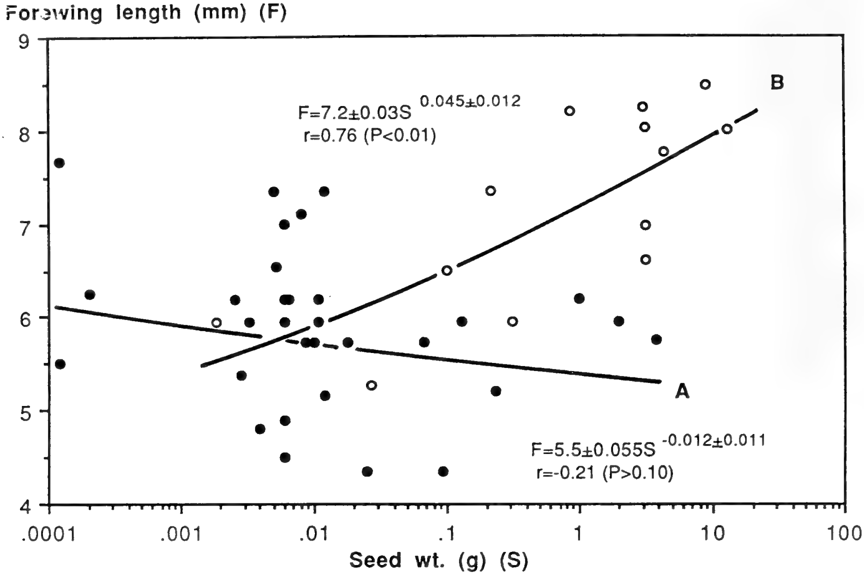


FIG. 2. *Cydia* body size as related to food-plant seed size in pooled medium and low food-quality classes. Each point represents a *Cydia* taxon or population enumerated in the Appendix. Line A (closed circles) depicts the nonseed-feeding subset; line B (open circles), the seed-predator subset. The symbol ± denotes standard error.

Cydia taxa with one recorded food plant and those with more than one are analogous to the specialist and generalist diet-breadth classes of Niemelä et al. (1981) and Wasserman and Mitter (1978). For "specialist" *Cydia* taxa, mean forewing length is 6.4 mm (37n), and for "generalist" taxa, 6.6 mm (42n). The difference, 0.2 mm, is statistically significant nonparametrically ($P < 0.001$, Mann-Whitney test), but not parametrically (Student *t*-test, $P > 0.40$). The first result matches findings of the above authors. When the high food-quality class is examined separately, however, results are reversed: mean forewing lengths are 6.9 mm (17n) for specialists and 6.6 mm (16n) for generalists. This reversal suggests that forewing length correlates more strongly with seed size than with diet breadth.

Cladistic Test of Results

Statistical analyses like the foregoing must be interpreted cautiously. Related taxa may simply inherit a given trait from a common ancestor rather than evolve it independently. If this happens, the assumption of statistical independence of observations is violated (Felsenstein 1985, Ridley 1983). It therefore seems necessary to test the assumption of independence, which is equivalent to the assumption that *Cydia* body-

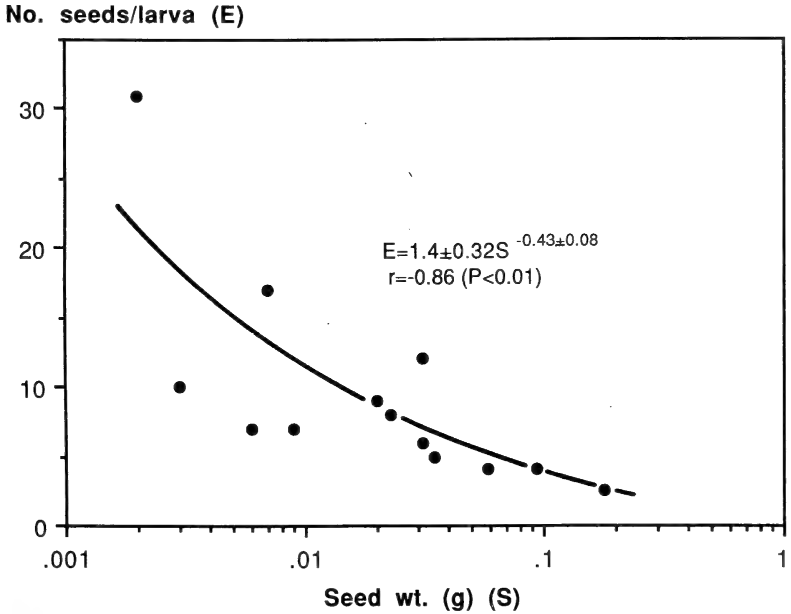


FIG. 3. Number of seeds eaten or destroyed per larva as related to food-plant seed size in the high food-quality class. Each point represents a *Cydia* taxon or population enumerated in Table 2 and the Appendix. The symbol ± denotes standard error.

size diversity represents many rather than a few evolutionary events. Below, I follow to the extent possible the test methodology advocated by Coddington (1988). I map food-quality classes indicated by the analysis on the *Cydia* phylogeny of Danilevsky and Kuznetsov (1968), then check for congruence. Congruence implies inheritance; lack of congruence, independence.

Danilevsky and Kuznetsov recognize three *Cydia* subgenera: *Cydia, Kenneliola,* and *Endopisa.* Their phylogeny to subgenera has the first two as sister taxa, with *Endopisa* in an outgroup position. Within each subgenus, Danilevsky and Kuznetsov further define a number of sections or species-groups, each of which represents a likely monophyletic lineage. The phylogeny to species is not resolved, but in three sections, four pairs of sister species are evident among study taxa.

Assignments to subgenus are made for 66 species in the study, 50 by Danilevsky and Kuznetsov, 16 by me. Food-quality class of each of these mapped on the phylogeny to subgenera produces the distribution in Table 3. All food-quality classes and associated body sizes occur among all subgenera, although most *Endopisa* species (12/15 = 0.80) are in the high class, and most *Kenneliola* species (13/14 = 0.93) are not. *Cydia* outgroup genera such as *Grapholita* also contain species

TABLE 3. Distribution of 66 *Cydia* species by food-quality class and subgenus.

Subgenus	Food-quality class		
	Low	Medium	High
Cydia	7	13	17
Kenneliola	3	10	1
Endopisa	1	2	12

assignable to high, medium, and low food-quality classes (Danilevsky & Kuznetsov 1968). Therefore, within *Cydia* outgroups as well as subgenera there is evidence that food-quality classes and associated body sizes evolved independently of subgeneric lineage.

Within subgenera, at the section or species-group level, the positions of 50 study species are available, almost entirely assigned by Danilevsky and Kuznetsov (1968). Two or more food-quality classes and associated body sizes occur in 7 of 15 sections overall, and in all 5 sections containing three or more species (Table 4). The detailed distribution of food-quality classes among sections shows 9 within-section shifts in food-quality class and associated body size out of 18 possible ones (Table 4). Thus evolutionary shifts in body size are likely to have occurred within sections.

TABLE 4. Distribution of 50 *Cydia* species by food-quality class and section, and inferred numbers of evolutionary shifts in food-quality class within sections.

Section	No. species in class			Minimal no. shifts	
	High	Medium	Low	Possible	Evident
Subgenus *Cydia*					
pactolanae	2	6	1	2	2
strobilellae	2	0	0	1	0
pomonellae	2	0	0	1	0
illutanae	1	1	2	2	2
servillanae	0	1	1	2	1
duplicanae	0	2	1	2	1
cosmophoranae	0	3	1	2	1
Subgenus *Kenneliola*					
splendanae	0	7	3	1	1
maackianae	1	0	0	0	0
trasias	1	0	0	0	0
exquisitanae	0	2	0	1	0
Subgenus *Endopisa*					
suceedanae	3	0	0	2	0
nigricanae	4	1	0	2	1
adenocarpae	1	0	0	0	0
semicinctanae	0	1	0	0	0
			Total	18	9

TABLE 5. Food-quality classes and associated body sizes of four *Cydia* sister-species pairs. Data are from the Appendix. (Ditto is abbreviated do.)

Pair no.	*Cydia* species	Food-quality class		Forewing length (mm)
1	*indivisa*	Medium		6.5
	cosmophorana	Low		4.9
2	*rana*	High		6.2
	laricana	do.		7.1
3	*strobilella*	do.	(Eurasia)	5.7
	do.	do.	(Midland No. America)	4.0
	ethelinda	do.		7.6
4	*pomonella*	do.		8.0
	pyrivora	do.		8.9

The four pairs of sister species mentioned earlier represent two sections (*strobilellae* and *pomonellae*) each containing only two species, and one section (*cosmophoranae*) containing four species that can be resolved into one Palearctic sister pair and one Nearctic sister pair. The four pairs, their food-quality classes, and forewing lengths are shown in Table 5. The members of the first pair belong to different food-quality classes, and differ in size by 25% ([6.5 − 4.9]/6.5 = 0.25). The remaining pairs all belong to the high class, but members of the third differ in size similarly to or more than members of the first, as expected from their differing food-plant seed sizes ([7.6 − 5.7]/7.6 = 0.25; [7.6 − 4.0]/7.6 = 0.47). Members of the second and fourth pairs differ least, from 10 to 13%; inherited similarity in their body sizes cannot be ruled out.

In sum, independence and number of degrees of freedom are no doubt overestimated, but only mildly. *Cydia* body-size evolution seems sufficiently independent of subgeneric, section, and species phylogeny to uphold rather than refute results of the statistical analysis.

DISCUSSION

Even though I consider only one independent variable, it relates well to body size (Table 1, Fig. 1). The correlation of body size and food-plant seed size among seed predators of all food-quality classes ultimately results from finite size and finite numbers of seeds. Seeds occur within seed-bearing parts of lesser food quality (Mattson 1980, Skerman 1977). The smaller the seed, the more feeding disruptions larvae experience as they finish one seed and seek another or eat seed-bearing tissue or both; the more feeding disruptions, the smaller the body size.

Potential number of seeds per fruit is reduced by frequent failure of some seeds to develop (Stephenson 1981, Tripp & Hedlin 1956) and by other seed predators. Intraspecific predation occurs in the high class (Bovey 1966, Coyne 1968, Hedlin 1967, Tripp & Hedlin 1956, Kraft 1968, Putman 1963) as well as in the medium and low classes (Bovey 1966). Intraspecific predation promotes net survival when the seed supply in one fruit or the nourishment in one large seed is not sufficient for all inhabitants.

I assume that food-plant seed size precedes *Cydia* body size, not the reverse. Evidence for this assumption is scant, except that many factors besides seed predation determine seed size (Harper et al. 1970).

In the medium and low food-quality classes, larvae probably eat more grams of food to support a given body size than in the high class. Smaller body size may lessen food needs of a larva. At least two members of the medium class, *C. zebeana* and *C. milleniana,* have evolved lengthened life cycles enabling their larvae to feed a second season (Kuznetsov 1987, Postner 1978). Forewing lengths of these species (7.0–7.3 mm) are greater than the class mean (6.4 mm) (Appendix, Table 1).

Among seed predators in the medium and low classes, food-plant seeds are mostly large and borne singly. Correlation between food-plant seed size and forewing length in seed predators of these classes (Fig. 2: line B) may exist because most such larvae use but one seed (Bovey 1966) through a range of seed sizes.

In conclusion, I interpret the correlation between *Cydia* body size and diet quality to reflect mechanisms whereby (a) larvae evolve body sizes for which they are able to obtain sufficient nourishment, and (b) body-size diversity arises as lineages colonize new larval food plants and plant parts of differing diet quality.

ACKNOWLEDGMENTS

I thank D. Prokrym, G. Terlemezian, D. A. Andow, M. Elling, and S. Lazzari for translating help, and D. L. Wagner, D. G. McCullough, W. J. Mattson, V. I. Kuznetsov, and two anonymous referees for reviewing the manuscript. Discussions I had with D. L. Wagner and A. H. Porter greatly aided the study.

Appendix. Enumeration of *Cydia* study taxa and populations. Asterisks denote food plants to which seed weights refer; brackets ([ ]), probable food plants; braces ({ }), seed weights estimated from relatives of similar seed dimensions; dashes, no data. Danilevsky and Kuznetsov (1968) is abbreviated D & K (1968); ditto, do.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
		High food-quality class (diet ca. 25% crude protein)			
adenocarpi (Ragonot) *Endopisa* *adenocarpi*	S Europe	*Adenocarpus* spp., *Cytisus scoparius* (L.)*	Seed (D & K 1968)	0.00789 (Gill & Pogge 1974)	6.1 (D & K 1968)
anaranjada (Miller) *Cydia* —	SE North America	*Pinus elliottii* Engelm.*	do. (Hedlin et al. 1981)	0.0314 (Krugman & Jenkinson 1974)	7.1 (Miller 1959)
blackmoreana (Walsingham) *Endopisa* *nigricanae*	N Africa	*Retama monosperma* (L.)	do. (D & K 1968)	—	6.9 (D & K 1968)
bracteatana (Fernald) *Cydia* —	W North America	*Abies bracteata* D. Don, *A. concolor* (Gord. & Gland.),* *A. magnifica* A. Murr.*	do. (Hedlin et al. 1981)	0.0518 (Franklin 1974)	5.3 (Heinrich 1926)
colorana (Kearfott) — —	SW North America	*Pinus edulis* Engelm.*	do. (do.)	0.239 (Krugman & Jenkinson 1974)	10.5 (do.)
conicolana (Heylaerts) *Cydia* *illutanae*	Britain	*P. sylvestris* L.,* *P. nigra* Arn.*	do. (Bradley et al. 1979)	0.00898 (do.)	5.0 (Bradley et al. 1979)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
dandana (Kearfott) (*nigricana* ssp.) *Endopisa* *nigricanae*	North America	*Lathyrus japonicus* Willd., *L. palustris* L., *Vicia angustifolia* L.*	Seed (Bovey 1966)	0.0135 (Barclay & Earle 1974, Hughes et al. 1962, Jones & Earle 1966)	6.0 (Heinrich 1926)
ethelinda (Meyrick) *Cydia* *strobilellae*	India	*Picea smithiana* (Wallich),* *Pinus wallichiana* A. B. Jacks*	do. (Cheema & Syed 1973)	0.0210 (Krugman & Jenkinson 1974, Safford 1974)	7.6 (Clarke 1958)
gilviciliana (Staudinger) *Endopisa* *nigricanae*	S Europe	*Pisum s. sativum* L.,* *P. s. elatius* (Bieb.)*	do. (Bovey 1966)	0.145 (Hughes et al. 1962, Makasheva 1973, Purseglove 1968, Wheeler & Hill 1957)	6.4 (Bovey 1966)
ingens (Heinrich) *Cydia* —	SE North America	*Pinus palustris* Mill.*	do. (Coyne 1968)	0.0926 (Krugman & Jenkinson 1974)	8.5 (Heinrich 1926)
injectiva (Heinrich) *Cydia* *pactolanae*	W North America	*P. jeffreyi* Grev. & Balf.*	do. (Hedlin et al. 1981)	0.123 (do.)	8.2 (do.)
latefemoris (Walsingham) *Endopisa* —	Hawaii	*Sophora chrysophylla* (Salisb.)	do. (Zimmerman 1978)	{0.0259} (Little & Skolmen 1989)	6.5 (Zimmerman 1978)
latisigna Miller *Cydia* —	Mexico	*Pinus engelmannii* Carr.,* *P. michoacana cornuta* Martinez*	do. (Cibrián-Tovar et al. 1986)	0.0305 (Patiño Valera & Villagómez Aguilar 1976)	7.8 (Miller 1986)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
maackiana (Danilevsky) *Kenneliola* *maackianae*	E Asia	*Maackia amurensis* (Rupr. & Maxim.)	Seed (D & K 1968)	{0.0204} (Zaborovsky 1962)	6.9 (D & K 1986)
malesana (Meyrick) *Endopisa* —	India	*Cassia auriculata* L., *C. corymbosa* Lam.*	do. (Beeson 1941)	0.0253 (Jones & Earle 1966, Sen Gupta 1936)	7.3 (Clarke 1958)
medicaginis (Kuznetsov) *Endopisa* *succedanae*	Eurasia	*Medicago sativa caerulea* (Less.),* *M.* spp.	do. (Bovey 1966)	{0.00200} (Lesins & Gillies 1972)	4.6 (Bovey 1966)
membrosa (Heinrich) — —	SW North America	*Prosopis juliflora velutina* (Woot.), *P. glandulosa* (Torr.)*	do. (Heinrich 1926)	0.0406 (Earle & Jones 1962, Harden & Zolfaghari 1988, Walton 1923)	6.4 (Heinrich 1926)
microgrammana (Guenée) *Endopisa* *microgrammanae*	SE Europe	*Ononis spinosa* L.	do. (D & K 1968)	{0.00247} (Brouwer & Stählin 1975)	5.0 (D & K 1968)
miscitata (Heinrich) *Cydia* —	SW North America	*Pinus ponderosa* Doug.*	do. (Hedlin et al. 1981)	0.0378 (Krugman & Jenkinson 1974)	6.5 (Heinrich 1926)
montezuma Miller *Cydia* —	Mexico	*P. montezumae* Lamb.,* *P. rudis* Endl.*	do. (Cibrián-Tovar et al. 1986)	0.0198 (Patiño Valera & Villagómez Aguilar 1976, Rafn ca. 1912)	8.8 (Miller 1986)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
nigra (Miller) *Cydia* —	Mexico	*P. ayacahuite veitchii* Shaw*	Seed (Cibrián-Tovar et al. 1986)	0.250 (Patiño Valera & Villagómez Aguilar 1976)	8.0 (Miller 1966)
n. nigricana (Fabr.) *Endopisa* *nigricanae*	Europe	*Lathyrus pratensis* L., *L. odoratus* L.,* *Vicia cracca* L.,* *V. sativa* L.*	do. (Bovey 1966)	0.0481 (Earle & Jones 1962, Hughes et al. 1962, Jones & Earle 1966, Stefferud 1961)	6.4 (Bovey 1966)
oxytropidis (Martini) *Endopisa* *nigricanae*	S Europe	*Oxytropis pilosa* (L.)	do. (D & K 1968)	—	6.5 (D & K 1968)
phyllisae Miller *Cydia* —	Mexico	*Picea chihuahuana* Martinez	do. (Cibrián-Tovar et al. 1986)	{0.00428} (Martinez 1963)	5.5 (Miller 1986)
piperana (Kearfott) *Cydia* —	SW North America	*Pinus ponderosa,* *P. jeffreyi**	do. (Koerber 1967)	0.0589 (Krugman & Jenkinson 1974)	8.2 (Heinrich 1926)
platydryas (Meyrick) *Endopisa* —	Africa	"*Acacia*"	do. (Clarke 1958)	—	6.6 (Clarke 1958, Diakonoff 1969)
pomonella (L.) *Cydia* *pomonellae*	E North America	*Malus sylvestris* (L.), *M. pumila* Mill.*	do. (Chapman & Lienk 1971)	0.0227 (Crossley 1974)	8.0 (Chapman & Lienk 1971)
pyrivora (Danilevsky) *Cydia* *pomonellae*	S Europe	*Pyrus communis* L.*	do. (Bovey 1966)	0.0315 (Gill & Pogge 1974)	8.9 (D & K 1968)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
strobilella (L.) *Cydia* *strobilellae*	Eurasia	*Picea abies* (L.),* *P. jezoensis* (S. & C.),* *P. koyamai* Shir.,* *P.* spp.	Seed (Postner 1978)	0.00466 (Safford 1974)	5.7 (D & K 1968)
do.	Midland North America	*P. glauca* (Moench)*	do. (Tripp 1954)	0.00201 (do.)	4.0 (Miller 1987)
succedana (D. & S.) *Endopisa* *succedanae*	Britain	*Ulex europaeus* L.,* "*Genista*", "*Lotus*", *Cytisus scoparius* (L.)*	do. (Bradley et al. 1979)	0.00728 (Gill & Pogge 1974, Rudolf 1974)	6.4 (Bradley et al. 1979)
tonosticha (Meyrick) — —	South America	*Cassia fistula* L.*	do. (Becker 1971)	0.169 (Barclay & Earle 1974, Guppy 1912, Sen Gupta 1936, Swingle 1939)	6.5 (Becker 1971, Costa Lima 1952)
toreuta (Grote) *Cydia* —	Midland North America	*Pinus resinosa* Ait.,* *P. banksiana* Lamb.	do. (Miller 1987)	0.00609 (Krugman & Jenkinson 1974)	6.0 (Miller 1987)
vallesiaca (Sauter) *Endopisa* *succedanae*	S Europe	*Ononis natrix* L.	do. (Kuznetsov 1987)	{0.00247} (Heywood & Ball 1968)	5.7 (Kuznetsov 1987)
		Medium food-quality class (diet ca. 12% crude protein)			
acerivora (Danilevsky) *Endopisa* *semicinctanae*	Asia	*Acer ginnala* Maxim.,* *A.* spp.	Seed (D & K 1968)	0.0267 (Olson & Gabriel 1974)	5.3 (D & K 1968)
amplana (Hübner) *Kenneliola* *splendanae*	Europe	*Corylus avellana* L.,* *C.* spp.	do. (Postner 1978)	0.848 (Brinkman 1974a)	8.2 (do.)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
amurensis (Danilevsky) *Kenneliola* *splendanae*	Japan	*Quercus mongolica* Fisch. ex Turcz.*	Seed (D & K 1968)	3.16 (Swingle 1939, Zaborovsky 1962)	6.6 (D & K 1968)
candana (Forbes) — —	E North America	"*Acer*"	do. (MacKay 1959)	—	6.4 (Heinrich 1926)
cognatana (Barret) *Cydia* *duplicanae*	Britain	*Pinus sylvestris**	Cortex (Bradley et al. 1979)	0.00650 (Krugman & Jenkinson 1974)	6.2 (Bradley et al. 1979)
coniferana (Saxesen) *Cydia* *illutanae*	Eurasia	*P.* spp. [*sylvestris,* nigra**], *Abies alba* Mill.,* *Picea abies**	do. (Postner 1978)	0.00859 (Franklin 1974, Krugman & Jenkinson 1974, Safford 1974)	5.7 (D & K 1968)
cornucopiae (Tengström) *Kenneliola* *splendanae*	S Asia	*Populus tremula* L.,* *Betula* spp.	do. (Kuznetsov 1986)	0.000124 (Schreiner 1974)	7.7 (D & K 1968)
cryptomeriae (Issiki) — —	Japan	*Cryptomeria japonica* (L. F.)*	Seed (Kawabe 1982)	0.00183 (Walters 1974)	6.0 (Kawabe 1982)
cupressana (Kearfott) *Cydia* *illutanae*	W North America	*Cupressus macrocarpa* Hartw.*	Cortex (Frankie & Koehler 1971)	0.00596 (Johnson 1974)	6.2 (Heinrich 1926)
danilevskii (Kuznetsov) *Kenneliola* *splendanae*	Japan	*Quercus mongolica**	Seed (Kuznetsov 1986)	3.16 (Swingle 1939, Zaborovsky 1962)	7.0 (D & K 1968)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
duplicana (Zetterstedt) *Cydia* *duplicanae*	Europe	*Abies alba*,* *Picea abies**	Cortex (Postner 1978)	0.0122 (Franklin 1974, Safford 1974)	7.3 (D & K 1968)
glandicolana (Danilevsky) *Kenneliola* *splendanae*	Japan	*Quercus mongolica**	Seed (D & K 1968)	3.16 (Swingle 1939, Zaborovsky 1962)	8.0 (do.)
indivisa (Danilevsky) *Cydia* *cosmophoranae*	Eurasia	*Picea* spp. [*abies*,* *asperata* Masters,* *jezoensis**]	Cortex (D & K 1968)	0.00527 (Safford 1974)	6.5 (do.)
inquinitana (Hübner) *Kenneliola* *splendanae*	Europe	*Acer* spp. [*campestre* L.,* *pseudoplatanus* L.*]	do. (Postner 1978)	0.0987 (Olson & Gabriel 1974)	6.5 (Hannemann 1961)
laricana (Busck) *Cydia* *cosmophoranae*	W North America	*Larix occidentalis* Nutt.,* *Pseudotsuga menziesii* (Mirb.)*	do. (Furniss & Carolin 1977)	0.00821 (Owston & Stein 1974, Rudolf 1974)	7.1 (Heinrich 1926)
laricicolana (Kuznetsov) *Cydia* *pactolanae*	Central Asia	*Larix gmelini* (Rupr.)*	do. (D & K 1968)	0.00378 (Rudolf 1974)	4.8 (D & K 1968)
latiferreana (Walsingham) — —	Midland North America	*Quercus alba* L.,* *Q. macrocarpa* Michx.,* *Q. rubra* L.,* *Q. velutina* Lam.*	Seed (Peacock et al. 1988)	4.45 (Olson 1974)	7.8 (Miller 1987)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
leguminana (Zeller) *Kenneliola* *exquisitanae*	Britain	"*Ulmus*" [*glabra* Huds.*]	Cortex (Bradley et al. 1979)	0.0113 (Brinkman 1974b)	6.2 (Bradley et al. 1979)
do.	Central Europe	*Acer*, *Fagus* spp. [*A. campestre*,* *A. platanoides* L.,* *A. pseudoplatanus*,* *F. sylvatica* L.*]	do. (D & K 1968)	0.131 (Olson & Gabriel 1974, Rudolf & Leak 1974)	6.0 (D & K 1968)
leucobasis (Busck) *Cydia* *pactolanae*	W North America	*Larix occidentalis*,* *Picea engelmannii* Parry*	do. (Furniss & Carolin 1977)	0.00333 (Rudolf 1974, Safford 1974)	6.0 (Heinrich 1926)
leucogrammana (Hofmann) *Endopisa* *nigricanae*	E Asia	*Peganum harmala* L.*	Flowers (D & K 1968)	0.00282 (Barclay & Earle 1974)	5.4 (D & K 1968)
leucostoma (Meyrick) — —	India	*Camellia sinensis* (L.)*	Foliage (Wyniger 1962)	1.97 (Purseglove 1968)	6.0 (Clarke 1958)
milleniana (Adamzewski) *Cydia* *pactolanae*	Eurasia	*Larix decidua* Mill.,* *L. gmelini*,* L. *siberica* Ledeb.*	Cortex (Kuznetsov 1987)	0.00519 (Rudolf 1974)	7.3 (Kuznetsov 1987)
p. pactolana (Zeller) *Cydia* *pactolanae*	Europe	*Picea abies**	do. (Postner 1978)	0.00594 (Safford 1974)	6.0 (D & K 1968)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
populana (Busck) *Kenneliola* *exquisitanae*	Midland North America	*Populus tremuloides* Michx.,* *P. trichocarpa* Torr. & Gray*	Cortex (Furniss & Carolin 1977)	0.000165 (Schreiner 1974)	6.2 (Miller 1987)
pseudotsugae (Evans) *Cydia* *pactolanae*	W North America	*Pseudotsuga menziesii**	do. (Evans 1969)	0.0110 (Owston & Stein 1974)	6.0 (Evans 1969)
rana (Forbes) *Cydia* *cosmophoranae*	E North America	*Picea engelmannii,** *P. glauca**	do. (Heinrich 1926, W. E. Miller unpubl.)	0.00251 (Safford 1974)	6.2 (Heinrich 1926)
servillana (Duponchel) *Cydia* *servillanae*	Britain	*Salix caprea* L., *S. cinerea* L.	do. (Bradley et al. 1979)	—	6.0 (Bradley et al. 1979)
splendana (Hübner) *Kenneliola* *splendanae*	do.	*Quercus* spp. [*petrea* (Mattushka),* *robur* L.*]	Seed (do.)	3.02 (Olson 1974)	8.2 (do.)
staphiditis (Meyrick) — —	India	*Bauhinia purpurea* L.*	Cortex (Beeson 1941)	0.239 (Earle & Jones 1962, Sen Gupta 1936, Swingle 1939)	5.3 (Clarke 1958)
stirpicola (Meyrick) — —	do.	*Butea frondosa* Koenig*	Multiple (do.)	0.987 (Swingle 1939)	6.2 (do.)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
trasias (Meyrick) *Kenneliola* *trasias*	E Asia	*Maackia amurensis* Rupr. & Maxim.,* *Sophora japonica* L.*	Multiple (Komai & Lantoh 1984)	0.0679 (Barclay & Earle 1974, Earle & Jones 1962, Rafn ca. 1912, Swingle 1939, Zaborovsky 1962)	5.7 (Komai & Lantoh 1984)
yasudai (Oku) (*pactolana* ssp.) *Cydia* *pactolanae*	Japan	*Abies sachalinensis* Fr. Schm.*	Cortex (Kawabe 1982, Oku 1968)	0.0103 (Franklin 1974)	5.7 (Oku 1968)
zebeana (Saxesen) *Cydia* *pactolanae*	Europe	*Larix decidua*,* *L. siberica**	do. (Postner 1978)	0.00581 (Rudolf 1974)	7.0 (Hannemann 1961)
Low food-quality class (diet ca. 6% crude protein)					
araucariae (Pastrana) — —	South America	*Araucaria angustifolia* (Bert.)*	do. (Schönherr 1987)	9.07 (Walters 1974)	8.5 (Schönherr 1987)
caryana (Fitch) — —	Midland North America	*Carya ovata* (Mill.),* *C. illinoensis* (Wangenh.),* *Juglans nigra* L.*	Seed husk (Moznette et al. 1940)	3.85 (Bonner & Maisenhelder 1974, Brinkman 1974c)	5.8 (Miller 1987)
commensalana (Danilevsky) *Kenneliola* *splendanae*	Asia	*Rosa* spp.	*Diplolepis* galls (D & K 1968)	—	6.0 (D & K 1968)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
corollana (Hübner) *Cydia* *illutanae*	Europe	*Populus tremula**	*Saperda* galls (Hannemann 1961)	0.000124 (Schreiner 1974)	5.5 (D & K 1968)
cosmophorana (Treitschke) *Cydia* *cosmophoranae*	W Europe	*Pinus sylvestris**	*Retinia* tunnels (Postner 1978)	0.00605 (Krugman & Jenkinson 1974)	4.9 (do.)
erotella (Heinrich) *Cydia* —	E North America	*P. taeda* L.*	do. (Heinrich 1926, W. E. Miller unpubl.)	0.0249 (do.)	4.4 (Heinrich 1926)
fagiglandana (Zeller) *Kenneliola* *splendanae*	Britain	*Fagus sylvatica**	Seed (Bradley et al. 1979)	0.216 (Rudolf & Leak 1974)	7.3 (Bradley et al. 1979)
gallaesaliciana (Riley) *Cydia* *servillanae*	E North America	"*Salix*"	Dipterous galls (Heinrich 1926)	—	5.5 (Heinrich 1926)
illutana (Herrich-Schäffer) *Cydia* *illutanae*	Eurasia	*Larix gmelini,* Picea abies,* Abies alba**	Cone scales (Postner 1978)	0.018 (Rudolf 1974)	5.7 (D & K 1968)
inopiosa (Heinrich) *Cydia* *pactolanae*	North America	*Pinus contorta* Doug.,* *P. resinosa**	Bark (Brown & Miller 1983, R. G. Dearborn pers. comm.)	0.00621 (Krugman & Jenkinson 1974)	4.5 (Miller 1987)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
interscindana (Möschler) *Cydia* *duplicanae*	S Europe	*Juniperus oxycedrus* L.	Sapwood (D & K 1968)	{0.0124} (Debazac 1964)	5.2 (D & K 1968)
kurokoi (Amsel) *Kenneliola* *splendanae*	E Asia	*Castanea mollissima* Blume,* *C. sequinii* Dode,* *C. crenata* Sieb. & Zucc.*	Seed (Komai & Ishikawa 1987)	13.1 (Olson 1974, Sander 1974)	8.0 (Komai & Ishikawa 1987)
palmetum (Heinrich) — —	SE North America	*Coccothrinax argentata* Jacq.	do. (Heinrich 1929)	{0.307} (Long & Lakela 1971)	6.0 (Heinrich 1928)
rufipennis (Butler) *Endopisa* —	Hawaii	*Acacia koa* Gray*	Multiple (Stein 1983)	0.0926 (Whitesell 1974)	4.4 (Zimmerman 1978)

LITERATURE CITED

ANDERSON, R. J. & W. L. KULP. 1921. An investigation of the seed of the silver maple (*Acer saccharinum*). New York Agric. Exper. Sta. Geneva Tech. Bull. 81, 20 pp.

ANDERSSON, E. 1965. Cone and seed studies in Norway spruce (*Picea abies* [L.] Karst.). Stud. Forest. Suecica 23, 214 pp.

BARCLAY, A. S. & F. R. EARLE. 1974. Chemical analysis of seeds III. Oil and protein content of 1253 species. Econ. Bot. 28:178–236.

BECKER, V. O. 1971. Microlepidópteros que vivem nas plantas cultivadas no Brasil. II. O nome correto da lagarta das favas da *Cassia fistula* L. (Lepidoptera, Tortricidae). Bol. Univ. Fed. Paraná (Zool.) 4(9):45–56.

BEESON, C. F. C. 1941. The ecology and control of the forest insects of India and the neighboring countries. Dehra Dun, India. 1007 pp.

BETTS, M. M. 1958. Notes on the life-history of *Enarmonia conicolana* (Heyl.) (Lep., Eucosmidae). Entomol. Monthl. Mag. 94:134–137.

BONNER, F. T. & L.C. MAISENHELDER. 1974. *Carya* Nutt. Hickory, pp. 269–272. *In* Schopmeyer (1974).

BONNER, J. T. 1965. Size and cycle: An essay on the structure of biology. Princeton Univ. Press, Princeton, New Jersey. 219 pp.

BOVEY, P. 1966. Super-famille des Tortricoidea, pp. 456–893. *In* Balachowsky, A. S. (ed.), Entomologie appliquée a l'agriculture. Vol. 2(1), Lepidoptères. Masson & Cie, Paris. 1057 pp.

BRADLEY, J. D., W. G. TREMEWAN & A. SMITH. 1979. British tortricoid moths. Tortricidae: Olethreutinae. Ray Society, London. 336 pp.

BRINKMAN, K. A. 1974a. *Corylus* L. Hazel, filbert, pp. 343–345. *In* Schopmeyer (1974).

——— 1974b. *Ulmus* L. Elm, pp. 829–834. *In* Schopmeyer (1974).

——— 1974c. *Juglans* L. Walnut, pp. 454–459. *In* Schopmeyer (1974).

BROUWER, W. & A. STÄHLIN. 1975. Handbuch der Samenkunde. ed. 2. DLG Verlag, Frankfurt (Main). 655 pp.

BROWN, R. L. 1979. The valid generic and tribal names for the codling moth, *Cydia pomonella* (Olethreutinae: Tortricidae). Ann. Entomol. Soc. Amer. 72:565–567.

BROWN, R. L. & W. E. MILLER. 1983. Valid names of the spruce seed moth and a related *Cydia* species (Lepidoptera: Tortricidae). Ann. Entomol. Soc. Amer. 76:110–111.

CALDER, W. A. 1984. Size, function, and life history. Harvard Univ. Press, Cambridge, Massachusetts. 431 pp.

CARDEMIL, L. & A. REINERO. 1982. Changes of *Araucaria araucana* seed reserves during germination and early seedling growth. Can. J. Bot. 60:1629–1638.

CHAPMAN, P. J. & S. E. LIENK. 1971. Tortricid fauna of apple in New York (Lepidoptera: Tortricidae). New York Agric. Exper. Sta. Spec. Publ. 122 pp.

CHEEMA, M. A. & R. A. SYED. 1973. Seed- and cone-insects, pp. 50–60. *In* Ghani, M. A. & M. A. Cheema (eds.), Biology, ecology and behaviour of principal natural enemies of major insect pests of forest trees in Pakistan. Commonwealth Inst. of Biol. Control Misc. Publ. 4, 100 pp.

CIBRIÁN-TOVAR, D., B. H. EBEL, H. O. YATES & J. T. MENDEZ-MONTIEL. 1986. Insectos de conos y semillas de las coniferas de Mexico. U.S. Dept. Agr. Forest Service Gen. Tech. Rept. SE-40, 110 pp. (Spanish and English).

CLARKE, J. F. G. 1958. Catalogue of the type specimens of Microlepidoptera in the British Museum (Natural History) described by Edward Meyrick. Vol. III. Tortricidae, Olethreutidae, Noctuidae. British Museum, London. 600 pp.

CODDINGTON, J. A. 1988. Cladistic tests of adaptational hypotheses. Cladistics 4:3–22.

COSTA LIMA, A. DA. 1952. Sôbre dois microlepidopteros (Tortricoidea, Grapholitidae). Mem. Inst. Oswaldo Cruz 50:249–257.

COYNE, J. F. 1968. *Laspeyresia ingens*, a seedworm infesting cones of longleaf pine. Ann. Entomol. Soc. Amer. 61:1116–1122.

CRANDALL, C. S. 1917. Seed production in apples. Ill. Agric. Exp. Sta. Bull. 203, [183]–213 pp.

CRISAN, E. V. & A. SANDS. 1978. Nutritional value, pp. 137–168. *In* Chang, S. T. & W. A. Hayes (eds.), The biology and cultivation of edible mushrooms. Academic Press, New York. 819 pp.

CROSSLEY, J. A. 1974. *Malus* Mill. Apple, pp. 531–534. *In* Schopmeyer (1974).

DANILEVSKY, A. C. & V. I. KUZNETSOV. 1968. [Leafroller family Tortricidae, fruit-moth tribe Laspeyresiini.] Fauna USSR. Lepidopterous insects. Vol. 5, pt. 1. Leningrad. 635 pp. (Russian).

DEBAZAC, E. F. 1964. Manuel des conifères. Nancy, France. 172 pp.

DENNO, D. N. & R. F. HARWOOD. 1973. Intraspecific larval competition by the codling moth, *Laspeyresia pomonella*. Environ. Entomol. 2:783–789.

DIAKONOFF, A. 1969. Tortricidae from the Seychelles and Aldabra (Lepidoptera). Tijd. Entomol. 112:81–100.

DICKMANN, D. I. & T. T. KOZLOWSKI. 1969. Seasonal changes in the macro- and micronutrient composition of ovulate strobili and seeds of *Pinus resinosa*. Can. J. Bot. 47:1547–1554.

EARLE, F. R. & Q. JONES. 1962. Analyses of seed samples from 113 plant families. Econ. Bot. 16:221–250.

EVANS, D. 1969. *Laspeyresia pseudotsugae* n. sp. (Lepidoptera: Olethreutidae), a bark miner in Douglas-fir. Can. Entomol. 101:955–963.

FELSENSTEIN, J. 1985. Phylogenies and the comparative method. Amer. Nat. 125:1–15.

FISHER, R. A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford. 272 pp.

FRANKIE, G. W. & C. S. KOEHLER. 1971. Studies on the biology and seasonal history of the cypress bark moth, *Laspeyresia cupressana* (Lepidoptera: Olethreutidae). Can. Entomol. 103:947–961.

FRANKLIN, J. F. 1974. *Abies* Mill. Fir, pp. 168–183. *In* Schopmeyer (1974).

FURNISS, R. L. & V. M. CAROLIN. 1977. Western forest insects. U.S. Dept. Agric. Misc. Publ. 1339, 654 pp.

GILL, J. D. & F. L. POGGE. 1974. *Pyrus* L. Pear, pp. 689–691. *In* Schopmeyer (1974).

GUPPY, H. B. 1912. Studies in seeds and fruits. Williams & Norgate, London. 528 pp.

GYÖRFI, J. 1956. Nadelholzzapfen- und Nadelholzsamenschädlinge und ihre Parasiten. Acta Agron. Acad. Sci. Hung. 6:321–373.

HANNEMANN, H. J. 1961. Kleinschmetterlinge oder Microlepidoptera I. Die Wickler (s. str.) (Tortricidae). 236 pp. Pt. 48, Die Tierwelt Deutschlands und der angrenzenden Meeresteile. Fischer, Jena.

HARDEN, M. L. & R. ZOLFAGHARI. 1988. Nutritive composition of green and ripe pods of honey mesquite (*Prosopis glandulosa*, Fabaceae). Econ. Bot. 42:522–532.

HARPER, J. L., R. H. LOVELL & K. G. MOORE. 1970. The shapes and sizes of seeds. Ann. Rev. Ecol. Syst. 1:327–356.

HAUT, I. C. 1938. Physiological studies on after-ripening and germination of fruit-tree seeds. Md. Agric. Expt. Sta. Bull. 420, 54 pp.

HEDLIN, A. F. 1967. The pine seedworm, *Laspeyresia piperana* (Lepidoptera: Olethreutidae), in cones of ponderosa pine. Can. Entomol. 105:113–122.

HEDLIN, A. F., H. O. YATES, D. CIBRIÁN TOVAR, B. H. EBEL, T. W. KOERBER & E. P. MERKEL. 1981. Cone and seed insects of North American conifers. Canadian Forestry Service, U.S. Forest Service, Secretaría de Agric. & Recursos Hidrául. Mexico. 122 pp.

HEINRICH, C. 1926. Revision of the North American moths of the subfamilies Laspeyresiinae and Olethreutinae. U.S. Natl. Mus. Bull. 132, 216 pp.

——— 1928. A new *Laspeyresia* from Florida (Lepidoptera: Olethreutidae). Proc. Entomol. Soc. Wash. 30:109.

——— 1929. A correction. Proc. Entomol. Soc. Wash. 31:19.

HERIOT, A. D. & D. B. WADDEL. 1942. Some effects of nutrition on the development of the codling moth. Sci. Agric. 23:172–175.

HEYWOOD, V. H. & P. W. BALL (Eds.). 1968. Leguminosae, pp. 80–191. *In* Tutin, T. G., V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters & D. A. Webb (eds.), Flora europaea. Vol. 2. Rosaceae to Umbelliferae. Cambridge Univ. Press, Cambridge, England. 455 pp.

HUGHES, H. D., M. E. HEATH & D. S. METCALFE. 1962. Forages: The science of grassland agriculture. Iowa State Univ. Press, Ames, Iowa. 707 pp.

JOHNSON, L. C. 1974. *Cupressus* L. Cypress, pp. 363–369. *In* Schopmeyer (1974).

JONES, Q. & F. R. EARLE. 1966. Chemical analyses of seeds II: Oil and protein content of 759 species. Econ. Bot. 20:127–155.

KATSUTA, M. & T. SATOO. 1964. Cone development in *Pinus thunbergii*. Nihon Ringakkai Shi (J. Jap. Forest. Soc.) 46:166–170.

KAWABE, A. 1982. Tortricidae, pp. 62–151. *In* Inoue, H., S. Sugi, H. Kuroko, S. Moriuti & A. Kawabe (eds.), Moths of Japan. Vol. 1. Kodansha, Tokyo. 966 pp. (Japanese).

KINZER, H. G., B. J. RIDGILL & J. G. WATTS. 1972. Seed and cone insects of ponderosa pine. New Mexico Agric. Expt. Sta. Bull. 594, 36 pp.

KOERBER, T. W. 1967. Studies of the insect complex affecting seed production of ponderosa pine in California. Ph.D. Dissertation, Univ. of California, Berkeley. 86 pp. (Diss. Abs. B 29:229 [1968]).

KOMAI, F. & K. ISHIKAWA. 1987. Infestation of chestnut fruits in China with two species of the genus *Cydia* (Lepidoptera: Tortricidae). Jap. J. Appl. Entomol. Zool. 31:55–62. (Japanese and English).

KOMAI, F. & S. LANTOH. 1984. *Cydia trasias* (Meyrick) (Lepidoptera, Tortricidae) attacking *Sophora* and *Maackia* in Japan. Tyô to Ga 35:145–151. (Japanese and English).

KRAFT, K. J. 1968. Ecology of the cone moth *Laspeyresia toreuta* in *Pinus banksiana* stands. Ann. Entomol. Soc. Amer. 61:1462–1465.

KRUGMAN, S. L. & J. L. JENKINSON. 1974. *Pinus* L. Pine, pp. 598–638. *In* Schopmeyer (1974).

KRÜSSMANN, G. 1978. Handbuch der Laubgehölze. Vol. 3. Parey, Berlin. 496 pp.

KUZNETSOV, V. I. 1986. [Review of tortricids of the subtribe Laspeyresiina (Lepidoptera, Tortricidae) from the south of the Far East], pp. 9–25. *In* Ler, P. A. (ed.), [Systematics and ecology of Lepidoptera from the Far East of the USSR.] Akad. Nauk USSR. 131 pp. (Russian).

——— 1987. Family Tortricidae (Olethreutidae, Cochylidae)—Tortricid moths, pp. 279–956. *In* Medvedev, G. S. (ed.), Keys to the insects of the European part of the USSR. U.S. Dept. Agric. & Natl. Sci. Foundation, Washington, D.C. 991 pp. (Translation).

KUZNETSOV, V. I. & I. M. KERZHNER. 1984. *Laspeyresia* Hübner, [1825], proposed conservation by the suppression of *Cydia* Hübner, [1825]. Bull. Zool. Nom. 41:110–113.

LESINS, K. & C. B. GILLIES. 1972. Taxonomy and cytogenetics of *Medicago*, pp. 53–86. *In* Hanson, C. H. (ed.), Alfalfa science and technology. Agronomy 15, 812 pp.

LITTLE, E. L. & R. G. SKOLMEN. 1989. Common forest trees of Hawaii (native and introduced). U.S. Dept. Agric. Agric. Handb. 679, 321 pp.

LONG, R. W. & O. LAKELA. 1971. A flora of tropical Florida. Univ. of Miami Press, Coral Gables, Florida. 962 pp.

LYONS, L. A. 1957. Insects affecting seed production in red pine III. *Eucosma monitorana* Heinrich, *Laspeyresia toreuta* Grote (Lepidoptera: Olethreutidae), *Rubsaamenia* sp. (Diptera: Cecidomyiidae), and other insects. Can. Entomol. 89:150–164.

MACKAY, M. R. 1959. Larvae of the North American Olethreutidae (Lepidoptera). Can. Entomol. 91, Suppl. 10, 338 pp.

MCCARTHY, M. A. & R. A. MATTHEWS (eds.). 1984. Composition of foods: Nut and seed products. U.S. Dept. Agric. Agric. Handb. 8–12, 137 pp.

MCCARTHY, M. A. & F. I. MEREDITH. 1988. Nutrient data on chestnuts consumed in the United States. Econ. Bot. 42:29–36.

MARTINEZ, M. 1963. Las Pináceas Mexicanas. ed. 3. Universidad nacional autónoma de México, México. 400 pp.

MAKASHEVA, R. K. 1973. The pea. U.S. Dept. Agric. & Natl. Sci. Foundation, Washington, D.C. 267 pp. (Translation).

MATTSON, W. J. 1977. Size and abundance of forest Lepidoptera in relation to host plant resources, pp. 429–441. *In* Labeyrie, V. (ed.), Comportement des insectes et milieu trophique. Colloq. Intern. Centre Nat. Recher. Sci. 265, 493 pp. Paris.

——— 1980. Herbivory in relation to plant nitrogen content. Ann. Rev. Ecol. Syst. 11: 119–161.

MATTSON, W. J. & J. M. SCRIBER. 1987. Nutritional ecology of insect folivores of woody plants: Nitrogen, water, fiber, and mineral considerations, pp. 105–146. *In* Slansky, F. & J. G. Rodriquez (eds.), Nutritional ecology of insects, mites, and spiders. Wiley, New York. 1016 pp.

MERKEL, E. P. 1967. Life history of the slash pine seedworm, *Laspeyresia anaranjada* Miller (Lepidoptera: Olethreutidae). Fla. Entomol. 50:141–149.

MILLER, W. E. 1959. A unique new North American species of pine-cone-feeding *Laspeyresia* related to *L. ingens* Heinrich (Lepidoptera: Olethreutidae). Fla. Entomol. 42:131–134.

——— 1966. A new species of moth destructive to pine cones in Mexico (Tortricoidea). J. Lepid. Soc. 20:251–253.

——— 1977. Wing measure as a size index in Lepidoptera: The family Olethreutidae. Ann. Entomol. Soc. Amer. 70:253–256.

——— 1986. New species of the genus *Cydia* that attack seeds of Mexican conifers (Lepidoptera: Tortricidae), pp. 5–7. *In* Cibrián-Tovar, D., B. H. Ebel, H. O. Yates & J. T. Mendez-Montiel (eds.), Insectos de conos y semillas de las coniferas de Mexico. U.S. Dept. Agric. Forest Service Gen. Tech. Rept. SE-40, 110 pp. (Spanish and English).

——— 1987. Guide to the olethreutine moths of Midland North America (Tortricidae). U.S. Dept. Agric. Agric. Handb. 660, 104 pp.

MOZNETTE, G. F., C. B. NICKELS, W. C. PIERCE, T. L. BISSELL, J. B. DEMAREE, J. R. COLE, H. E. PARSON & J. R. LARGE. 1940. Insects and diseases of the pecan and their control. U.S. Dept. Agric. Farm. Bull. 1829, 70 pp.

NAS (NATIONAL ACADEMY OF SCIENCES). 1979. Tropical legumes: Resources for the future. Washington, D.C. 331 pp.

NIEMELÄ, P., S. HANHIMÄKI & R. MANNILA. 1981. The relationship of adult size in noctuid moths (Lepidoptera: Noctuidae) to breadth of diet and growth form of host plants. Ann. Entomol. Fenn. 47:17–20.

OBRAZTSOV, N. S. 1959. Die Gattungen der palaearktischen Tortricidae II. Die Unterfamilie Olethreutinae, pt. 2. Tijd. Entomol. 102:175–216.

OKU, T. 1968. New or little known species of the subfamily Olethreutinae injurious to coniferous trees from Japan (Lepidoptera: Tortricidae). Kontyû 36:227–236.

OLSON, D. F. 1974. *Quercus* L. Oak, pp. 692–703. *In* Schopmeyer (1974).

OLSON, D. F. & W. J. GABRIEL. 1974. *Acer* L. Maple, pp. 187–194. *In* Schopmeyer (1974).

OPLER, P. A. 1978. Interaction of plant life history components as related to arboreal herbivory, pp. 23–31. *In* Montogomery, G. G. (ed.), The ecology of arboreal folivores. Smithsonian Institution, Washington, D.C. 574 pp.

OWSTON, P. W. & W. I. STEIN. 1974. *Pseudotsuga* Carr. Douglas-fir, pp. 674–683. *In* Schopmeyer (1974).

PATIÑO VALERA, F. & Y. VILLAGÓMEZ AGUILAR. 1976. Los analisis de semillas y su utilizacion en la propagacion de especies forestales. Inst. Nac. Invest. Forest. (Mexico). 40, 26 pp.

PEACOCK, J. W., S. L. WRIGHT & J. R. GALFORD. 1988. Attraction of acorn-infesting *Cydia latiferreana* (Lepidoptera: Tortricidae) to pheromone-baited traps. Great Lakes Entomol. 21:151–156.

PETERS, R. H. 1983. The ecological implications of body size. Cambridge Univ. Press, Cambridge, England. 329 pp.

POSTNER, M. 1978. Olethreutinae. Laspeyresiini, pp. 89–109. *In* Schwenke, W. (ed.), Die Forstschädlinge europas. Vol. 3. Schmetterlinge. Parey, Hamburg. 467 pp.

PULLIAINEN, E. & L. H. J. LAJUNEN. 1984. Chemical composition of *Picea abies* and *Pinus sylvestris* seeds under subarctic conditions. Can. J. Forest. Res. 13:214–217.

PURSEGLOVE, J. W. 1968. Tropical crops. Dicotyledons 2, pp. 333–719. Wiley, New York.

PUTMAN, W. L. 1963. The codling moth, *Carpocapsa pomonella* (L.) (Lepidoptera

Tortricidae): A review with special reference to Ontario. Proc. Entomol. Soc. Ontario 93:22–60.

RÄDER-ROITZSCH, J. E. 1957. Quantitative Stoffänderungen bei der Keimung von *Pinus silvestris* L. Forstwiss. Cbl. 76:229–245.

RAFN, J. ca. 1912. The testing of forest seeds during 25 years 1887–1912. Privately printed. 91 pp.

RIDLEY, M. 1983. The explanation of organic diversity: The comparative method and adaptations for mating. Clarendon, Oxford. 272 pp.

ROFF, D. 1981. On being the right size. Amer. Nat. 405–422.

RUDOLF, P. O. 1974. *Larix* Mill. Larch, pp. 478–485. *In* Schopmeyer (1974).

RUDOLF, P. O. & W. B. LEAK. 1974. *Fagus* L. Beech, pp. 401–405. *In* Schopmeyer (1974).

SAFFORD, L. O. 1974. *Picea* A. Dietr. Spruce, pp. 587–597. *In* Schopmeyer (1974).

SANDER, I. L. 1974. *Castanea* Mill. Chestnut, pp. 273–275. *In* Schopmeyer (1974).

SCHMIDT-HEBBEL, H. & I. PENNACCIOTTI M. (eds.). 1979. Tabla de composicion quimica de alimentos chilenos. ed. 6. Univ. Chile Facultad Ciencias Quimicas y Farmacologicas. unpaged.

SCHÖNHERR, J. 1987. Zwei neue *Cydia*-Arten aus Brasilien (Lep., Tortricidae). J. Appl. Entomol. 102:284–287.

SCHOPMEYER, C. S. (Ed.). 1974. Seeds of woody plants in the United States. U.S. Dept. Agric. Agric. Handb. 450, 883 pp.

SCHREINER, E. J. 1974. *Populus* L. Poplar, pp. 645–655. *In* Schopmeyer (1974).

SCRIBER, J. M. & F. SLANSKY. 1981. The nutritional ecology of immature insects. Ann. Rev. Entomol. 26:183–211.

SEN GUPTA, J. N. 1936. Seed weights, plant percents, etc., for forest plants in India. Indian Forest Rec. (n.s.) Silvic. 2(5):175–221.

SHEPARD, R. K. 1975. Radial distribution of corticular photosynthate in stems of bigtooth and trembling aspen. Forest Sci. 21:370–372.

SHORT, H. L. & E. A. EPPS. 1976. Nutrient quality and digestibility of seeds and fruits from southern forests. J. Wildl. Manage. 40:283–289.

SKERMAN, P. J. 1977. Tropical forage legumes. FAO Plant Prod. Prot. Ser. 2. Food and Agric. Organization of the United Nations, Rome. 609 pp.

SMARTT, J. 1980. Evolution and evolutionary problems in food legumes. Econ. Bot. 34: 219–235.

STEFFERUD, A. (Ed.). 1961. Seeds: The yearbook of agriculture, 1961. U.S. Dept. Agric., Washington, D.C. 591 pp.

STEIN, J. D. 1983. The biology, host range, parasites, and hyperparasites of koa seed insects in Hawaii: A review. Proc. Hawaiian Entomol. Soc. 24:317–326.

STENMARK, A. 1971. Studies on the pea moth (*Laspeyresia nigricana* Steph.) in central Sweden. I & II. Medd. Stat. Växtskyddsanst. 15:1–47.

STEPHENSON, A. G. 1981. Flower and fruit abortion: Proximate causes and ultimate functions. Ann. Rev. Ecol. Syst. 12:253–279.

SWINGLE, C. F. 1939. Seed propagation of trees, shrubs, and forbs for conservation planting. U.S. Dept. Agric. SCS-TP 27, 198 pp.

TRIPP, H. A. 1954. Description and habits of the spruce seedworm (*Laspeyresia youngana* (Kft.) (Lepidoptera; Olethreutidae). Can. Entomol. 86:385–402.

TRIPP, H. A. & A. F. HEDLIN. 1956. An ecological study and damage appraisal of white spruce cone insects. Forest. Chron. 32:400–410.

WAINIO, W. W. 1941. The chemical composition of forest fruits and nuts from Pennsylvania. J. Agric. Res. 62:627–635.

WALTERS, G. A. 1974. *Araucaria* (Jussieu). Araucaria, pp. 223–225. *In* Schopmeyer (1974).

WALTON, G. P. 1923. A chemical and structural study of mesquite, carob, and honey locust beans. U.S. Dept. Agric. Bull. 1194, 19 pp.

WASSERMAN, S. S. & C. MITTER. 1978. The relationship of body size to breadth of diet in some Lepidoptera. Ecol. Entomol. 3:155–160.

WHEELER, W. A. & D. D. HILL. 1957. Grassland seeds. Van Nostrand, Princeton, New Jersey. 734 pp.

WHITESELL, C. D. 1974. *Acacia* Mill. Acacia, pp. 184–186. *In* Schopmeyer (1974).

WILLIAMS, G. C. 1966. Adaptation and natural selection. Princeton Univ. Press, Princeton, New Jersey. 307 pp.

WILLIAMS, S. (Ed.). 1984. Official methods of analysis of the Association of Official Analytical Chemists. 14th ed. Arlington, Virginia. 1141 pp.

WINTON, A. L. & K. B. WINTON. 1932. The structure and composition of foods. Vol. 1. Cereals, starch, oil seeds, nuts, oils, forage plants. Wiley, New York. 710 pp.

——— 1935. The structure and composition of foods. Vol. 2. Vegetables, legumes, fruits. Wiley, New York. 904 pp.

WYNIGER, R. 1962. Pests of crops in warm climates and their control. Verlag f. Recht u. Gesellschaft A.G., Basel. 555 pp.

YOON, H. S., C. CHOI & M. J. OH. 1983. Studies on the development of food resources from waste seeds II. Chemical composition of apple seed. Korean J. Food Sci. Technol. 15:128–132. (Korean and English).

ZABOROVSKY, E. P. 1962. [Fruits and seeds of trees and shrubs]. Goslesbumizdat, Moscow. 303 pp. (Russian).

ZIMMERMAN, E. C. 1978. Insects of Hawaii. Vol. 9. Microlepidoptera, pt. 1. Monotrysia, Tineoidea, Tortricoidea, Gracillarioidea, Yponomeutoidea, and Alucitoidea. Univ. Press of Hawaii, Honolulu. 881 pp.

Received for publication 10 February 1990; revised and accepted 11 July 1990.

Journal of the Lepidopterists' Society
44(3), 1990, 143–155

BODY TEMPERATURE, BEHAVIOR, AND GROWTH OF EARLY-SPRING CATERPILLARS (*HEMILEUCA LUCINA*: SATURNIIDAE)

NANCY E. STAMP

Department of Biological Sciences, State University of New York,
Binghamton, New York 13901

AND

M. DEANE BOWERS

University of Colorado Museum and Department of E.P.O. Biology,
Campus Box 334, University of Colorado, Boulder, Colorado 80309

ABSTRACT. Buckmoth caterpillars (*Hemileuca lucina*: Saturniidae) hatch in May, are then exposed to considerable variation in spring thermal conditions, and thus may benefit by basking. We found that larvae exposed to full sunlight reached body temperatures as much as 5°C above ambient temperatures. When sunlight was obscured by clouds, their body temperatures rapidly cooled to that of ambient. However, during partly sunny conditions, larvae in groups were often warmer than solitary larvae. The advantages for buckmoth caterpillars in attaining body temperatures warmer than ambient are discussed in terms of their food plant and predators.

Additional key words: basking, gregarious, predators, *Spiraea latifolia*, Massachusetts.

Thermal conditions affect the foraging patterns of and food plant exploitation by herbivorous insects. For example, raising the body temperature by basking may speed up physiological processes enabling larvae to consume and digest food faster and, thus, develop more quickly (Sherman & Watt 1973, Casey 1976, Grossmueller & Lederhouse 1985). Shortened developmental time for larvae may decrease availability to parasitoids (Porter 1983) and predators (Evans 1982) and maximize the intake of high quality food, which may be available only for a limited time during the growing season (Feeny 1970, Stamp & Bowers 1990a).

Our objective was to examine, under natural conditions, body temperature, behavior, and growth of buckmoth caterpillars (*Hemileuca lucina* Hy. Edw.: Saturniidae), which are typical of gregarious caterpillars feeding early in the spring. Larvae of *H. lucina* are specialists on meadowsweet (*Spiraea latifolia* Ait. Bork.: Rosaceae), a shrub common in wet fields in New England. In late September in Massachusetts, buckmoths deposit egg masses around stems of their hostplant. The eggs hatch in May. Although the mean size of egg masses was 146 eggs (Bowers & Stamp 1987), larval aggregations found in the field were often much smaller (Stamp & Bowers 1988). Reduced group size reflects the declining tendency to aggregate, subdivision as a result of escape responses to predators and parasitoids, and mortality (Cornell et al.

1987, Stamp & Bowers 1988). The caterpillars are conspicuous due to aggregation and aposematic coloration (i.e., black with urticating spines). Like many other early spring feeders (Porter 1982, Capinera et al. 1980, Knapp & Casey 1986), they bask. The larvae develop in early spring over 6–8 weeks, pupate in late June in the soil, and remain there through the summer.

METHODS

Depending on local larval densities, we used various sites over the three year study period (1983–85). To assess foraging behavior of first instar larvae, we used a population in 1985 at Leverett (Franklin Co.), Massachusetts. To determine larval temperatures, we used populations in 1984 and 1985 at Leverett and Gardner (Worcester Co.), Massachusetts. We used a population in 1983 at Dover (Norfolk Co.), Massachusetts, to examine growth rate of larvae under natural conditions.

To determine the feeding location of first instar larvae, 58 aggregations were observed on 19 May 1985 at Leverett. The following were recorded: height of the stem used by larvae, height of aggregation above the ground and relative to foliage, and behavior of larvae.

To ascertain maximal body temperatures of larvae under field conditions and to compare the thermoregulatory ability of solitary versus aggregated larvae, we observed aggregations of third and fourth instar caterpillars at two field sites (Leverett and Gardner). The size (wet weight) of mid-instar third and fourth instar larvae is 191.7 mg ± 34.5 SD (n = 36) and 216.0 mg ± 38.7 SD (n = 36), respectively. An infrared thermometer (Everest Interscience) was used to measure surface temperature of larval groups and air temperature at the corresponding microsites, 3 cm from the aggregations (with air temperature determined by a shielded sensor on the antenna of the infrared thermometer). This instrument allowed thermal measurements (of an area with a 2.5 mm diameter) without disturbing the larvae, which thrash and drop off the food plant with the slightest provocation. In 1984, a black-body instrument was used to estimate solar radiation (Porter 1982). Black-body measurements represent a combination of factors: radiation (solar and thermal), convection, and conduction. Although such measurements have limited value when the geometry and reflectance properties of the probe in the black-body instrument are different from those of the animals being measured (as is usually the case), black-body measurements do serve as an indicator of the thermal input available. In 1985, a pyranometer (LI-COR 200SB sensor attached to a LI-COR 185B radiometer) was used to determine solar radiation and to calibrate the black-body instrument used the previous year. Temperatures of live individuals were determined with a calibrated thermistor probe inserted into the thoracic segments (Porter 1982). These larvae were

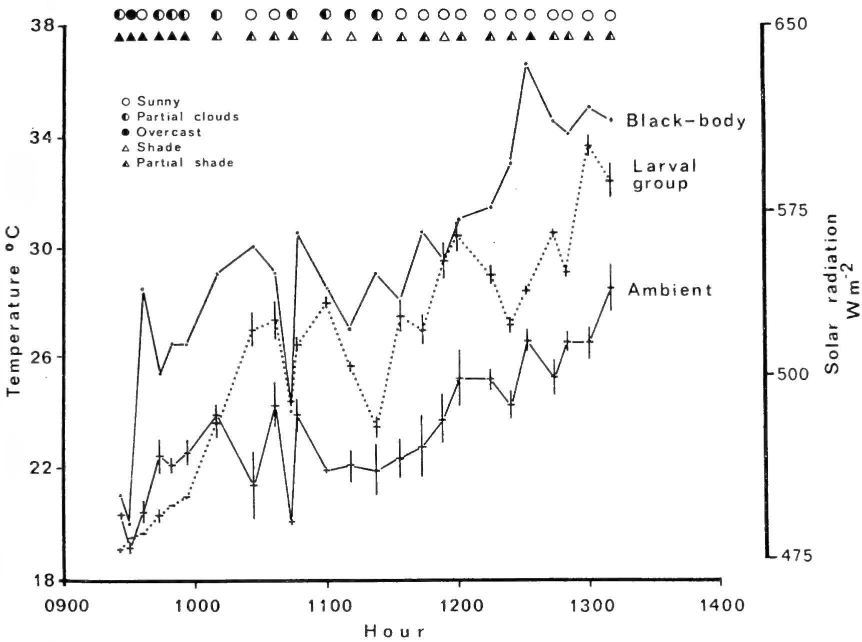


FIG. 1. Thermal measurements of aggregated third instar caterpillars at Leverett, Massachusetts, on 15 June 1984. Mean ambient temperature and surface temperature of the aggregation are shown with ± SE. Solar radiation (W m^{-2} = watts per square meter) was measured with a black-body instrument. Available sunlight is indicated with: open circles = full sunlight, half circles = partial clouds, and dark circles = overcast. Triangles represent shading by vegetation, with open triangles = no shade, half triangles = partial shade, and dark triangles = full shade.

placed 2.5 cm away from the group to be measured and in a vertical position, the most common position of buckmoth larvae whether they are feeding on leaves or massed during molting; larvae remained in this position throughout the measurements.

To examine the growth rate of caterpillars under natural conditions, five aggregations of buckmoth larvae were monitored in spring 1983 at Dover. Starting on 14 May, then again on 25 May, 1 June, 9 June, and finally on 14 June, 10 larvae from each aggregation were taken to the laboratory, weighed individually, and returned to the aggregation the next day. Monitoring began with first instar caterpillars and continued until the fifth instar, after which it was no longer possible to determine from which aggregation individuals had come.

RESULTS

Buckmoth caterpillars hatch in May in Massachusetts, for example, 7 May 1983 and 20 May 1984 at Dover, 15 May 1986 and 20 May 1987 at Belchertown, and 17 May 1985 at Leverett. The phenology of the

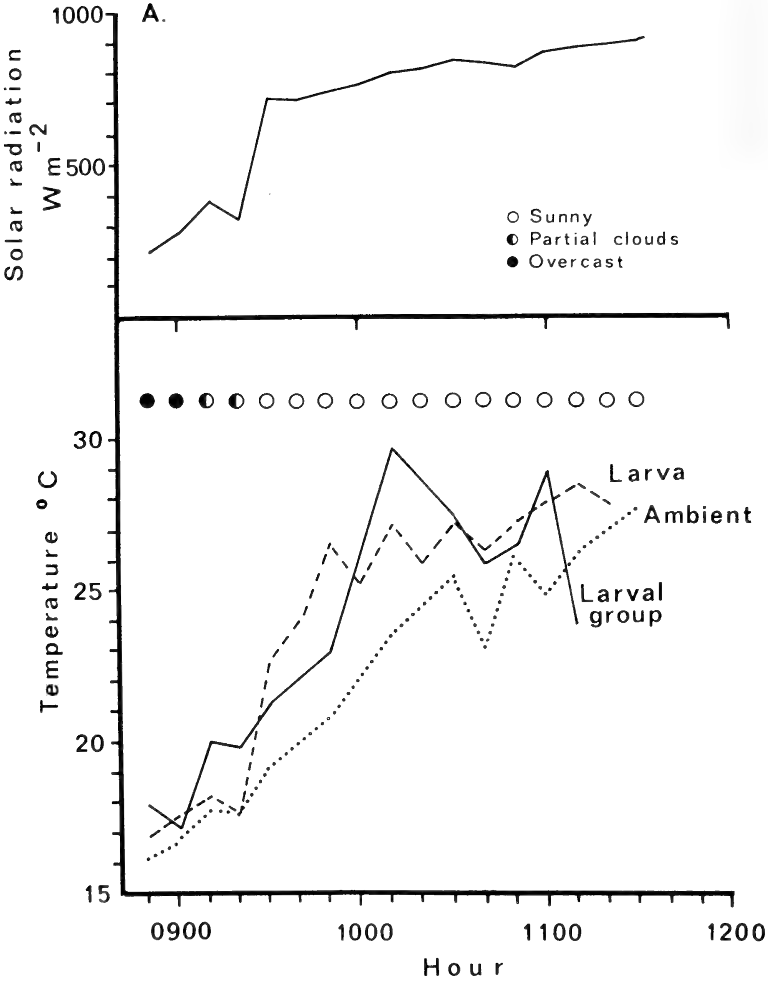
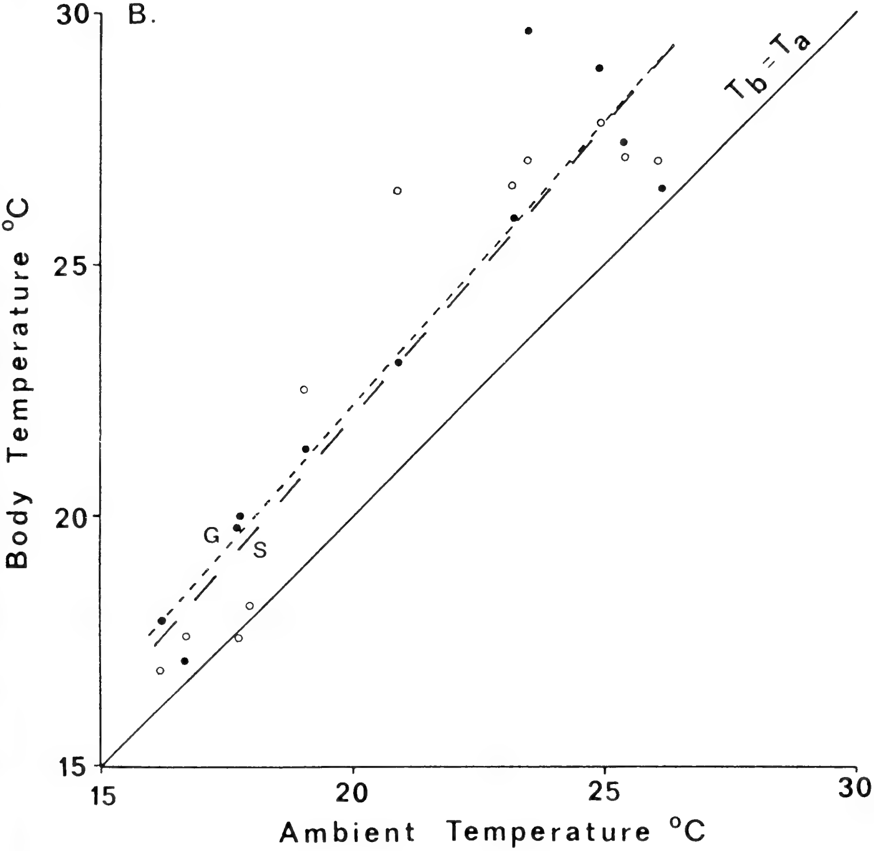


FIG. 2. Thermal measurements of fourth instar larvae at Gardner, Massachusetts, on 9 June 1985. A. The larval group (7 larvae) was 56 cm above the ground at the top of a branch. B. Relationship of larval body temperature (T_b) and ambient temperature (T_a), with black dots for grouped larvae (G) and open circles for solitary larva (S). Lines were fit by least squares method.

⟶

H. lucina larvae parallels that of the food plant (*S. latifolia*), with larvae hatching about a week after budbreak. The newly-hatched larvae move up the stems, about 30 cm, to the top of branches and begin feeding. First instar larvae spend considerable time basking. Observations of 58 aggregations in mid-May (on a day with alternating full sunlight and



clouds, and air temperatures of 13–16°C at the height of the aggregations) showed that all aggregations were exposed on stems, either at the height of the uppermost leaves or above them. The mean height of the stems was 92 cm (±36 SD) and larvae were located at a mean height of 76 cm (±32 SD). Thus, the groups were located on the top fifth of the stems. Of 58 aggregations, 12.1% were molting to the second instar, and 65.5% were resting (i.e., massed with some on top of others and not feeding or moving around). The other groups (22.4%) were feeding gregariously on new leaves.

Fluctuations in temperature of aggregations of mid-instar larvae corresponded to changes in availability of direct sunlight, which depended upon the degree of cloudiness and the amount of shade from vegetation. For example, one morning (at 1044 h), conditions changed from full to partial sunlight and both the black-body and larval aggregation temperatures dropped several degrees (Fig. 1). When in full sunlight

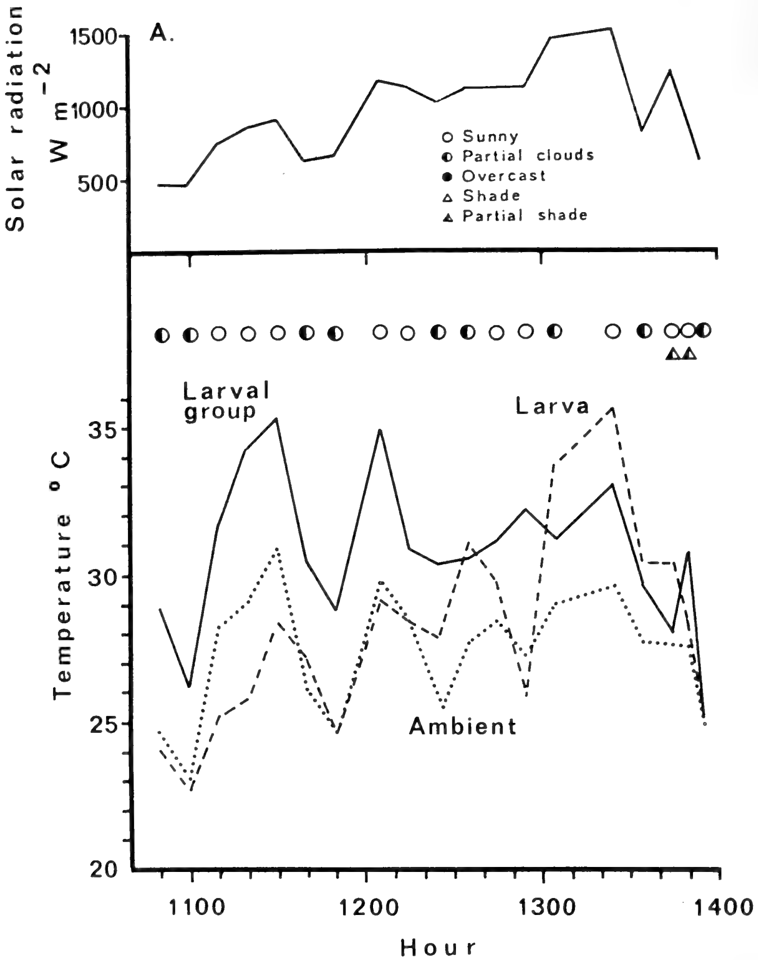
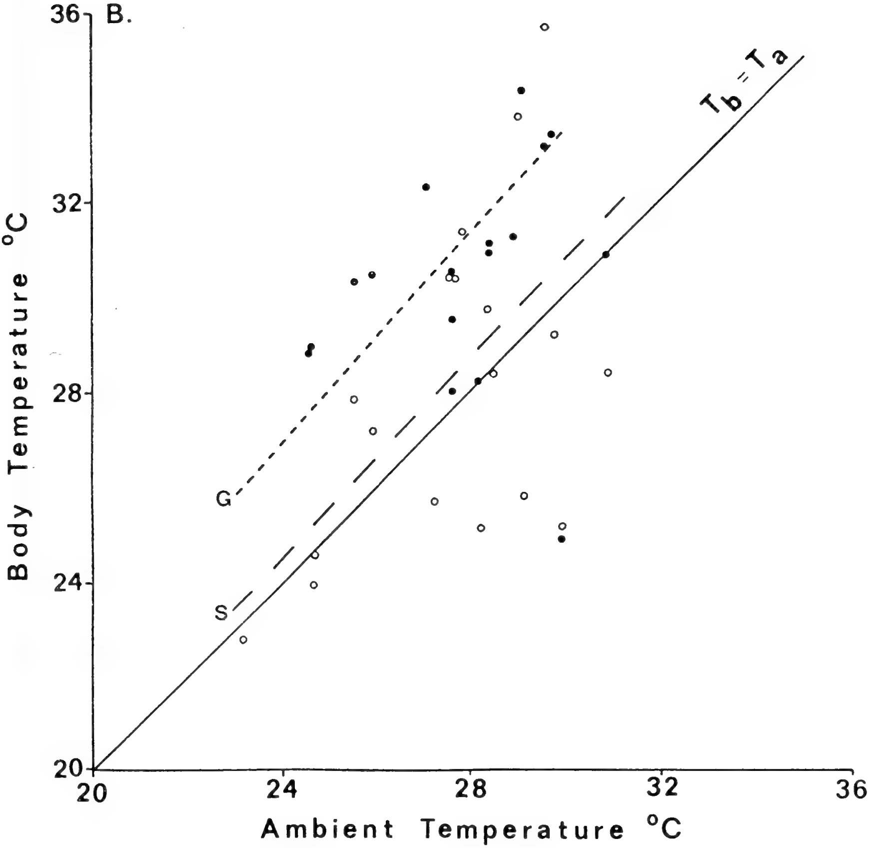


FIG. 3. Thermal measurements of fourth instar larvae at Gardner, Massachusetts, on 11 June 1985. A. The aggregation of 15 larvae was feeding on new leaves at the top of a branch, 39 cm above the ground. B. Relationship of larval body temperature (T_b) and ambient temperature (T_a) for larvae, with black dots for grouped larvae (G) and open circles for solitary larva (S). Lines were fit by least squares method.

→

(e.g., from 1153 to 1201 h, with no clouds and no shade), the larval aggregation temperatures approached that of the black-body measurements. Without direct sunlight (e.g., around 0930 h), the aggregation temperature was similar to ambient temperature (Fig. 1).

With full sunlight and steadily increasing solar radiation through the morning, groups and individuals quickly warmed from 17°C at 0900



h to 25°C by 1000 h (Fig. 2A) and, during this morning observation, maintained body temperatures that were above ambient temperatures (Fig. 2B). On a day with partial cloudiness, both groups and individuals cooled rapidly when cloud cover occurred, thereby reducing solar radiation and ambient temperature (Fig. 3A). Consequently, throughout this observation period, isolated individuals' temperatures oscillated around ambient temperature, whereas group temperatures were higher (Fig. 3B). Partially shaded larvae had body temperatures similar to ambient (Fig. 4A), but, for a while at least, grouped larvae were warmer than solitary larvae (Fig. 4B). Data points for body temperatures that were below those of ambient temperature probably were due to high levels of evaporative cooling.

The growth rates (slopes of larval weight regressed on days) were the same for all five field aggregations in spring 1983 at Dover (ANOCOVAR, $P > 0.20$, df = 4, 14; Fig. 5A). The slopes were 0.053, 0.054,

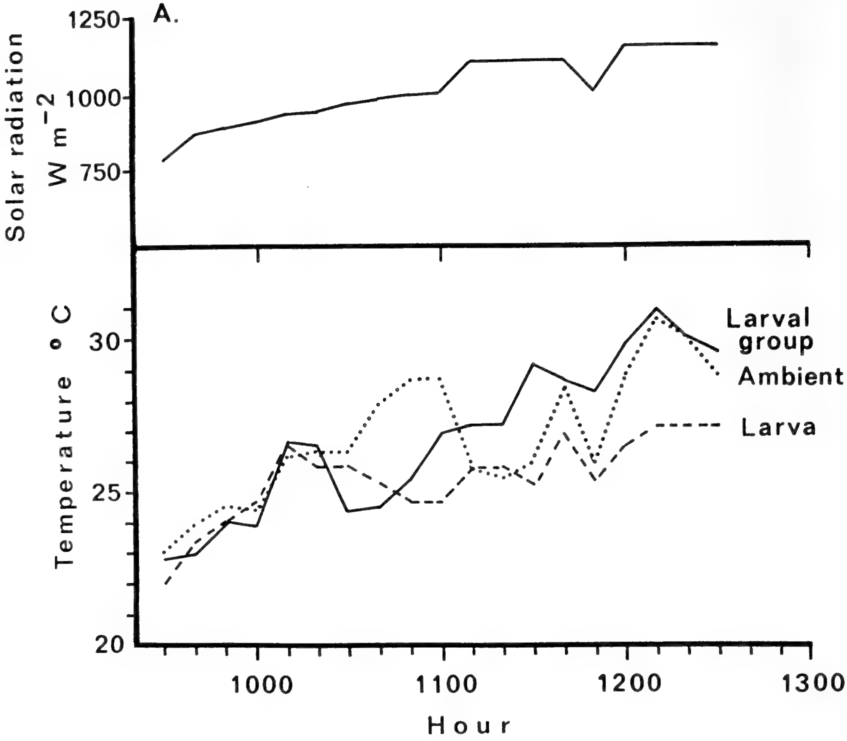
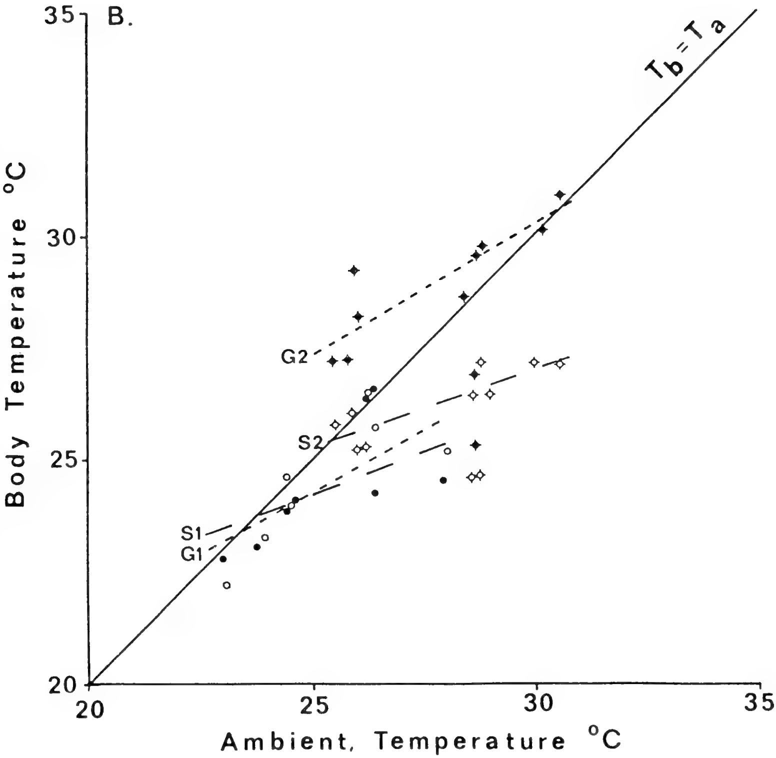


FIG. 4. Thermal measurements of pre-molt, non-feeding fourth instar larvae at Gardner, Massachusetts, on 10 June 1985. A. The aggregation of 26 larvae was 13–29 cm above the ground and in partial shade, and there were no clouds. B. Relationship of body temperature (T_b) and ambient temperature (T_a). S1 and G1 refer to temperatures before 1100 h of solitary (open circles) and grouped larvae (black dots), respectively; S2 (open stars) and G2 (black stars) refer to temperatures of those same larvae, solitary and grouped respectively, after 1100 h.

→

0.062, 0.064 and 0.067. The hatch dates of the egg masses, estimated by extrapolating the regression lines, were 2–10 May. Although the larvae hatched about 1–2 weeks earlier than usual that year, they were subject to typical (and considerable) fluctuations in temperature and available sunshine (National Climatic Center 1979, 1983; Fig. 5B, C). In May in particular, caterpillars were frequently subject to days with either less than 10% of potential sunshine or more than 85% of potential sunshine. By the fifth week (14 June), larvae in the field aggregations were in the fifth instar, and the aggregations had become subdivided into smaller groups.



Discussion

Buckmoth caterpillars that were exposed to full sunlight reached body temperatures as much as 5°C above ambient temperatures (Figs. 1, 2A, 3A) and, during partly sunny conditions, larvae in groups were warmer than the solitary larvae (Figs. 3B, 4B). Growth is faster at warmer temperatures; for instance, relative growth rate of buckmoth caterpillars doubled when the daytime rearing temperature was increased from 20 to 30°C (Stamp & Bowers 1990b). By growing faster, larvae can spend more of the developmental period eating when leaves are highest in nutritional quality, which is the first few weeks after budburst in May (Stamp & Bowers 1990a). By basking during cool but sunny springs, larvae may escape predators and parasitoids temporally. For instance, stinkbugs, such as *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae), are important predators of gregarious caterpillars (Mukerji & LeRoux 1965; including *H. lucina*, Stamp, pers. observ.) but are relatively few in number early in the spring (Evans 1982).

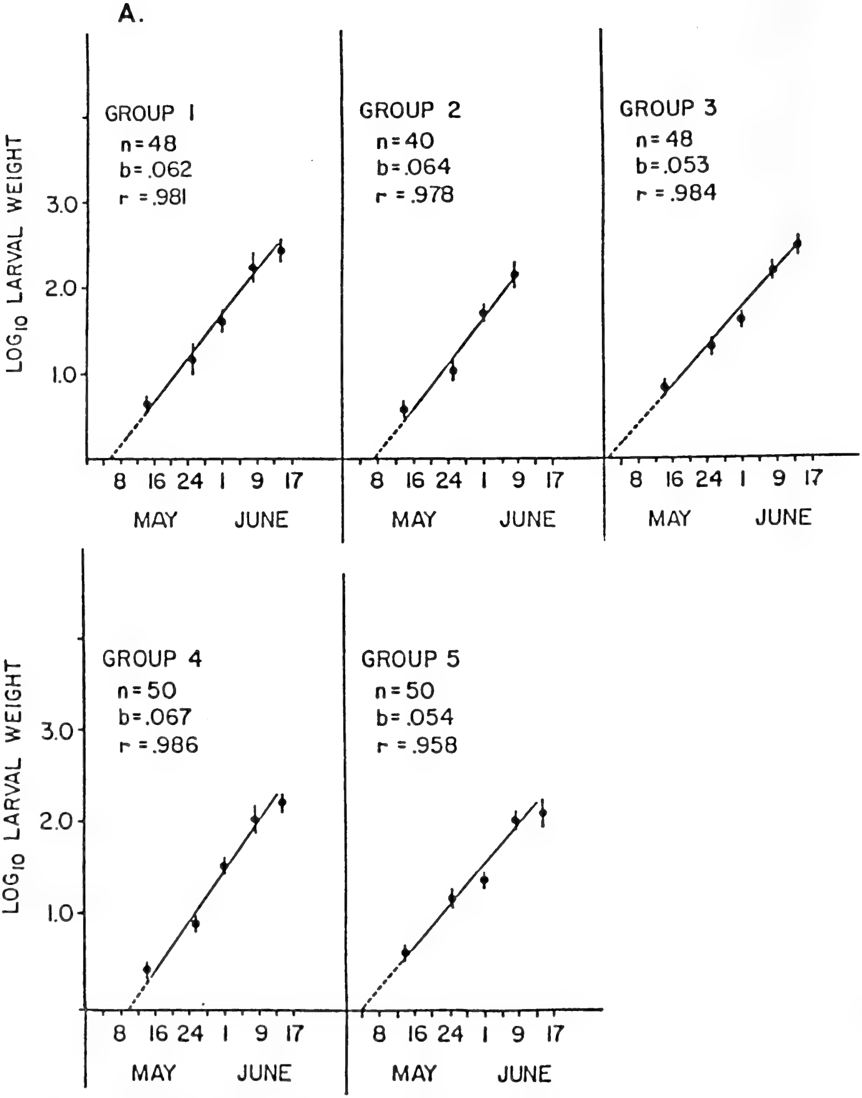
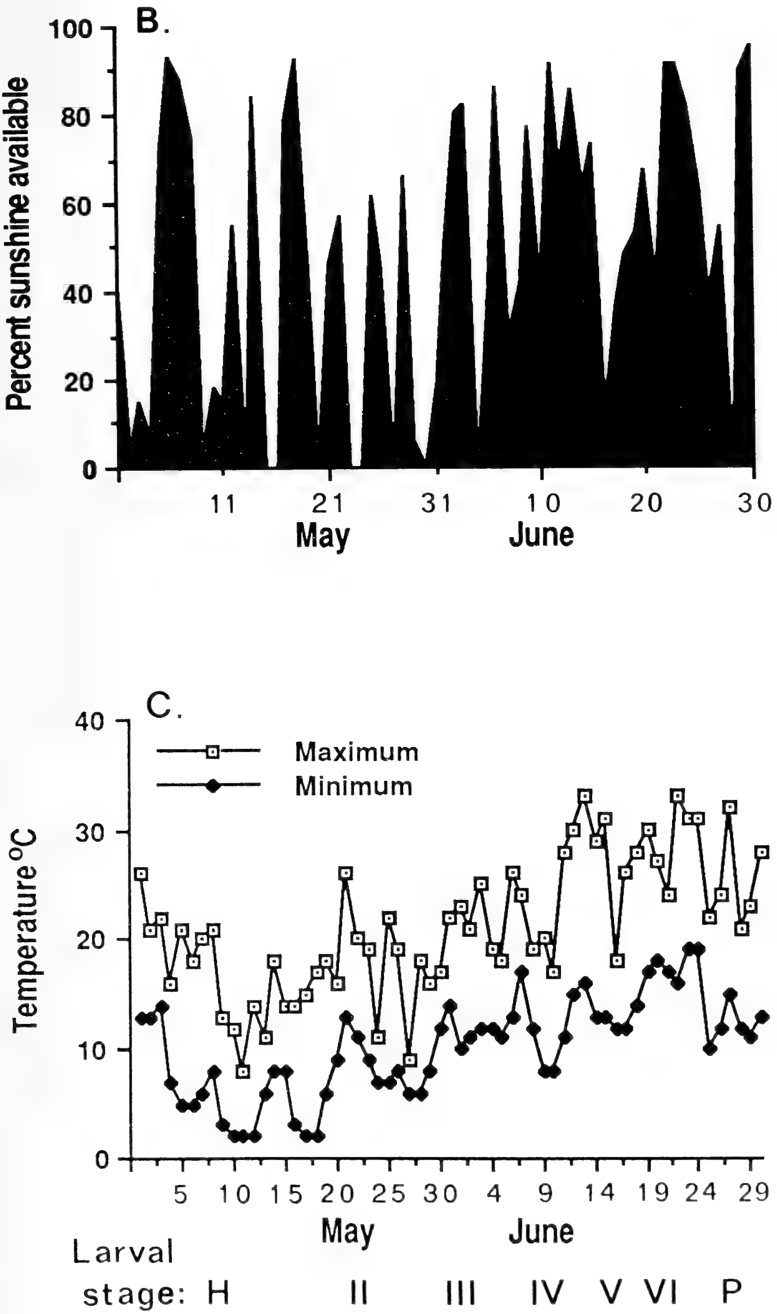


FIG. 5. Phenology of buckmoth caterpillars at Dover, Massachusetts, and typical climatic conditions in spring 1983. Data shown in B and C are from Blue Hill Observatory, 14 km from Dover, Massachusetts (National Climatic Center 1983). A. Growth of larvae under natural conditions at Dover, Massachusetts, with mean ± SE shown. Dashed portions of lines indicate extrapolation to determine hatch date. B. Availability of sunshine during growth period of larvae shown in A. C. Air temperatures during growth period of larvae shown in A. Developmental stages are indicated: estimated hatch (H), larval instars (II–VI) as observed, and estimated pupation (P).

→


B.
Percent sunshine available
100
80
60
40
20
0
11
21
31
10
20
30
May
June
C.
Maximum
Minimum
Temperature °C
40
30
20
10
0
5
10
15
20
25
30
4
9
14
19
24
29
May
June
Larval stage: H
II
III
IV
V
VI
P

Consequently, when the thermal conditions are in their favor, tent caterpillars, which also bask (Knapp & Casey 1986), can more quickly grow beyond the size in which they are vulnerable to these predators (Evans 1982). Another lepidopteran species (*Euphydryas aurinia*; Nymphalidae), by basking and thus growing quickly in cool sunny springs, is better able to avoid parasitism by braconid wasps than in overcast springs, in which caterpillar development is much slower (Porter 1982, 1983).

Buckmoth larvae were subject to considerable variation in maximal body temperatures from day to day, especially in May, which may have important consequences for growth and survival. In addition, our results show that buckmoth caterpillars were subjected unpredictably to periods of relatively cool temperatures during the daylight hours (Figs. 3A, 5). Cool temperatures slow down molting rate more than growth rate (Ayres & MacLean 1987; Stamp 1990). Thus, larvae that enter the molting phase during an overcast period are likely to have an extended developmental period compared to those that are feeding then and molting during warmer periods.

The pattern of local populations of *Hemileuca lucina* becoming extinct (Bowers & Stamp, pers. observ.) and the "boom and bust" phenomenon of *Euphydryas phaeton* (Nymphalidae) (Clench 1979; Stamp & Bowers, pers. observ.), another species with larvae that feed early in the spring and bask, may be largely a function of consecutive springs with favorable conditions (cool but sunny) followed by a series of unfavorable springs (overcast). It is in the latter case that natural enemies and deteriorating food quality are likely to have the greatest negative impact on growth and survival of early spring feeding caterpillars.

ACKNOWLEDGMENTS

We thank E. Bernays, S. Collinge, E. Fajer, J. Kingsolver, J. Schultz, F. Slansky, and E. Williams for comments on a previous draft. P. Johnson and T. Sargent helped locate populations of the buckmoths. J. Cornell helped with the project. MDB was supported by the Clark Fund of Harvard University and NSF grant BSR-8307353. NES was supported by a postdoctoral research fellowship from the University of California at Davis and by the New York State-United University Professors Professional Development Committee.

LITERATURE CITED

AYRES, M. P. & S. F. MACLEAN, JR. 1987. Molt as a component of insect development: *Galerucella sagittariae* (Chrysomelidae) and *Epirrita autumnata* (Geometridae). Oikos 48:273–279.

BOWERS, M. D. & N. E. STAMP. 1987. Patterns of oviposition in the buckmoth, *Hemileuca lucina* (Saturniidae). J. Lepid. Soc. 41:131–140.

CAPINERA, J. L., L. F. WIENER & P. R. ANAMOSA. 1980. Behavioral thermoregulation by late-instar range caterpillar larvae *Hemileuca oliviae* (Saturniidae). J. Kansas Entomol. Soc. 53:631–638.

CASEY, T. M. 1976. Activity patterns, body temperatures and thermal ecology in two desert caterpillars (Lepidoptera: Sphingidae). Ecology 57:485–497.

CLENCH, H. K. 1979. How to make regional lists of butterflies: Some thoughts. J. Lepid. Soc. 33:216–231.

CORNELL, J. C., N. E. STAMP & M. D. BOWERS. 1987. Developmental change in aggregation, defense and escape behavior of buckmoth caterpillars, *Hemileuca lucina* (Saturniidae). Behav. Ecol. Sociobiol. 20:383–388.

EVANS, E. W. 1982. Influence of weather on predator/prey relations: Stinkbugs and tent caterpillars. J. N. Y. Entomol. Soc. 90:241–246.

FEENY, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51:565–581.

GROSSMUELLER, D. W. & R. C. LEDERHOUSE. 1985. Oviposition site selection: An aid to rapid growth and development in the tiger swallowtail butterfly, *Papilio glaucus*. Oecologia 66:68–73.

KNAPP, R. & T. M. CASEY. 1986. Thermal ecology, behavior, and growth of gypsy moth and eastern tent caterpillars. Ecology 67:598–608.

MUKERJI, M. K. & E. J. LEROUX. 1965. Laboratory rearing of a Quebec strain of the pentatomid predator, *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae). Phytoprotection 46:40–60.

NATIONAL CLIMATIC CENTER. 1979. Comparative climatic data for the United States through 1978. National Oceanic and Atmospheric Administration, Asheville, NC.

——— 1983. Local climatological data: Monthly summary for Blue Hill Observatory. National Oceanic and Atmospheric Administration, Asheville, NC.

PORTER, K. 1982. Basking behaviour in larvae of the butterfly *Euphydryas aurinia*. Oikos 38:308–312.

——— 1983. Multivoltinism in *Apanteles bignellii* and the influence of weather on synchronisation with its host *Euphydryas aurinia*. Entomol. Exp. Appl. 34:155–162.

SHERMAN, P. W. & W. B. WATT. 1973. The thermal ecology of some *Colias* butterflies. J. Comp. Physiol. 83:25–40.

STAMP, N. E. 1990. Growth versus molting time of caterpillars as a function of temperature, nutrient concentration and the phenolic rutin. Oecologia 82:107–113.

STAMP, N. E. & M. D. BOWERS. 1988. Direct and indirect effects of predatory wasps (*Polistes* sp.: Vespidae) on gregarious caterpillars (*Hemileuca lucina*: Saturniidae). Oecologia 75:619–624.

——— 1990a. Phenology of nutritional differences between new and mature leaves and its effect on caterpillar growth. Ecol. Entomol. 15. In press.

——— 1990b. Variation in food quality and temperature constrain foraging of gregarious caterpillars. Ecology 71:1031–1039.

Received for publication 12 August 1989; revised and accepted 23 June 1990.

Journal of the Lepidopterists' Society
44(3), 1990, 156-162

INTERACTION OF *PYRAUSTA PANOPEALIS* (PYRALIDAE) WITH A NEWLY-REPORTED HOST, THE ENDANGERED MINT *DICERANDRA FRUTESCENS* (LABIATAE)*

SCOTT R. SMEDLEY,[1] KEVIN D. MCCORMICK[2]
AND THOMAS EISNER[1]

[1]Section of Neurobiology and Behavior, [2]Department of Chemistry,
Cornell University, Ithaca, New York 14853

ABSTRACT. *Dicerandra frutescens* (Labiatae), an endangered mint endemic to Florida, is a previously unrecorded food plant for *Pyrausta panopealis* (Pyralidae). *Pyrausta panopealis* tolerates the plant's terpene-based defenses, which it uses to its own advantage. As a defensive response, the larva regurgitates fluid containing pulegone, the principal terpene within its foliar diet. Preliminary findings indicate that the oral discharge has anti-insectan activity.

Additional key words: food plant, chemical defense, terpenes, defensive regurgitation, silk.

Pyrausta panopealis (Walker), a pyralid of the *phoenicealis* species group, is distributed pantropically (Munroe 1976). Its sole previously recorded larval food plant is *Hyptis capitata* Jacquin (Labiatae) in Puerto Rico (Schaus 1940). Although Schaus lists the species as *phoenicealis*, current understanding of the two species (Munroe 1976) indicates that the Puerto Rican record is actually *panopealis*. We here report a new larval host of *P. panopealis*, the endangered scrub balm, *Dicerandra frutescens* Shinners (Labiatae), and also examine some aspects of the moth's behavior in light of its host's phytochemistry.

D. frutescens is a low-growing shrub, flowering in August-September. It is endemic to the sand pine scrub habitat of Highlands County in central Florida (Kral 1982, Huck 1987). Due to its limited distribution of probably no more than 100 ha (M. Deyrup, pers. comm.), *D. frutescens* has been declared a federally endangered species (Code of Federal Regulations 1988). As is typical for mint plants, damage to the foliage of *D. frutescens* results in emission of a strong terpenoid odor. Twelve monoterpenes responsible for the fragrance of the plant have been characterized. These chemicals are concentrated in glandular capsules, distributed over the entire leaf surface (Eisner et al. 1990).

MATERIALS AND METHODS

During 17-21 October 1989 at the Archbold Biological Station, Lake Placid, Florida, USA, we examined one of the more extensive remaining

---

* Paper no. 97 in the series *Defense Mechanisms of Arthropods*. Paper no. 96 is Mason et al., *Naturwissensch.* (in press).

stands of *D. frutescens* plants. In a subplot covering about 40 m^2 that we inspected in detail, 25 mid- to late-instar larvae of a pyralid (Fig. 1D) were found. These were collected and reared to adults (Fig. 1A), which were identified as *P. panopealis*. An adult was also collected when it was flushed from a *D. frutescens* patch. Voucher specimens of the adults are deposited in the Cornell University Insect Collection, lot #1184.

To determine if *P. panopealis* larvae consume the terpene-bearing capsules of *D. frutescens,* foliage was prepared for scanning electron microscopy. Three chewed leaves, each from a different larva, were frozen by rapid immersion in liquid Freon 22 (jacketed by liquid nitrogen) and immediately freeze-dried. [Freon 22 is preferable to Freon 12 for this purpose, because as a hydrochlorofluorocarbon (rather than a chlorofluorocarbon), it degrades environmentally more quickly, supposedly before reaching the upper atmosphere.]

When disturbed by pinching with forceps, *P. panopealis* caterpillars writhe vigorously, coating themselves and their immediate environs with vomit. To determine whether the egested fluid contains the food plant's terpenes in unaltered form, vomit was obtained from a last instar larva collected on 4 February 1990 at the Archbold Station and transported to Cornell where it was allowed to consume fresh *D. frutescens* foliage. The larva was disturbed on a chilled depression slide, and its regurgiated fluid was collected with calibrated microcapillary tubes. A capillary tube containing ca. 0.4 μL of fluid was stored in a capped reaction vial at −78°C, and its contents were examined directly, without solvent, by gas chromatography (Attygalle & Morgan 1988). Instrumentation included a Hewlett Packard 5890 series II gas chromatograph equipped with a solid sample injector and a J & W Scientific DB1 30 m × 0.25 mm capillary column held at 40°C for 5 min then ramped up to 200°C at 10°C/min. Foliage fed to the larva supplying the vomit sample was itself analyzed for terpene content as previously described (Eisner et al. 1990).

To determine whether larval regurgitated fluid has anti-insectan potential, it was tested for topical irritancy using a cockroach scratch bioassay (Eisner et al. 1976, 1990). In this assay, a fluid sample is applied to the integument of decapitated roaches (last instar nymphs of *Periplaneta americana* (L.), Blattidae), and the delay to onset of leg-scratching of the stimulated site is timed to provide the criterion of irritancy. Active samples usually produce scratching in less than 30 sec. Due to the limited quantity of vomit available from the single *P. panopealis* that was "milked", only one application could be performed. The single sample (ca. 0.1 μL) was applied with a microcapillary tube to one side of the fifth abdominal tergite of a roach. As a control, a comparable volume of distilled water was applied shortly thereafter to the opposite side of the same tergite.

OBSERVATIONS AND RESULTS

The solitary larvae of *P. panopealis* construct a loose, silken retreat, in which they incorporate *D. frutescens* leaves, including those upon which they feed (Fig. 1B, C). Only after persistent prodding with forceps did the caterpillars leave their enclosures. Individual strands of the webbing were densely beset with tiny fluid droplets (Fig. 1E).

In the field there was some tendency for larvae to feed upon leaves of branches bearing recently senesced blossoms (Fig. 1B). However, both field and laboratory observations showed that they are capable of consuming foliage of non-flowering branches as well. Scanning electron microscopic examination of the three leaves that were being eaten by larvae indicated that *P. panopealis* fully consumes the terpene-containing glandular capsules (Fig. 1F).

Gas chromatographic analysis of the oral effluent of the larva revealed the presence of a single major terpene, pulegone. Pulegone was also found to be the principal monoterpene in the leaves upon which the larva had fed.

The vomit of the *P. panopealis* larva proved irritating in the cockroach scratch test. Application of the fluid elicited vigorous scratching at 19 sec, unlike the control, which failed to induce a response.

DISCUSSION

Plant terpenes commonly have anti-insectan properties. This is true for the scrub balm's terpene mixture and its major components, including pulegone (Eisner et al. 1990). A diet of 0.2% pulegone (fresh *D. frutescens* foliage is ca. 1.0% pulegone) adversely affects the development and reproduction of the generalist lepidopteran *Spodoptera eridania* (Cramer) (Noctuidae) (Gunderson et al. 1985). The pulegone-rich oil of pennyroyal, *Mentha pulegium* (L.) (Labiatae), is an antifeedant with high toxicity for larval *Spodoptera frugiperda* (J. E. Smith) (Noctuidae) (Zalkow et al. 1979).

P. panopealis is undeterred by the mint's chemical defense. It ingests the glandular capsules, and must therefore be exposed to its host's terpenes, both orally and enterically. Beyond its tolerance of the plant's chemicals, *P. panopealis* evidently uses the compounds for its own benefit: the single pulegone-laden oral discharge sample that we tested had anti-insectan properties. By the same *Periplaneta* assay used to test the vomit, pulegone itself has been shown to be irritating (Eisner et al.

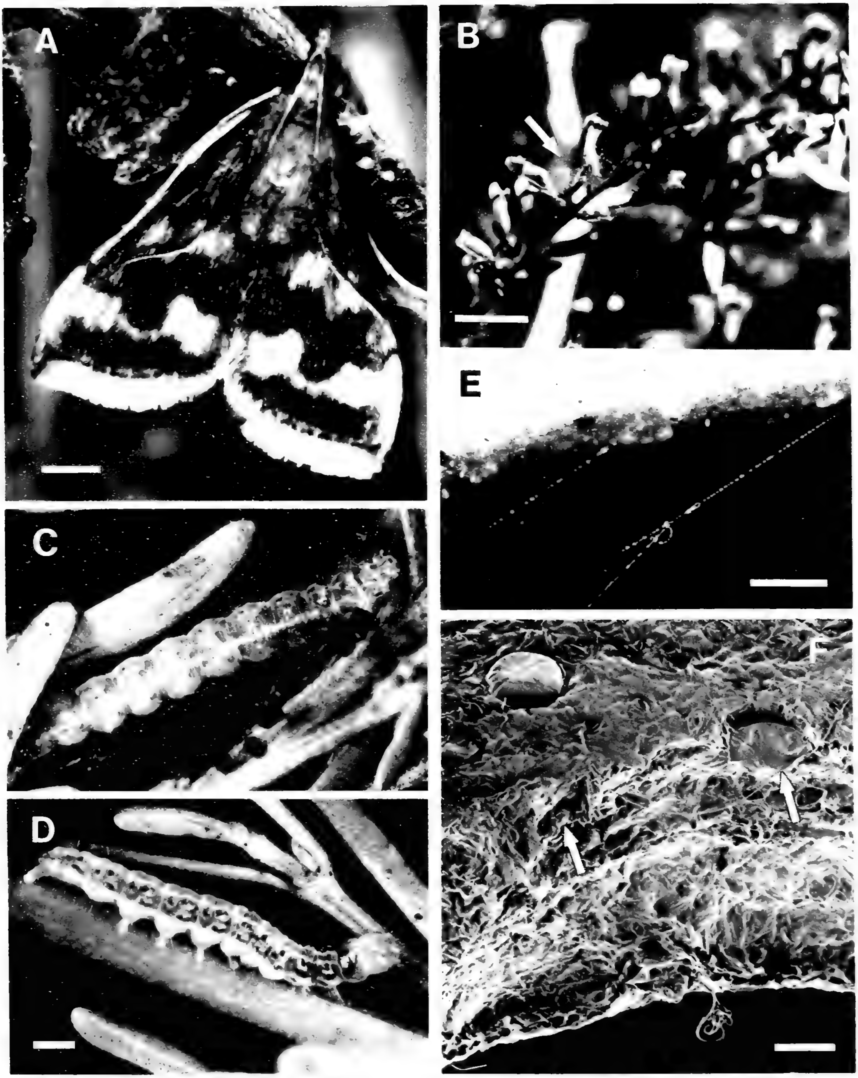


FIG. 1. *Pyrausta panopealis* and its host plant *Dicerandra frutescens*. A, Adult female (brownish purple, markings golden yellow); B, Larva within silken enclosure (arrow) on branch with senesced flowers; C, Enlarged view (ventral) of larva in enclosure; D, Larva (pale green, stripes greenish yellow, tubercles black) removed from enclosure; E, Anchoring threads of larval enclosure. Note fluid droplets on threads; F, Scanning electron micrograph of chewed leaf margin. Note intact (upper left) and ruptured glandular capsules. Arrows point to chewed margin of capsules. Scale bars: (A) 1 mm; (B) 1 cm; (D) 1 mm; (E) 0.5 mm; (F) 50 μm.

1990). Defensive regurgitation of diet-derived materials has been documented for other larval Lepidoptera as well (Common & Bellas 1977, Eisner et al. 1980, Peterson et al. 1987).

Terpene tolerance is likely characteristic of the majority of the congeners of *P. panopealis*, for they too are specialists on Labiatae (Munroe 1976). One possibility is that these mint-feeders possess an enzymatic means of detoxifying dietary terpenes. Induction of cytochrome P-450 dependent monooxygenases, glutathione transferases, and 1-naphthyl acetate esterase has been implicated in terpene degradation by lepidopterans (Yu 1986). A survey of the midgut aldrin epoxidase activity (an indicator of cytochrome P-450 dependent oxygenase activity) of 58 species of larval lepidopterans reports high activity invariably associated with the ingestion of host plants containing monoterpenes (Rose 1985).

Hyptis, the labiate genus upon which *P. panopealis* had previously been reported to feed, occurs within both the New and Old World tropics (Mabberley 1987). *Hyptis* may therefore potentially serve as a host over much of the range of *P. panopealis*. At least two species of *Hyptis* are sympatric with *D. frutescens* (Vander Kloet 1986). *Hyptis* and D. *frutescens* share a minimum of five monoterpenes (Luz et al. 1984, Tanowitz et al. 1984, Malan et al. 1988, Eisner et al. 1990). The shared chemistry may well play a role in the use of both mint genera by *P. panopealis*, particularly if the terpenes, either singly or in combination, have ovipositional or phagostimulatory activity for the moth. Monoterpenes are known ovipositional stimulants (Fatzinger & Merkel 1985, Hanula et al. 1985, Leather 1987) and phagostimulants (Harborne 1988) for lepidopterans.

The use of silken enclosures by larval lepidopterans is common and likely provides protection against certain predators, parasitoids, and abiotic factors. However, to our knowledge, presence of fluid droplets on the strands of such retreats has not been previously reported. These droplets may enhance the webbing's defensive function. They could act physically as an adhesive or chemically as a deterrent, depending on their specific properties. Defensive placement of droplets on silken strands has been noted in certain chrysopids, where such droplets are spaced along the egg stalk and act to repel ants (Eisner 1970, fig. 16B).

A minor point concerns the chemical composition here reported for *D. frutescens* leaves. We previously noted for spring foliage the presence of *trans*-pulegol and pulegone as the main terpene constituents of the plant (Eisner et al. 1990). The analysis of winter foliage reported here did not detect trans-pulegol. This may well reflect seasonal variation in the terpene composition of *D. frutescens*, a phenomenon reported for other mints (Cabo et al. 1987, Holm et al. 1988).

ACKNOWLEDGMENTS

This work was supported in part by NIMH (to S.R.S.) and NIH (to K.D.McC.) predoctoral traineeships and grants AI-02908 and AI-12020 from NIH. We thank Dr. Athula B. Attygalle for advice on chromatographic technique, Maria Eisner for electron microscopy, Dr. John G. Franclemont for identification of the moth, and the staff of the Archbold Biological Station for help and hospitality.

LITERATURE CITED

ATTYGALLE, A. B. & E. D. MORGAN. 1988. Pheromones in nanogram quantities: Structure determination by combined microchemical and gas chromatographic methods. Angew. Chem. Int. Ed. Engl. 27:460–478.

CABO, J., M. E. CRESPO, J. JIMENEZ, C. NAVARRO & S. RISCO. 1987. Seasonal variation of essential oil yield and composition of *Thymus hyemalis*. Planta Medica 53:380–382.

CODE OF FEDERAL REGULATIONS. 1988. Wildlife and fisheries 50, parts 1 to 199. National Archives and Records Administration, Washington, D.C. 595 pp.

COMMON, I. F. B. & T. E. BELLAS. 1977. Regurgitation of host-plant oil from a foregut diverticulum in the larvae of *Myrascia megalocentra* and *M. bracteatella* (Lepidoptera: Oecophoridae). J. Aust. Entomol. Soc. 16:141–147.

EISNER, T. 1970. Chemical defense against predation in arthropods, pp. 157–217. *In* Sondheimer, E. & J. B. Simeone, (eds.). Chemical ecology. Academic Press, New York. 336 pp.

EISNER, T., I. KRISTON & D. J. ANEHANSLEY. 1976. Defensive behavior of a termite (*Nasutitermes exitiosus*). Behav. Ecol. Sociobiol. 1:83–125.

EISNER, T., K. D. MCCORMICK, M. SAKAINO, M. EISNER, S. R. SMEDLEY, D. J. ANESHANSLEY, M. DEYRUP, R. L. MYERS & J. MEINWALD. 1990. Chemical defense of a rare mint plant. Chemoecology 1:30–37.

EISNER, T., S. NOWICKI, M. GOETZ & J. MEINWALD. 1980. Red cochineal dye (carminic acid): Its role in nature. Science 208:1039–1042.

FATZINGER, C. W. & E. P. MERKEL. 1985. Oviposition and feeding preferences of the southern pine coneworm (Lepidoptera: Pyralidae) for different host-plant materials and observations on monoterpenes as an oviposition stimulant. J. Chem. Ecol. 11: 689–699.

GUNDERSON, C. A., J. H. SAMUELIAN, C. K. EVANS & L. B. BRATTSTEN. 1985. Effects of the mint monoterpene pulegone on *Spodoptera eridania* (Lepidoptera: Noctuidae). Environ. Entomol. 14:859–863.

HANULA, J. L., C. W. BERISFORD & G. L. DEBARR. 1985. Monoterpene oviposition stimulants of *Dioryctria amatella* in volatiles from fusiform rust galls and second-year lobolly pine cones. J. Chem. Ecol. 11:943–952.

HARBORNE, J. B. 1988. Introduction to ecological biochemistry. 3rd ed. Academic Press, New York. 356 pp.

HOLM, Y., B. GALAMBOSI & R. HILTUNEN. 1988. Variation of the main terpenes of dragonhead (*Dracocephalum moldavica* L.) during growth. Flavour Fragance J. 3: 113–115.

HUCK, R. B. 1987. Systematics and evolution of *Dicerandra* (Labiatae). Phanerogamarum Monographiæ Tomus XIX. J. Cramer, Berlin. 343 pp.

KRAL, R. 1982. Some notes on *Dicerandra* (Lamiaceae). SIDA 9:238–262.

LEATHER, S. R. 1987. Pine monoterpenes stimulate oviposition in the pine beauty moth, *Panolis flammea*. Entomol. Exp. Appl. 43:295–303.

LUZ, A. I. R., M. G. B. ZOGHBI, L. S. RAMOS, J. G. S. MAIA & M. L. DA SILVA. 1984. Essential oils of some Amazonian Labiatae, 1. Genus *Hyptis*. J. Natural Products 47: 745–747.

MABBERLEY, D. J. 1987. The plant book: A portable dictionary of the higher plants. Cambridge University Press, Cambridge. 706 pp.

MALAN, K., Y. PELISSIER, C. MARION, A. BLAISE & J.-M. BESSIERE. 1988. The essential oil of *Hyptis pectinata*. Planta Medica 54:531–532.

MUNROE, E. G. 1976. Pyraloidea, Pyralidae (in part), Fasc. 13.2B. *In* Dominick, R. B. et al. (eds.), The moths of America north of Mexico. E. W. Classey, Ltd. and Wedge Entomological Research Foundation, London.

PETERSON, S. C., N. D. JOHNSON & J. L. LEGUYADER. 1987. Defensive regurgitation of allelochemicals derived from host cyanogenesis by eastern tent caterpillars. Ecology 68:1268–1272.

ROSE, H. A. 1985. The relationship between feeding specialization and host plants to aldrin epoxidase activities of midgut homogenates in larval Lepidoptera. Ecol. Entomol. 10:455–467.

SCHAUS, W. 1940. Insects of Porto Rico and the Virgin Islands. Moths of the families Geometridae and Pyralidae. New York Acad. Sci., Scientific Survey of Porto Rico and the Virgin Islands 12:291–417.

TANOWITZ, B. D., S. A. JUNAK & D. M. SMITH. 1984. Terpenoids of *Hyptis emoryi*. J. Natural Products 47:739–740.

VANDER KLOET, S. P. 1986. Plant List of the Archbold Biological Station, Lake Placid, Florida. 2nd ed. Archbold Biological Station. 74 pp.

YU, S. J. 1986. Consequences of induction of foreign compound-metabolizing enzymes in insects, pp. 153–174. *In* Brattsten, L. B. & S. Ahmad (eds.), Molecular aspects of insect-plant associations. Plenum Press, New York. 346 pp.

ZALKOW, L. H., M. M. GORDON & N. LANIR. 1979. Antifeedants from rayless goldenrod and oil of pennyroyal: Toxic effects for the fall armyworm. J. Econ. Entomol. 72: 812–815.

Received for publication 12 March 1990; revised and accepted 12 June 1990.

Journal of the Lepidopterists' Society
44(3), 1990, 163–173

LOCALIZED INTERSPECIFIC HYBRIDIZATION BETWEEN MIMETIC *LIMENITIS* BUTTERFLIES (NYMPHALIDAE) IN FLORIDA

DAVID B. RITLAND

Department of Zoology, University of Florida, Gainesville, Florida 32611

ABSTRACT. Viceroy and red-spotted purple butterflies (*Limenitis archippus* and *Limenitis arthemis astyanax*) are broadly sympatric in the eastern United States, but very rarely interbreed in most areas. However, the butterflies hybridize relatively frequently in northern Florida and southern Georgia; I recorded seven hybrid individuals in a 13-month period in 1986–87, as well as two mating pairs of viceroy and red-spotted purple. I propose that this elevated hybridization is due to a unique combination of ecological and biogeographic (genetic) factors, which interact to locally weaken the premating reproductive barrier between viceroys and red-spotted purples. First, habitat overlap (and therefore encounter rate) between the two species of butterflies is unusually high because they share a larval foodplant. Second, red-spotted purples may be less discriminating in mate choice because of their comparative rarity (viceroy : red-spotted purple ratio is 9:1), which must affect the economics of mate choice. Finally, viceroys in northern Florida also may be prone to mismating because they represent intraspecific hybrids between two geographic races (*L. a. archippus* and *L. a. floridensis*), the latter of which is largely allopatric from red-spotted purples and may not have evolved effective pre-mating isolating mechanisms. This combination of ecological and genetic factors apparently creates a unique conduit of gene flow (introgression) between red-spotted purples and viceroys.

Additional key words: *Limenitis archippus, Limenitis arthemis astyanax, Salix caroliniana,* introgression, mate choice.

Interspecific hybrids are often striking individuals, blending the morphological, behavioral, and ecological traits of two parental types into novel patterns. Studying natural hybridization can elucidate ecological and genetic barriers between taxa and plays an important and continuing role in the development of evolutionary thought and speciation theory (e.g., Wallace 1889, Fisher 1930, Mayr 1963, Barton & Hewitt 1985). "Hybridization" encompasses a spectrum of phenomena, ranging from clinal intergradation involving geographic subspecies to *bona fide* hybridization between nominally distinct species. Most investigations of interspecific hybridization have focussed on "hybrid zones" (geographically-limited regions of contact and interbreeding between parapatric species: e.g., Remington 1968). However, isolated interspecific hybrids also occur between species that are broadly sympatric; two species may be well-isolated reproductively in some locales but interbreed in others (e.g., the sparrows *Passer domesticus* and *P. hispaniolensis* in Europe: Mayr 1963).

In contrast to the extensive literature on hybrid zones between parapatric taxa, few studies have addressed the causes and implications of such localized hybridization events involving distinct, broadly-sympatric species. In this paper, I consider a case involving southeastern United States populations of two congeneric nymphalid butterflies: the viceroy, *Limenitis archippus* (Cramer), and the red-spotted purple, *L. arthemis astyanax* (Fabricius) (Nymphalidae).

Parapatric taxa of the genus *Limenitis* provide the best examples of interspecific hybridization among North American butterflies. *Limenitis* taxonomy is currently being reassessed (Porter 1989), but four nominal species are generally recognized in North America: *L. arthemis* (Drury), *L. archippus*, *L. weidemeyerii* (Edwards), and *L. lorquini* (Boisduval). Each of these hybridizes (sometimes frequently) with its parapatric congeners in areas where they meet in narrow contact zones (e.g., Remington 1968, Platt 1983, Porter 1989). In contrast, the two taxa that are most broadly sympatric—the viceroy (*L. archippus*) and the red-spotted purple (*L. arthemis astyanax*)—interbreed surprisingly infrequently. From 1872 to present, only 33 natural hybrids between these butterflies have been reported, all as single, isolated individuals (Platt 1983, 1987a). These hybrids are designated as form "rubidus" (Strecker 1878). Platt (1975) has crossed viceroys and red-spotted purples in the laboratory, confirming that wild-collected "rubidus" phenotypes are indeed interspecific hybrids (Platt & Greenfield 1971).

The rarity of "rubidus" hybrids in nature presumably is due to a combination of genetic incompatibility (evidenced by a deficit of females in laboratory crosses: Platt 1987a) and effective premating reproductive isolation of the two butterflies resulting from morphological, behavioral, and habitat differences (Platt et al. 1978). In addition, it has been suggested that "rubidus" may be selected against by attracting increased adult predation (Platt & Greenfield 1971). Viceroys and red-spotted purples both mimic distasteful butterflies (viceroys resemble monarchs, *Danaus plexippus* (L.), and queens, *Danaus gilippus* (Cramer) (Danainae); red-spotted purples mimic the pipevine swallowtail, *Battus philenor* (L.) (Papilionidae)). The efficacy of each mimetic pattern has been experimentally demonstrated (Brower 1958, Platt et al. 1971, Ritland unpubl.). The intermediate coloration of "rubidus" hybrids, however, does not closely approximate either the monarch or the pipevine swallowtail, so the hybrids may lose their mimetic protection (although this hypothesis is untested).

HYBRIDIZATION RECORDS

Collection records of individual "rubidus" hybrids extend from New Mexico to New York, but only two individuals have been reported previously from the southeastern U.S. (Platt et al. 1978, Platt 1987a). I now report seven new "rubidus" hybrids discovered in Florida and

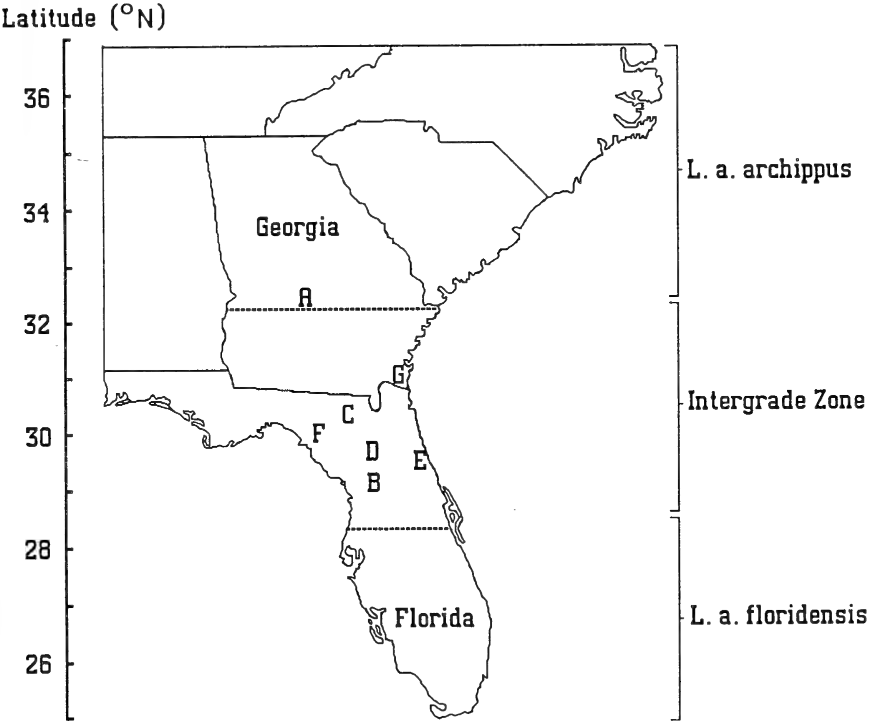


FIG. 1. Collections and observations of "rubidus" hybrids (A–E) and interspecific matings (F–G) between viceroys (*Limenitis archippus*) and red-spotted purples (*L. arthemis astyanax*) in 1986–88. Letters refer to individual records described in text. Also indicated (by two dotted lines) is the approximate location of a phenotypic intergrade zone between northern viceroys (*Limenitis a. archippus*) and Florida viceroys (*L. a. floridensis*) (Ritland 1990).

Georgia between June 1986 and July 1987, as well as two observations of interspecific mating between viceroy and red-spotted purple. Each independent hybridization event is designated by a letter, and the corresponding collection locales are depicted in Fig. 1.

Hybrids Collected as Adults

An adult male "rubidus" (A) was captured near Perry, Houston County, Georgia (32°22'N, 83°45'W) on 8 June 1986 in a thicket of black willow (*Salix nigra* Marsh) (Salicaceae).

A very small male "rubidus" (B) was sighted, but not captured, in a clump of coastal-plain willow (*Salix caroliniana* Michx.) (Salicaceae) near Dunnellon, Marion County, Florida (29°02'N, 82°31'W) on 7 July 1987.

Hybrids Reared from Wild-collected Larvae

One male "rubidus" (C) emerged on 15 June 1986 from a group of seven fifth-instar larvae collected on a single *S. caroliniana* tree near White Springs, Hamilton County, Florida (30°20′N, 82°45′W) on 7 June 1986. The remaining six larvae yielded viceroys.

Two male "rubidus" (D) were reared from a group of 17 wild larvae (fourth and fifth instars) collected on a single *S. caroliniana* in Gainesville, Alachua County, Florida (29°39′N, 82°20′W) on 6 June 1986. The two adult "rubidus" emerged on 16 June and 18 June; their proximity in space and time suggests that perhaps they were the progeny of a single female. The remaining larvae yielded 11 viceroys and four red-spotted purples.

Two "rubidus" (E) emerged from a group of six fifth-instar larvae collected on a single *S. caroliniana* near Espanola, Flagler County, Florida (29°30′N, 81°21′W) on 8 June 1987. The adults emerged on 21 and 24 June; presumably they were siblings. Although their pupae appeared superficially normal, both butterflies eclosed with deformed wings (one was severely deformed); whether this was due to developmental abnormality or environmental conditions is unknown. The other four larvae were viceroys.

Natural Interspecific Matings

Two mating pairs of male viceroy and female red-spotted purple were collected in 1988; one pair (F) was taken near Mayo, Lafayette County, Florida (30°03′N, 83°11′W) on 29 April, and the other (G) was collected near Woodbine, Camden County, Georgia (30°56′N, 81°45′W) on 14 June. Both viceroys involved were *L. a. archippus–L. a. floridensis* intergrades. These mismatings may not have resulted necessarily in successful hybridization, but they do provide evidence of mate-choice breakdown (see below). Attempts to obtain eggs from the females failed in both cases, possibly due to interruption of spermatophore transfer during their capture *in copula* (although captive female *Limenitis* often fail to oviposit: A. P. Platt, pers. comm.).

Further sampling is required to determine the magnitude and persistence of interbreeding between viceroys and red-spotted purples in Florida and Georgia; such influences as winter survivorship and population dynamics of the two species presumably affect the degree of interaction and hybridization that occurs between them.

DISCUSSION

All of the "rubidus" discovered were males (a female "rubidus" has never been taken in the wild: Platt 1987a) and all were intermediate in wing pattern between viceroys and red-spotted purples. They resembled wild-caught and lab-reared hybrids depicted by Platt and Greenfield (1971) and Platt et al. (1978), and included both the "light" (viceroy-like) and "dark" (red-spotted purple-like) phenotypes described by these authors. In fact, the specimen from Houston County, Georgia, has such a preponderance of viceroy characteristics that it may be a "rubidus"—viceroy backcross ("rubidus" are often fertile in laboratory crosses).

The seven hybrid specimens represent 1.1% of the entire *Limenitis* sample (n = 629) collected during the study period (Apr 1986–Aug 1987) in willow thickets from Houston County, Georgia, to Marion County, Florida. The hybrids were discovered while surveying willow habitats as part of another investigation; while this might yield a higher estimate of hybrid frequency than casual observation, it should be noted that intensive *Limenitis* collections (involving hundreds of butterflies) have not turned up "rubidus" hybrids in other areas (Remington 1968; Platt & Brower 1968; Bergman 1971; Platt 1975, 1987b; Waldbauer et al. 1988; pers. obs.).

Postulated Causes of Increased Hybridization in Florida and Georgia

The discovery of seven "rubidus" hybrids and two interspecific matings within two years contrasts with the rarity of "rubidus" records elsewhere. Furthermore, other workers have reported "rubidus" from northern Florida: one collected in Volusia County by G. W. Rawson (Platt et al. 1978) and three collected in Columbia County by James Maudsley (Platt & Maudsley, unpublished). Why should Florida/Georgia populations of viceroy and red-spotted purple hybridize more frequently than populations elsewhere? At least two possibilities exist: (1) matings between viceroys and red-spotted purples occur more frequently in this area than elsewhere (i.e., there is reduced pre-mating reproductive isolation), or (2) interspecific matings are no more frequent, but the few hybrids that are produced are more viable than those elsewhere (i.e., there is reduced post-mating reproductive isolation).

There is no *a priori* reason to expect that post-mating isolating mechanisms (genetic incompatibility or hybrid breakdown) are any weaker in Florida and Georgia than elsewhere, but the appropriate breeding studies have not been conducted. On the other hand, I propose three reasons to suspect a partial breakdown of pre-mating isolating mechanisms, which could result in more frequent intermating.

1) Habitat overlap

Although the two butterflies share a broad geographic range, red-spotted purples commonly rely on a different larval foodplant (black cherry, *Prunus serotina* Ehrh.; Rosaceae) than do viceroys (willows and poplars; Salicaceae) (e.g., Remington 1968, Opler & Krizek 1984). Willow and black cherry often occur in different microhabitats (Elias 1987), and viceroys and red-spotted purples feeding on them are reportedly somewhat habitat-segregated (Shapiro & Biggs 1968). In fact, in Maryland and Wisconsin willow patches, larvae of viceroys outnumber those of red-spotted purples by from 30:1 to 100:1 (A. Platt & D. Flaim, pers. comm.; pers. obs.). This habitat segregation has been proposed as one component of pre-mating isolation between the two species (Platt et al. 1978).

However, in northern Florida and southern Georgia, red-spotted purples occasionally switch from black cherry to the viceroy's larval foodplants, coastal plain willow (*Salix caroliniana*) and black willow (*S. nigra*). In fact, red-spotted purples comprise up to 35% of mixed *Limenitis* larvae collected from Florida willow thickets (pers. obs.), and the adult butterflies are forced into microsympatry (Table 1). Thus, the butterflies probably encounter one another more frequently in this region than elsewhere. Such habitat overlap is commonly cited as a cause of hybridization between normally habitat-segregated species (e.g., Chapin 1948, Anderson 1949, Mayr 1963, Williams 1983), including *Limenitis* (Greenfield & Platt 1974). In sampled willow thickets, adult red-spotted purples were most abundant early in the year (26% of combined *Limenitis* sample), becoming virtually absent later (Fig. 2). Perhaps autumnal senescence of black cherry in northern Florida forces late-season red-spotted purples to oviposit primarily on willow; the overwintering larvae then give rise to early-spring adults that find themselves in willow thickets surrounded by viceroys. This elevated encounter rate in the spring may explain why the Florida hybrids occurred fairly early in the year (median date = 8 June), rather than in late summer, as Platt (1987a) reported for "rubidus" elsewhere. Likewise, the two mismated pairs of viceroy and red-spotted purple were discovered early in the season.

2) "Economics" of red-spotted purple mate choice

The low density of red-spotted purples relative to viceroys in willow habitats may compel red-spotted purples to "settle for" viceroys as mates. In willow thickets where both butterflies were observed (Apr 1986–Aug 1987), viceroys outnumbered red-spotted purples by approximately 9:1 (Table 1). Increased hybridization when one species is comparatively rare is well documented in various taxa (e.g., Hubbs 1955, Mayr 1963, Wittenberger 1983), including butterflies (*Limenitis*: Greenfield & Platt 1974, Simpson & Pettus 1976, Platt et al. 1978; *Pieris*: Chew 1980). Theoretical considerations of mate choice "eco-

TABLE 1. Documented microsympatry of adult viceroys (*Limenitis archippus*) and red spotted purples (RSPs; *L. arthemis astyanax*) in willow thickets in Florida and Georgia (April 1986–August 1987). Data include only thickets in which both butterflies were found, and sites at which "rubidus" or interspecific matings were observed have the city name underlined. Note: localities are in N to S order; north of Houston County, Georgia (32°30′N), RSPs occur but were not observed in willow thickets; south of Marion County, Florida (29°N), RSPs do not occur.

Location		Total number of *Limenitis*	Percent RSPs
County	City		
Georgia			
Houston	Perry	10	10
Dooly	Unadilla	14	7
Liberty	Flemington	13	8
McIntosh	Eutonia	16	12
Tift	Chula	26	8
Cook	Adel	15	13
Camden	Woodbine	13	8
Lowndes	Valdosta	49	10
Brooks	Quitman	17	6
Georgia subtotals:		173	9
Florida			
Hamilton	Wht. Sprgs	39	8
Duval	Baldwin	7	14
Columbia	Lake City	9	11
Lafayette	Mayo	15	7
Union	Lake Butler	28	14
Alachua	Waldo	28	7
	Gainesville	163	10
	Hawthorne	35	14
	Micanopy	24	17
Gilchrist	Bell	12	25
Flagler	Espanola	9	11
Marion	Dunnellon	30	3
Florida subtotals:		404	10
Overall:		577	10

nomics" (Wilson & Hedrick 1982) predict that female red-spotted purples will be less discriminating in choosing mates if conspecific males are absent (which they often are; most red-spotted purples that I encountered in willow thickets were single females). Likewise, male red-spotted purples that are unable to locate conspecific females may be unusually persistent in courting female viceroys. Probably it is the combination of microsympatry and red-spotted purple mate-choice economics that sets the stage for hybridization.

3) Biogeography and genetics

An intriguing biogeographic correlation suggests that in northern Florida, red-spotted purples encounter viceroys that differ in mate

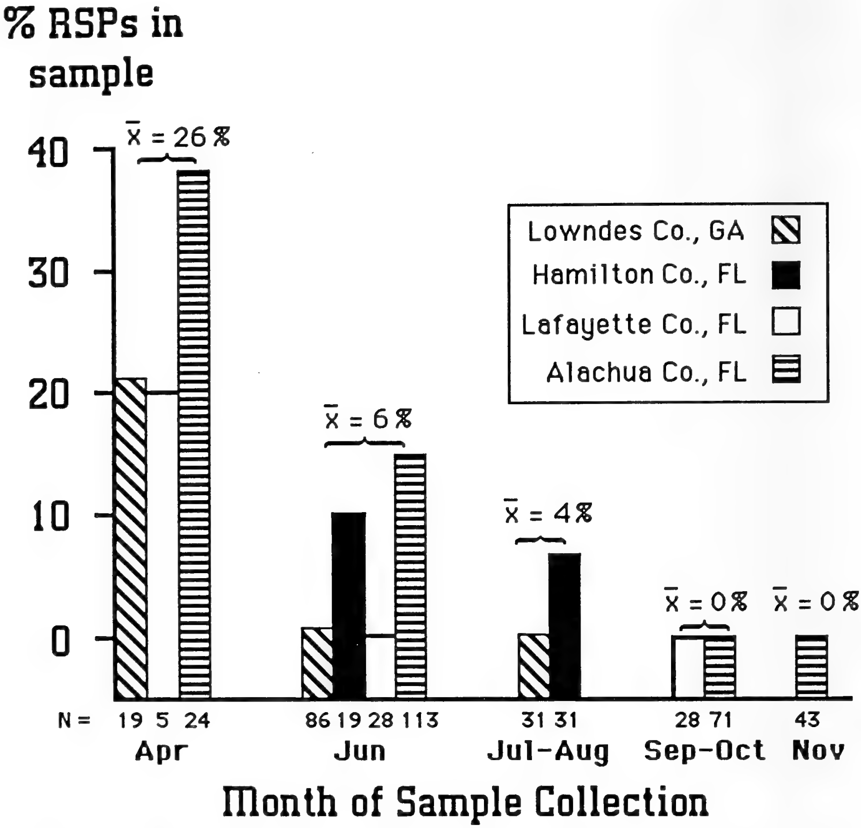


FIG. 2. Seasonal decline in the relative frequency of red-spotted purples (RSPs; *Limenitis arthemis astyanax*) in willow thickets from four areas in northern Florida and southern Georgia (1986–88). Bars (coded by site as indicated) depict percentage of RSPs in the total adult *Limenitis* sample collected during different months. Mean RSP percentage across all sites is indicated by month as well. A seasonal decline in RSPs is evident in both individual and pooled site data. Total sample size (no. viceroys + no. RSPs) is indicated beneath each bar. Some sites were not sampled every month.

choice behavior from viceroys they encounter elsewhere. The "rubidus" collection sites coincide geographically with an intraspecific hybrid zone between two subspecies of the viceroy (Fig. 1). This hybrid zone, which is characterized by a latitudinal cline in wing color, connects the light orange northern viceroy, *L. a. archippus* (Cramer), and the dark mahogany-brown Florida viceroy, *L. a. floridensis* (Strecker). *L. a. archippus* ranges widely over eastern North America and is broadly sympatric with the red-spotted purple, but *L. a. floridensis*, in peninsular Florida, occupies a largely disjunct geographic range to the south of other *Limenitis* species. Thus, *L. a. floridensis* may have "escaped" selection for sensitive mate-discrimination abilities (Bigelow 1965, Dobzhansky et al. 1968, Barton & Hewitt 1985), and *L. a. floridensis* genotypes immigrating into the intergrade zone could therefore be prone to mismating with the unfamiliar red-spotted purples that they encounter there. Furthermore, the dark wing color of Florida viceroys perhaps masks critical pattern elements that normally allow a red-spotted purple to recognize a viceroy as a heterospecific.

Moreover, "hybrid" viceroys may exhibit atypical mate choice because they represent mixtures of the *L. a. archippus* and *L. a. floridensis* genomes. These genomes apparently differ in alleles besides those for wing color (e.g., larval characters: Edwards 1884; and diapause control: Williams and Platt 1987), so hybrid viceroy mating behavior conceivably could be affected by novel allele combinations or intragenic recombination (e.g., Spieth 1968, Barton et al. 1983, Golding & Strobeck 1983; but *cf.* Barton 1983 *re* polygenic traits). This hypothesis is supported by the two observations of intergrade viceroys *in copula* with red-spotted purples. Finally, to the extent that mate choice and courtship in *Limenitis* are mediated by wing pattern or coloration, the variable ground color of viceroys within the intergrade zone (ranging from light orange to dark mahogany-brown: Ritland, 1990) may contribute to more frequent mismating by viceroys here than occurs in monotypic populations. These arguments remain speculative, because mate choice in viceroys and red-spotted purples is poorly understood; however, the proposed mechanisms identify several avenues of research that should be pursued in attempting to explain the elevated hybridization in this area.

Potential Consequences of Viceroy–Red-spotted Purple Hybridization

Locally-elevated hybridization between red-spotted purple and viceroy populations may allow limited genetic introgression (Anderson 1949) between the two species. Introgression is possible because "rubidus" males are fertile in laboratory backcrosses to both parental species (Platt 1983). The unpredictable effects of novel allele combinations created through introgression (Alston 1967, Ford 1971, Naveira & Fontdevila 1985) and the diffusion of adaptive alleles from one taxon to another (Barton 1979) represent potential evolutionary catalysts in Lepidoptera (e.g., Clarke & Sheppard 1960, Hovanitz 1963). Introgressive hybridization between red-spotted purples and viceroys conceivably could affect traits ranging from mimetic coloration and chemical defense to diapause dynamics and foodplant utilization ability. Thus, if local hybridization in Florida and Georgia does represent a significant and persistent breach in the normal species barrier, this area may be a "hot spot" in the continuing evolution of the two butterflies.

ACKNOWLEDGMENTS

I sincerely appreciate the insightful and stimulating thoughts offered by A. P. Platt, L. P. Brower, A. H. Porter, D. Flaim, T. C. Emmel, T. J. Walker and R. L. Ritland during the evolution of this manuscript. Financial support from the National Geographic Society (Grant # 3417-86 to L. P. Brower) and Sigma Xi (two grants-in-aid of research to the author) facilitated the field surveys.

LITERATURE CITED

ALSTON, R. E. 1967. Biochemical systematics. Evol. Biol. 1:197–305.

ANDERSON, E. 1949. Introgressive hybridization. Wiley, New York. 109 pp.

BARTON, N. H. 1979. Gene flow past a cline. Heredity 43:333–339.

——— 1983. Multilocus clines. Evolution 37:454–471.

BARTON, N. H. & G. M. HEWITT. 1985. Analysis of hybrid zones. Ann. Rev. Ecol. Syst. 16:113–148.

BARTON, N. H., R. B. HALLIDAY & G. M. HEWITT. 1983. Rare electrophoretic variants in a hybrid zone. Heredity 50:139–146.

BERGMAN, W. A. 1971. A study of interspecific hybridization of *Limenitis arthemis* in Minnesota. The Mid-Continent Lepidoptera Series 2(31):1–11 (privately published by J. H. and W. L. Masters, St. Paul, Minnesota).

BIGELOW, R. S. 1965. Hybrid zones and reproductive isolation. Evolution 19:449–458.

BROWER, J. VZ. 1958. Experimental studies of mimicry in some North American butterflies. I. The monarch, *Danaus plexippus,* and viceroy, *Limenitis archippus*. Evolution 12:32–47.

CHAPIN, J. P. 1948. Variation and hybridization among the paradise flycatchers of Africa. Evolution 2:111–126.

CHEW, F. S. 1980. Natural interspecific pairing between *Pieris virginiensis* and *P. napi oleracea* (Pieridae). J. Lepid. Soc. 34:259–261.

CLARKE, C. A. & P. M. SHEPPARD. 1960. The evolution of mimicry in the butterfly *Papilio dardanus*. Heredity 14:163–173.

DOBZHANSKY, T., L. EHRMAN & P. A. KASTRESIS. 1968. Ethological isolation between sympatric and allopatric species of the *obscura* group of *Drosophila*. Anim. Behav. 16:79–87.

EDWARDS, W. H. 1884. The butterflies of North America. Vol. 2. Houghton Mifflin, Boston. 357 pp.

ELIAS, T. E. 1987. The complete trees of North America. Gramercy Pub. Co., New York. 948 pp.

FISHER, R. A. 1930. The genetical theory of natural selection. Oxford Univ. Press, Oxford. 272 pp.

FORD, E. B. 1971. Ecological genetics. 3rd ed. Chapman and Hall, Ltd., London. 410 pp.

GOLDING, G. B. & C. STROBECK. 1983. Increased number of alleles found in hybrid populations due to intragenic recombination. Evolution 37:17–29.

GREENFIELD, J. C., JR. & A. P. PLATT. 1974. Report of the capture of an additional hybrid between *Limenitis arthemis astyanax* and *L. archippus* (Nymphalidae). J. Lepid. Soc. 28:72–75.

HOVANITZ, W. 1963. The origin of a sympatric species in *Colias* through the aid of natural hybridization. J. Res. Lepid. 1:261–274.

HUBBS, C. L. 1955. Hybridization between fish species in nature. Syst. Zool. 4:1–20.

MAYR, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, Massachusetts. 797 pp.

NAVEIRA, H. & A. FONTDEVILA. 1985. The evolutionary history of *Drosophila buzzatii*. IX. High frequencies of new chromosome rearrangements induced by introgressive hybridization. Chromosoma 91:87–94.

OPLER, P. A. & G. O. KRIZEK. 1984. Butterflies east of the Great Plains. Johns Hopkins University Press, Baltimore, Maryland. 294 pp.

PLATT, A. P. 1975. Monomorphic mimicry in nearctic *Limenitis* butterflies: Experimental hybridization of the *L. arthemis-astyanax* complex with *L. archippus*. Evolution 29:120–141.

——— 1983. Evolution of North American admiral butterflies. Bull. Entomol. Soc. America 29:10–22.

——— 1987a. Recent observations on North American admirals (Lepidoptera: Nymphalidae). Maryland Entomol. 3:18–20.

——— 1987b. Banded admirals from western Maryland: analysis of the *Limenitis* (*Basilarchia*) *arthemis-astyanax* complex (Lepidoptera: Nymphalidae) at Green Ridge State Forest. Proc. Entomol. Soc. Washington 89:633–645.

PLATT, A. P. & L. P. BROWER. 1968. Mimetic versus disruptive coloration in intergrading populations of *Limenitis arthemis* and *astyanax* butterflies. Evolution 22:699–718.

PLATT, A. P., R. C. COPPINGER & L. P. BROWER. 1971. Demonstration of the selective advantage of mimetic *Limenitis* butterflies presented to caged avian predators. Evolution 25:692–701.

PLATT, A. P. & J. C. GREENFIELD, JR. 1971. Inter-specific hybridization between *Limenitis arthemis astyanax* and *L. archippus* (Nymphalidae). J. Lepid. Soc. 25:278–284.

PLATT, A. P., G. W. RAWSON & G. BALOGH. 1978. Inter-specific hybridization involving *Limenitis archippus* and its congeneric species (Nymphalidae). J. Lepid. Soc. 32: 289–303.

PORTER, A. H. 1989. Genetic evidence for reproductive isolation between hybridizing *Limenitis* butterflies (Lepidoptera: Nymphalidae) in southwestern New Mexico. Am. Midl. Nat. 122:275–80.

REMINGTON, C. L. 1968. Suture zones of hybrid interaction between recently-joined biotas. Evol. Biol. 2:321–428.

RITLAND, D. B. 1990. Geographic variation in wing color of viceroy butterflies (*Limenitis archippus*): Description and significance. 41st Ann. Mtg. of the Lepid. Soc. Abstracts, p. 9.

SHAPIRO, A. M. & J. D. BIGGS. 1968. A hybrid *Limenitis* from New York. J. Res. Lepid. 7:149–152.

SIMPSON, R. G. & D. PETTUS. 1976. Records of *Limenitis* hybrids from Colorado. J. Res. Lepid. 15:163–168.

SPIETH, H. T. 1968. Evolutionary implications of reproductive behavior in *Drosophila*. Evol. Biol. 2:157–193.

STRECKER, H. 1878. Lepidoptera, Rhopaloceres, and Heteroceres, indigenous and exotic, with descriptions and colored illustrations. Privately publ. by author, Reading, Pennsylvania. 143 pp.

WALDBAUER, G. P., J. G. STERNBURG & A. W. GHENT. 1988. Lakes Michigan and Huron limit gene flow between the subspecies of the butterfly *Limenitis arthemis*. Can. J. Zool. 66:1790–1795.

WALLACE, A. R. 1889. Darwinism. An exposition of the theory of natural selection. Macmillan, London. 494 pp.

WILLIAMS, D. M. 1983. Mate choice in the mallard, pp. 297–310. *In* Bateson, P. (ed.), Mate choice. Cambridge Univ. Press, New York. 462 pp.

WILLIAMS, T. F. & A. P. PLATT. 1987. Absence of diapause in a laboratory strain of the Florida viceroy butterfly. Am. Midl. Nat. 117:346–352.

WILSON, D. S. & A. HEDRICK. 1982. Speciation and the economics of mate choice. Evol. Theory 6:15–24.

WITTENBERGER, J. F. 1983. Tactics of mate choice, pp. 435–448. *In* Bateson, P. (ed.), Mate choice. Cambridge Univ. Press, New York. 462 pp.

Received for publication 23 December 1989; revised and accepted 30 June 1990.

Journal of the Lepidopterists' Society
44(3), 1990, 174–179

VERTICAL STRATIFICATION OF HILLTOPPING BEHAVIOR IN SWALLOWTAIL BUTTERFLIES (PAPILIONIDAE)

JON D. TURNER
208 Westmoreland Avenue, Huntsville, Alabama 35801

ABSTRACT. A study of hilltopping behavior in Papilioninae on a forested hilltop in Tennessee has revealed a vertical zone for *Papilio glaucus* L. separate from other Papilioninae. These findings suggest that perception of "hilltop" differs among species. Separate hilltop vertical zones for species occupying the same horizontal habitat increase the species-packing capacity of the habitat and may increase the likelihood of successful mate location by reducing the interspecific encounter rate.

Additional key words: *Papilio glaucus,* mate locating behavior, patrolling, Tennessee.

Hilltopping behavior is common in butterflies and is characteristic of many swallowtails. A number of excellent studies and reviews detail this mate locating behavior (Shields 1967; Scott 1968, 1975, 1982; Guppy 1969; Lederhouse 1982; Alcock 1985). Studies of hilltopping Lepidoptera in the United States have been predominantly in western areas with open hilltops. In this study I examined the behavior of Papilioninae on a forested hilltop in the southeastern United States.

STUDY AREA

The hill studied is located in southeast Giles County, Tennessee, an area of rough topography with high winding ridges, hills, and deep meandering valleys of the Highland Rim. The underlying rocks are sedimentary, primarily limestone. The hilltop is 262 m in elevation, entirely tree covered, relatively flat, and oval shaped. The surrounding valley is 200–213 m elevation with hill slopes ranging in grade from 30 to 45% and slightly steeper to the west. The canopy on the hilltop is 15–25 m high, with crowns beginning at approximately 10 m. Canopy height is greater on the eastern slope than on the western slope. Trees 6–12 m in height are present in the understory. The predominant tree species are hickory (*Carya ovata*) (Juglandaceae) and hackberry (*Celtis occidentalis*) (Ulmaceae). Other deciduous tree species are scattered throughout, but no evergreen trees are present.

Tree density allowed 20–50% of the forested ground area to receive sunlight even during seasonally maximal crown development, depending on the time of day. Ground cover consisted primarily of vines and small bushes with some native grasses and weeds, but generally was devoid of flowers. Although this hill is one of the highest within a 2 km radius, at least 20 other hills over 245 m in elevation occur in the area.

METHODS

The oval, relatively flat summit was divided into four quadrants with the long-axis of the oval running N/S and the short axis running E/W. The study site was defined as the area extending from the center point of the hill to 2 m descent, resulting in an oval area 69 m long and 48 m wide. Each quadrant of the study area was divided into vertical zones defined by height above ground as low (<3 m), intermediate (3–6 m), and high (>6 m).

Butterfly surveys of five minutes duration were conducted between 1000 h and 1500 h (CDST) in all four quadrants in counterclockwise sequence, rotating the initial quadrant and providing rest intervals of 20–40 min after all four quadrants were observed. Papilioninae in each quadrant were counted and recorded as to vertical zone location. A single butterfly was counted for each vertical zone entered in each quadrant, but only once for each zone while in that quadrant. Thus, a single species flying from low to high vertical zone in the same quadrant was counted in all three zones. In addition to the author, one to three observers counted and followed each butterfly in each quadrant. The primary purpose of the observers was to insure that a butterfly was not missed or counted twice, particularly in the canopy area. Dull or camouflage clothing was worn by all observers and no specimens were collected during observation periods. Non-Papilioninae species interacting with Papilioninae species were observed and their behaviors recorded, but quantitative data were collected only for Papilioninae.

Observations were made between 3 April and 27 August 1989 and quantitative data were collected between 8 July and 27 August 1989. Wind direction and velocity at the summit ground level were measured by WinDial (Edmund Scientific, Barrington, New Jersey 08007). Relative wind velocity was estimated at treetop level by visually assessing movement of the tree crowns. Ambient air temperature in the shade at the hilltop was recorded with an Ultimeter (Edmund Scientific), and general weather conditions were noted.

RESULTS

Species of Papilioninae (Papilionidae) visiting the hilltop included *Eurytides marcellus* Cramer, *Papilio cresphontes* Cramer, *Papilio glaucus* L., *Papilio troilus* L., *Battus philenor* L., and *Papilio polyxenes asterius* Stoll. Collectively, *P. troilus, P. cresphontes, B. philenor,* and *E. marcellus* were seen 288 times, 286 of which were in the low vertical zone (Table 1). The intermediate and high vertical zones were entered only rarely by these species. *Papilio troilus* and *B. philenor* were each present only once, in the intermediate vertical zone. *Papilio cresphontes*

TABLE 1. Summary of hilltop observations of Papilioninae according to vertical zone location.

Species	Vertical zone High	Intermediate	Low
P. glaucus	319	13	8
P. troilus	0	1	128
B. philenor	1	1	83
P. cresphontes	0	3	63
E. marcellus	0	0	12

moved from low to intermediate zone three times on leaving the hilltop and once, when pursued by another butterfly, *B. philenor* moved from the low to the intermediate vertical zone and briefly into the high vertical zone before returning to the low vertical zone after the pursuit ended. The low number of observations of *E. marcellus* probably results from the study taking place late in this species' flight season. *Papilio polyxenes* was encountered so infrequently as to preclude its assignment to a characteristic vertical zone.

Typical patrolling behavior (Scott 1974) was exhibited by all Papilioninae in the low vertical zone, although *B. philenor* often perched on vines and small bushes. *Papilio troilus* occasionally exhibited similar perching behavior. *Papilio cresphontes* tended to fly higher above the ground in the low vertical zone than the other species, but remained in the low vertical zone on the summit. Interaction among all species in the low vertical zone was common. The intermediate vertical zone was not patrolled by Papilioninae.

There were 320 observations of *P. glaucus*, of which 319 were in the high vertical zone (Table 1). *P. glaucus* entered the intermediate vertical zone from the high vertical zone only 13 times, continuing into the low vertical zone 7 times. All 7 episodes of entrance into the low vertical zone occurred when *P. glaucus* was being pursued by another *P. glaucus* or by another species. At the end of each such encounter, the *P. glaucus* returned to the high vertical zone without interaction with another butterfly. *Papilio glaucus* predominated in the high vertical zone and other Papilioninae predominated in the low vertical zone. This difference is highly significant (Chi square, *P. glaucus* versus non-*glaucus* and high zone versus low zone, is 578.7: $P < .0005$).

Other species present on the hilltop that interacted with Papilioninae in all three vertical zones included *Asterocampa celtis* Bvd. & Lec. (Apaturidae) and *Limenitis arthemis astyanax* Fabr. (Nymphalidae). These two perching species were present in all three vertical zones although *L. arthemis astyanax* was observed predominantly in the intermediate and high vertical zones. Perching male *A. celtis* appeared to be as frequent in surrounding nonhilltop areas as in the study area, whereas perching male *L. arthemis astyanax* were uncommon off the hilltop. Although *P. glaucus* interacted with these two species, there was no pursuit interaction between *P. glaucus* and other Papilioninae on the hilltop.

There were no changes in vertical zone location for any of the species that could be correlated with direction or velocity of wind, intensity of sunlight, or time of day. Wind direction was almost always from the west, northwest, or southwest. At high wind velocities, *P. glaucus* was more likely to be observed in the leeward side of the study area. With calm or light wind, *P. glaucus* was equally represented in all four quadrants in the high vertical zone. In the low vertical zone, wind velocity never reached more than 8 kmp because of the windbreak effect of the trees. Species in the low vertical zone were present in all hilltop quadrants equally.

DISCUSSION

This study clearly demonstrates a three-dimensional aspect to hilltopping behavior in a forested area, a result not previously reported. Previous studies examining hilltopping behavior have dealt primarily with treeless or predominantly treeless hilltops, most often in the western United States (Shields 1967, Lederhouse 1982, Scott 1982, Alcock 1985). Guppy (1969) reported that he had never seen butterflies on a particular densely wooded hilltop area, but that a sparsely wooded summit was frequented by butterflies. The forested hilltop in this study is probably representative of many such areas in the southeastern United States.

Scott (1968, 1982) demonstrated that hilltopping behavior is a mate-locating behavior characteristic of low density species. Shields (1967) provided evidence that "hilltopping" in butterflies is a phenomenon in which males and virgin (or multiple-mating) females instinctively seek a topographic summit to mate.

In the present study, there is an apparent species-specific difference in perception of what constitutes the "hilltop." *Papilio glaucus* seeks a higher vertical zone than other Papilioninae, flying mostly at treetop level on forested summits. Other Papilioninae prefer ground level at the summit (similar to any open hilltop area). Possible explanations for *P. glaucus*'s preference for the high vertical zone in this forested area include the following: greater requirement for sunlight, presence of attractants in the tree crown region, safety from predators, more efficient use of air currents and thermal uplifts for gliding movements, and reduced interaction with non-*glaucus* species.

Weather conditions such as temperature and solar radiation levels have been shown to influence the male density of hilltopping species, but not their behavior (Wickman 1988). Similarly, no vertical zone changes occurred with any species in this study despite changing sunlight exposure (sunny, partly cloudy, or cloudy). Furthermore, *P. glaucus* was observed in the high vertical zone in early spring prior to the appearance of treetop foliage. Thus, sunlight intensity is an unlikely cause for the vertical zone behavior.

There was no evidence of any attractant in the canopy, and *P. glaucus* exhibited typical patrolling behavior. Although *P. glaucus* did occasionally alight in the canopy, there was no predilection for any particular tree species and patrolling behavior soon resumed.

Potentially, *P. glaucus* would have greater ability to descend rapidly and maneuver away from predators by patrolling in the high vertical zone, but this seems an unlikely reason for its persistence in the high zone location. Furthermore, there may be greater numbers of predators in the canopy than in the low vertical zone.

Shields (1967) found that hilltopping species confine their activities to the leeward side of the summit during windy periods. My observations of *P. glaucus* reported here extend these findings to the canopy level on forested summits. Soaring and gliding movement of *P. glaucus* is reminiscent of avian species (Brown 1963, Dorst 1974), which take advantage of wind currents and thermal uplifts for energy conservation during flight. Reduced energy expenditure may be even more important to patrolling male butterflies and this could be a factor in *P. glaucus*'s preference for the high vertical zone. But this reasoning should apply to all patrolling species and thus does not explain why *P. glaucus* is the only papilionid found in the high vertical zone.

Reduced interaction with non-*glaucus* species is probably the most important factor responsible for high vertical zone behavior of *P. glaucus*. Scott (1974) discussed energy conservation and the importance of separate mating sites to reduce interference between species. He suggested that if closely related species already mate in one site, then interference between those species may select for mating in another site. Exploiting an area unoccupied by other Papilioninae would result not only in energy conservation for the patrolling male, but would increase the likelihood that any encounter would result in locating a conspecific female. Separate vertical zones for species occupying the same horizontal habitat increase the species-packing capacity of the habitat and reduce the chances of interspecific interaction, thus increasing the likelihood of successful encounters among potential mates.

ACKNOWLEDGMENTS

I wish to acknowledge my son, Jonathan, for asking why the tiger swallowtails were in the treetops and why they would not come down. I thank Matt, Jonathan, Jeff, and

Nancy Turner for field assistance. I am grateful to Drs. James Scott, Thomas Emmel, and Boyce Drummond for their reviews of the manuscript.

LITERATURE CITED

ALCOCK, J. 1985. Hilltopping in the nymphalid butterfly *Chlosyne california* (Lepidoptera). Am. Midl. Nat. 113:69–75.

BROWN, R. H. J. 1963. The flight of birds. Biol. Rev. 38:460–489.

DORST, JEAN. 1974. The life of birds. Vol 1. Columbia University Press, New York. 349 pp.

GUPPY, R. 1969. Further observations on "Hilltopping in *Papilio zelicaon*." J. Res. Lepid. 8:105–117.

LEDERHOUSE, R. C. 1982. Territorial defense and lek behavior of the black swallowtail butterfly, *Papilio polyxenes*. Behav. Ecol. Sociobiol. 10:109–118.

SCOTT, J. A. 1968. Hilltopping as a mating mechanism to aid the survival of low density species. J. Res. Lepid. 7:191–204.

——— 1974. Mate-locating behavior of butterflies. Am. Mid. Nat. 91:103–117.

——— 1975. Mate-locating behavior of the western North American butterflies. J. Res. Lepid. 14:1–40.

——— 1982(83). Mate-locating behavior of western North American butterflies. II. New observations and morphological adaptations. J. Res. Lepid. 21:177–187.

SHIELDS, O. 1967. Hilltopping. J. Res. Lepid. 6:69–178.

WICKMAN, P. 1988. Dynamics of mate-searching behavior in a hilltopping butterfly. J. Linn. Soc. 93:357–377.

Received for publication 22 September 1989; revised and accepted 18 July 1990.

Journal of the Lepidopterists' Society
44(3), 1990, 180–187

BIOLOGY AND TAXONOMIC STATUS OF *BOLORIA NATAZHATI* (GIBSON) (NYMPHALIDAE)

J. T. TROUBRIDGE
23847-36A Avenue, RR #12, Langley, B.C. V3A 7B9, Canada

AND

D. M. WOOD
Research Associate, Biosystematics Research Centre,
Agriculture Canada, Ottawa, Ontario K1A 0C6, Canada

ABSTRACT. *Boloria natazhati* (Gibson 1920) is briefly redescribed and its known occurrences documented. The subspecific name, *nabokovi* (Stallings & Turner 1947), is synonymized under *B. natazhati* and its type locality is relocated and restricted.

Additional key words: arctic, scree, dolomite, *Boloria freija*, *Dryas integrifolia*.

Boloria natazhati has been one of the least collected and least understood insects of the North American Arctic. It was described from six specimens from Mt. Natazhat, St. Elias Mountains, Yukon Territory (Y.T.), at an elevation of 2470–2620 m (Gibson 1920). Two other specimens from Bernard Harbour, Northwest Territories (N.W.T.), were recognized at that time. Since 1920, *B. natazhati* has been encountered infrequently, probably because of the inaccessibility of its habitat.

Soon after its description, the status of *B. natazhati* was questioned. Stallings and Turner (1947) suggested that it probably represented a dark race of *Boloria freija* (Thunberg 1791), and dos Passos (1964) placed *B. natazhati* as a subspecies of *B. freija*. Nothing of the biology or habitat of this species was known by Stallings, Turner, or dos Passos; therefore, given the superficial similarity between *B. freija* and *B. natazhati*, it is not surprising that they were considered conspecific at the time.

While reviewing specimens of *Boloria* in the Canadian National Collection (CNC) in 1981, J. D. Lafontaine and J. H. Shepard noted that specimens from Victoria Island, N.W.T., Coppermine, N.W.T., and the types of *B. natazhati* were larger and darker than the remaining specimens of *B. freija*. Specimens of the latter had been common at Coppermine and the existence of two unusually large, dark specimens, which matched the types of *B. natazhati*, prompted Lafontaine and Shepard to contact the collector, Mr. S. Hicks. He recalled that he had collected on rocky areas as well as on wet tundra, and that the nominal "Coppermine" locality included some of the offshore islands as well as the mainland in the vicinity of Coppermine, N.W.T. If not necessarily sharing the same habitat, it appeared that specimens identifiable as both *B. freija* and *B. natazhati* were at least nearby.

Following the advice of one of us (JTT) and J. D. Lafontaine, and based on appearance and presumed sympatry at Coppermine, Scott (1986) restored *B. natazhati* from the status of a subspecies of *B. freija* to full species status. Although at that time we felt confident that *B. natazhati* was indeed a distinct species, we had no supporting evidence until now.

On 13 July 1982 one of us (DMW) collected a pair of *B. natazhati* in a barren valley of the White Mts., a limestone massif within the northern Richardson Mts., Y.T. Together, we were able to visit this valley again, from 30 June to 9 July 1987, where we obtained sufficient specimens of both *B. natazhati* (n = 125) and *B. freija* (n = 24) (specimens in the Troubridge collection and the CNC), flying together, to enable us to determine that they look and behave as separate species. Similar observations were made when the senior author visited Bernard Harbour, N.W.T., from 2–17 July 1988, and Mt. St. Paul, British Columbia (B.C.) from 19–25 June, 1989, and 16–18 June, 1990.

Synonymy for *boloria natazhati* (Gibson)

Brenthis natazhati Gibson 1920; Holland 1947. Report of the Canadian Arctic Expedition, 3(i):21i–22i. [Type locality: 141st meridian N. of Mt. Natazhat, Yukon; Canadian National Collection, Ottawa].

Boloria freija natazhati: dos Passos 1964; Howe 1975.

Clossiana freija natazhati: Miller & Brown 1981; Ferris et al. 1983; Hodges 1983; Tilden & Smith 1986.

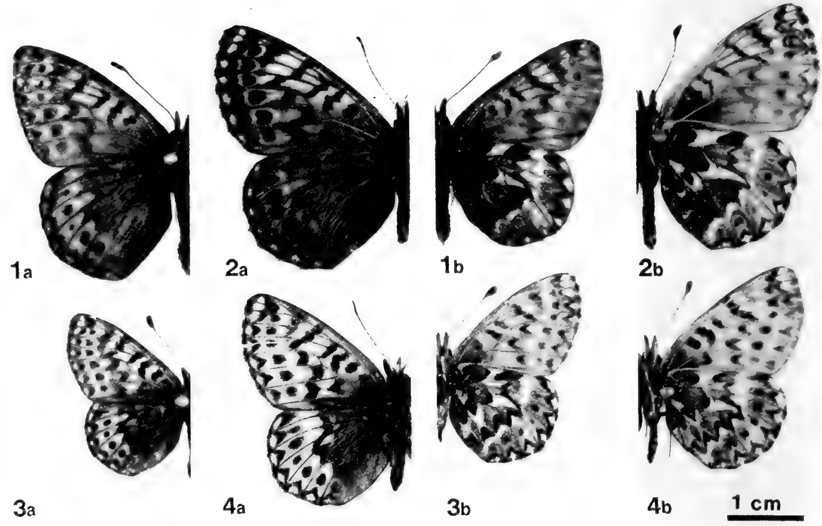
Boloria natazhati: Scott 1986.

Boloria freija nabokovi Stallings & Turner 1947; dos Passos 1964; Howe 1975. [Type locality: Alaska Military Highway, 102 miles north of Summit 2, Ravine, 1830 m; Museum of Comparative Zoology, Harvard University.] **NEW SYNONYMY**

Clossiana freija nabokovi: Miller & Brown 1981; Hodges 1983; Tilden & Smith 1986.

DIAGNOSIS

Boloria natazhati may be distinguished from *B. freija* as follows (Figs. 1–4): many *B. natazhati* have a blue, iridescent sheen to the upper wing surface, absent in *B. freija*; *B. natazhati* is larger (mean male forewing length 22.5 mm (n = 20) among specimens from the White Mts., Y.T.) than *B. freija* (mean male forewing length 19.0 mm (n = 18) from the same habitats as the former); the upper wing surface of *B. natazhati* is darker and duskier (ground color a dull, brownish-orange) than that of *B. freija* (ground color a brighter orange); the color of the ventral surface of the abdomen of *B. freija* is light brown in individuals from all populations we have studied with the single exception of Baffin Island, N.W.T., where it is black as is that of *B. natazhati*; the basal half of the ventral hindwing of *B. natazhati* is covered with long (2 mm), dark hairs, absent in *B. freija*; the submarginal area of ventral hindwing cells Rs, Ml, and Cul of *B. natazhati* is



FIGS. 1–4. *Boloria natazhati* and *B. freija* from the White Mts., Yukon Territory, 29 June to 9 July, 1987, J. Troubridge.
Fig. 1. *B. natazhati*, male; a. upperside, b. underside.
Fig. 2. *G. natazhati*, female; a. upperside, b. underside.
Fig. 3. *B. freija*, male; a. upperside, b. underside.
Fig. 4. *B. freija*, female; a. upperside, b. underside.

often purplish-gray, but that of *B. freija* is usually orange to reddish-orange, and the wing surface of fresh *B. natazhati* has a greasy appearance (reminiscent of *Charidryas damoetas* (Skinner 1902)), which is absent in *B. freija*. The male genitalia are similar to those of *B. freija*. The juxta is lyre-shaped and the number of spines at the tip of the lower arm of the valva is variable.

Distribution and Habitat

Thus far, *B. natazhati* has been found at the following sites (Fig. 5): Holman, N.W.T.; Kuujjua Valley, N.W.T.; in the vicinity of Coppermine, N.W.T. (probably Seven Mile Island); Bernard Harbour, N.W.T.; Canyon Range, MacKenzie Mts., N.W.T.; Mt. Natazhat, Y.T.; 8 km west of Sheep Mt., Y.T.; White Mts., Y.T.; Montana Mt., Y.T.; Sentinel Range, Rocky Mts., B.C. (the type locality of *nabokovi*, here restricted); Mt. St. Paul, B.C., and on the ridge above Slana, Alaska.

In the White Mts., Y.T., *B. natazhati* was found only on white dolomite scree slopes and alluvium from 900–1500 m (Fig. 6). Where the more acidic sandstone formations abut the dolomite, *B. natazhati* was found commonly on the dolomite, but was not seen over the sandstone, nor did it venture more than a few meters from the rocks into

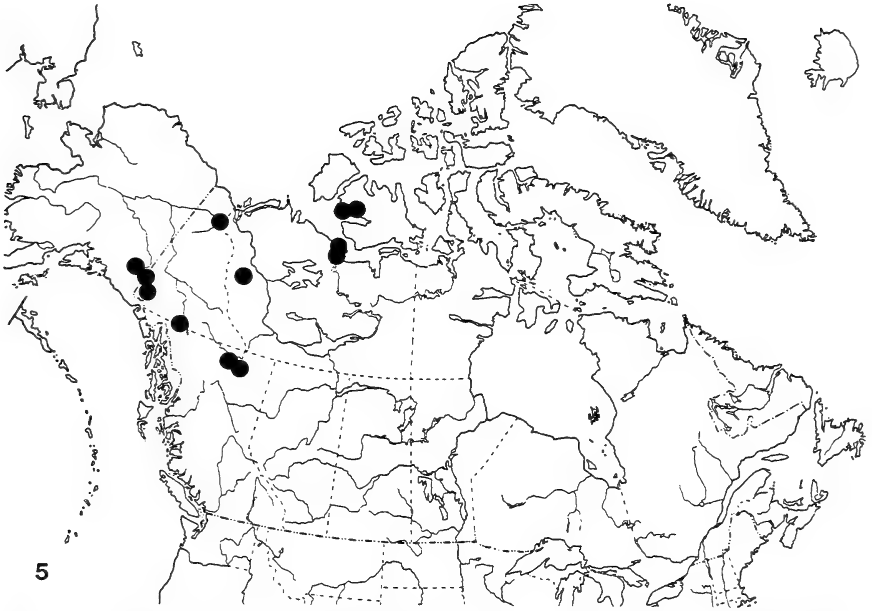


FIG. 5. The known distribution of *B. natazhati* (see text exact locality descriptions).

vegetated areas. The valleys and scree slopes that supported the greatest densities of *B. natazhati* were also the least vegetated. The habitat in the White Mts. is similar to the habitat in which *B. natazhati* occurs in the Sentinel and Stone Ranges of the northern Rocky Mts.

The habitat at Coppermine, N.W.T., is primarily wet tundra. Outcrops of gabbro are present on ridges but no extensive areas of scree are present. The wet tundra at Coppermine does not provide suitable habitat for *B. natazhati,* although *B. freija* is present. Our collecting at Coppermine in 1984 and 1988 did not produce *B. natazhati*; however, extensive areas of dolomite and gabbro scree were observed but not investigated on some of the offshore islands. We assume that the "Coppermine" specimens in the CNC came from one of these islands.

The unnamed peninsula bordered by Dolphin and Union Strait to the north and Coronation Gulf to the south is dominated by vast areas of barren dolomitic bedrock outcrops. *B. natazhati* is abundant throughout this peninsula. Bernard Harbour, N.W.T., is more heavily vegetated than most other areas on this peninsula. *B. natazhati* flies in low numbers with *B. freija* on the south slopes of the drumlins at Bernard Harbour, most commonly in unvegetated areas, but is abundant on the dolomite scree of the raised beaches that occur along the entire length of the south shore of Dolphin and Union Strait (Fig. 7).

FIGS. 6–8. Typical habitat for *B. natazhati*.
Fig. 6. Barren limestone scree slopes and alluvium in the White Mts., Y.T.
Fig. 7. Raised beaches of dolomite cobbles along Dolphin and Union Strait, at Bernard Harbour, N.W.T. Patches of the probable foodplant, *Dryas integrifolia* are seen in hollows at the left of the photo. The white strip through the upper part of the photo is sea ice.
Fig. 8. Dolomite block field, north of Holman, Victoria Island, N.W.T.

On Victoria Island, *B. natazhati* is widely distributed but *B. freija* has not yet been found. Our work has been restricted to the vicinity of Holman (Fig. 8) and the Kuujjua River valley on the Diamond Jenness Peninsula. Both sites are thinly vegetated with diverse geology. Most hills are composed of dolomite, capped with extrusive igneous rock, that occurs as gabbro. The gabbro is dominated by calcic feldspar and darker, mafic minerals and the pH is therefore basic as opposed to the acidic nature of intrusive igneous rocks. In the Kuujjua River valley, *B. natazhati* is generally distributed but most common on the hilltops, which were covered with gabbro scree. At Holman, *B. natazhati* is generally distributed on the gravel areas but most common on scree, which was not always located on hilltops. It did not seem to prefer white dolomite over dark gabbro at this location.

Larval Foodplant

At Holman and at Bernard Harbour, several females of *B. natazhati* were observed ovipositing on *Dryas integrifolia* Vahl (Rosaceae). At each of these sites, *D. integrifolia* was found growing in matts in depressions among the rocks. No other plants were found in the immediate area and females were almost always found in association with patches of *D. integrifolia*. Although no larvae were found feeding, this is the assumed foodplant of *B. natazhati*.

DISCUSSION

In the White Mts., Y.T., at Mt. St. Paul, B.C., and at Bernard Harbour, N.W.T., *B. freija* flies together with *B. natazhati* at the same time and in the same habitat. Although scree habitat is normal for *B. natazhati*, *B. freija* is usually found in wet tundra and taiga habitats. We found no intermediate specimens, therefore we have evidence of sympatry without hybridization. This alone is adequate evidence that *B. natazhati* and *B. freija* are distinct species. The presence of a lyre-shaped juxta and lateral lobes on the aedeagus are synapomorphies that link *B. natazhati* and *B. freija* as sister species.

The geographic variation found between colonies of *B. natazhati* is of note. When compared to specimens from the type locality, specimens from the other locations differ as follows: those from the White Mts., Y.T., average larger and darker; those from the Sentinel and Stone Ranges, B.C., are similar to those from the White Mts., Y.T., in size, but are darker in color; those from the MacKenzie Mts., N.W.T., are similar; those from Bernard Harbour, N.W.T., are similar in size but are darker and less colorful and most closely resemble those from the Sentinel Range, B.C.; and those from Victoria Island are smaller and more orange.

Although most of the populations of *B. natazhati* that we have studied are not genetically continuous and vary slightly in color and size, we see no need to clutter the literature with subspecific names.

Restriction of Type Locality of *nabokovi*

We regard the holotype of *B. freija nabokovi* as being conspecific with *B. natazhati* and we therefore place *nabokovi* as a junior synonym of *B. natazhati*. Until specimens were found in the Stone Range, B.C., in 1989, additional specimens of *nabokovi* had not been found since the holotype and paratype were collected in 1943. We believe this is because the type locality has been misinterpreted in the literature (Howe 1975, Miller & Brown 1981, Tilden & Smith 1986). Although Miller and Brown (1981) list the type locality as "mile 102, Alaska Military Highway, British Columbia," Stallings and Turner (1947) actually published a different account in the following words: "Alaska Military Highway, 102 miles *north of Summit 2* [italics ours], Ravine, 6000'." The second summit crossed by the Alaska Highway in 1943 was Steamboat Mountain (elevation 1067 m). Habitat we have associated with colonies of *B. natazhati* can be found 102 miles north of Steamboat Mountain in the Sentinel Range, Muncho Lake Provincial Park, B.C. Although this now seems to be an awkward way of describing Muncho Lake Provincial Park, there were no named landmarks in 1943 when the *nabokovi* types were collected, the year after the opening of the highway, and this may have been the only logical way of describing the location. Therefore, we here restrict the type locality of *nabokovi* to the Sentinel Range of the Rocky Mts., B.C., at 1830 m elevation. With on-going construction and straightening of the highway, the current kilometer measurement at this location is subject to change. Although we have not found *B. natazhati* in the Sentinel Range because of seemingly endless bad weather, it was found on Mt. St. Paul in the nearby Stone Range in 1989 and 1990 by the senior author.

Justification for the Use of *Boloria*

Synapomorphies for the genus *Boloria* Moore, 1900 *s. lat.*, *sensu* North American authors prior to 1981 (including synonyms *Clossiana* Reuss, 1919 and *Proclossiana* Reuss, 1926 but not including *Brenthis* Hübner, 1819 or any other genus of Argynninae), are described as follows: 1) loss of all lobed, spine-like or serrated blade-like structures on the dorsomedian surface of the valve, *viz.* basal lobe of cucullus, apical spine of sacculus, and crista; 2) rounded anterior end of the juxta; 3) bifid uncus; and 4) aedeagus closed basally. These synapomorphies indicate that the species of *Clossiana* and *Proclossiana* are subsets of a larger concept, *Boloria sensu* North American authors before 1981, and justify our use of *Boloria* for *B. natazhati*.

ACKNOWLEDGMENTS

Without the logistical support of the Polar Continental Shelf Project, under the direction of Dr. G. D. Hobson, this study would not have been possible. We also thank J. D. Lafontaine, S. A. Marshall, K. W. Philip, and D. A. St-Onge for their help and advice, and M. D. Bowers, for arranging the loan of the *nabokovi* types. This project was partially funded by a grant from the Canadian Department of Indian Affairs and Northern Development.

LITERATURE CITED

DOS PASSOS, C. F. 1964. A synonymic list of the Nearctic Rhopalocera. Lepid. Soc. Mem. 1., 145 pp.

FERRIS, C., C. F. DOS PASSOS, J. A. EBNER & J. D. LAFONTAINE. 1983. An annotated list of the butterflies (Lepidoptera) of the Yukon Territory, Canada. Can. Entomol. 115:823–840.

GIBSON, A. 1920. The Lepidoptera collected by the Canadian arctic expedition 1913–1918. Part I *in* Report of the Canadian arctic expedition 1913–18. Vol. III, Insects: 21i–22i.

HODGES, R. W. ET AL. 1983. Checklist of the Lepidoptera of America north of Mexico. E. W. Classey Ltd. & The Wedge Entomol. Res. Found., London. 284 pp.

HOLLAND, W. J. 1947. The butterfly book. New and thoroughly revised edition. Doubleday and Co., New York. 424 pp.

HOWE, W. H. 1975. The butterflies of North America. Doubleday and Co., New York. 633 pp.

HÜBNER, J. 1819. Verz. bekannt. Schmett. (2):30.

MILLER, L. D. & F. M. BROWN. 1981. A catalogue/checklist of the butterflies of America north of Mexico. The Lepid. Soc. Mem. 2, 280 pp.

MOORE, F. 1900. Lepidoptera Indica 4:243.

REUSS, T. 1919. Die Androconien von *Ramea cytheris* Drury und die nachststehenden analogen Schuppenbildungen bei *Dione* Hbn. und *Brenthis* Hbn. (Lep.). Entomol. Mitt. 8:192.

——— 1926. Systematischer Ueberblik der Dryadinae T. Rss. mit einigen Neubeschreibungen (Lep. Rhopal.). Deutche Entomol. Zeit. 51:168.

SCOTT, J. A. 1986. The butterflies of North America: A natural history and field guide. Stanford University Press. Stanford, California. 583 pp.

SKINNER, H. 1902. A new species of *Melitaea*. Entomol. News. 13:304.

STALLINGS, D. & J. R. TURNER. 1947. New American butterflies. Can. Entomol. 78: 134–135.

THUNBERG, 1791. D. D. Dissert Ent. Sist. Ins. Svecica (2):34–36.

TILDEN, J. W. & A. C. SMITH. 1986. A field guide to the western butterflies. Houghton Mifflin, Boston. 370 pp.

Received for publication 14 July 1989; revised 1 June 1990; accepted 5 July 1990.

Journal of the Lepidopterists' Society
44(3), 1990, 188–193

HIGH ANDEAN *CHLOROSTRYMON* (LYCAENIDAE) AND A NEW SPECIES FROM MT. LARANCAGUA, CHILE

KURT JOHNSON

Department of Entomology, American Museum of Natural History,
Central Park West at 79th Street, New York, New York 10024

ABSTRACT. *Chlorostrymon larancagua*, new species, is described and contrasted to another, little known, sympatric high Andean endemic, *C. kuscheli* (Ureta). Additional records are provided for *C. kuscheli* and a recently described austral endemic, *C. patagonia* Johnson. Previously unknown male genitalia of *C. kuscheli* are illustrated.

Additional key words: Eumaeini, systematics, biogeography, *Chlorostrymon larancagua, Chlorostrymon kuscheli.*

I recently revised *Chlorostrymon* Clench (Lycaenidae) to comprise six species, including as a new combination high Andean *C. kuscheli* (Ureta) and the new austral species *C. patagonia* and *C. chileana* (Johnson 1989). Local or regional endemism in these latter three species contrasts with cosmopolitanism in the mainland Neotropical type species *C. telea* (Hewitson), Antillean *C. maesites* (Herrich-Schaeffer) and pan-Neotropical *C. simaethis* (Drury).

Subsequently, Z. D. Ajmat de Toledo (Instituto Miguel Lillo, Tucumán, Argentina "IML") sent the American Museum of Natural History (AMNH) specimens believed to be additional representatives of *C. kuscheli* from Mt. Larancagua (18°08'S, 69°08'W), Tarapacá State, Chile. *Chlorostrymon kuscheli,* a small species (forewing, base to apex ["FW"] 8.0–9.5 mm, n = 4) with white forewing and hindwing under surface bands somewhat similar to *C. simaethis,* has been known only from the short type series collected from 2700–3650 m on Mt. Larancagua by Ureta (Ureta 1949). Male genitalia of the type series were not fully intact though generic placement was readily confirmed from the extant male aedeagus and female genitalia (Johnson 1989).

The three specimens forwarded from IML included a male and female of *C. kuscheli* (Figs. 1, 2), easily identified by small size (FW's, respectively, 9.5, 8.5 mm), narrow but continuous white under surface bands, and upper surface hindwing rufous limbal patch. The third specimen, however, clearly represented an undescribed species of the *C. telea*-like complex of *Chlorostrymon.* Under surface bands in *C. telea, C. maesites,* and *C. patagonia* are limited to a jagged or broken postmedial line on the hindwing.

Because cosmopolitan *C. simaethis, C. telea,* and *C. maesites* are widely sympatric throughout the neotropics (Johnson 1989, Fig. 4) discovery of sympatric high Andean elements of the genus is of great interest. This paper describes the new species, further documents *C. kuscheli,* and, because high Andean and austral members of *Chlorostry-*

FIG. 1. Females of *C. larancagua* (A) and *C. kuscheli* (B) from Mt. Larancagua, Chile (dorsal, left; ventral, right). Medial <-shaped mark on *C. larancagua* VHW is wing damage.

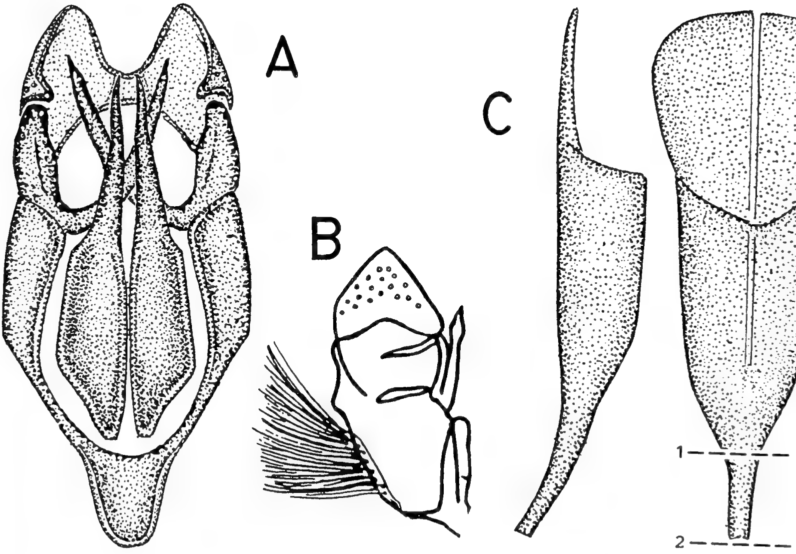


FIG. 2. Genitalia. A, B. Previously unknown male genitalic parts of *C. kuscheli* (AMNH): A, ventral view, aedeagus removed (for aedeagus see Johnson 1989, Fig. 5N); B, lateral view, vinculum dorsal margin with brush organs abutting (for *C. kuscheli* female, see Johnson 1989, Fig. 6M). C. Female genital plate, *C. larancagua* holotype (lateral view, left; ventral view, right); lines 1, 2 for comparative purposes (1, juncture of maximal ductal sclerotin and elongate membranous tube preceding corpus bursae in *C. patagonia* and *C. chileana*; 2, location of direct attachment of corpus bursae in *C. larancagua*).

mon have only recently been recognized (Johnson 1989), provides further records of the Patagonian endemic, *C. patagonia*. *Chlorostrymon patagonia* and the new species lack prominent under surface bands.

The new species can be distinguished by the following addition to couplet 3 of the generic wing character key (Johnson 1989, p. 123).

3[A] VHW postdiscal band distinctive only costad vein M3 .... *chileana*
VHW postdiscal band distinctive only caudad vein M3 .... 3[B]
3[B] VHW ground green, FW costal fold extremely wide ($\geq$1 mm) and rufous colored .... *patagonia*
VHW ground mottled yellow-brown, FW costa fuscus and not otherwise outstanding (width $<$1 mm) .... *larancagua*, new species

Description below follows on the generic diagnosis, species criteria and character terminology of the generic revision ("DFW, DHW" and "VFW, VHW" refer to dorsal and ventral fore- and hindwing surfaces, respectively).

Chlorostrymon larancagua, new species

(Figs. 1A, 2C)

DIAGNOSIS. Superficially distinguished by small size (FW 8.0 mm), VFW, VHW mottled yellow & brown ground, VHW with banding restricted to slight white dashes (cells CuA1 to CuA2) and limbal suffusion limited to a brown tint. Sympatric *C. kuscheli* (FW 8.0–9.5 mm) distinguished on VFW, VHW by green ground with narrow but continuous white bands and DHW rufous limbal patch. Female genitalia of *C. larancagua* distinctive with wide terminal lamellae, steeply tapering antrum and short, thin (but fully sclerotized) ductus bursae (see below and Johnson 1989, Fig. 6).

DESCRIPTION. Female: Fig. 1A. DFW, DHW, brown, slightly suffused blue at bases. VFW dusky yellow, distally tinted brown; VHW ground dusky yellow mottled with brown, postmedial area of cells CuA2 and CuA1 with obscure white dashes, limbal area tinted darker brown. **Female Genitalia:** Fig. 2C. Terminal lamella wide and antrum steeply tapered; ductus bursae short *sensu* Johnson 1989 (Fig. 7B, ratio of transparent dorsal suture line of ductus bursae to remaining length of ductus bursae ["d.s.l./d"] = 5.00), and thin (maximal ductus bursae width/maximal antrum width = 0.15) [d.s.l./d other taxa (Johnson 1989): *simaethis* = 0.37, *telea* = 0.39, *maesites* = 0.30, *patagonia* (all types) = 0.31, *chileana* (all types) = 0.62]; corpus bursae lacking signa (see Discussion).

TYPE. Holotype female, CHILE, Tarapacá State, Mt. Larancagua, 2700 m, 9 December, collector and year not noted (see Discussion); deposited IML.

ETYMOLOGY. The name is taken from the local area of endemism.

DISCUSSION

COLLECTION DATA. All three IML Larancagua specimens have identical month/day notations and the altitudes recorded are similar; the male specimen of *C. kuscheli* is marked as a Ureta collection. No label gives a year but day/month notations correspond to the data on Ureta's 1946 collections (Ureta 1949). Thus, it is probable that all three specimens derive from the 1940–48 Ureta samples (see Ureta 1949, Johnson 1989). If so, it is apparent why Ureta did not include them in his 1949 description of *Thecla kuscheli* or recognize the species described herein: the specimens were given to K. Hayward in 1946. According to affixed labels, Hayward took the specimens to the British Museum (Natural History) where they were all identified as "sp. nr. telea" and returned to the IML in 1948.

CHARACTERS. Wings: except for occasional dwarf *C. telea* or *C. maesites*, both *C. kuscheli* and *C. larancagua* appear consistently much smaller than congeners (see above and Johnson 1989). From generic characters it can be suggested that the dorsal wing coloration in male *C. larancagua* is probably iridescent blue (as in *C. telea* and *C. maesites*) or red-violet (as in *C. patagonia*). Of the *C. telea*-like complex, only *C. patagonia* displays limited VFW-VHW markings like *C. larancagua*. However, *C. patagonia* (FW 10.0–13.0 mm, n = 12) has a green ground color, rusty red and gray VHW limbal suffusion and a distinctive rufous FW costal fold.

Female genitalia: the ductus bursae in all *Chlorostrymon* species terminates with a widely fluted antrum (Johnson 1989, Fig. 6). In *C. simaethis, C. telea, C. maesites,* and *C. kuscheli,* a constricted, elongate, sclerotized tube joins the antrum to the corpus bursae. In *C. chileana* and *C. patagonia,* connection of the antrum to the corpus bursae, although elongate, is completely membranous. In *C. larancagua* there is a distinct sclerotized tube cephalad of the antrum (Fig. 2C1, 2) but, although it connects directly with the corpus bursae, it is extremely short and constricted.

Male genitalia: genitalia of the type series of *C. kuscheli* were not fully intact (Johnson 1989). Based on new specimens, genital parts of *C. kuscheli* not previously illustrated are included in Fig. 2A, B. Distinctive are a broad valval ventrum (2A), centro-terminal production of the labides (2A, B), and a curvate ventral vincular margin with consequent clustering of the brush organs (2B).

BIOGEOGRAPHY. Both *C. kuscheli* and *C. larancagua* are recorded from 2700–3650 m, Mt. Larancagua, Chile. Cerro Larancagua (summit 5368 m), located along the border between Chile and Bolivia (18°08′S, 69°08′W), exhibits a high altitude desert flora and altiplano fauna more typical of immediately adjacent high volcanic mountains of Bolivia and Peru than the rest of Chile (A. M. Shapiro, pers. comm.). It is possible that *C. larancagua* and *C. kuscheli* occur throughout this immediate high montane region. Johnson (1989) and Nicolay (1980) noted that other montane *Chlorostrymon* populations (occurring up to 1820 m in Ecuador [Baños, Brown 1941]) fit the species diagnoses of either *C. simaethis* or *C. telea.* Records of these two species from Argentina (Johnson 1989 and below) are from lowland (250–500 m) chaco biomes.

Ventral wing pattern and genitalia indicate *C. kuscheli* and *C. larancagua* are high montane endemics of the respective "simaethis" and "telea" subgroups of *Chlorostrymon.* Johnson (1989) suggested that widespread neotropical sympatry of these subgroups, and lack of a clear eumaeine outgroup, imply *Chlorostrymon* may be very old. High montane sympatry of *C. larancagua* and *C. kuscheli* might be similarly construed since a vicariant origin for the distribution would require simultaneous, *in situ,* upland isolation of ancestral elements representing both *Chlorostrymon* subgroups. Andean uplift in the Mt. Larancagua region began in the Miocene (Gansser 1973).

MATERIAL EXAMINED (high Andean, temperate & austral S American records additional to Johnson 1989): New records of *C. kuscheli*: CHILE. Mt. Larancagua, 2800 m, 9 December, leg. Ureta (one male, IML), same data but 2700 m and no leg. (one female, AMNH). New southern range extreme for *C. telea*: ARGENTINA. Catamarca Prov., San Antonio, 18 February 1958, leg. R. Golbach (one male, IML) (typical of Fig. 2B, Johnson 1989); additional new N Argentina records: Sante Fe Prov., Villa Ana [at 250 m], December 1928, leg. K. Hayward (one male, IML); Salta Prov., Santa María, 250 m, 5 November 1974, leg. B. MacPherson (one male, MacPherson Collection "MC"), same data but leg. R. Eisele (one male, Eisele Collection "EC"), Pichanal, 300 m, 17 May 1972, leg. R. Eisele (one female, EC), Tartagal, 500 m, 20 December 24, leg. B. MacPherson (one female, MC) (all typical of figs. 2B, females figs. 6K, Johnson 1989). New records of *C. patagonia*: ARGENTINA. Río Negro Prov. [Patagonia], San Carlos de Bariloche, 2 January 1950, leg. not noted (four males, AMNH).

ACKNOWLEDGMENTS

I thank Z. D. Ajmat de Toledo (IML), Robert C. Eisele, and Ruth Eisele for facilitating hand delivery of IML specimens. I again thank L. D. Miller (Allyn Museum, Florida Museum of Natural History) for facilitating the original loans of *C. kuscheli* and David Matusik (Field Museum of Natural History) for aiding in specimen acquisition. Arthur M. Shapiro (University of California, Davis) made extremely helpful review comments.

LITERATURE CITED

BROWN, F. M. 1941. A gazetteer of entomological stations in Ecuador. Ann. Entomol. Soc. Amer. 34:809–851.

GANSSER, A. 1973. Facts and theories of the Andes. J. Geol. Soc. London 13:93–131.

JOHNSON, K. 1989. Revision of *Chlorostrymon* Clench and description of two new austral Neotropical species (Lycaenidae). J. Lepid. Soc. 43:120–146.

——— in press. *Penaincisalia*, a new genus of "elfin"-like butterflies from the high Andes (Lepidoptera: Lycaenidae). Pan-Pacific Entomol.

NICOLAY, S. S. 1980. The genus *Chlorostrymon* and a new subspecies of *C. simaethis*. J. Lepid. Soc. 34:253–256.

URETA, R. E. 1949. Lepidopteros de Chile (Rhopalocera). IV Parte. Familia Lycaenidae. Bol. Mus. Nac. Hist. Nat. Chile 24:93–123.

Received for publication 17 October 1989; revised and accepted 5 July 1990.

PROFILES

Journal of the Lepidopterists' Society
44(3), 1990, 194–198

THE JOHN T. MASON COLLECTION AT THE DENVER MUSEUM OF NATURAL HISTORY

ELIZABETH A. WEBB AND RICHARD S. PEIGLER

Department of Zoology, Denver Museum of Natural History,
2001 Colorado Boulevard, Denver, Colorado 80205

ABSTRACT. John T. Mason (1853–1928) was an amateur lepidopterist who amassed a large collection of butterflies and moths, most of which is now housed in the Denver Museum of Natural History in Colorado. The collection was made by Mason's own field collecting as well as by purchases from other well-known collectors and dealers including William Barnes, Otto Staudinger, and others. The majority of the material is from Europe and Jalapa, Veracruz, Mexico. At least eight patronyms of Lepidoptera honor Mason. Six primary type specimens of Lepidoptera have been located in Mason's collection, and the Museum also has three additional butterfly type specimens added in more recent years.

Additional key words: type specimens, biography, patronyms, Colorado, Mexico.

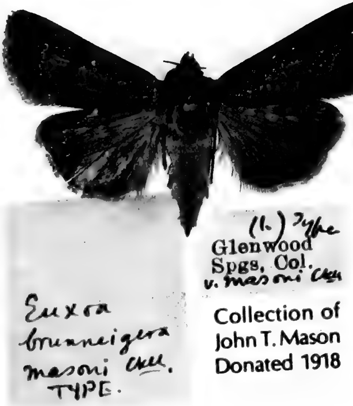
John T. Mason worked with the founders of the Colorado [now Denver] Museum of Natural History (incorporated in 1900), served as Curator during the Museum's formative years, and was in charge of operations until the first Director, Jesse D. Figgins, was appointed in 1910. Born in Lincolnshire, England, in 1853, Mason joined the ranks of avid natural history collectors as a boy of twelve. By the age of fifteen, Jack had amassed a fine collection of birds, bird eggs, and butterflies. When schoolmates traveled to Australia and sent home specimens of birds, the young naturalist mounted them, and kept one specimen of each species for his private collection.

Mason came to the United States in 1872 and lived for short periods in New York, Mississippi, and Galveston, Texas, then eventually settled in Houston, Texas. There he married a Miss Schaffter of Galveston in 1877 and opened a large department store, accumulating a fortune in the mercantile business from 1880 to 1892. Mason moved to Denver, Colorado, in 1895. By the time he retired from business, his zeal for collecting had grown into a scientific avocation. He was sent to Mexico by the United States as government collector of butterflies. In 1928, he died in Pasadena, California, eight years after moving there from Colorado. The John T. Mason Park in Houston is located on land donated in 1930 by his second wife. The house where Mason resided in Denver was restored and opened in 1989 as a bed and breakfast inn (Castle Marne, 1572 Race Street). Fig. 1 is a portrait of Mason given to us by Edward D. White, a great-nephew of John Mason.

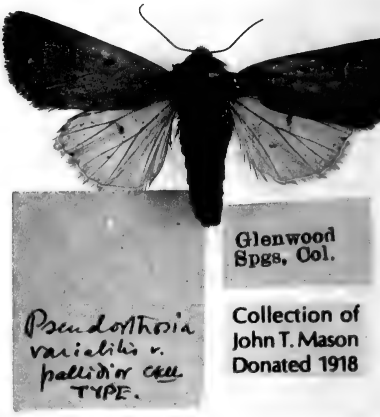
FIG. 1. Portrait of John T. Mason.

The Mason Lepidoptera Collection

Mason donated his worldwide collection of over 20,000 butterflies and moths to the Museum in 1918. This forms the basis for the Museum's Lepidoptera collection. Many of the specimens in the Mason Collection were obtained in the field by Mason, others through purchase and exchange with renowned collectors such as the Grand Duke Michael of Russia, the great collectors for the Natural History Museum in London (formerly British Museum (Natural History)), and William Schaus of New York. It is surmised that Mason did his own collecting in Jalapa, Veracruz; Harris County, Texas; and Glenwood Springs, Colorado. Smaller collections have been added in recent years from staff fieldwork and donations. Mason's collection is particularly strong in all families of butterflies from North America, Mexico, and Europe, with occasional specimens from India, Africa, Japan, New Guinea, and Cuba. The moth families best represented are Sphingidae, Arctiidae, and Geometridae, although there are modest series of Noctuidae, Pyralidae, Notodontidae, and Saturniidae. The Microlepidoptera (except Pyralidae and Cossidae)



2



3

FIG. 2. Holotype of *Euxoa brunneigera masoni* Cockerell.
FIG. 3. Holotype of *Pseudorthosia variabilis pallidior* Cockerell.

are weakly represented. The genus *Catocala* is well represented, filling several drawers.

Mason's second wife, Dora Porter Mason, assisted him in building the collection and was a patron of the Museum. Selected specimens from the Mason Collection first went on exhibit from 1929 to 1938, when they were temporarily withdrawn to design a more contemporary exhibit. The Colorado Butterflies and Moths Exhibit, which opened in 1940, was funded by Mrs. Mason and named the Dora Porter Mason Butterfly Hall. The exhibit closed in 1986 when the wing in which it was housed was demolished to make room for Museum expansion. Because of the historical significance of the Mason Collection, specimens will remain in storage in the Zoology Department research collection and will be available for study. In 1990, a new exhibit on Colorado butterflies and moths was installed, for which the primary consultant was Dr. Ray Stanford who selected and identified all of the butterflies.

There is evidence that Mr. Frank Howland, Curator of Geology and Mineralogy, was caretaker for the collection from the late 1920s through 1935. Mr. Frank Clay Cross, Honorary Curator of Entomology, began curating the collection in 1936 (Cross 1937). Under Cross' direction, Robert Potts and Charles W. Dawson reorganized the collection. During the reorganization, several types and paratypes of moths and butterflies came to light which were to have been published by Cross, but apparently this was not done. Some of these were rediscovered by R. S. Peigler and Andrew D. Warren in 1987–89 during the most recent reorganization of the collection. The purpose of this paper is to make the existence of the collection known to the scientific community and to cite the primary type material that it contains. We provide illustrations of two holotypes that have not been figured previously.

Patronyms

Patronyms honoring Mason, aside from those listed below under the section on type material, include the following which were all described from Jalapa, Veracruz, Mexico:

Plusia masoni Schaus, Noctuidae. See Schaus (1894).
Eacles masoni Schaus, Saturniidae. See Oiticica (1956) and Lemaire (1988).
Halysidota masoni (Schaus), Arctiidae. See Watson (1980).
Psychonoctua masoni (Schaus), Cossidae. See Blanchard and Knudson (1985).
Charadra masoni Schaus, Noctuidae. See Schaus (1894).

Type Specimens

Noctuidae: *Rhododipsa masoni* J. B. Smith (1896). Paralectotype male, figured by Byers (1989). Now known as *Schinia masoni*. We have "Type 2" from the series of four syntypes bearing labels written by Smith. Todd (1982) reported this specimen as lost and selected Type 1 as lectotype among the remaining three syntypes in the National Museum of Natural History.

Euxoa brunneigera masoni Cockerell (1905). Holotype female (Fig. 2). A junior synonym of *Euxoa comosa comosa* (Morrison) according to Lafontaine (1987), who reported that the holotype of *masoni* had not been located. The specimen agrees fairly well with Lafontaine's color figures 2 and 3 on Plate 5, and we therefore agree with the synonymy. The holotype of *masoni* is from Glenwood Springs, Colorado, and bears a type label in Cockerell's handwriting.

Pseudorthosia variabilis pallidior Cockerell (1906). Holotype female (Fig. 3). This specimen is from Glenwood Springs, Colorado, and also has a type label written by Cockerell.

Arctiidae: *Eupseudosoma floridum* Grote (1882). Syntype male. Now considered a subspecies of the Neotropical *E. involutum* (Sepp). The type label is in Grote's handwriting (Horn & Kahle 1935–37). Grote routinely labeled every specimen in a type series with the word "Type" (Todd 1982: 1).

Zygaenidae: *Triprocris martenii* French (1883). Syntype female. Now known as *Pyromorpha martenii* (see Hodges et al. 1983: 66). The specimen bears the following three labels: Ariz./Type/Aglaope Ariz. French. The latter is in Mason's handwriting.

Satyridae: *Cercyonis masoni* Cross (1937). Holotype male figured in original description. Now considered to be a subspecies of *C. sthenele* (Boisduval) (see Miller & Brown 1981: 196).

Nymphalidae: *Chlosyne definita* (E. M. Aaron). This syntype is probably the individual specimen intended by Aaron to be the type (Roy O. Kendall, pers. comm.).

Lycaenidae: *Satyrium behrii crossi* (Field). Paratype number 14 of *Callipsyche behrii crossi*.

Incisalia polia obscura Ferris & Fisher. Paratype number 163.

ACKNOWLEDGMENTS

We thank the following who provided literature references and other pertinent information: Julian P. Donahue (Natural History Museum of Los Angeles County), Ronald W. Hodges (National Museum of Natural History), Roy O. Kendall (San Antonio, Texas), Allan Watson (The Natural History Museum, London), Timothy P. Friedlander, Edward C. Knudson (Bellaire, Texas), and Kristine Haglund (Archivist, Denver Museum of Natural History). Gary D. Hall photographed the type specimens. Significant curatorial assistance on the Mason Collection has been given by Andrew D. Warren, who located all of the butterflies cited in this paper as well as specimens of extinct species, and Nancy K. Hendler.

Diane and Jim Peiker, owners of the house where Mason lived in Denver, and Edward D. White generously shared historical and biographical information.

LITERATURE CITED

BLANCHARD, A. & E. C. KNUDSON. 1985. *Psychonoctua masoni* (Schaus), new combination (Lepidoptera: Cossidae: Zeuzerinae), redescription and first records from Texas and USA. Proc. Entomol. Soc. Wash. 87:426–431.

BYERS, B. A. 1989. Biology and immature stages of *Schinia masoni* (Noctuidae). J. Lepid. Soc. 43:210–216.

COCKERELL, T. D. A. 1905. Miscellaneous notes. Can. Ent. 137:361–362.

——— 1906. [Untitled note]. Entomol. News 17:204.

CROSS, F. C. 1937. Butterflies of Colorado. Proc. Colo. Mus. Nat. Hist. 16:9–10.

FRENCH, G. H. 1883 [1884]. A new zygaenid: Triprocris martenii, n. sp. Papilio 3:191–192.

GROTE, A. R. 1882. New moths. Can. Ent. 14:181–188.

HODGES, R. W. ET AL. 1983. Check list of the Lepidoptera of America north of Mexico including Greenland. E. W. Classey, Ltd., and The Wedge Entomol. Res. Found., London. xxiv + 284 pp.

HORN, W. & I. KAHLE. 1935–1937. Ueber entomologische Sammlungen, Entomologen & Entomo-Museologie (Ein Beitrag zur Geschichte der Entomologie), parts 1–3. Entomol. Beihefte, Berlin-Dahlem, Vols. 2–4. vi + 536 pp., 38 pls.

LAFONTAINE, J. D. 1987. Noctuoidea, Noctuidae (part), Noctuinae (part—*Euxoa*), fasc. 27.2. *In* Dominick, R. B. et al., The moths of America north of Mexico including Greenland. Wedge Entomol. Research Foundation, Washington, 237 pp., 8 col. pls.

LEMAIRE, C. 1988. Les Saturniidae américains . . . The Saturniidae of America . . . Los Saturniidae americanos (=Attacidae), Ceratocampinae. Mus. Nac. Costa Rica, San José. 479 pp., 64 pls. (62 col.).

MILLER, L. D. & F. M. BROWN. 1981. A catalogue/checklist of the butterflies of America north of Mexico. Lepid. Soc. Mem. 2, vii + 280 pp.

OITICICA, J., JR. 1956. Tipos do Saturnioidea no United States National Museum, 1—Gênero *Eacles* Hübner, [1819], (Lepidoptera, Citheroniinae). Bol. Mus. Nac., Zool. (n. sér.), Rio de Janeiro, No. 137:1–53.

SCHAUS, W. 1894. New species of Noctuidae from tropical America. Trans. Amer. Entomol. Soc. 21:223–244.

SMITH, J. B. 1896. A new species of Rhododipsa. Entomol. News. 7:284–285.

TODD, E. L. 1982. The noctuid type material of John B. Smith (Lepidoptera). U.S. Dept. Agric. Techn. Bull. 1645. iii + 228 pp.

WATSON, A. 1980. A revision of the *Halysidota tessellaris* species-group (*Halysidota* sensu stricto) (Lepidoptera: Arctiidae). Bull. Brit. Mus. (Nat. Hist.) Ent. 40:1–65.

Received for publication 1 February 1990; revised and accepted 5 July 1990.

GENERAL NOTES

Journal of the Lepidopterists' Society
44(3), 1990, 199–200

PARASITISM OF NEW ENGLAND BUCKMOTH CATERPILLARS (*HEMILEUCA LUCINA*: SATURNIIDAE) BY TACHINID FLIES

Additional key words: *Compsilura concinnata,* defense, gregarious, *Hyposoter fugitivus*.

We report here the interactions of larvae of *Hemileuca lucina* Hy. Edw. (Saturniidae) and tachinid parasitoids (Diptera: Tachinidae) and the resulting level of parasitism of aggregated versus solitary larvae at Leverett (Franklin Co.), Massachusetts in 1985. On 2 June, tachinid flies were observed attacking three aggregations of third instar *H. lucina* larvae feeding on *Spiraea latifolia* Ait. Bork (Rosaceae). One fly was attacking each aggregation. Although in some instances the flies were able to land on the larvae, walk on them and probe with the ovipositor, in many cases the larvae began thrashing as the flies (either flying or walking) approached within 2.5 cm. Once the larvae began thrashing, the flies retreated to nearby branches (<15 cm away) and periodically resumed attacking the larvae. Larvae in two of the aggregations being attacked were in the process of molting. The third group of (non-molting) larvae was attacked repeatedly by a fly during the two-hour observation period and consequently fed little.

Attacks were also observed on 7 June, and larvae collected then were reared to identify the parasitoids. In addition, to determine the level of parasitism at the site, 234 fourth instar larvae were collected and reared to pupation. During collection, some larvae were found aggregated. Others were solitary, which can occur: 1) throughout the larval period but is most frequent in the later instars as aggregation tendency declines (Cornell, J. C., N. E. Stamp & M. D. Bowers 1987, Behav. Ecol. Sociobiol. 20:383–388) and 2) when predators trigger escape behaviors after which the larvae fail to re-aggregate (Stamp, N. E. & M. D. Bowers 1988, Oecologia 75:619–624). Of the 49 larvae that were found at least 20 cm from other individuals and 50 cm or more from aggregations, 53% were parasitized. In contrast, of the 185 larvae in groups, with mean group size of 10 (±4 SD, $n = 18$), only 26% were parasitized. That the solitary larvae more frequently contained parasites ($\chi^2 = 11.95$, $P < 0.001$) may mean that: 1) solitary larvae are more vulnerable to the flies; 2) larvae attacked by the flies are more likely to drop to the ground, an escape behavior exhibited by these larvae, and then fail to rejoin an aggregation; and/or 3) parasitized larvae have less of an aggregation tendency than unparasitized larvae.

The majority of the parasitism was due to the tachinid fly *Compsilura concinnata* (Mg.) (identified by Monty Wood, Biostematics Research Institute, Ottawa, Ontario). This parasitoid deposits live larvae into its hosts (Clausen, C. P. 1940, Entomophagous insects, McGraw-Hill, New York–London, 688 pp.). It was introduced for biological control of gypsy moths, but it has been recorded from about 200 species (Clausen, C. P. 1956, Biological control of insect pests in the continental United States, U.S.D.A. Tech. Bull. 1139, 151 pp.).

Three of the larvae from groups were parasitized by an ichneumonid wasp *Hyposoter fugitivus* (Say) (Hymenoptera: Ichneumonidae) (identified by Scott Shaw, Univ. of Wyoming). This parasitoid is also a generalist and has been reported from *Hemileuca maia* (Drury) (Carlson, R. W. 1979, Ichneumonidae, p. 677 *in* Krombein, K. V., P. D. Hurd, Jr., D. R. Smith & B. D. Burks (eds.), Catalog of Hymenoptera in America north of Mexico, Smithsonian Inst., Washington, D.C., 1198 pp.).

We also observed the behavior of the tachinid flies attacking third and fourth instar *H. lucina* larvae in screened cages (60 × 60 × 80 cm length) in the laboratory. These flies had emerged from *H. lucina* larvae in the laboratory. After discovering the larval aggregation, the flies perched on nearby leaves or branches before attacking. Not all fly attacks resulted in contact with a larva. When a fly disturbed the larvae, the entire aggregation often began thrashing for up to 20 min and that often appeared to prevent fly contact with the larvae. As noted in field observations, some larvae attacked by the flies immediately dropped to the ground.

NANCY E. STAMP, *Department of Biological Sciences, State University of New York, Binghamton, New York 13901,* AND M. DEANE BOWERS, *University of Colorado Museum and Department of E.P.O. Biology, Campus Box 334, University of Colorado, Boulder, Colorado 80309.*

Received 12 August 1989; revised and accepted 23 June 1990.

Journal of the Lepidopterists' Society
44(3), 1990, 200–201

URBAN BIOLOGY OF *LEPTOTES MARINA* (REAKIRT) (LYCAENIDAE)

Additional key words: *Plumbago auriculata*, myrmecophily, predators, parasitoids, ecology.

Leptotes marina (Reakirt) is a widespread lycaenid butterfly, ranging from southwestern United States to northern Central America. Ecologically versatile, it occurs in a wide range of habitats from xeric deserts to coniferous forests or tropical lowlands. As early as the 1920s, *L. marina* had become a common backyard species in southern California; J. A. Comstock (1930:177, Butterflies of California, published by the author, Los Angeles, 334 pp.) reported the ornamental *Wisteria* (Fabaceae) as the larval host in these situations. Since that time, *L. marina* has become increasingly urbanized. Although larvae feed on Fabaceae in native situations, the primary host in urban environments today is the perennial Cape Plumago (*Plumbago auriculata* Lam.; Plumbaginaceae), a bush introduced from South Africa and used widely as a garden ornamental and in freeway landscaping. In contrast to the spring blooming *Wisteria, P. auriculata* may bloom year round, providing larval resources throughout the year.

An urban site approximately 2.5 km east of Imperial Beach, San Diego County, California, harbors a large population of *L. marina,* and this locality was the source of the following observations.

Eggs are laid singly on the calyx and developing buds of *P. auriculata.* The young larva bores a hole into the bud near the base, where it feeds primarily on plant reproductive tissue. Later instars may devour nearly the entire bud or developing seeds. Flower petals are eaten rarely; larvae were never observed to feed on foliage. A single bush of *P. auriculata* may support a substantial population of the butterfly without exhibiting noticeable damage from larval feeding. The butterfly appears to be continually brooded. Although adults may be taken throughout the year, population density is conspicuously depressed from December to February or March in most years.

All larvae observed in the field (n = 15) were closely associated with Argentine ants [*Iridomyrmex humilis* (Mayr); Hymenoptera: Formicidae]; ants were either on or within a centimeter of larvae. Larvae were never observed in the absence of ants; three to five ants on a single inflorescence always indicated the presence of one or more larvae. Larvae reared in the laboratory in cardboard cartons at ambient temperature developed normally in the absence of ants. As reported previously for *L. marina* and for many other lycaenids (Ballmer, G. & G. Pratt 1989, J. Res. Lepid. 27:1–81), larval coloration and markings are extremely variable. Of 20 larvae brought into the laboratory, 3 produced single braconid parasitoids (*Cotesia* sp.; Hymenoptera: Braconidae: Microgastrinae) that pupated in silken white cocoons attached either to the host material or to the paper-towel substrate. In the laboratory, larvae of *L. marina* left the host material to pupate. Pupae were attached to the substrate by a cremaster and a silken girdle. The pupation period lasted seven days.

The only nectar source at which I observed adults was Brazilian Pepper (*Schinus terebinthifolius* Raddi; Anacardiaceae). The small white flowers of Brazilian Pepper attract a large number of hymenopteran and dipteran visitors, but few, if any other Lepidoptera. Ornamental *Cassia* sp. (Fabaceae) and *Lantana* sp. (Verbenaceae) are used occasionally as perching substrates, but I never observed *L. marina* nectaring on these plants. Although the butterfly literally may swarm around the host, I never observed *L. marina* nectaring on the larval host. This probably is due to the long corolla compared to the length of the butterfly's proboscis (Opler, P. & G. Krizek 1984:32, Butterflies east of the Great Plains, Johns Hopkins Univ. Press, 294 pp.).

A small noctuid larva, inadvertently collected while gathering inflorescences of plumbago, produced an adult of *Heliothis virescens* (Fabricius) (Noctuidae). This was the only other lepidopterous larva observed feeding on plumbago.

On 13 August 1989, 1130 hours, I observed a female *L. marina* that had been captured by a green lynx spider [*Peucetia viridans* (Hentz); Oxyopidae] on a *Cassia* bush. These spiders ambush their prey, which consists primarily of moths, both adults and larvae, but also many other kinds of insects (Whitcomb, W., M. Hite & R. Eason 1966, J. Kansas Entomol. Soc. 39:259–267).

Leptotes marina is one of few native North American butterflies that has benefited from the activities of man by its remarkable switch to a new larval host introduced from South Africa and to a nectar source and an ant introduced from South America, none of which are closely related to the butterfly's native resources. This flexibility undoubtedly has led to an expansion in range, at least ecologically and temporally, over the past 60 years, resulting in the butterfly's invasion and successful colonization of urban environments.

I thank Roy Snelling for identifying the ants associated with the larvae, and James Whitfield for identifying the parasitoids. I gratefully acknowledge Sterling Mattoon and Ronald Flaspohler for many helpful suggestions that improved the quality of this brief manuscript.

JOHN W. BROWN, *Entomology Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.*

Received for publication 28 November 1989; revised and accepted 18 June 1990.

Journal of the Lepidopterists' Society
44(3), 1990, 201–202

NORTHWARD DISPERSAL OF *EUPTOIETA CLAUDIA* (NYMPHALIDAE) IN CALIFORNIA AND NEVADA IN 1988

Additional key words: distribution, biogeography.

The Variegated Fritillary, *Euptoieta claudia* (Cramer), is a highly dispersive species whose late-summer range in North America frequently extends far beyond those areas where it is a permanent resident. Because of its frequent and occasionally massive northward movements, dot maps of its distribution tend to disguise its transient nature. J. A. Scott (1986, The butterflies of North America, Stanford University Press, Stanford, California, pp. 335–336) maps its transient range as covering most of North America, but it is conspicuously unmapped on the Pacific Coast north of the California Transverse Ranges. Except for a passing reference to a record in Mono County (J. A. Comstock, 1927, Butterflies of California, published by the author, Los Angeles, California, 334 pp.), the

California literature, both antique and recent, consistently treats *E. claudia* as a rare species confined to the southeastern corner of the state. This is especially significant given the long history and intensity of collecting in the state.

At least three *E. claudia* were taken far north of previous records in California in 1988. S.O.M. took an apparently very fresh female near Queen Lily Campground, N Fork Feather River, 4.8 km N Highway 70 near Belden, Plumas Co., el. 730 m, 19 August 1988 at almost exactly 40°00'N Lat. A.M.S. took an also apparently fresh female at the Burrowing Owl Reserve adjacent to the Recreation Pool at the University of California campus at Davis, Yolo Co., el. 17 m, 7 October 1988, 38°33'N. Both of these were taken nectaring at Yellow Star Thistle, *Centaurea solstitialis* L. (Compositae). O.S. took yet another very fresh female at Jerseydale, 13.6 km NE Mariposa, Mariposa Co., 1070 m, 23 October 1988, 37°34'N.

Although spread over two months, these records together suggest a significant northward movement in 1988, an interpretation borne out by the Nevada records compiled by G.T.A. Prior to 1988, Nevada records were as follows: Churchill Co. (1), Clark Co. (11), Douglas Co. (1), Lincoln Co. (3), Nye Co. (1) and White Pine Co. (1), distributed among years as follows: one each in 1969, 1972, 1975, 1978, 1981, 1983 and 1986; two (both Clark Co.) in 1968 and 7 in 1984 (4 Clark Co., 2 Lincoln Co., 1 Douglas Co.). G.T.A.'s 1988 records total 6: Lincoln Co.: Meadow Valley Wash, Grapevine Canyon, 12 April (sight); Lander Co.: Reese River Valley, U.S. 50, 4 mi E Reese River, 28 June (1 male); Clark Co.: Spring Mts., Lee Canyon Ski Area, 29 June (1 male) and Kyle Canyon Ski Area, 24 July (1 male); Elko Co.: Ruby Valley, NV 229, 3.5 km N jct. NV 789, 28 July (1 male); Pershing Co.: Humboldt Mts., Buena Vista Canyon, 30 July (1 male).

The early-season Nevada records combined with the apparently fresh condition of all the northern California specimens suggest that early immigrants west of the Sierra, themselves undetected, succeeded in breeding in 1988. It is not possible on internal evidence to rule out cross-Sierran dispersal, however. Two of the three California localities were in the Sierra Nevada and relatively close to the Great Basin localities apparently reached by *E. claudia* in 1988.

Our collective field experience of over a century leads us to regard this as a very unusual and noteworthy event which may or may not be significant in terms of the long-range dynamics of the species. No northern California records are known to us for 1989 or the first half of 1990. Atmospheric circulation in western North America was highly unusual in late winter-early spring 1988, producing an unprecedented ten-week drought from mid-January to March. Summer 1988 was one of the two hottest of record in much of northern and central California west of the Sierra Nevada; flight seasons of many low-altitude species were advanced by as much as a month, and extremely large northward migrations of the Painted Lady, *Vanessa cardui* L. (Nymphalidae) were observed beginning in February. Correlation is interesting, but cannot prove causation.

ARTHUR M. SHAPIRO, *Department of Zoology, University of California, Davis, California 95616;* STERLING O. MATTOON, *2109 Holly Avenue, Chico, California 95926;* GEORGE T. AUSTIN, *Nevada State Museum, 700 Twin Lakes Drive, Las Vegas, Nevada 89158;* AND OAKLEY SHIELDS, *6506 Jerseydale Road, Mariposa, California 95338.*

Received for publication 24 October 1988; revised 19 January 1989; revised and accepted 7 June 1990.

Journal of the Lepidopterists' Society
44(3), 1990, 203–204

BOOK REVIEWS

PORTRAITS OF SOUTH AUSTRALIAN GEOMETRID MOTHS, by Noel McFarland. 1988. Published and distributed by the author, P.O. Box 1404, Sierra Vista, Arizona, 85636 U.S.A. 408 pp., over 1400 B + W photographs. Soft cover, Quarto (26 × 35 mm), ISBN 0-935868-32-1, $80.00 (postpaid in USA).

This is a remarkable book. Never before, and probably never again, has so much information and so many photographs been assembled in one book on the metamorphosis of 72 species of moths. In a sense, this book is an autobiography of Noel McFarland, showing by example the kind of detailed, accurate and innovative scientific work he has done all his life.

The life history work upon which the book is based was performed by McFarland in 1965–69 while he was assistant curator at the South Australian Museum in Adelaide. The specimens remained there, but notes and photographs were retained by the author, allowing publication almost 20 years later. Private publication has permitted the author to include as much data on whatever topics he wished, limited only by the practicalities of publishing. This has resulted in the inclusion of many topics rarely seen in ordinary moth books. Nomenclature systems are proposed for adult and larval resting positions, which are diverse and complex in the Geometridae. Categories of larval crypsis are established, and each of the 72 species discussed is assigned to a category for the final instar. Items of "quoted wisdom" are interspersed throughout the book: this is an enjoyable touch not seen since the writings of W. J. Holland.

Rearing techniques not already published in articles in the *Journal of the Lepidopterists' Society* are given, including pupal handling and larval storage vial technology. Several sections encourage amateur entomologists to pursue independent studies and document their efforts in a complete and accurate manner, concluding with a philosophy of life for a true scientist.

The organization of the book is somewhat unusual, starting with the fact that the indices are up front. This is not chance; the author gives his reasons for every arrangement and inclusion. Other introductory material includes complete descriptions of localities, habitats and foodplants, with maps and photos. On page 45, the first of 46 life history chapters begins for *Ennominae* and *Oenochrominae*. A middle section, perhaps better put at the end, contains appendices, generalizations, and a Topic Index. While this is mostly valid material (e.g., the resting position nomenclature), its appearance in the middle of the life histories does seem disjointed. After 32 pages, the remaining 26 life histories are given, for all other Geometrid subfamilies. The volume concludes with a glossary, lists of references sorted three ways, and more explanatory material.

The life history chapters have been prepared according to a standard format that includes a place for every conceivable detail. There is information on the species name (original description reference, type locality, etc.), habitat, foodplant, adult, egg, larva, and pupa. There are photographs of each stage from various angles, with an average of 20 per chapter. There are cross references to the general sections of the book (which in turn are referenced to the chapters). Almost any detail that you can think of has been described in these truly complete portraits.

The photographs themselves deserve special attention. All are crystal clear and properly lighted to bring out every detail. The larvae display a variety of shapes, colors and resting positions—all perfectly matched to blend in with their respective foodplants. There is a cumulative effect in seeing so many diverse and clever adaptations in one book: it starts one pondering on the mysteries of nature. Then there are the adults. Many are pinned, spread specimens that adequately show the maculation. But an equal number of photos are of live adults, resting in a natural settled position on a glass plate. This shows an element of beauty not found in museum specimens. With just a bit of imagination, these moths can be seen as aerodynamic works of art. *Monoctenia falernaria*, viewed head on, is a Stealth Bomber with legs. *Oenochroma vinaria* is an amphibious high wing Patrol Plane. *Phallaria ophiusaria* has a most pleasing shape even without an airplane counterpart.

Every book with broad scope is bound to have a weakness, and this one is no exception. Taxonomy is one area in which McFarland has little interest, and thus it receives little attention in this book. Every attempt has been made to use the correct names for the 72 moths portrayed. One new combination has been published, where larval information made the previous generic assignment obviously wrong. Despite the desire for correct names, and the existence of life history data for almost 20 years, there are three (possibly four) un-named new species among the 72 in this book. This is certainly ironic; never has an un-named species been described in such detail in a publication. But Noel McFarland is not interested in creating zoological nomenclature, and apparently no one else is either, so that is the way it stands. E. Strand, who named all of Sir George Hampson's un-named aberrations, would have seized this opportunity with relish.

In closing, McFarland states that the primary purpose of the book was to "communicate my pleasure in the thrill of discovery, while undertaking the documentation of these 72 life history investigations." This goal has been admirably achieved. For the future, I hope that a companion volume will some day document the many life histories he has detailed subsequently in over 20 years of observations in Ash Canyon, Cochise Co., Arizona.

RON LEUSCHNER, *Research Associate, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.*

Journal of the Lepidopterists' Society
44(3), 1990, 204–205

MOTHS OF THAILAND, Vol. 1: SATURNIIDAE, by Amnuay Pinratana and Rudolf E. J. Lampe. 1990. Brothers of St. Gabriel in Thailand, St. Gabriel's College, Bangkok 10300, Thailand. v + 47 pp., 44 color plates. Hard cover, 19 × 26.5 cm, no ISBN, $22.00 U.S. (postpaid).

After producing a six-volume set on butterflies of Thailand (1977–88) of over 1000 pages of text, Brother Pinratana has now embarked on a treatment of Thai moths beginning with saturniids. The junior author is already a well-known saturniid specialist in Germany, having established his reputation with about 20 brief papers on life-histories of various species plus a lengthy paper on Saturniidae of West Malaysia. Their joint effort in the present volume is a fine success.

The book is attractive and well made, having been produced with sturdy binding and glossy pages, with gold lettering on the spine and front cover. The latter may be seen only rarely as it is covered by a beautiful dust jacket depicting on the back cover a life-sized male of *Actias rhodopneuma,* arguably among the most beautiful lepidopterans in the world with its long tails and pink and yellow coloration, and on the front cover, perhaps appropriately, a female of *Saturnia pinratanai* Lampe, described in 1989. The color plates are excellent, depicting the large moths life size (consequently only one or two specimens appear on most plates). Color reproduction ranges from good to perfect, except for a couple of the blue-green *Actias,* which are too yellow, and the pair of *Saturnia zuleika* (Plate 40), which are definitely too brown and yellow. The first seven plates depict mature larvae, several of which have never been illustrated or described. Also illustrated for the first time is the bizarre-looking female of *Salassa lemaii,* a species very rare in collections.

The authors indicate that their book is based on material collected mainly in northern Thailand, and that further collecting in southern Thailand would certainly increase the number of species above the 29 currently known for the country. They also state at the onset that no taxonomic changes are proposed in this book, a wise decision in my judgment, considering that most genera of Indo-Australian Saturniidae still need revision. I agree with their identifications, notably that *Samia canningii* is indeed the correct name for what occurs in northern Thailand, a conclusion I reached a few years ago based on material in my own collection. The text, in English, is sparse, but gives specific localities, dates of collection, and descriptions of the adult moths. The subspecies concept is explicitly rejected in a short discussion on page 32. I found no misspellings nor typographical errors.

The book is an essential addition to the bookshelf, especially considering the impressive and numerous color plates and low price. We have relatively few modern treatments of the saturniid fauna of Southeast Asia and this one fills a definite gap.

RICHARD S. PEIGLER, *Department of Zoology, Denver Museum of Natural History, 2001 Colorado Boulevard, Denver, Colorado 80205.*

Journal of the Lepidopterists' Society
44(3), 1990, 205

THE BUTTERFLIES OF EGYPT, by Torben B. Larsen. 1990. Apollo Books and The American University in Cairo Press. Distributed by Apollo Books, Lundbyvej 36, DK-5700 Svendborg, Denmark. 112 pp., 8 color plates, 6 halftone illustrations. Hard cover, 16.5 × 24 cm, ISBN 87-88757-14-5, Danish kroner 240 (plus postage) (about $32.00).

This volume is based on Dr. Larsen's painstaking searches of major museum collections for Egyptian butterfly records, which were augmented by six weeks' field work from late March to mid-May 1987. As he states (p. 7), "I did not wish to publish such a review without personal acquaintance with *all* the varied habitat types . . ." (emphasis mine). He further admits that the book is less based on his personal research than were his previous excellent faunal reviews.

This volume has been produced beautifully by Apollo Books and the American University in Cairo Press. The color plates are outstanding and much superior to those of his previous works. The text is very readable and relatively free of typographic errors, although a few notable ones demand attention. A pioneer collector, A. Alfieri, is referred to as "Alfierii" on pages 30 and 31, though correctly elsewhere, and Esper is listed (p. 60) as having described *Carcharodus alceae* in "1870", 90 years after he did so.

In the introductory section, Larsen gives lucid descriptions of most major Egyptian biotic areas, and his discussion of past collecting activities is extensive. The species discussions are adequate, but obviously not based on much personal experience. The biogeography section almost is equal to his others for the region. The first and last of these, and to a lesser extent, other sections, suffer from a common problem: a lack of cooperation by the host country. Larsen was not allowed to visit the Gebel Elba in southeasternmost Egypt, an area interesting for its Afro-tropical elements that remain almost unknown today, though the species that have been found are tantalizing. The book should have been much stronger had access to the Gebel Elba not been denied. A comprehensive bibliography for Egyptian butterflies completes the treatment.

I have the impression that publication of this volume, for whatever reason, was premature. Larsen's entire series on middle Eastern butterflies, which concludes with this volume, should not be judged on this book alone.

Anyone with an interest in Mediterranean butterflies should buy this book to complete an otherwise excellent series. Others may or may not wish to buy this work: it is really not a "coffee table" book, nor does it have the "meat" of his other faunal works.

LEE D. MILLER, *Allyn Museum of Entomology, Florida Museum of Natural History, 3621 Bay Shore Road, Sarasota, Florida 34234.*

Journal of the Lepidopterists' Society
44(3), 1990, 206–207

BUTTERFLIES OF CALIFORNIA, by John A. Comstock (facsimile reprint of the 1927 edition). Introduction, Biography, and Revised Checklist by Thomas C. Emmel & John F. Emmel. 1989. Nature Guide No. 2, Scientific Publishers, P.O. Box 15718, Gainesville, Florida 32604. lviii + 334 pp., 63 color plates (reprinted in black & white). Hard cover, 16 × 23.5 cm, ISBN 0-945417-21-7, $27.50 ($1.50 S&H).

My first acquaintance with Comstock's *Butterflies of California* came in August 1979 when I responded to an offer made by the Audubon Nature Training Society in Oakland, California. In exchange for a donation of $20 (which was to be shared with the Xerces Society), the Audubon Society sent a set of color plates from Comstock's book. (Well, almost a set. What I received were Plates 1–41 and 43; missing were Plates 42 and 44–63.) These were, apparently, left over after the book was published privately by Comstock himself in Los Angeles in 1927. I ordered them for two reasons: a long-standing historical (and esthetic) interest in butterfly books and because the donation went to a good cause. I did not own a copy of Comstock's book but knew of its importance to western lepidopterology.

Butterflies of California (with the subtitle "A Popular Guide to a Knowledge of the Butterflies of California, embracing all of the 477 species and varieties at present recorded for the state") originally was printed in two editions. The Regular Edition was bound in green leatherette and sold for $9.00. The De Luxe Edition, sporting the imprint of a butterfly embossed on its brown leather cover, was advertised as "hand illuminated and inscribed by the author" and sold for $15.00. Although the De Luxe Edition was supposed to be limited to 200 numbered copies, the actual number issued was probably much smaller. Nor is it known for sure how many of the Regular Edition were actually printed. But in the 63 years since the appearance of this classic work, surviving copies have appreciated in value at least fifty-fold. The Regular Edition now sells for over $500 on the rare book market, putting it well out of reach of all but the most serious collectors.

The facsimile reprint reviewed here is a handsome volume issued in brown leatherette with gold lettering on the spine. True to its billing, it includes the entire text of the original, printed on coated paper in crisp photo-reproduction. Over a hundred line drawings and half-tone photographs are interspersed throughout the text and are only slightly less sharp than in the original. The 63 color plates (reproduced in black & white) illustrate spread specimens and were made from 62 Riker mounts prepared by Comstock. These still survive in the Natural History Museum of Los Angeles County. The 63rd plate depicts 17 larvae and pupae drawn in color by R. F. Sternitzky.

Added to the reprint of the original book is an extensive and informative introduction by the Emmel brothers, whose lifetimes of field work with California butterflies have produced dozens of publications, including *The Butterflies of Southern California* (1973, Natural History Museum of Los Angeles County, Science Series 26, 148 pages, 10 color plates), and the forthcoming *The Butterflies of California* (with Sterling O. Mattoon), to be published by Stanford University Press. The Emmels' Introduction to the Comstock reprint includes a seven-page biography, a complete chronological listing of the 236 scientific papers and books that Dr. Comstock published over 67 years (from 1902–69), and an updated synonymic list of California butterflies, providing currently recognized names for the 236 taxa recognized by Comstock. (Numerologists will no doubt divine great meaning from the fact that Comstock produced one publication for every butterfly species known in California!)

Why, one might ask, would anyone want to purchase a "popular guide" to California butterflies that (a) is six decades out of date and (b) will soon be replaced by the mammoth compendium being prepared by Emmel, Emmel & Mattoon? Not for identifying specimens, certainly, but there are several reasons for owning the book, and Scientific Publishers is banking on lepidopterists recognizing some of them. One, it is a classic and important work that is otherwise unavailable. Two, it is affordable by today's book prices (lapse of copyright helped by eliminating the need to pay royalties) and cheap compared to the going rate for the original. Three, it is filled with valuable information on where and when to collect in remote localities. Four, it covers extinct species such as the Xerces Blue (considered rare even in Comstock's day) and the Unsilvered Fritillary, *Speyeria* (=*Argynnis*) *adiaste atossa*, providing insight into their past abundance and of the efficacy (and ethics?) of early collectors (Comstock claims he once took over 500 *atossa* in a single day). Five, it is historically fascinating, revealing details of a vanished era when a collector could take over 100 species in the Los Angeles area. Six, if you, like me, obtained a set of color plates back in the 1970's, now you can have the text that goes with them. Seven, the writing is good, sometimes excellent, and occasionally inspired (e.g., "[*Parnassius clodius baldur*] is commonly encountered in our upland meadows of the Sierra Nevadas, or sporting about precipitous cliffs, where it is by no means easy of capture."). Eight (if you're still interested, dear reader), the Emmel, Emmel & Mattoon (EEM) volume has been "forthcoming" for some time—in the Introduction to the Comstock reprint it is cited (optimistically) as having a 1989 publication date (publication is currently projected for fall 1991)—and purchase of the Comstock reprint will give you something to read until *The Butterflies of California* finally appears.

It will be fascinating to compare what was known about California butterflies in 1927 with what we will know in 1991 after *The Butterflies of California* is published. For example, the EEM volume will be twice as long as Comstock's (>700 pages), will include 1200 life history illustrations and more than 50 habitat photographs, and will contain detailed distribution maps for every species and subspecies. Although EEM's *The Butterflies of California* will treat a similar number of species (267 compared to Comstock's 236), over 100 of these are new since Comstock's volume was published, a paradox that results largely from substantial taxonomic rearrangements during the past sixty years. For example, many of the *Speyeria* (=*Argynnis*) and *Euphydryas* that Comstock treated as species are now considered subspecies or forms (in the entire state fauna, over 760 subspecies are recognized by EEM). On the other wing, some species from Comstock's day have been split into as many as five or six species (*Philotes battoides*, for example).

The vast amount of information to be incorporated into EEM's *The Butterflies of California* has been made possible by the huge increase in the number of California collectors (who now make up 15% of the Society's membership) and to the much greater ease with which collectors can reach most areas of the state. The primitive roads in the 1920's meant that it took three days just to get to the desert from Los Angeles; today the trip is a matter of hours by car. As Thomas Emmel says, "It's astonishing how much information Comstock was able to gather for his book considering the logistical obstacles he faced in those early days." Indeed. And what better reminder of that astonishing effort than this timely reprint of one of this country's first and best treatments of the butterflies of a single state.

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

Journal of the Lepidopterists' Society
44(3), 1990, 208

ANNOUNCEMENT

PROFILES: A NEW CATEGORY IN THE *JOURNAL*

Profiles is a new *Journal* category that will feature informative and descriptive articles about prominent lepidopterists, significant collections of Lepidoptera, and institutions of special importance to lepidopterology. Manuscripts submitted for publication as **Profiles** should conform to the same style and format requirements as Articles and will be subject to peer review.

This new category is meant to provide an outlet for information of lasting value about the people and places of importance to the study of Lepidoptera, thereby increasing the value and interest of the *Journal* to readers.

BOYCE A. DRUMMOND, Editor

Date of Issue (Vol. 44, No. 3): 6 December 1990

NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of Lepidoptera study. Categories are Articles, Profiles, 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 111 in Volume 44(2). *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 submit manuscripts in *triplicate*, typewritten, *entirely double-spaced*, with wide margins, on one side only of white, letter-sized paper. Prepare manuscripts according to the following instructions, and submit them flat, not folded.

Abstract: An informative abstract should precede the text of Articles and Profiles.

Key Words: Up to five key words or terms not in the title should accompany Articles, Profiles, General Notes, and Technical Comments.

Text: Contributors should write with precision, clarity, and economy, and should use the active voice and first person whenever appropriate. Titles should be explicit, descriptive, and as short as possible. The first mention of a plant or animal in the text should include the *full scientific name* with *author*, and *family*. Measurements should be given in metric units; times in terms of the 24-hour clock (0930 h, not 9:30 AM). Underline only where *italics* are intended.

Literature Cited: References in the text of Articles and Profiles should be given as Sheppard (1959) or (Sheppard 1959, 1961a, 1961b) and listed alphabetically under the heading LITERATURE CITED, in the following format without underlining:

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

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

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

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.

Tables: Tables should be numbered consecutively in Arabic numerals. Headings for tables should not be capitalized. Tabular material must be typed *on separate sheets*, and placed following the main text, with the approximate desired position indicated in the text. Vertical lines as well as vertical writing should be avoided.

Voucher specimens: When appropriate, manuscripts must name a public repository where specimens documenting identity of organisms can be found. Kinds of reports that require vouchering include life histories, host associations, immature morphology, and experimental enquiries.

Proofs: The edited manuscript and galley proofs will be mailed to the author for correction of printer's errors. Excessive author's changes at this time will be charged to authors at the rate of $2 per line. A purchase order for reprints will accompany proofs.

Page charges: For authors affiliated with institutions, page charges are $20 per *Journal* page. For unaffiliated authors, page charges are $10 per *Journal* page with a $50 maximum. Authors of Book Reviews and Obituaries are exempt from page charges. Authors unable to pay page charges for reasons such as difficulties with foreign exchange should apply to the editor for free publication.

Correspondence: Address all matters relating to the *Journal* to the editor.

PRINTED BY THE ALLEN PRESS, INC., LAWRENCE, KANSAS 66044 U.S.A.

CONTENTS

PROFILES

GENERAL NOTES

BOOK REVIEWS

ANNOUNCEMENT

ne 44 1990 Number 4

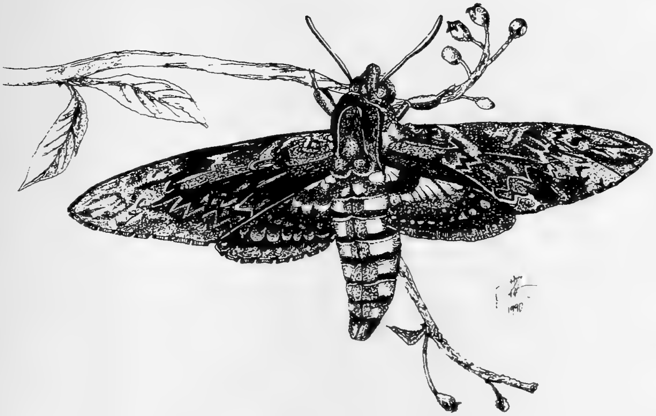
ISSN 0024-0966

JOURNAL

of the

LEPIDOPTERISTS' SOCIETY

Published quarterly by THE LEPIDOPTERISTS' SOCIETY
Publié par LA SOCIÉTÉ DES LÉPIDOPTÉRISTES
Herausgegeben von DER GESELLSCHAFT DER LEPIDOPTEROLOGEN
Publicado por LA SOCIEDAD DE LOS LEPIDOPTERISTAS



16 May 1991

THE LEPIDOPTERISTS' SOCIETY

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.

Active members—annual dues	$25.00
Student members—annual dues	$15.00
Sustaining members—annual dues	$35.00
Life members—single sum	$500.00
Institutional subscriptions—annual	$40.00

Send remittances, payable to *The Lepidopterists' Society*, to: Fay H. Karpuleon, Treasurer, 1521 Blanchard, Mishawaka, Indiana 46544, U.S.A.; and address changes to: Julian P. Donahue, Natural History Museum, 900 Exposition Blvd., Los Angeles, California 90007-4057 U.S.A. For information about the Society, contact: William D. Winter, Secretary, 257 Common St., Dedham, Massachusetts 02026-4020, U.S.A. (617-326-2634). To order back issues of the *Journal, News*, and *Memoirs*, write for availability and prices to the Publications Coordinator: Ronald Leuschner, 1900 John St., Manhattan Beach, California 90266-2608, U.S.A.

Journal of the Lepidopterists' Society (ISSN 0024-0966) is published quarterly for $40.00 (institutional subscription) and $25.00 (active member rate) by the Lepidopterists' Society, % Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, California 90007-4057. Second-class postage paid at Los Angeles, California and additional mailing offices. POSTMASTER: Send address changes to the Lepidopterists' Society, % Natural History Museum, 900 Exposition Blvd., Los Angeles, California 90007-4057.

Cover illustration: Female of *Manduca sexta* (L), the Carolina Sphinx, one of the most common hawkmoths in North America. The larva is known as the Tobacco Hornworm because of the damage it causes to solanaceous crops such as tobacco, potato, and tomato. Original drawing by J. D. Dietrich Larsen, 4201 North 20th Street, Suite 216, Phoenix, Arizona 85016.

JOURNAL OF
THE LEPIDOPTERISTS' SOCIETY

Volume 44 1990 Number 4

Journal of the Lepidopterists' Society
44(4), 1990, 209–214

HIGH ALTITUDE AGGREGATIONS OF *ANETIA BRIAREA* GODART ON HISPANIOLA (NYMPHALIDAE: DANAINAE)

MICHAEL A. IVIE, T. KEITH PHILIPS AND KATHLEEN A. JOHNSON

Department of Entomology, Montana State University,
Bozeman, Montana 59717

ABSTRACT. High altitude aggregations of the danaine *Anetia briarea* Godart were observed near the summit of Pico Duarte (2500–3000 m) in the Dominican Republic. These observations represent the highest elevation record in the West Indies for butterflies and the first report of high elevation aggregations in the genus *Anetia*. *Anetia briarea* and *Danaus plexippus* are now the only two neotropical danaines known to form high altitude aggregations, suggesting that this behavior may be a plesiomorphic character for the Danainae.

Additional key words: Dominican Republic, migration, diapause.

Several aggregations of adult *Anetia briarea* Godart (Nymphalidae: Danainae), with interesting similarities to those of another danaine, the Monarch (*Danaus plexippus*), were discovered on Pico Duarte in the Dominican Republic, the highest peak in the West Indies (3175 m), in September 1988. The aggregations are apparently well known to the local guides who frequent the mountain, as they repeatedly told us of this phenomenon before we reached the area involved. This situation is similar to that of the now-famous Mexican Monarch colonies in Michoacan, the "discovery" of which came as a surprise to locals who had always known they were there (Urquhart 1976).

Seasonal aggregation of Monarch butterflies is a well known phenomenon in the nearctic region (Calvert & Brower 1986 and citations therein), but adults of few other species of Lepidoptera are known to form such aggregations. The Old World danaine, *Euploea core* (Cramer), forms overwintering aggregations in the temperate portions of its range in Asia and Australia (Ackery & Vane-Wright 1984 and citations within). In the Neotropics, only *Eurema daira* (Godart) (Pieridae), *Smyrna karwinskii* (Hübner) (Nymphalidae), and *Calaenorrhi-*

nus fritzgaertneri (Bailey) (Hesperiidae) are reported to form aggregations (Denlinger 1986, DeVries et al. 1987); however, these three species aggregate in moist microhabitats at low to moderate elevations (Muyshondt & Muyshondt 1974, Janzen 1983, Devries et al. 1987). The southern "tropical" Monarch colonies are high elevation phenomena (Calvert & Brower 1986).

Seasonal aggregation by adult tropical insects is usually associated with reproductive diapause (Denlinger 1986). Adult diapause is reported in only seven species of tropical butterflies (Denlinger 1986, Devries et al. 1987), including *E. daira, S. karwinskii* and *C. fritzgaertneri* as well as in the Monarch (Brower et al. 1977). Aggregation during diapause can have several functions in tropical insects. Aposematic species can reduce the chance of predation (Wolda & Denlinger 1984). Aggregation may also reduce evaporative water loss, lower incident radiation, and facilitate mate searching at the end of diapause (Denlinger 1986).

One of five species in the neotropical genus *Anetia* (Ackery & Vane-Wright 1984), *A. briarea* is endemic to the Greater Antillean islands of Cuba, Isla de la Juventud (Isle of Pines), and Hispaniola. Ackery and Vane-Wright (1984) point out that virtually nothing is known of the biology of *Anetia* species. Alayo and Hernández (1987) have summarized knowledge of the Cuban subspecies [*A. b. numida* (Hübner)], repeating the old larval host record of *Jacquinia* (Theophrastaceae) (Gundlach 1881). Schwartz (1989) recently summarized what is known about the nominate subspecies (*A. b. briarea*) on Hispaniola, reporting adults to be inhabitants of mesic hardwood forest, and alluding to possible migratory behavior. Of 46 localities Schwartz recorded for the species on Hispaniola, only 8 are below 900 m elevation. At one of these low elevation sites (Haiti: Fond Parisien, sea level), Gali and Schwartz (in Schwartz 1989) suggest that the many fresh individuals in the area indicated a downward migration from higher elevations. Schwartz' collection records indicate a pronounced seasonality of abundance, the number of records (i.e., specimens) per month being January (1), March (2), April (7), June (45), July (106), August (11), September (1), October (2), December (3). To our knowledge there are no published reports of high elevation seasonal aggregations in this genus.

OBSERVATIONS ON PICO DUARTE

In August and September 1988 we made several trips into high elevation areas of the Dominican Republic, including an ascent of Pico Duarte, the highest peak in the West Indies. Apparently, we were the first entomologists to collect on Pico Duarte. These localities are within Parque Nacional de Almando Bermudez and persons collecting in the

Parque without the proper permits are subject to arrest and prosecution under Dominican law. Enforcement by park personnel is active, and should be taken very seriously.

On 5 September 1988, on Pico Duarte between La Compartacion (2350 m) and the weather station (3075 m), at elevations ranging from 2500 to 3000 m, over a distance of 2 km, we observed several aggregations of *A. briarea* on branches of *Pinus occidentalis* Swartz (Pinaceae). The area was unique in that the trees were festooned with fruticose *Usnea* lichens (Ascolichen: Lecanorales: Lecanorineae) (Plate 1, upper). The forest both above and below this area was also pine, but lacked the heavy loads of lichen.

Aggregations were from 4 m to ca. 10 m above the ground, and rather widely spaced, on mostly east-facing slopes. We estimated that the half-dozen colonies closely examined each had 75–250 individuals. Other individuals were basking or flying nearby. The vast majority in each colony were simply hanging in a clump. The appearance of the colonies was very much like some of the smaller California Monarch colonies on a warm, sunny winter day (Plate 1, lower).

DISCUSSION

The occurrence of high-elevation aggregations of a danaine on Hispaniola brings several questions to mind. First, what is the function of this behavior? As no mating pairs of *A. briarea* were seen in the aggregations we observed, we suggest reproductive diapause is the most likely physiological condition of the aggregating individuals, an hypothesis we plan to investigate on future visits.

Second, what are the seasonal and physical factors involved in this behavior? We have no information beyond our one day of observation, and the testimony of the guides. That the behavior is of long duration and in stable locations cannot be doubted, as it is well known to local people. Schwartz (1989) records a seasonal abundance of *A. briarea* at middle elevations in June and July, and virtually none from September to March. If these dates are indicative of a 7-month reproductive diapause, it would not be unique among tropical insects. Wolda and Denlinger (1984) report reproductive diapause and aggregation of a Panamanian beetle lasting 10 months. Seasonal cues, though less obvious than in the temperate zone, are known to work in the tropics, with daylength and humidity being the best studied (Tanaka & Denlinger 1984, Denlinger 1986). Within the high areas of the Cordillera Central, there are many entomologically unexplored peaks that could be used to isolate and identify the required geographical factors involved.

Lastly, how does this discovery impact our view of better studied danaines and their evolution? Hispaniola occupies a central place in

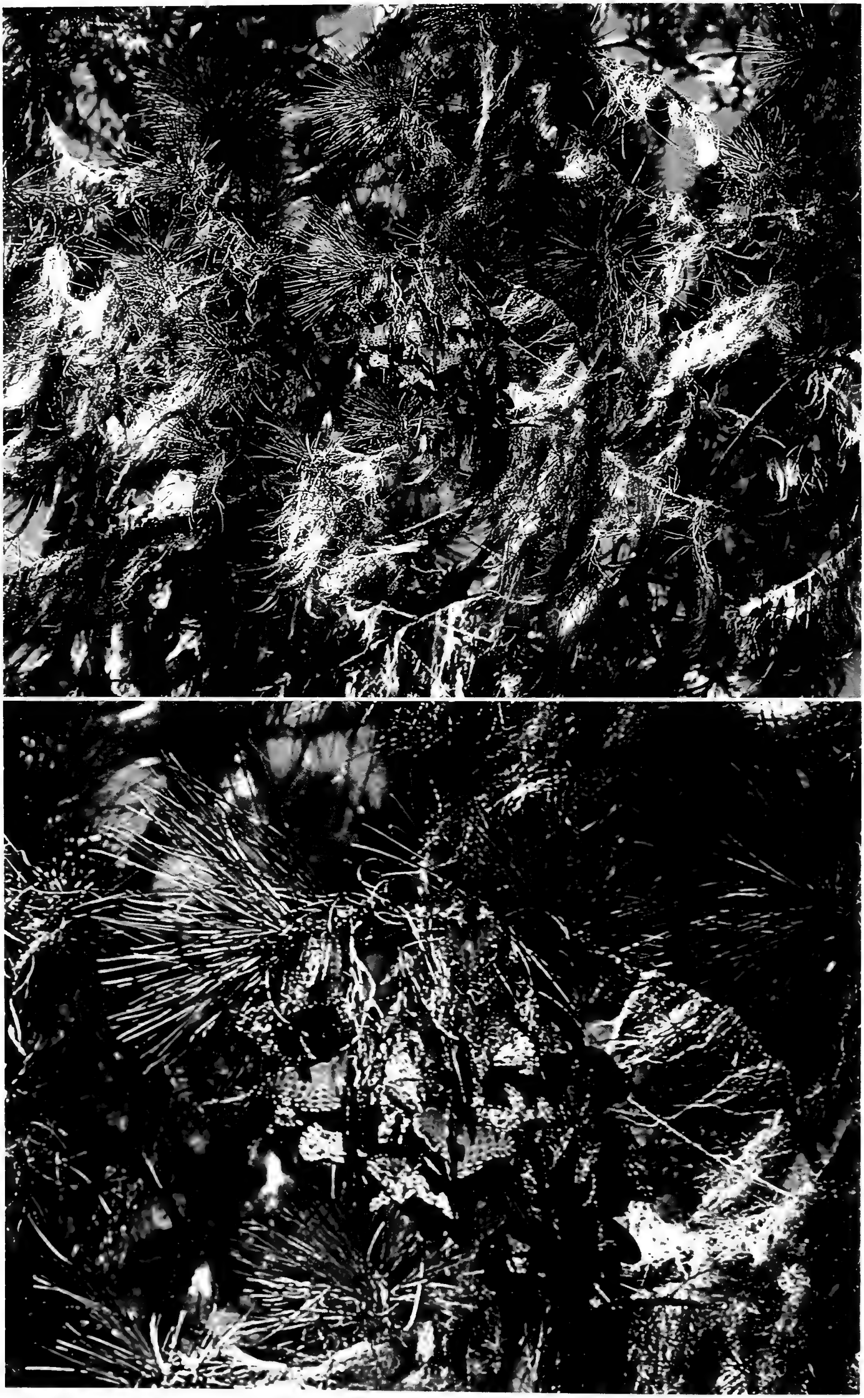


PLATE 1. Aggregation of *Anetia briarea* in *Pinus occidentalis* on slopes of Pico Duarte, Dominican Republic. Upper: lichen-festooned trees with *Anetia* cluster in center. Lower: close-up of *Anetia* aggregation shown above.

Western Hemisphere danaine evolution. Of the 14 species in the New World, 8 occur on Hispaniola. Of the five spp. of *Anetia*, three occur there. *Anetia* possesses many plesiomorphic characters (Ackery & Vane-Wright 1984), and is considered by some (Forbes 1939) to represent the sister-group of the rest of the subfamily. All five species are montane, with *A. thirza* being recorded up to 3500 m in Costa Rica (Hall 1983). Schwartz (1989) records *A. briarea* and *A. pantherata* up to 2288 m, which is previously the highest elevation record of a butterfly in the Dominican Republic. He records *A. jaegeri* up to 2300 m in Haiti, which is previously the highest elevation record for a butterfly from Hispaniola and the West Indies. Alayo and Hernández (1987) do not record elevations for the Cuban species, but indicate that all are montane.

It is intriguing to compare the behavior of a primitive group of montane danaines, one of which has now been demonstrated to exhibit seasonal migrations and aggregation on high elevation sites dominated by conifers, with the Monarch, which exhibits similar behavior. In fact, a comparison of the Mexican Monarch overwintering sites with those discovered for *Anetia briarea* shows some interesting similarities (Monarch data from Calvert & Brower 1986). The Monarch sites are between 19 and 20°N latitude, whereas the Hispaniolan sites are at 19°02′N. The Mexican sites are between 2928 and 3357 m, whereas the Hispaniolan are between 2500 and 3000 m. In each locality, the two danaines aggregate on conifers on mountain slopes. It is possible that a tropical montane ancestor of the Monarch, similar to *Anetia*, with seasonal high elevation roosts, later evolved to exploit a temperate resource by returning from increasingly long migrations to high-elevation tropical roosts during adverse weather conditions (i.e., winter). Perhaps it is more parsimonious, in light of the very little information known about the New World Danainae, to think of high-elevation aggregation and reproductive diapause as a plesiomorphic behavior for the modern species, and synapomorphic for the subfamily.

These high elevation phenomena are by definition difficult to reach. The fact that this discovery comes so late in the exploration of the West Indies points out the limitations of previous road-based collecting. It will take many more observations by lepidopterists willing to search far beyond the end of the road to test the hypothesis proposed here.

ACKNOWLEDGMENTS

We thank Julio Cesar Canelas and Vijo Peralta of La Cienega, Dominican Republic for their help as guides and mule skinners on Pico Duarte. For help with permits and logistics, we thank J. and M. Brodzinsky (Santo Domingo); L. Dominquez, R. O. Rimoli, and A. Jimenez (Museo Nacional de Historia Natural, Santo Domingo); and G. Valdez

Sierra (Parques Nacionales, Santo Domingo). The lichens were identified by S. Eversman of Montana State University. Helpful reviews were provided by W. Kemp, K. O'Neil, J. Shuey, T. Emmel, and an anonymous reviewer. This work was funded by MONTS-NSF, and is contribution J-2404 of the Montana Agricultural Experiment Station.

LITERATURE CITED

ACKERY, P. R. & R. I. VANE-WRIGHT. 1984. Milkweed butterflies, their cladistics and classification. Cornell University Press, Ithaca, New York. 425 pp.

ALAYO, D. & L. R. HERNÁNDEZ. 1987. Atlas de las mariposas diurnas de Cuba (Lepidoptera: Rhopalocera). Editorial Científico-Técnica, La Habana. 148 pp.

BROWER, L. P., W. H. CALVERT, L. E. HEDRICK & J. CHRISTIAN. 1977. Biological observations on an overwintering colony of Monarch butterflies (*Danaus plexippus*, Danaidae) in Mexico. J. Lepid. Soc. 31:232–242.

CALVERT, W. H. & L. P. BROWER. 1986. The location of Monarch butterfly (*Danus plexippus* L.) overwintering colonies in Mexico in relation to topography and climate. J. Lepid. Soc. 40:164–187.

DENLINGER, D. L. 1986. Dormancy in tropical insects. Ann. Rev. Entomol. 31:239–264.

DEVRIES, P. J., J. SCHULL & N. GREIG. 1987. Synchronous nocturnal activity and gregarious roosting in the neotropical skipper butterfly *Celaenorrhinus fritzgaertneri* (Lepidoptera: Hesperiidae). Zool. J. Linn. Soc. 89:89–103.

FORBES, W. T. M. 1939. Revisional notes on the Danainae. Entomol. Americana (N.S.) 19:101–140.

GUNDLACH, J. 1881. Contribution â la entomologia Cubana 1. Havana. 480 pp.

HALL, A. 1983. A monograph of the butterflies of the subfamily Nymphalinae. 180 microfiche. Brighton. [Not seen, as cited by Ackery & Vane-Wright 1984.]

JANZEN, D. H. (ed.). 1983. Costa Rican natural history. Univ. Chicago Press, Chicago. 816 pp.

MUYSHONDT, A. & A. MUYSHONDT JR. 1974. Gregarious seasonal roosting of *Smyrna karwinskii* adults in El Salvador (Nymphalidae). J. Lepid. Soc. 28:224–229.

SCHWARTZ, A. 1989. The butterflies of Hispaniola. Univ. Florida Press, Gainesville. 580 pp.

TANAKA, S. & D. L. DENLINGER. 1984. Daylength and humidity as environmental cues for diapause termination in a tropical beetle. Physiol. Entomol. 12:213–224.

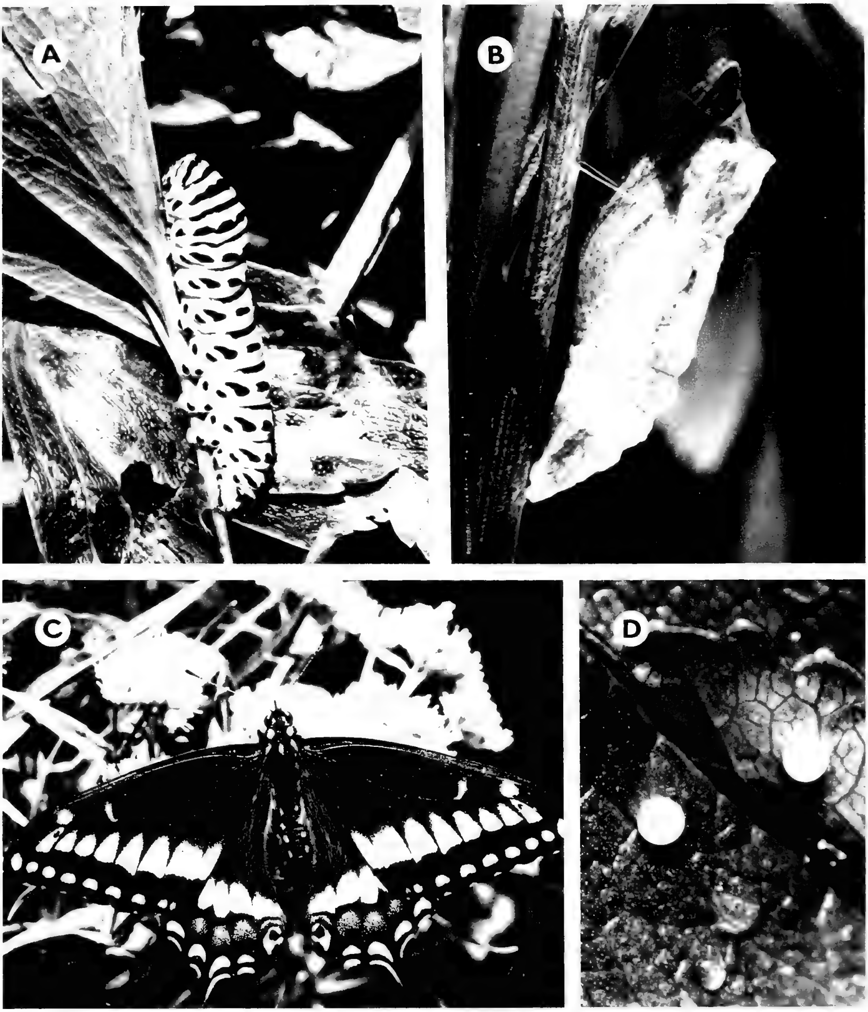
URQUHART, F. A. 1976. Found at last: The monarch's winter home. Nat. Geogr. Mag. 150:160–173.

WOLDA, H. & D. L. DENLINGER. 1984. Diapause in a large aggregation of a tropical beetle. Ecol. Entomol. 9:217–230.

Received for publication 27 September 1989; revised and accepted 17 June 1990.

Journal of the Lepidopterists' Society
44(4), 1990, 215

FEATURE PHOTOGRAPH



***Papilio brevicauda* Saunders—Evidence for a second generation:** On 2 August 1989, one *P. brevicauda* was seen ovipositing on *Ligusticum scothicum* Linn. (Umbelliferae) at Neguac, Northumberland Co., New Brunswick, Canada, where mature larvae also were present, and one freshly-emerged male *P. brevicauda* was captured at Shippagan, Gloucester Co., N.B. (larvae also present), where eggs of the first generation were common on 24 June 1989. These photographs were taken on 3 August 1989 on a salt marsh, Bathurst, Gloucester Co., N.B., Canada. **A**: mature larva of the first generation on *L. scothicum*; **B**: pupa of first generation on *L. scothicum*; **C**: female of second generation nectaring on goldenrod (*Solidago* sp.: Asteraceae); **D**: eggs of second generation on *L. scothicum* leaves. Photographed with a Nikon FE2, 200-mm micro-Nikkor lens, and extension tubes (Kodachrome 64; A, B & D in natural light, C with Nikon SB15 flash; f16; speed not recorded).

Anthony W. Thomas, *P.O. Box 4000, Fredericton, New Brunswick, E3B 5P7, Canada.*

Journal of the Lepidopterists' Society
44(4), 1990, 216–228

MIGRATION AND OVERWINTERING AGGREGATIONS OF NINE DANAINE BUTTERFLY SPECIES IN TAIWAN (NYMPHALIDAE)

HSIAU YUE WANG
Taiwan Museum, Tapiei, Taiwan 100, Republic of China

AND

THOMAS C. EMMEL[1]
Department of Zoology, University of Florida, Gainesville, Florida 32611

ABSTRACT. Nine species of danaine butterflies regularly participate in fall migrations of 300 km or more from the temperate northern and montane areas of Taiwan to several warmer sheltered valleys in the southern part of that island. There they aggregate by November and December in overwintering colonies at 300–500 m above sea level. *Salatura genutia* generally forms single-species colonies of up to 50,000 butterflies. The other eight species form mixed-species colonies of thousands of individuals. The winter temperatures in the colony sites normally remain above 10°C. In late March, the overwintered danaines begin courting and mating, and then individually fly north to the breeding areas.

Additional key words: *Euploea, Parantica, Radena, Tirumala, Salatura.*

Apparently in response to the strongly seasonal climate on the northern half of Taiwan, an extraordinary intra-island migration and subsequent formation of a series of overwintering aggregations takes place annually among at least 9 of the 18 species of Danainae (Nymphalidae) among the 400 species of butterflies living on this Asian island. These danaine butterflies fly southward in groups before the onset of winter, and congregate in several warm and windless valleys located in the southern part of Taiwan where they pass the winter. Local people have long known of the existence of these overwintering valleys, calling them "Butterfly Valley" or "Purple Butterfly Valley," but only recently have scientists investigated these phenomena. Here we summarize the known information about these extraordinary migrations and overwintering aggregations.

Taiwan Geography and the Locations of Overwintering Sites

The Southeast Asian island of Taiwan covers some 36,000 square km and is approximately 394 km in length from north to south. A plains area occupies the western third of Taiwan while the remainder of the island is covered by the Central Mountain Range, which runs some 320 kilometers from north to south. The main Taiwanese peak of Yushan

---

[1] Research Associate, Florida State Collection of Arthropods, Allyn Museum of Entomology, and Natural History Museum of Los Angeles County. Reprint requests may be addressed to either author.

rises 3997 m above sea level and is the highest mountain in Southeast Asia. More than 130 mountain peaks on Taiwan reach higher than 3000 m elevation. As elevation increases, even in the areas of Taiwan south of the Tropic of Cancer, temperature decreases correspondingly; above 2500 m elevation, winter snows occur.

The first overwintering aggregation of butterflies was discovered by an unknown Taiwanese lepidopterist in 1971. Today, four locations have been found where large overwintering aggregations of these danaines occur regularly. All of the butterfly valleys are located in the low mountains of Kaoshung County, Pinton County, and Taiton County, three of the southernmost counties of Taiwan (Fig. 1). From north to south, these sites are: Lukuea, Taiwu, Laiyi (all on the western side of the Central Mountain Range), and the most recently discovered overwintering site, Dawu, found by Wang during the winter of 1988–89 and located 46 km S of Chipen Hotspring in Taiton County, on the eastern slope of the Central Mountain Range.

The three sites on the western side of the Central Mountain Range are occupied primarily by overwintering species of the genus *Euploea*, whereas at the single eastern slope site, half of the danaines in the overwintering colony are species of *Radena*, *Tirumala*, and *Parantica*. The most abundant species is *Radena similis similis*. A preliminary hypothesis (Wang unpublished) relates this interesting distributional difference to the distribution of the food plants of these genera. Initially, the butterflies occupy sites with altitudes in excess of 1000 m, but, as winter progresses, the butteflies move downslope to the final overwintering sites at elevations between 300 and 500 m.

Species Involved in the Overwintering Aggregations

The overwintering species of danaine butterflies in Taiwan include the following (larval food plant observations by Wang):

1. *Euploea sylvester swinhoei* (Wallace) (Plate 1: k)

   The larval food plants are species of *Ficus* (Moraceae). Widely distributed in Asia, this species occurs from Sri Lanka and southern India to southern China and south through Indonesia and Malaysia to New Guinea, as well as the Philippines and northern Australia. Elsewhere, individuals of *E. sylvester* have been observed migrating through the Port Moresby area in Papua New Guinea (Ackery & Vane-Wright 1984).

2. *E. eunice hobsoni* Butler (Plate 1: l, m)

   Three species of the fig family are the larval food plants: *Ficus microcarpa*, *F. ampelos*, and *F. formosana*. The butterfly and its

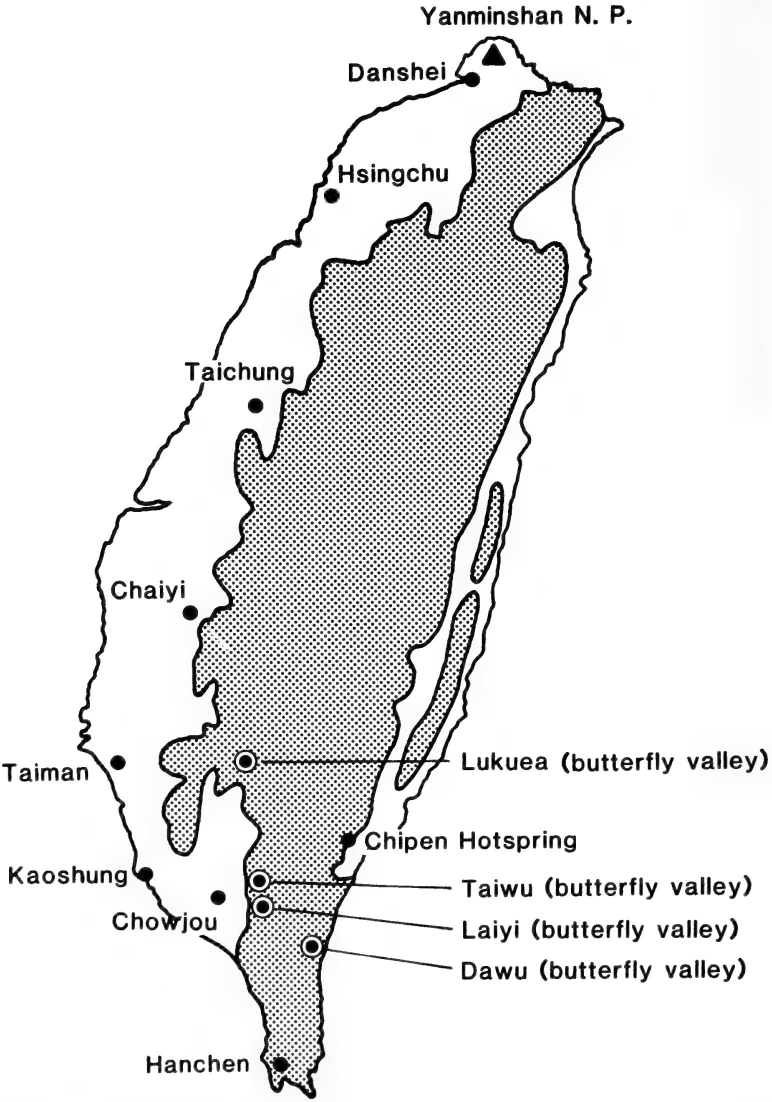


FIG. 1. A map showing the mountain areas (shaded) of Taiwan, and the locations of the known overwintering valleys and major landmarks.

food plants are distributed in all montane areas of the island, from the lowlands to 1500 m. Elsewhere, the species occurs from the southern coast of China through Indo-China and the Philippines. Williams (1930) reported *eunice* as a migrant in December 1885 in Java (under the name *leucostictos*).

3. *E. mulciber barsine* (Fruhstorfer) (Plate 1: f, o, p)

Six species of *Ficus* are larval food plants in Taiwan: *Ficus microcarpa, F. pumila, F. sarmentosa, F. vasculosa, F. erecta,* and *F. formosana.* The butterfly ranges from lowland elevations to 2000 m in all mountain areas of Taiwan. On mainland Asia, *E. mulciber* is widespread from India to the Philippines and southern China. Williams (1930) notes several records of this species migrating in vast numbers with other butterflies in Burma (January) and Thailand (May).

4. *E. tulliolus koxinga* (Fruhstorfer) (Plate 1: n, q)

This species feeds on unidentified *Ficus* in Taiwan; elsewhere, it uses *Malaisia* species (Moraceae) and *Nerium oelander* (Apocynaceae) (Ackery & Vane-Wright 1984). It is widespread across Asia and the South Pacific islands to Australia; there is one report of a large-scale migration of *E. tulliolus* in Malaysia (Batchelor 1960).

5. *Parantica aglea maghaba* (Fruhstorfer)

Two species of Asclepiadaceae serve as larval food plants: *Tylophora lanyuensis* and *T. ovata.* The butterfly is distributed from the lowlands to 1000 m in all the mountains of the island. Widespread across Asia from India and Sri Lanka to China, this species has been reported to occur occasionally in small numbers in migratory flocks of other butterflies in February, August, and October in south India and Sri Lanka (Williams 1930).

6. *Ideopsis (Radena) similis similis* (Linnaeus) (Plate 1: e)

The food plants of *I. s. similis* are *Tylophora ovata, Cynanchum atratum,* and *Marsdenia tinctoria,* all in the family Asclepiadaceae. The butterfly occurs in all mountain regions from the lowlands to 2500 m. There is one record (Williams 1930) of this species migrating in a mixed species flock on 23 May 1926, in Thailand, moving southward in the morning by the millions and to the north the same afternoon in low numbers.

7. *Tirumala limniace limniace* Cramer

The larval food plants are *Dregea formosana* (Moraceae) and *Heterostemma brownii* (Asclepiadaceae). The butterfly ranges from the lowlands to 1500 m in all mountain areas of the island. On the Asian mainland, this species is widespread from India to China, the Philippines, and south through the Indonesian islands. Williams (1930) records a number of southern migrations of *T. limniace* on the island of Sri Lanka from late September to early December, and cites a 1912 report that "it migrates annually from the plains in the district of Kodaikanal, S. India, in October and November with many other species" (Williams 1930:159).

8. *T. hamata septentrionis* (Butler) (Plate 1: i)

   The larval food plant is *Heterostemma brownii* (Asclepiadaceae). The butterfly is distributed in all montane areas of Taiwan, from the lowlands to 2000 m. It is primarily a mainland Indo-Oriental species, with relatively few island populations in Asia. Williams (1930) cites a number of reports of *hamata* migrating in low numbers in mixed-species flocks in October, January, and March in India, Sri Lanka, and Burma. In southern India, it is reported (Williams 1930) to move annually from the plains in October and November.

9. *Danaus (Salatura) genutia genutia* (Cramer) (Plate 1: j)

   Danaus genutia feeds on three species of Asclepiadaceae: *Asclepias curassavica*, *Cynanchun lanhsuense*, and *C. taiwanianum*. It flies from the lowlands to 1000 m in all island mountains. Elsewhere, *D. genutia* flies from China and the Philippines through Indonesia to northwestern Australia (but not in New Guinea) and west to India (Ackery & Vane-Wright 1984). There are no previous reports of migratory behavior in this species. However, Longstaff (1912:756) observed a group of about 20 *Danaus genutia* gathering to roost communally under a palm leaf in the evening on 8 December 1903, in the Botanic Gardens at Howrah near Calcutta, India.

The relative proportions of eight of these species found at the Lukuea overwintering site in Kaoshung County in mid-winter 1989 are shown in Table 1. Here, at 400 m elevation, the quiescent adults were sitting on the upper surfaces of leaves and twigs on a variety of tree species. Most resting butterflies were between 3 and 10 m above the ground.

Most (86%) of the overwintering danaine butterflies in this sample (counted by H. Y. Wang) belonged to the genus *Euploea*. The two most common were *Euploea mulciber barisine* and *E. tulliolus koxinga*. All four species of *Euploea* are widespread over the island of Taiwan, but can be collected only from April to September in the northern and central part of Taiwan. In other words, these four species of *Euploea*, along with the other migratory danaine species, "disappear" from the northern and central areas of Taiwan from October to March of the

TABLE 1. The proportions of individuals among eight species of danaines in an overwintering site sample (206 specimens) counted 17 February 1989 by H. Y. Wang, at Lukuea, Kaoshung County, Taiwan (400 m).

Species	Number	Percentage of aggregation
1. *Euploea tulliolus koxinga*	76	36.9%
2. *E. mulciber barsine*	68	33.0%
3. *E. eunice hobsoni*	22	10.7%
4. *E. sylvestor swinhoei*	12	5.8%
5. *Tirumala hamata septentrionis*	12	5.8%
6. *Ideopsis similis similis*	10	4.9%
7. *Parantica algea maghaba*	1	0.5%
8. *Danaus genutia genutia*	5	2.4%
Total	206	100.0%

following spring, apparently concentrating in these several southern valleys for the winter (Table 2). Incidentally, all of these species formerly were placed in the "catch-all" genus *Danaus*, congeneric with the well-known migrant North American monarch butterfly, *Danaus plexippus*.

Danaus genutia, although rare in the mixed aggregations (Table 1), forms large single-species overwintering colonies, as does the monarch in Mexico. Unlike the huge aggregations of monarchs in Mexico, however, which number in the millions, colonies of *D. genutia* number in the hundreds or thousands, and have never been found to exceed 50,000 individuals. This species has a beautiful orange and black color pattern on the dorsal wing surface, similar to the monarch.

In contrast to *D. genutia*, *Ideopsis similis similis*, a beautiful pale green butterfly with black veins, overwinters in low numbers in the same valleys as other danaine species.

In the summer season, a time of maximum flight activity, individuals of local populations of *I. similis* congregate in small groups in late afternoon, sitting on adjacent leaves to pass the night.

Characteristics of the Migratory Behavior

Although the first butterfly valley in Taiwan was not reported by a lepidopterist until 1971, considerable local interest has focused on the phenomenon since. One central fact already known is that before the first major cold front sweeps across Taiwan, usually in late November, all the overwintering species of danaines have reached the butterfly valleys or nearby areas (Wang, pers. obs.). A general outline of other behavioral observations to date is as follows.

Initially, danaines at the same elevations in the higher mountains form small mixed-species groups that fly south along the Central Moun-

TABLE 2. Seasonal occurrence of migratory and non-migratory danaine butterfly species at Yanminshan National Park, located at the most northern point on Taiwan (Fig. 1). (The symbol "+" indicates the resident occurrence of the species in that season.)

Species	Spring	Summer	Autumn	Winter	Migratory in Taiwan or not
Euploea sylvestor swinhoei	+	+			yes
E. mulciber barsine	+	+	+		yes
E. tulliolus koxinga	+	+	+		yes
E. eunice hobsoni	+	+	+		yes
Tirumala hamata septentrionis	+	+			yes
T. limniace limniace	+	+			yes
Ideopsis similis similis	+	+			yes
Parantica aglea maghaba	+	+			yes
P. malaneus swinhoei	+	+	+	+	no
P. sita niphonica	+	+	+	+	no
Danaus genutia genutia	+	+			yes
Limnas chrysippus	+	+		+	no

tain Range. Other small groups form and join together to increase the size of the migrating aggregations. As the large migratory groups reach the southern area of the Central Mountain Range, they settle temporarily in valleys in the higher mountains, at altitudes in excess of 1000 m. When an arriving cold front from mainland Asia (Fig. 2) lowers the air temperature, the large group flies downslope into the warmer valleys. In the process, larger and larger groups of butterflies form as smaller groups encounter each other. The result is like a snowball rolling downhill, with the migrating group growing steadily on the way to its winter home. This portion of the migration, forced by the arrival of cold fronts from the Asian continent, presents spectacular scenes, but it is difficult to observe movements of these large aggregations for the following reasons:

(1) The *migratory distances* involved in the last stages of the migration route are short.
(2) The *migratory time* required for these relatively local movements from high mountains to lower valleys is brief, taking place in only a day or so.
(3) Most of the species in these groups are black and purplish or green, and are well *camouflaged* within the forest. Additionally, they fly only a meter or two above ground and thus are frequently inconspicuous within the thick tropical vegetation at the southern end of the island.

The number of times that this kind of local migration is repeated during a single year depends on how many strong cold fronts arrive

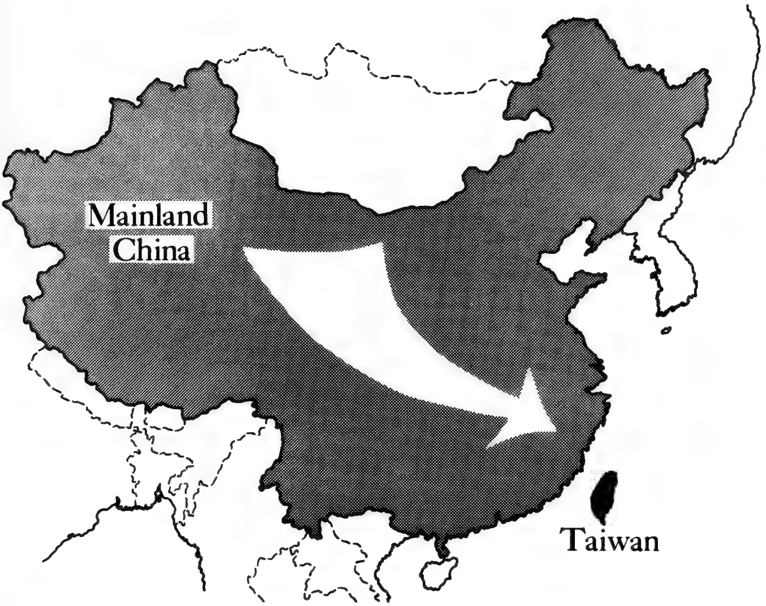


FIG. 2. The geographic position of Taiwan and the direction of cold fronts arriving from mainland Asia in winter.

during the late fall and winter. Finally, however, the huge group of danaines finishes migration and arrives at the lowest and warmest valleys, where it stays until the coming of spring. Usually, these last sites in the overwintering valleys range from 300 to 500 meters in elevation. After their arrival at these locations, no matter how cold the weather is, the danaines never have been observed to move to other places or to leave the mountain valleys to enter the lower but developed (urbanized and agriculturalized) plains areas.

If an extraordinarily strong cold front arrives and causes the temperature in these final overwintering valley locations to drop below 4°C, disastrous losses occur in the colonies. Frozen danaids cannot hold their positions on the leaves and fall to the ground in quick succession. The forest floor becomes carpeted with dead butterflies, coloring the ground with masses of black, purple, and green wings and bodies. Normally, however, the temperature in the southern low mountain areas very seldom drops below 4°C.

The southward and downard movement of danaines that normally live in high mountains results in their arrival at these southern warmer valleys where past generations have survived the winter. At higher elevations, nighttime temperatures regularly drop below 4°C during the winter. However, the lowest temperatures in the now-cleared and uninhabitable plains areas during the winter are above this level. For example, between December 1988 and February 1989, the lowest temperatures anywhere in the plains occurred at dawn on 12 February 1989. Minimum temperatures on the plains, which occur in February, are lowest in the North and increase gradually from north to south as follows (refer to Fig. 1): 6.4°C (Danshei), 7.2°C (Hsingchu), 6.9°C (Taichung), 7.2°C (Chaiyi), 8.5°C (Taiman), 10.2°C (Kaoshung), and 10.7°C (Hanchen). This temperature gradient suggests an ecological reason for the southward movement and the selection of lower-elevation sites by populations of overwintering danaines, where they seek winter shelter on trees still existing in foothill valleys just above the developed plains area.

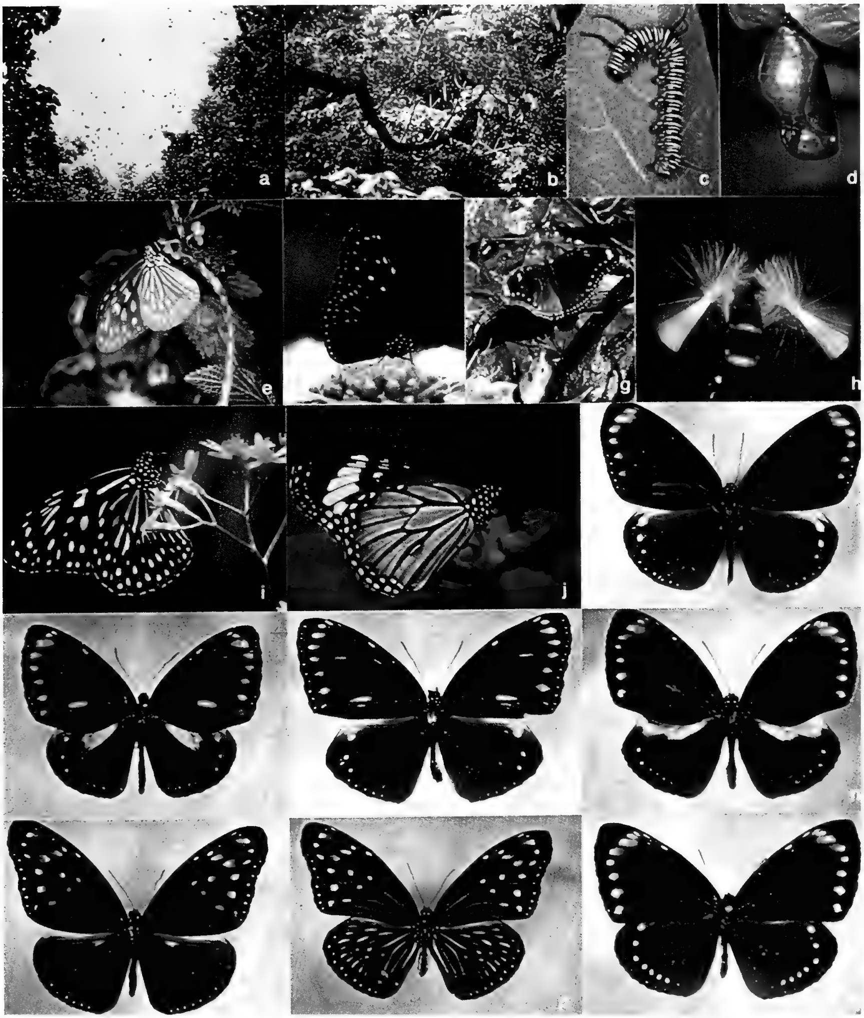
Some of these migrations reach spectacular numbers. A local lepidopterist named Chan reported to Wang that he saw "a flying black river" of danaine butterflies flowing from the sea to the nearby valley at Chow-Jou Beach (in Pinton County) in early December 1972. Chan hypothesized that the danaines living in the lowlands or the western plains fly from the breeding area directly to the coast, and then fly southward above the Taiwan Strait and the adjacent coastline, gradually joining with other groups. The migrating danaines then become a very large group when they approach the turning point at the Sea of Chow-Jou. At that point, the danaines form a huge and lengthy flying river from sea to the land as they fly inland towards the overwintering valleys. This use of a coastal route by migrating danaines may result from the fact that the entire western plain of Taiwan is now developed. Urbanization and industrialization of these western lowlands have eliminated any past favorable nectaring areas or other natural habitats and navigational landmarks that might have been used by the danaines.

Behavior in the Aggregation Valleys

In the latter part of November and December, danaines that have just arrived at the overwintering valleys take up positions on the leaves, but fly around actively from approximately 0930 to 1130 h (Plate 1). They also visit nearby streams for drinking water during the same period. However, when cold fronts come, the butterflies remain motionless on tree leaves in the valley until warmer temperatures return.

→

PLATE 1. Scenes of the overwintering phenomenon in Taiwanese danaine species. (a) Overwintering danaine aggregations take flight on warm days or when disturbed by people entering a colony area. (b) Hundreds of dark *Euploea* individuals rest in scattered array on the top surfaces of leaves of deciduous trees while overwintering. They are not



as densely packed as individuals in overwintering North American monarch colonies. (c) The larva of a *Euploea* species; only the adult stage overwinters. (d) A *Euploea* pupa. (e) *Ideopsis similis similis* female nectaring on a flower in a colony on a warm day in late January. (f) *Euploea mulciber barsine* adult nectaring on a flower at an overwintering site in early December. (g) A mimetic nymphaline, *Hypolimnas bolina kezia* (Butler) female, here seen drinking water at a stream in a danaine colony site, may also overwinter in the adult stage, but any migratory behavior is unknown. (h) *Euploea* males evert yellow androconial brushes from their abdomens at times while flying at mid-day in an overwintering colony. (i) *Tirumala hamata septentrionis* male nectaring at a flower in an overwintering valley. (j) *Danaus genutia genutia* male visiting a flower in December in a colony. (k) *Euploea sylvester swinhoei* male. (l) *Euploea eunice hobsoni*, male. (m) *Euploea eunice hobsoni*, female. (n) *Euploea tulliolus koxinga*, male. (o) *Euploea mulciber barsine*, male. (p) *Euploea mulciber barsine*, female. (q) *Euploea tulliolus koxinga*, female.

In some of the valleys, the aggregations get so dense that twigs, branches, and leaves are covered with danaines perched shoulder-to-shoulder. Even the green color of the foliage is replaced by the predominantly black color of the underside of the wings. On warm nights, the overwintering danaines can be attracted off their perches by electric lights or flashlights, many of them flying just like moths around the light source.

Wang (unpublished) has noted that, at least in *Euploea tulliolus koxinga*, males evert and display their brushes of yellow hair pencils from their abdominal tips (Plate 1:h) while flying around at the overwintering sites in early February, before any courtship and mating activity is observed. He postulates that the pheromones of these *Euploea* may play an important role as an aggregation stimulus for the overwintering danaines, in addition to their role at other times of the year in courtship and mating.

As the warmer weather of March comes, the overwintering danaines become more and more active, leaving the roost daily for water and nectar (Plate 1:a). In late March, the butterflies begin courting and mating, and soon after mating, the females begin to fly north, back to the high elevation breeding areas in the northern parts of the island. Presumably, males die within a short time after mating. The departure from the overwintering sites is gradual, in striking contrast to the mass arrival during the fall.

DISCUSSION

The most important point of this report is that the monarch is not unique among the Danainae in its migration and over-wintering behavior. The fact that other members of the Danaini, and Euploeini, show similar behaviors suggests that it is a well-established ancestral trait in the Danainae in general.

The regular southward and northward migratory behavior and overwintering aggregations of the Monarch, *Danaus plexippus*, in response to cold weather has been well documented on the continent of North America (e.g., Williams 1930, 1958, Urquhart 1960, 1987, Brower 1977, 1985, Calvert & Brower 1981, Ackery & Vane-Wright 1984). Otherwise, few studies have been done on danaine migrations and overwintering behavior, although this behavior may be widespread in the subfamily as a response to either cold or dry seasons. Some observations of dry-season movements of neotropical danaines through mountain passes in Venezuela and Costa Rica have been reported (Beebe 1950, DeVries 1987). Scattered observations of migrations of certain species in the genera *Danaus, Tirumala, Parantica, Ideopsis,* and *Euploea* have been made in East Africa, southern India, and Sri Lanka (Ackery & Vane-

Wright 1984). A detailed study of a subtropical, locally-overwintering aggregation of the common crow butterfly, *Euploea core corinna* (W. S. Macleay), has been made in Brisbane, Australia (Kitching & Zalucki 1981). In addition to this Indo-Australian danaine species, winter aggregations (May–September) are recorded for the dry season in northeastern Australian populations of *E. sylvester* (F.) and *E. tulliolus* (F.), *Tirumala hamatus* (W. S. Macleay), and *Danaus affinis* (F.). *Euploea core* is capable of living as long as 160 days, but it is not migratory (Kitching & Zalucki 1981), unlike the nine danaines (including four *Euploea* species) in Taiwan and *Danaus plexippus* in North America.

The observations reported here show that there are still many questions to be answered about these migrations in Taiwan. The details of the migratory route are unknown, especially during the early parts of the movement from the northern and central parts of the island to the southern higher mountain areas, prior to the movement downhill to the low-elevation valleys. Additional locations of overwintering sites are certain to be found with further searching. Detailed studies need to be made of the relation between climatic and weather conditions and the particular overwintering locations chosen by these danaids, similar to the work that has been done by Lincoln P. Brower (e.g., 1977, 1985) and his colleagues (e.g., Calvert & Brower 1981) in the overwintering sites of *Danaus plexippus* in central Mexico. The permanence of the overwintering sites needs to be ascertained, although all observations to the present indicate that the same sites are used year after year.

It is known that the nine migratory species of danaines in Taiwan have two to four generations a year (Hamano 1986). The adult danaines of the summer season live only about one month, but the overwintering adults of these species can live about six months, from October to at least March of the following year. All nine species of overwintering danaines share the characteristic of having a very tough integument that makes them difficult to kill (as tested by squeezing the thorax between thumb and forefinger). It is also relatively difficult to rub the scales off these butterflies. It would be valuable to test the palatability of these danaines to insectivorous birds and other potential predators in both the summer ranges and the overwintering sites.

Additional unanswered questions include: Are there any overwintering valleys along the eastern side of the Central Mountain Range in addition to the recently discovered one in Taiton County at Dawu? Is the true migratory route in the western plains area actually along the coastline, or over the sea itself? Do the danaines that come from the northern part of Taiwan congregate in the same valleys as those that come from the mountains in the southern part of Taiwan?

Expanded research on the overwintering danaines of Taiwan should generate fascinating comparative material for those interested in studying and preserving the tremendous overwintering aggregations of the Monarch (*Danaus plexippus*) in North America. In the meantime, preserving the very few overwintering sites of danaine butterflies in Taiwan will be of the greatest importance for conservationists in that country, and, indeed, for lepidopterists and others around the world who may wish to travel to see these great natural phenomena for themselves. The aggregations offer great potential for winter tourism in Taiwan, and perhaps admission fees could be collected to help defray protection costs. Currently, the sites occupied by the colonies are only marginally attractive for agricultural clearing and development, but that could change with increasing population pressures.

ACKNOWLEDGMENTS

We thank Philip Ackery, John B. Heppner, Lincoln P. Brower, Robert Michael Pyle, and Peter J. Eliazar for helpful comments and critical discussion in reviewing the manuscript. The Taiwan Museum and its Director, Young Shih-Chun, provided very helpful support for this research.

LITERATURE CITED

ACKERY, P. R. & R. I. VANE-WRIGHT. 1984. Milkweed butterflies. British Museum (Natural History), London. 425 pp.

BATCHELOR, D. M. 1960. A large scale migration of *Euploea modesta* Butler. Malayan Nature Journal, Kuala Lumpur 14:90–93.

BEEBE, W. 1950. Migration of Danaidae, Ithomiidae, Acraeidae and Heliconidae (Butterflies) at Rancho Grande, north-central Venezuela. Zoologica, New York 35:27–32.

BROWER, L. P. 1977. Monarch migration. Natural History 84:40–53.

——— 1985. New perspectives on the migration biology of the Monarch butterfly, *Danaus plexippus* L., pp. 748–785. *In* Rankin, M. A. (ed.), Migration: Mechanisms and adaptive significance. Univ. Texas Contrib. Marine Sci. Suppl. 27.

CALVERT, W. H. & L. P. BROWER. 1981. The importance of forest cover for the survival of overwintering monarch butterflies (*Danaus plexippus*, Danaidae). J. Lepid. Soc. 35:216–225.

DEVRIES, P. J. 1987. The butterflies of Costa Rica and their natural history. Princeton Univ. Press, Princeton, New Jersey. 327 pp.

HAMANO, EIJI. 1986. Ecological encyclopedia of Taiwanese butterflies. Kodansha Ltd., Tokyo, Japan. 474 pp.

KITCHING, R. L. & M. P. ZALUCKI. 1981. Observations on the ecology of *Euploea core corina* (Nymphalidae) with special reference to an overwintering population. J. Lepid. Soc. 35:106–119.

LONGSTAFF, G. B. 1912. Butterfly-hunting in many lands. Longmans, Green, and Co., London. 729 pp.

URQUHART, F. A. 1960. The Monarch butterfly. Univ. Toronto Press, Toronto, Ontario. 361 pp.

——— 1987. The Monarch butterfly: International traveler. Nelson-Hall, Chicago, Illinois. 232 pp.

WILLIAMS, C. B. 1930. The migration of butterflies. Oliver and Boyd, Edinburgh and London. 473 pp.

——— 1958. Insect migration. Collins, London. 235 pp.

Received for publication 7 August 1990; revised and accepted 18 October 1990.

Journal of the Lepidopterists' Society
44(4), 1990, 229–244

FEMALE COLOR AND SEX RATIO IN HYBRIDS BETWEEN *PAPILIO GLAUCUS GLAUCUS* AND *P. EURYMEDON*, *P. RUTULUS*, AND *P. MULTICAUDATUS* (PAPILIONIDAE)

J. MARK SCRIBER,[1] ROBERT V. DOWELL,[2] ROBERT C. LEDERHOUSE[1]
AND ROBERT H. HAGEN[1]

[1] Department of Entomology, Michigan State University,
East Lansing, Michigan 48824
[2] 1681 Pebblewood Dr., Sacramento, California 95833

ABSTRACT. Female offspring of black *Papilio glaucus glaucus* females handpaired to *P. eurymedon*, *P. rutulus*, or *P. multicaudatus* males show variable expression of the black phenotype. Hybridization with *P. rutulus* yielded black, yellow, and intermediate females, in agreement with previous observations. Hybridization with *P. multicaudatus* also yielded black and intermediate females, which has not been reported previously. Hybridization with *P. eurymedon* yielded only one yellow female. Suppression of the black phenotype in interspecies hybrids is not complete and may not have a simple genetic basis.

The sex ratio among progeny of these hybridizations was skewed drastically towards males, with most females dying prior to adult eclosion. This "Haldane effect" appears to be much less severe among progeny of *P. glaucus glaucus* males paired to *P. eurymedon* or *P. rutulus* females than in the case of reciprocal pairings using *P. g. glaucus* females.

Additional key words: Haldane effect, mimetic coloration, suppressor genes, enabler genes, pupal diapause.

Papilio glaucus glaucus (Papilionidae) females show a striking color dimorphism that has attracted considerable study for over 100 years (Edwards 1884, Clarke & Sheppard 1959, 1962, Brower 1958, Brower 1959a, 1959b, Brower & Brower 1962, Scriber et al. 1987, Lederhouse & Scriber 1987). Female *P. g. glaucus* may have a yellow ground color and resemble the monomorphic males, or they may have a dark or black ground color and act as Batesian mimics of *Battus philenor* (Brower 1958).

Papilio g. glaucus appears to be unique among taxa within the *Papilio glaucus* species group in exhibiting this dimorphism. Only monomorphic females occur in *P. glaucus canadensis*, *P. rutulus*, *P. eurymedon*, *P. multicaudatus*, and *P. alexiares alexiares*. Only black females are known in *P. alexiares garcia* (Beutelspacher & Howe 1984). Valuable insight into the evolution of mimicry in *P. g. glaucus* can be obtained through comparative study of the genetic basis for female color in these closely related species and subspecies.

Female color in *P. g. glaucus* is almost always maternally inherited, implying that it is determined primarily by a Y-linked gene (Clarke & Sheppard 1959, 1962, Clarke & Clarke 1983). Exceptions to the usual rule of maternal inheritance (cases of black females producing yellow daughters and the reverse) have been noted repeatedly, however (Edwards 1884, Clarke & Sheppard 1959, 1962, Scriber & Evans 1986, Scriber et al. 1987). Chromosome abnormalities have been invoked as explanations for some of these cases (Clarke & Sheppard 1959, Clarke & Clarke 1983, Scriber & Evans 1987, West & Clarke 1987).

Cases of non-maternal inheritance may also result from effects of autosomal or X-linked "suppressor" alleles that inhibit the production or deposition of black ground color (Clarke & Willig 1977, Clarke & Clarke 1983, Scriber et al. 1987, West & Clarke 1987, Hagen & Scriber 1989). An X-linked suppressor of this type has been identified and mapped in *P. g. canadensis* (Hagen & Scriber 1989). Presence of the *canadensis* suppressor allele is probably responsible for reported cases of non-maternal inheritance involving females collected near the *P. g. glaucus/P. g. canadensis* hybrid zone (Scriber et al. 1987, Scriber 1988).

In the case of *P. g. canadensis*, laboratory hybridizations with *P. g. glaucus* have revealed that the absence of black females is due both to lack of the black-determining Y-linked allele and to high frequency of the X-linked suppressor allele in natural populations (J. M. Scriber, R. Hagen & R. C. Lederhouse, unpublished). Do homologous suppressors occur in other taxa also lacking a black female form?

Interspecies hybrids within the *glaucus* species group may be obtained through hand-pairing (Clarke & Sheppard 1955, 1957, West & Clarke 1987, Scriber et al. 1988, 1991). Based on such crosses, West and Clarke (1987) presented evidence for suppressors in *P. eurymedon, P. rutulus*, and *P. multicaudatus*. Here we report results of additional laboratory hybridizations between *P. g. glaucus* and *P. eurymedon, P. rutulus*, and *P. multicaudatus*. Results of hybridization with *P. alexiares garcia* have been presented elsewhere (Scriber et al. 1988).

Reduced viability of hybrid females, the heterogametic sex, may result from genetic differentiation after speciation (the "Haldane effect": Haldane 1922, Ae 1979, Oliver 1979, Coyne & Orr 1989a). Recent studies have implicated sex chromosome interactions as primary factors in sex-biased hybrid viability and fertility (Coyne 1985, Coyne & Orr 1989b). Imperfect integration of the genome of hybrid Lepidoptera can result in a syndrome of developmental and diapause abnormalities, possibly from hormonal imbalances between regulatory and secretory positions of sex-linked co-adapted gene complexes (Oliver 1983). Prolonged post-diapause development of pupae may result in delays of adult females, and diapause may extend for one or more years (Oliver 1983, Scriber et al. 1987). More extreme cases may result in death of female hybrids at the egg, larval, or pupal stage, and therefore skewed sex-ratios may serve as indicators of the negative effects of the X- and Y-chromosome interactions. Sex ratios for interspecific crosses within the *glaucus* species group are presented here.

METHODS

Male and female *P. rutulus* and *P. eurymedon* were collected from Orange, Placer, Solano, Sacramento, and Mono counties, California and the Blue Mountains (Columbia County) of Washington during 1982–90 and mailed in envelopes or carried on ice to our laboratory. *Papilio multicaudatus* were collected from Placer and Solano counties in California and Columbia County, Washington and also from Nuevo Leon, Mexico.

Male *P. rutulus, P. eurymedon,* and *P. multicaudatus* were hand-paired to lab-reared virgin *P. glaucus* females. Field collected and laboratory-mated females were set up in plastic oviposition boxes (10 cm × 20 cm × 27 cm) with a sprig of foodplant under saturated humidity. The boxes were placed 0.7–1.0 m from continuously lighted 100 watt incandescent bulbs. From 1987–90 a repeating 4:4 h photo: scotophase was used. Females were fed a mixture of 1 part honey to 4 parts water at least once daily. Most females were allowed to oviposit until death. Eggs were collected and counted at 2-day intervals. Larvae were removed as they eclosed, and the remaining eggs were monitored for 10 days after the first larva hatched. First instar (neonate) larvae were gently placed on fresh leaves of various host plants. Leaf moisture was maintained using Aquapics® and fresh leaves were provided three times a week throughout larval development. Pupae were held at room temperature (23°C) for a minimum of three months after pupation. Those that had not emerged were then refrigerated six months at 5–7°C and then held at room temperature the following summer. This procedure was repeated for those apparently alive, healthy pupae that did not emerge by the end of the second summer. Some progeny of the field-collected females were used in the subsequent matings. Hybrid crosses are given with the female parent listed first.

RESULTS

Hybridization with *Papilio eurymedon*

A total of 25 pairings of *P. g. glaucus* females and *P. eurymedon* males was successful as judged by production of offspring reaching at least the pupal stage (Table 1). Only one female eclosed successfully from these broods whereas 223 males eclosed. The number of dead or developmentally delayed pupae (250) was not greatly different from the total number of males eclosing, suggesting that the majority may have been females (sex of pupae was not determined for this portion of our study). Extremely low viability of female hybrids was independent of maternal color phenotype. Black *P. g. glaucus* females were

TABLE 1. Hybrids between *Papilio glaucus* and *P. eurymedon*.

			Offspring		
Brood no.	Mother (source)	Father (source)	Males	Females	Dead pupae
1083	black *Pgg* (OH)	*eurymedon* (CA)	13	0	5
1170	black *Pgg* (OH)	*eurymedon* (CA)	1	0	3
1196	black *Pgg* (WI)	*eurymedon* (CA)	6	0	9
2309	black *Pgg* (WVA)	*eurymedon* (CA)	0	0	1
2311	black *Pgg* (IL)	*eurymedon* (CA)	11	0	11
2312	black *Pgg* (IL)	*eurymedon* (CA)	1	0	4
2313	black *Pgg* (IL)	*eurymedon* (CA)	21	0	27
2314	black *Pgg* (WVA)	*eurymedon* (CA)	1	0	0
2315	black *Pgg* (WVA)	*eurymedon* (CA)	6	0	9
2321	black *Pgg* (WVA)	*eurymedon* (CA)	24	0	21
2322	black *Pgg* (WVA)	*eurymedon* (CA)	0	0	4
2327	black *Pgg* (IL)	*eurymedon* (CA)	14	1*	29
2328	black *Pgg* (IL)	*eurymedon* (CA)	33	0	41
2518	black *Pgg* (GA)	*eurymedon* (CA)	4	0	9
2547	black *Pgg* (WI)	*eurymedon* (WA)	1	0	1
2671	black *Pgg* (WI)	*eurymedon* (CA)	16	0	16
	Subtotal		(148)	(1)	(190)
544	yellow *Pgg* (PA)	*eurymedon* (CA)	22	0	14
1084	yellow *Pgg* (OH)	*eurymedon* (CA)	3	0	5
1117	yellow *Pgg* (OH)	*eurymedon* (CA)	2	0	0
1119	yellow *Pgg* (OH)	*eurymedon* (CA)	21	0	23
1168	yellow *Pgg* (FL)	*eurymedon* (CA)	5	0	3
1187	yellow *Pgg* (FL)	*eurymedon* (CA)	1	0	0
1198	yellow *Pgg* (FL)	*eurymedon* (CA)	0	0	1
2269	yellow *Pgg* (WVA)	*eurymedon* (CA)	15	0	11
2318	yellow *Pgg* (WVA)	*eurymedon* (CA)	6	0	3
	Subtotal		(75)	(0)	(60)
4465	*eurymedon* (WA)	*Pgg* (FL)	6	1*	0

Pgg = *Papilio glaucus glaucus*, * = yellow.

used in 16 of the pairings and yellow females in the remaining nine; the only daughter produced was from a black mother (brood 2327).

Female viability appears to be higher in the reciprocal cross (*P. eurymedon* female × *P. g. glaucus* male). Few crosses in this direction were attempted in our study and only one was successful (Table 1: brood 4465). However, one of two successful crosses in the same direction reported by West and Clarke (1987) produced 13 females and 13 males; the other produced two males only. The overall sex ratio from these three crosses was 1.5 male : 1.0 female (n = 35 offspring).

The color of the single hybrid (*P. g. glaucus* × *P. eurymedon*) female was yellow, which could indicate that her phenotype resulted from a suppressor contributed by her father. Additional evidence of a *P. eurymedon* suppressor is provided by the yellow daughters from 2 back-

TABLE 2. Backcrosses involving *P. eurymedon*.[1]

Brood no.	Mother (source)	Father (source)	Offspring Males	Offspring Females	Offspring Dead pupae
1278	black *Pgg* (TX)	F_1 (yellow *Pgg* × *Pe*)	2	1*	4
1544	black *Pgg* (TX)	F_1 (black *Pgg* × *Pe*)	3	5*	3

[1] The *P. g. glaucus* female numbers for the g × e hybrid males are 544 and 1083, respectively, for pairings 1278 and 1544.
Pgg = *Papilio glaucus glaucus*, *Pe* = *Papilio eurymedon*, * = yellow.

crosses of hybrid (*P. g. glaucus* × *P. eurymedon*) males to black *P. g. glaucus* females (Table 2). Too few offspring (6 females) were produced to determine whether yellow and black phenotypes depart significantly from the 1:1 ratio expected of a single suppressor allele contributed from the *P. eurymedon* grandparent.

The combined sex ratio among the backcross progeny (0.83 male: 1.0 female, n = 11) was similar to the combined ratio from three similar backcross families obtained by West and Clarke (1987) (1.33:1, n = 21) and neither differed significantly from a 1:1 ratio (χ^2, both P's > 0.50). Fertility of the hybrid males did not appear to be greatly reduced relative to that of other laboratory-reared males (Lederhouse et al. 1990).

Hybridization with *Papilio rutulus*

There were 26 successful pairings of *P. g. glaucus* females with *P. rutulus* males using 13 black and 13 yellow females (Table 3). As in the case of pairings with *P. eurymedon* males, most of the progeny that eclosed were male: 362 males versus 12 females (28:1 ratio). Also similar to crosses with *P. eurymedon,* a large number of pupae (407) failed to develop. Live pupae of 1987 crosses (brood #4562, 4564, and 4664) that had not emerged by August 1988 were sexed. Only 2 of the 34 pupae were male and all died subsequently without emerging. No effect of maternal color on sex ratio was apparent (Table 3). West and Clarke (1987) reported a total of 19 males and two females from two crosses of this type; two additional females were obtained by ecdysone injection of pupae (Clarke & Willig 1977).

Far fewer reciprocal crosses (*P. rutulus* female × *P. g. glaucus* male) were attempted, but the one that was successful (#4447) yielded an equal number of males and females. A similar, nearly equal, ratio of sexes (10 males, 8 females) was obtained by Clarke and Sheppard (1955) in an earlier cross of this type. Fertility of hybrid males, backcrossed to *P. g. glaucus* females did not appear to be substantially impaired (Table 4; also West & Clarke 1987). The sex ratio among backcross

TABLE 3. Hybrids between *Papilio glaucus* and *P. rutulus*.

			Offspring		
Brood no.	Mother (source)	Father (source)	Males	Females	Dead pupae
1115	black *Pgg* (WI)	*rutulus* (CA)	0	0	2
1152	black *Pgg* (FL)	*rutulus* (CA)	0	0	1
1153	black *Pgg* (FL)	*rutulus* (CA)	1	1+	0
1155	black *Pgg* (WI)	*rutulus* (CA)	15	2+	18
1156	black *Pgg* (OH)	*rutulus* (CA)	16	0	16
1181	black *Pgg* (FL)	*rutulus* (CA)	3	0	4
1183	black *Pgg* (OH)	*rutulus* (CA)	5	1*	7
2517	black *Pgg* (GA)	*rutulus* (WA)	43	1*	33
2553	black *Pgg* (GA)	*rutulus* (WA)	2	0	1
2830	black *Pgg* (WVA)	*rutulus* (CA)	40	0	15
4562	black *Pgg* (FL)	*rutulus* (CA)	47	2*	41
4564	black *Pgg* (FL)	*rutulus* (CA)	2	0	1
4664	black *Pgg* (OH)	*rutulus* (CA)	24	0	12
	Subtotal		(198)	(7)	(151)
2	yellow *Pgg* (PA)	*rutulus* (CA)	18	0	30
277	yellow *Pgg* (PA)	*rutulus* (CA)	15	2*	25
433	yellow *Pgg* (PA)	*rutulus* (CA)	12	0	17
546	yellow *Pgg* (WI)	*rutulus* (CA)	6	0	4
547	yellow *Pgg* (PA)	*rutulus* (WA)	30	1*	68
548	yellow *Pgg* (WI)	*rutulus* (WA)	9	0	11
1179	yellow *Pgg* (WI)	*rutulus* (CA)	33	0	23
334	yellow *Pgg* (FL)	*rutulus* (CA)	7	0	19
335	yellow *Pgg* (FL)	*rutulus* (CA)	2	0	8
336	yellow *Pgg* (FL)	*rutulus* (CA)	6	0	29
343	yellow *Pgg* (FL)	*rutulus* (CA)	0	0	2
1178	yellow *Pgg* (FL)	*rutulus* (CA)	9	2*	2
1180	yellow *Pgg* (FL)	*rutulus* (CA)	17	0	18
	Subtotal		(164)	(5)	(256)
4465	*rutulus* (CA)	*Pgg* (FL)	5	5	2

Pgg = *Papilio glaucus glaucus*, * = yellow, + = black.

progeny was 2.4 male:1.0 female (n = 150 offspring), similar to the ratio 2:1 (n = 71) reported by West and Clarke (1987).

Five pairings with black *P. g. glaucus* females produced a total of 3 black and 4 yellow hybrid (F1) daughters (Table 3, Fig. 1). Mixed phenotypes (two yellow, two intermediate) were also reported by West and Clarke (1987) from crosses of this type. (Hybrid intermediates are figured in Clarke & Willig [1977] and Clarke & Clarke [1983].) Three successful backcrosses of F1 males to black *P. g. glaucus* females also produced a range of color phenotypes among daughters (Table 4). The majority of backcross females were intermediate in color, with varying proportions of black and yellow scales intermixed (Fig. 1c–f). Four backcrosses of this type reported by West and Clarke (1987) also yielded

TABLE 4. Backcrosses involving *Papilio rutulus*.[1]

Brood no.	Mother (source)	Father (source)	Offspring					
				Females				
			Males	Black	Mostly dark	Mostly yellow	Yellow	Dead pupae
630	black *Pgg* (WI/SC)	F_1 (yellow *Pgg* × *Pr*) (CA)	32	3	5	4	1	15
1875	black *Pgg* (WI)	F_1 (black *Pgg* × *Pr*) (CA)	23	5	7	3	1	39
1876	black *Pgg* (WI)	F_1 (black *Pgg* × *Pr*) (CA)	51	2	12	1	8	27

Pgg = *Papilio glaucus glaucus*, *Pr* = *Papilio rutulus*.

[1] The *P. g. glaucus* female numbers for the g × r hybrid males are 433, 1155, and 1183 respectively for pairings 630, 1875, and 1876.

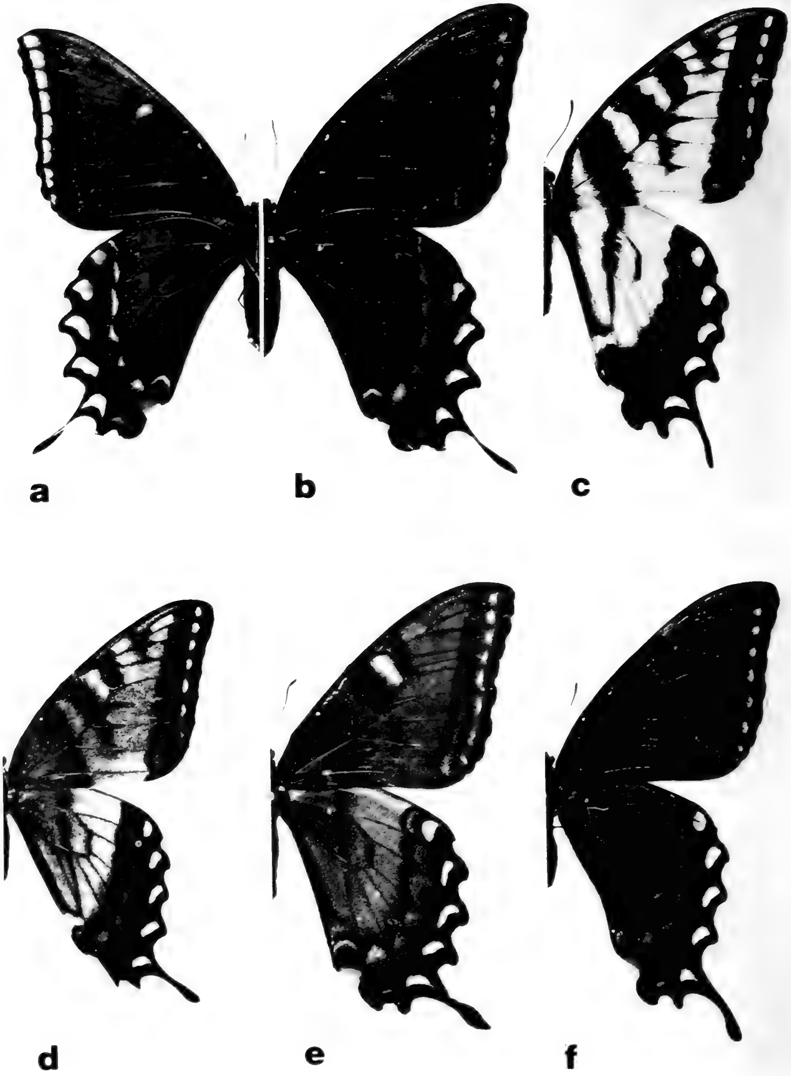


FIG. 1. Ventral (a) and dorsal (b) views of a black female hybrid from a black female *P. g. glaucus* × male *P. rutulus* (brood #1153). Backcross offspring exhibiting four female color forms (yellow [c], "intermediate" mostly yellow [d], "intermediate" mostly black [e], and black [f]). These 4 females are from a single backcross (brood #1876) between a dark *P. g. glaucus* female and a hybrid male (from a black female *glaucus* × male *rutulus*).

TABLE 5. Hybrids between *Papilio glaucus* and *P. multicaudatus*.

			Offspring				
Brood no.	Mother (source)	Father (source)	Males	Black females	Intermediate females	Yellow females	Dead pupae
2265	black *Pgg* (OH)	*multicaudatus* (CA)	10	2	3	0	10
3619	black *Pgg* (GA)	*multicaudatus* (WA)	4	1	0	0	0
3660	black *Pgg* (OH)	*multicaudatus* (Mex)	1	0	0	0	3
4473	black *Pgg* (OH)	*multicaudatus* (Mex)	2	0	0	0	4
4475	black *Pgg* (IN)	*multicaudatus* (Mex)	1	0	0	0	1
4498	black *Pgg* (FL)	*multicaudatus* (Mex)	10	0	0	0	9
4512	black *Pgg* (IN)	*multicaudatus* (Mex)	0	0	0	0	3
4516	black *Pgg* (OH)	*multicaudatus* (Mex)	2	0	0	0	1
	Subtotal		(30)	(3)	(3)	(0)	(31)

Pgg = *Papilio glaucus glaucus*.

a mixture of phenotypes (16 black; 5 intermediate; 3 yellow). Differences in the proportions of black and intermediate females between studies may reflect differences in criteria used for phenotype classification.

Hybridization with *Papilio multicaudatus*

We obtained eight successful pairings of black *P. g. glaucus* females with *P. multicaudatus* males (Table 5). No pairings with yellow females were successful and we did not have sufficient *P. multicaudatus* females to attempt reciprocal pairings using *P. g. glaucus* males. Two pairings yielded a total of six female offspring, for an overall sex ratio of 5:1 male : female (n = 36 offspring). Pupae from broods #2265, 3660, 4473, 4498, and 4516 that were alive, but had not eclosed after one year were sexed. All ten were female and all died without eclosing. West and Clarke (1987) report only male offspring in crosses in this type.

The hybrid females consisted of three black and three intermediate individuals (Fig. 2). The intermediate phenotype may indicate partial suppression of the black color in these hybrids. West and Clarke (1987) postulate the occurrence of a *P. multicaudatus* suppressor on the basis of 2 yellow daughters obtained from a backcross of a hybrid male to a black *P. g. glaucus* female.

Miscellaneous Interspecific Crosses

Five pairings of *P. rutulus* females with *P. eurymedon* males and five of the reciprocal pairings were successful (Table 6, Fig. 3). Despite overall low numbers of emerging adults, hybrid females were obtained from both types. The one successful hybridization between a *P. eurymedon* female and a *P. multicaudatus* male also yielded both male

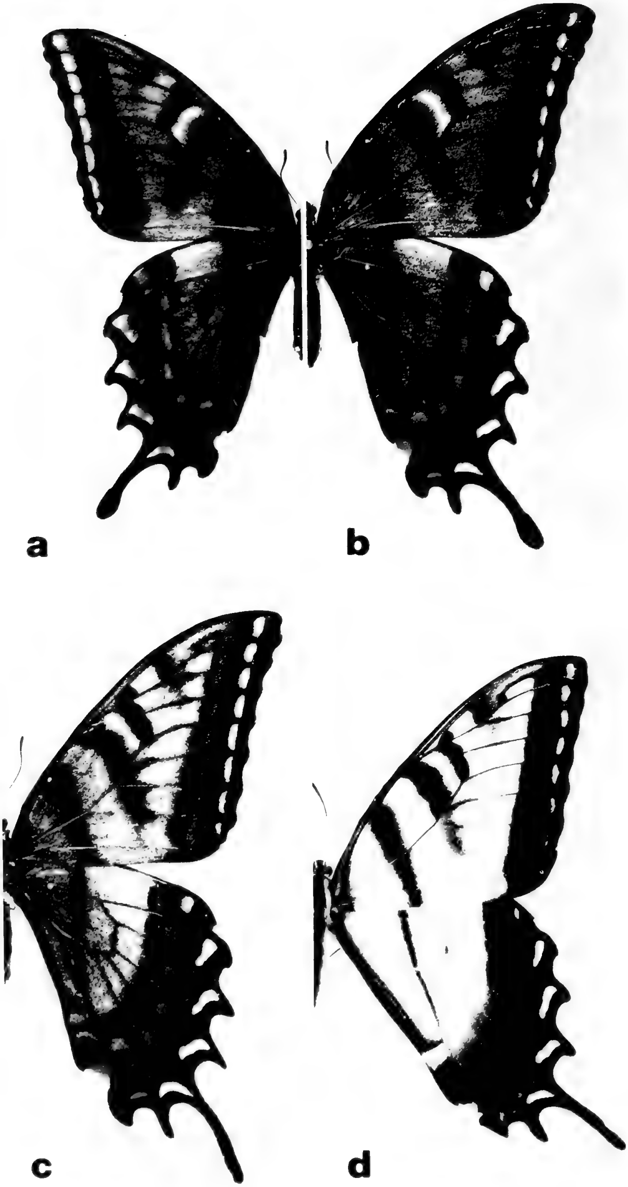


FIG. 2. Hybrid offspring (brood #2265) of a black female of *P. g. glaucus* × male *P. multicaudatus*. Ventral (a) and dorsal (b) views of a black female with some yellow scaling and the dorsal view (c) of an intermediate female are shown. The lower right (d) is a sibling hybrid male.

TABLE 6. Hybrids and backcrosses between *P. rutulus*, *P. eurymedon*, and *P. multicaudatus*.

			Offspring		
Brood no.	Mother (source)	Father (source)	Males	Females	Dead pupae
4539	*rutulus* (CA)	*eurymedon* (OR)	0	1	0
5653	*rutulus* (OR)	*eurymedon* (CA)	1	0	0
88008	*rutulus* (CA)	*eurymedon* (CA)	9	3	6
89028*	*rutulus* (CA)	*eurymedon* (CA)	22	9	0
7807*	*rutulus* (CA)	*eurymedon* (CA)	9	9	0
	Subtotal		(41)	(22)	(6)
1112	*eurymedon* (CA)	*rutulus* (CA)	3	1	3
3468	*eurymedon* (CA)	*rutulus* (WA)	1	0	15
3471	*eurymedon* (CA)	*rutulus* (WA)	0	2	27
3472	*eurymedon* (CA)	*rutulus* (WA)	1	0	7
89009*	*eurymedon* (CA)	*rutulus* (WA)	3	0	0
	Subtotal		(8)	(3)	(52)
88009	(*Pr* × *Pe*)	*rutulus* (CA)	9	9	2
7805	*rutulus* (CA)	*multicaudatus* (CA)	0	1	0
7806*	*rutulus* (CA)	*multicaudatus* (CA)	4	4	0
7819*	*rutulus* (CA)	*multicaudatus* (CA)	5	5	0
	Subtotal		(9)	(10)	(0)
4515	*eurymedon* (CA)	*multicaudatus* (Mex)	4	3	7

Pr = *Papilio rutulus*, *Pe* = *Papilio eurymedon*.
* Numbers reported are for sexed pupae.

and female offspring (Table 6). Three pairings of *P. rutulus* females with *P. multicaudatus* males produced a nearly equal sex ratio in pupae although more female pupae diapaused. All of the hybrid females in these crosses were yellow (Fig. 3).

DISCUSSION

In general, results from interspecific hybridizations in our laboratory agree with those summarized by West and Clarke (1987), with respect to relative viability of sexes and inheritance of color in female progeny. In both studies, however, relatively small sample sizes limit our ability to infer the genetics underlying these observations. Nonetheless, some generalizations can be suggested on the basis of present knowledge.

Suppressors of Black Female Color

Our results provide additional evidence to support West and Clarke's claim that suppressors of the black female phenotype occur in *P. eurymedon*, *P. rutulus*, and *P. multicaudatus*.

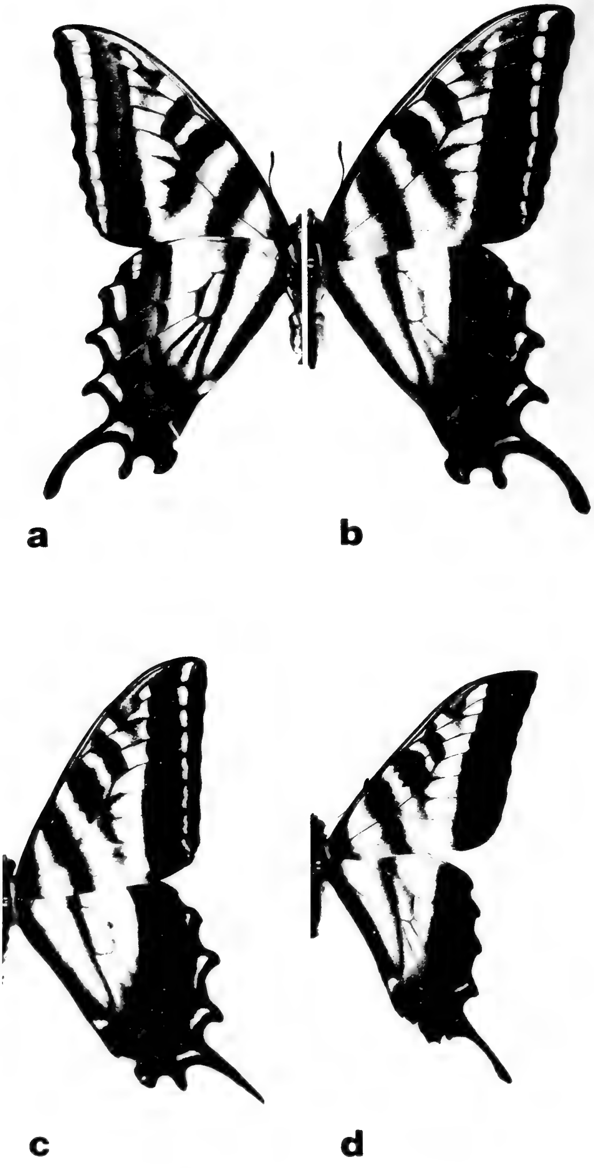


FIG. 3. Hybrid offspring of a female *P. eurymedon* × *P. multicaudatus* (brood #4515). Ventral (a) and dorsal (b) views of a female and the dorsal (c) view of a male are shown. The dorsal view (d) of a male offspring of a female *P. rutulus* × a male *P. eurymedon* (brood #88008) is also shown.

West and Clarke (1987) argue that suppression in *P. eurymedon* is due to an autosomal gene, in contrast to the X-linked suppressor of *P. glaucus canadensis* (Hagen & Scriber 1989). However, their argument is based on the occurrence of one yellow female in a backcross family, and should be accepted with caution. Unfortunately, our data provide little additional evidence of the mode of inheritance for any of the suppressors.

The *P. rutulus* and *P. multicaudatus* suppressors appear to be less effective than that of *P. eurymedon*, based on presence of intermediate and black females among hybrid or backcross progeny. As noted by West and Clarke (1987) and others (Scriber & Evans 1986, Hagen & Scriber 1989, J. M. Scriber, R. Hagen, and R. C. Lederhouse unpublished), inheritance of female color in *P. g. glaucus* crosses does not always follow simple Mendelian patterns. Further *P. g. glaucus* × *P. eurymedon* crosses and backcrosses are needed to determine whether there is consistent autosomal inheritance of suppression, and whether the "*eurymedon* suppressor" is truly different from those of other species.

From an evolutionary perspective, the presence of suppressors in *P. eurymedon, P. rutulus, P. multicaudatus,* and *P. g. canadensis* is puzzling if their only function is to prevent expression of the black female phenotype. All four taxa lack the Y-linked allele that is required to produce black females in the first place. Moreover, ranges of the three western species overlap considerably with that of *Battus philenor* (Ferris & Brown 1981, Scott 1986), so there is a potential selective advantage favoring black females if they were to appear in these species. One plausible explanation is that suppression is a pleiotropic effect of genes that play other, more significant roles in these butterflies. Their effect in hybrids may be an artifact of the disruption of both parental genomes.

Another possibility is that "suppressor" loci are actually "enabler" genes in *P. g. glaucus* and *P. alexiares garcia*. Suppression of the black phenotype may be a consequence of the absence of a required factor, rather than the presence of a specific inhibitor. If true, this would account for the simultaneous absence of the Y-linked allele and presence of suppression in *P. glaucus* group taxa lacking black females (i.e., *P. rutulus, eurymedon, multicaudatus,* and *P. g. canadensis*). The origin of the black female phenotype may have required evolution at two or more loci: at a Y-linked "black pigment" locus, and at X-linked or autosomal "enabler/suppressor" loci. The variable expression of female color in hybrids may represent a preadaptation for the black phenotype that was present in the ancestor of *P. g. glaucus* before the evolution of the Y-linked allele.

Sex Ratios and Viability of Interspecies Crosses

Analysis of inheritance patterns for female color in this study was limited primarily by low viability of female progeny in crosses of the type best able to demonstrate suppression: *P. g. glaucus* female × *P. eurymedon, rutulus,* or *multicaudatus* male. These females will have *P. g. glaucus* cytoplasm and Y-chromosome but have only a *eurymedon, rutulus,* or *multicaudatus* X-chromosome. Since low female viability occurred among daughters of both yellow and black *P. g. glaucus,* the Y-linked color gene appears not to be directly responsible.

Differential mortality of hybrid females appears to occur in the pupal stage. The numbers of dead pupae are roughly equal to the number of males that emerged in each family (Tables 1, 3, 5). When the sex of pupae was determined, the majority of those pupae that failed to develop were female. If these subsamples were representative of all dead hybrid pupae, family sex ratios would much more closely approximate the 1:1 ratio shown by intraspecific crosses.

In *P. g. canadensis,* the X-linked suppressor is closely linked to a locus responsible for regulation of pupal diapause (Hagen & Scriber 1989). The *canadensis* allele at this diapause locus causes individuals carrying it to enter an "obligate" pupal diapause, irrespective of photoperiod, temperature, or other cues (Rockey et al. 1987a, 1987b, Hagen & Scriber 1989). The *canadensis* allele appears to be recessive to the *glaucus* allele which permits environmental avoidance of diapause. Therefore, among hybrid *P. g. glaucus* × *P. g. canadensis* progeny reared under diapause-averting conditions, individuals entering pupal diapause were nearly all females.

Female mortality in interspecies crosses may involve homologous sex-linked regulatory loci that prevent triggering of pupal development in hybrids. Ecdysone injected into hybrid pupae has proven effective for stimulating ecolsion of hybrids and may provide a means for overcoming this block artificially (Clarke & Willig 1977, Hagen & Scriber 1989).

West and Clarke (1987) summarize the genetic basis underlying the human "fragile-X" syndrome as an example of the potential for subtle genotype-by-environment interactions affecting phenotype at the chromosomal level. Gilbert et al. (1987) described multiple pathways for genetic control of coloration in *Heliconius* species. It remains to be seen whether a single genetic mechanism underlies the diverse patterns of inheritance of color phenotype in the *Papilio glaucus* group, and whether it is connected directly with evolution of barriers to reproduction between species.

ACKNOWLEDGMENTS

This research was supported by Michigan State University College of Natural Sciences and the Agricultural Experiment Station (Project 1644) and in part by the National Science

Foundation (BSR 8306060, BSR 8718448), USDA grants #85CRCR-1-1598 and #87-CRCR-1-2851, and the Graduate School and College of Agricultural and Life Sciences (Hatch 5134) of the University of Wisconsin. We particularly thank the following people for valuable discussion and/or their assistance in field collections for this study: Janice Bossart, Mark Evans, Robert Krebs, Jim Maudsley, Ric Peigler, Adam Porter, David Robacker, Frank Slansky Jr., John Thompson, William Warfield, Wayne Wehling, and David West. We also thank Ralph Common for the photography, and Keith Brown and David West for constructive criticism of our manuscript.

LITERATURE CITED

AE, S. A. 1979. The phylogeny of some *Papilio* species based on interspecific hybridization data. Syst. Entomol. 4:1–16.

BEUTELSPACHER, C. R. & W. H. HOWE. 1984. Mariposas de Mexico. Fasc. 1. La Prensa Medica Mexicana, S.A. Mexico. D.F.

BROWER, J. V. Z. 1958. Experimental studies of mimicry in some North American butterflies. Part II. *Battus philenor* and *Papilio troilus, P. polyxenes,* and *P. glaucus.* Evolution 12:123–136.

BROWER, L. P. 1959a. Speciation in butterflies of the *Papilio glaucus* group. I. Morphological relationships and hybridization. Evolution 13:40–63.

——— 1959b. Speciation in butterflies of the *Papilio glaucus* group. II. Ecological relationships and interspecific sexual behavior. Evolution 13:212–228.

BROWER, L. P. & J. V. Z. BROWER. 1962. The relative abundance of model and mimic butterflies in natural populations of the *Battus philenor* mimicry complex. Ecology 43:154–158.

CLARKE, C. A. & F. M. M. CLARKE. 1983. Abnormalities of wing pattern in the eastern tiger swallowtail butterfly, *Papilio glaucus*. Syst. Entomol. 8:25–28.

CLARKE, C. A. & P. M. SHEPPARD. 1955. The breeding in captivity of the hybrid *Papilio rutulus* female × *P. glaucus* male. Lepid. News 9:46–48.

——— 1957. The breeding of the hybrid *Papilio glaucus* female × *P. eurymedon* male. Lepid. News 11:201–205.

——— 1959. The genetics of some mimetic forms of *Papilio dardanus,* Brown, and *Papilio glaucus*. Linn. J. Genetics 56:236–260.

——— 1962. The genetics of the mimetic butterfly, *Papilio glaucus*. Ecology 43:159.

CLARKE, C. A. & A. WILLIG. 1977. The use of α-ecdysone to break permanent diapause of female hybrids between *Papilio glaucus* L. female and *Papilio rutulus* Lucas male. J. Res. Lepid. 16:245–248.

COYNE, J. A. 1985. The genetic basis of Haldane's rule. Nature 314:736–738.

COYNE, J. A. & H. A. ORR. 1989a. Two rules of speciation, pp. 180–207. *In* Otte, D. & J. A. Endler (eds.), Speciation and its consequences. Sinauer Assoc., Sunderland, Massachusetts. 679 pp.

——— 1989b. Patterns of speciation in *Drosophila*. Evolution 43:362–381.

EDWARDS, W. H. 1884. The butterflies of North America. Vol. II. Houghton Mifflin Co., Boston, Massachusetts. 358 pp., 51 pls.

FERRIS, C. D. & F. H. BROWN. 1981. Butterflies of the Rocky Mountain states. Univ. of Oklahoma Press, Norman, Oklahoma. 422 pp.

GILBERT, L. E., H. S. FORREST, T. D. SCHULTZ & D. J. HARVEY. 1987(1988). Correlations of ultrastructure and pigmentation suggest how genes control development of wing scales of *Heliconius* butterflies. J. Res. Lepid. 26:141–160.

HAGEN, R. C. & J. M. SCRIBER. 1989. Sex-linked diapause, color, and allozyme loci in *Papilio glaucus*: Linkage analysis and significance in a hybrid zone. Heredity 80: 179–185.

HALDANE, J. B. S. 1922. Sex ratio and unisexual sterility in hybrid animals. J. Genet. 12:101–109.

LEDERHOUSE, R. C., M. P. AYRES & J. M. SCRIBER. 1990. Adult nutrition affects male virility in *Papilio glaucus*. Functional Ecology 4:743–751.

LEDERHOUSE, R. C. & J. M. SCRIBER. 1987. Increased relative frequency of dark morph females in the tiger swallowtail *Papilio glaucus* (Lepidoptera: Papilionidae) in s-central Florida. Amer. Midl. Nat. 118:211–213.

OLIVER, C. G. 1979. Genetic differentiation and hybrid viability within and between some Lepidoptera species. Am. Nat. 114:681–694.

——— 1983. Disturbance of eclosion sequence in hybrid Lepidoptera. Can. Ent. 115: 1445–1452.

ROCKEY, S. J., J. H. HAINZE & J. M. SCRIBER. 1987a. A latitudinal and obligatory diapause reponse in three subspecies of the eastern tiger swallowtail *Papilio glaucus* (Lepidoptera: Papilionidae). Amer. Midl. Nat. 118:162–168.

——— 1987b. Evidence of a sex-linked diapause response in *Papilio glaucus* subspecies and their hybrids. Physiol. Entomol. 12:181–184.

SCOTT, J. A. 1986. The butterflies of North America. Stanford Univ. Press, Stanford, California. 583 pp.

SCRIBER, J. M. 1988. Tale of the tiger: Beringial biogeography, bionomial classification, and breakfast choices in the *Papilio glaucus* complex of butterflies, pp. 241–301. *In* Spencer, K. C. (ed.), Chemical mediation of coevolution. Academic Press, New York. 609 pp.

SCRIBER, J. M. & M. H. EVANS. 1986(1987). An exceptional case of paternal transmission of the dark form female trait in the tiger swallowtail butterfly, *Papilio glaucus* (Lepidoptera: Papilionidae). J. Res. Lepid. 25:110–120.

——— 1987(1988). Bilateral gynandromorphs, and sexual and/or color mosaics in the tiger swallowtail butterfly, *Papilio glaucus* (Lepidoptera: Papilionidae). J. Res. Lepid. 26:39–57.

SCRIBER, J. M., M. H. EVANS & R. C. LEDERHOUSE. 1988(1990). Hybridization of the Mexican tiger swallowtail, *Papilio alexiares garcia* with other *Papilio glaucus* group species and survival of pure and hybrid larvae on potential host plants. J. Res. Lepid. 27:222–232.

SCRIBER, J. M., M. H. EVANS & D. RITLAND. 1987. Hybridization as a casual mechanism of mixed color broods and unusual color morphs of female offspring in the eastern tiger swallowtail butterflies, *Papilio glaucus*, pp. 119–134. *In* Huettel, M. (ed.), Evolutionary genetics of invertebrate behavior. Plenum Press, New York. 355 pp.

SCRIBER, J. M., R. C. LEDERHOUSE & R. H. HAGEN. 1991. Foodplants and evolution within *Papilio glaucus* and *Papilio troilus* species groups (Lepidoptera: Papilionidae), pp. 341–373. *In* Price, P. W., T. M. Lewinsohn, G. W. Fernandes & W. W. Benson (eds.), Plant-animal interactions: Evolutionary ecology in tropical and temperate regions. John Wiley, New York. 639 pp.

WEST, D. A. & C. A. CLARKE. 1987(1988). Suppression of the black phenotype in females of the *P. glaucus* group (Papilionidae). J. Res. Lepid. 26:187–200.

Received for publication 24 November 1989; revised and accepted 14 September 1990.

Journal of the Lepidopterists' Society
44(4), 1990, 245–251

ROLE OF THE OSMETERIAL GLAND IN SWALLOWTAIL LARVAE (PAPILIONIDAE) IN DEFENSE AGAINST AN AVIAN PREDATOR

ANDREA JO LESLIE
316 N. Fleming Rd., Woodstock, Illinois 60098

AND

MAY R. BERENBAUM*
Department of Entomology, 320 Morrill Hall, University of Illinois,
505 S. Goodwin, Urbana, Illinois 61801-3795

ABSTRACT. The importance of the osmeterial gland, a universal characteristic of larvae in the Papilionidae, in defense against vertebrate predators has rarely been examined. In this study, third and fifth instar larvae of *Papilio polyxenes* with and without a functional osmeterium were presented to *Coturnix coturnix* (Japanese quail), a representative avian predator. Virtually all larvae were rejected by *C. coturnix* irrespective of osmeterial function. Larvae of *P. cresphontes* with functional osmeteria were also universally rejected by *C. coturnix*; in contrast, larvae of *P. glaucus* were readily consumed. In view of the fact that osmeterial secretions in these three species are similar in composition, they are unlikely to play a major role in determining palatability of these species to this avian predator.

Additional key words: *Papilio polyxenes, Papilio glaucus, Papilio cresphontes, Coturnix coturnix*, palatability.

The osmeterium, a Y-shaped eversible gland located mid-dorsally behind the head, is a universal characteristic of swallowtail caterpillars (Papilionidae). Its function has long been assumed to be defensive (Merian 1705, as cited in Crossley & Waterhouse 1969). There is indeed evidence of the efficacy of the osmeterial gland and its secretions against invertebrate predators. Eisner and Meinwald (1965) demonstrated that *Papilio machaon* L. larvae use osmeterial secretions to deter ant predation; Damman (1986) determined that the presence of a functional osmeterial gland of *Eurytides marcellus* (Cramer) reduces predation by ants and small spiders, and Chow and Tsai (1989) showed that *Papilio memnon* L. larvae are rejected by praying mantids. Honda (1983) confirmed that many components of osmeterial secretions from a variety of papilionid species are toxic and/or repellent to ants.

The role of the osmeterial gland in defense against vertebrate predators, however, is less clear. Jaervi et al. (1981) demonstrated that the osmeterial gland was ineffective at protecting third instar *Papilio machaon* larvae against predation by the great tit *Parus major* L. (Paridae) (that is, birds refused to eat intact larvae as well as decapitated larvae with osmeteria removed), and Honda (1983) reported that osmeterial

---

* To whom correspondence may be addressed.

eversion does not deter Japanese tree sparrow predation on late instar *Papilio protenor* Cramer larvae. However, in many species of swallowtails the chemical composition of osmeterial secretions varies ontogenetically. In six species of *Papilio,* osmeterial secretions of early instar caterpillars consist primarily of mono- and sesqui-terpenes; in later instars (fourth and fifth), osmeterial secretions consist primarily of aliphatic acids and their esters (Honda 1981). Accompanying the change in osmeterial gland chemistry is a major change in morphology. Early instar larvae are black with a white saddle, a pattern generally assumed to be cryptic and reminiscent of bird droppings, and later larvae are solid green with eyespots ("snake mimic"), mottled brown and white, or striped green and black (Tyler 1975). Although most ultimate instar patterns are thought to be cryptic, Jaervi et al. (1981) argue that the striped pattern is aposematic at short distances; indeed, the presence of yellow or orange spots interrupting the black bands on most larvae in the *P. machaon* complex may enhance any aposematic effect.

The possibility exists, therefore, that the defensive importance of the osmeterium changes over the course of development. Accordingly, in this study we tested the palatability of early and late instar larvae, with and without a functional osmeterium, to a representative avian predator. In addition, the differential conspicuousness of different species of swallowtail larvae suggests differences in efficacy of chemical defense against visually orienting predators; cryptic or homotypic species may be relatively vulnerable in comparison with aposematic species. Therefore, in this study we also compared the palatability to an avian predator of larvae of three papilionids differing in ultimate instar coloration.

MATERIALS AND METHODS

All of the swallowtail larvae used in this study were laboratory-reared and originated from adults caught in east central Illinois. *Papilio polyxenes* Fabricius feeds exclusively on herbaceous representatives of Rutaceae and Apiaceae (=Umbelliferae) (Tyler 1975). Early instar larvae are black with a white saddle; fourth and fifth instar larvae are green with black stripes interrupted with yellow spots. Caterpillars in the laboratory were reared on greenhouse-grown foliage of *Petroselinum crispum* (Mill.) Nym. ex A. Hill (parsley) (Apiaceae). *Papilio cresphontes* Cramer feeds exclusively on rutaceous shrubs. Whereas first instar larvae are black with a white saddle, subsequent instars are characterized by a mottled brown and white color pattern (Opler & Krizek 1984). In the laboratory, *P. cresphontes* larvae were reared on foliage of greenhouse-grown *Citrus limon* (L.) Burm. (Rutaceae). *Papilio glaucus* L. has the broadest food plant range of any swallowtail species and is reported to feed on foliage of trees in over a dozen plant families (Tyler 1975). Early instar *P. glaucus* larvae are brownish-black with a white saddle, but late instar larvae are green and snake-like in appearance with conspicuous eyespots on the thorax. *P. glaucus* larvae were reared in the laboratory on foliage of *Liriodendron tulipifera* L. (Magnoliaceae) or *Prunus serotina* Ehrh. (Rosaceae) collected from wild trees.

The avian predator used in this study was *Coturnix coturnix* L., the Japanese quail (Phasianidae). *C. coturnix* feeds freely on insects and has been used previously in investigations of insect palatability as a representative ground-feeding insectivorous bird (Wiklund & Jaervi 1982, Wiklund & Sillen-Tullberg 1985). The individuals used in this study were reared from egg hatch on commercial chicken feed and had no prior exposure to insect prey.

Palatability trials were similar in design to those described by Wiklund and Sillen-Tullberg (1985). Trials were run in one of two large (2.13 m × 2.13 m) cages containing 14 quail. In the center of the cage, two watchglasses were placed on the floor 76.2 cm apart. Five mealworms were placed in each dish and were consumed by the quail. This process was repeated with five additional mealworms in each dish after the first five were consumed. After the second ten mealworms were eaten, five swallowtail caterpillars were placed in one watchglass and five mealworms in the other watchglass. Observations were made for a ten-minute interval. This process was repeated four times so that a total of 20 swallowtail larvae were exposed to the quail (with the exception of *P. cresphontes*, for which only a limited number of larvae of the appropriate age were available).

Two separate experiments were conducted. In the first series of trials, the palatability of larvae of three different species was compared. In all species, the osmeterium was fully functional. For *P. polyxenes* and *P. glaucus*, trials were run with both third instar larvae (bird-dropping morphs in both species) and late instar larvae (striped or "snake" morph, respectively). In the second series of trials, two developmental stages—third instar and fifth instar larvae—of only one species, *Papilio polyxenes*, were examined. Within each developmental stage, the palatability of larvae with and without a functional osmeterium was tested. Osmeterial glands were rendered nonfunctional by the method of Damman (1986). A dab of Liquid Paper correction fluid (Liquid Paper Corp., Boston, Maryland) was placed directly on the fold from which the osmeterium everts. Larvae treated in this fashion were unable to evert their osmeterium even when prodded by the investigators. A dab of Liquid Paper was also placed on mealworms in the control watchglasses at a comparable location behind the head.

Differences in the numbers of individuals eaten or not eaten over

TABLE 1. Survival of *Papilio* caterpillars with functional osmeteria in the presence of *Coturnix coturnix*.

Species[a]	Instar	No. eaten	No. not eaten
P. cresphontes	4/5	0	8
P. glaucus	3	20	0
P. glaucus[b]	4/5	8	0
P. polyxenes	3	0	20
P. polyxenes[c]	5	0	20

[a] Survival is not independent of species ($\chi^2 = 36$, $P < 0.05$)

[b] Survival of *P. glaucus* is independent of instar (Fisher exact $P = 0.09$)

[c] Survival of *P. polyxenes* is independent of instar (Fisher exact $P = 1.00$)

the trial period were evaluated with a test of independence; in comparing late instar individuals of the three different species, a chi-square test was used and for all 2 × 2 tables a Fisher's exact test was used.

RESULTS AND DISCUSSION

The three species of *Papilio* examined in this study differ in their susceptibility of predation by Japanese quail (Table 1). Whereas 100% of *P. polyxenes* larvae (40/40) and *P. cresphontes* larvae (8/8) survived encounters with quail, 100% (28/28) of the *P. glaucus* larvae were consumed. The unpalatability of *P. polyxenes* was unaffected by developmental stage; both third and fifth instar larvae were consistently rejected. By the same token, the palatability of *P. glaucus* was unaffected by developmental stage; all caterpillars were consumed irrespective of instar. The unpalatability of *P. polyxenes* was also independent of the presence of a functional osmeterium; 39/40 caterpillars with occluded osmeteria survived encounters with quail (Table 2).

In general, while *C. coturnix* showed no reluctance to seize and consume ultimate instar *P. glaucus* caterpillars, they were hesitant to touch the green and black striped ultimate instar *P. polyxenes* larvae. They showed less reluctance to sample the third instar *P. polyxenes* "bird dropping" morphs and in fact picked up several individuals out of the watchglass and entirely consumed one. This inclination to sample third instar larvae was reported also by Wiklund and Jaervi (1982), who noted that *C. coturnix* seized 13 of 18 *P. machaon* larvae in a similar feeding trial; of these 13, 12 were subsequently dropped and one eaten.

The basis for rejecting third instar *P. polyxenes* larvae does not appear to be visual; indeed, from the human perspective, third instar *P. glaucus* larvae, which are seized and consumed by Japanese quail, are virtually indistinguishable from third instar *P. polyxenes* larvae. Moreover, the unpalatability of third instar *P. polyxenes* larvae cannot be attributed solely to the osmeterial gland, since larvae that could not evert their

TABLE 2. Survival of *Papilio polyxenes* larvae with and without functional osmeteria in the presence of *Coturnix coturnix* (osmeteria rendered nonfunctional by occlusion with Liquid Paper).

Instar	Osmeterium	No. eaten	No. not eaten
3	functional	0	20
3[a]	nonfunctional	1	19
5	functional	0	20
5[b]	nonfunctional	0	20

[a] Survival of third instar larvae is independent of osmeterial function (Fisher exact P = 1.0)
[b] Survival of fifth instar larvae is independent of osmeterial function (Fisher exact P = 1.0)

glands when seized were equally as unacceptable to *C. coturnix* as were larvae with functional osmeteria. It is also unlikely that osmeterial secretions are primarily responsible for differences in acceptability of late instar *Papilio* species as well, since the known chemical composition of osmeterial secretions is extremely similar in the three species (Eisner et al. 1970).

The fact that, of the three species of *Papilio* examined in this study, two oligophagous species were unpalatable and one polyphagous species was palatable suggests that larval diet may be involved in relative acceptability of swallowtail larvae to *C. coturnix*. Oligophagous Lepidoptera, including papilionids, have long been known to sequester toxins from their food plants; sequestration of aristolochic acids from *Aristolochia* food plants, for example, is documented throughout the Troidini (Papilionidae) (Rothschild 1972). Although sequestration of food plant allelochemicals has not been demonstrated for *Papilio* species, the possibility exists that oligophagous species in the genus sequester toxins from food plants for defensive purposes. Consistent with this suggestion is the report by Jaervi et al. (1981) that the "obnoxious properties" of *P. machaon* larvae (which are oligophagous, as are *P. polyxenes*, on Apiaceae and Rutaceae) are detectable in the cuticle by birds; the presence of diet-derived defensive compounds in cuticle has been reported in other species (Bernays & Woodhead 1982). The rutaceous food plants of *P. crespohontes* are known to contain a variety of toxic allelochemicals, including furanocoumarins and furanoquinoline, beta-carboline, and benzylisoquinoline alkaloids; the apiaceous food plants of *P. polyxenes* contain sesquiterpene lactones, furanocoumarins, and polyacetylenes (Hegnauer 1973), which may be sequestered (Berenbaum 1990). On the other hand, despite the presence of toxic allelochemicals such as cyanogenic glycosides, benzylisoquinoline alkaloids, sesquiterpene lactones, and saponins in food plants of *P. glaucus* (Scriber et al. 1987), including those species used as food plants in this study, these polyphagous caterpillars are not demonstrably distasteful to predators and give no other indications of any ability to sequester food plant toxins.

Osmeterial eversion in the presence of vertebrate prey may not be without survival value in all cases. The possibility exists that other vertebrate predators (e.g., those with a long ecological association with these North American species) may be adversely affected by osmeterial secretions. Another possibility is that osmeterial secretions, while not themselves toxic, may serve a function analogous to that of pyrazines in many species of unpalatable butterflies (Rothschild et al. 1984)—that is, they may serve as olfactory aposematic signals. The high volatility and pungent aroma of osmeterial secretions, particularly the aliphatic acid esters typical of late instar *Papilio* larvae (Eisner et al. 1970, Honda 1981), may provide a warning signal of distastefulness to potential predators. The value of such an olfactory signal is that it may reduce the risk of handling and subsequent rejection based on contact chemoreception of cuticular defenses and increase the probability that an individual caterpillar would survive an encounter with a would-be predator (Wiklund & Jaervi 1982, Wiklund & Sillen-Tullberg 1985). Naive quail, unfamiliar with insect prey in general and swallowtail caterpillars in particular, may require prior experience with distasteful individuals to learn to associate osmeterial secretions with unpalatability. If osmeterial secretions are indeed primarily warning signals, rather than effective allomones in their own right, the possibility exists that palatable caterpillars such as *P. glaucus* may actually be olfactory Batesian mimics of sympatric unpalatable papilionids. This suggestion must remain speculative until additional information is obtained on the composition and mode of action of osmeterial secretions of both palatable and unpalatable swallowtails.

ACKNOWLEDGMENTS

We thank J. K. Nitao for valuable discussion and Christer Wiklund and an anonymous reviewer for improving the manuscript. Voucher specimens of adults of all three species are on deposit in the University of Illinois Department of Entomology collection. This project was supported in part by NSF grant BSR8818205.

LITERATURE CITED

BERENBAUM, M. R. 1990. Evolution of specialization in insect-umbellifer associations. Ann. Rev. Entomol. 35:319–343.

BERNAYS, E. A. & S. WOODHEAD. 1982. Plant phenols utilized as nutrients by a phytophagous insect. Science 216:201–203.

CHOW, Y. S. & R. S. TSAI. 1989. Protective chemicals in caterpillar survival. Experientia 45:390–392.

CROSSLEY, A. C. & D. F. WATERHOUSE. 1969. The ultrastructure of the osmeterium and the nature of its secretion in *Papilio* larvae (Lepidoptera). Tissue & Cell 1:525–554.

DAMMAN, H. 1986. The osmaterial [sic] glands of the swallowtail butterfly *Eurytides marcellus* as a defense against natural enemies. Ecol. Entomol. 11:261–265.

EISNER, T., T. E. PLISKE, M. IKEDA, D. F. OWEN, I. VAZQUEZ, H. PEREZ, J. G. FRANCLEMONT & J. MEINWALD. 1970. Defense mechanisms of arthropods. XXVII. Osmeterial secretions of papilionid caterpillars (*Baronia, Papilio, Eurytides*). Ann. Entomol. Soc. Amer. 63:914–915.

EISNER, T. & Y. MEINWALD. 1965. Defensive secretion of a caterpillar (*Papilio*). Science 150:1733–1735.

HEGNAUER, R. 1973. Chemotaxonomie der Pflanzen. Vol. 6. Birkhauser Verlag, Basel. 882 pp.

HONDA, K. 1981. Larval osmeterial secretions of the swallowtails. J. Chem. Ecol. 7: 1089–1113.

——— 1983. Defensive potential of the larval osmeterial secretion of papilionid butterflies against ants. Physiol. Entomol. 8:173–179.

JAERVI, T., B. SILLEN-TULLBERG & C. WIKLUNG. 1981. The cost of being aposematic. An experimental study of predation on larvae of *Papilio machaon* by the great tit *Parus major*. Oikos 36:267–272.

MERIAN, M. S. 1705. Veraenderung der Surinamische Insekten. Amsterdam.

OPLER, P. A. & G. O. KRIZEK. 1984. Butterflies east of the Great Plains. Johns Hopkins Univ. Press, Baltimore. 294 pp.

ROTHSCHILD, M. 1972. Secondary plant substances and warning colouration in insects, pp. 59–83. *In* van Emden, H. F. (ed.), Insect/plant relationships, Symp. Roy. Ent. Soc. Lond. 6. Blackwell Sci. Publ., Oxford.

ROTHSCHILD, M., B. MOORE & W. V. BROWN. 1984. Pyrazines as warning odour components in the Monarch butterfly, *Danaus plexippus*, and in moths of the genera *Zygaena* and *Amata* (Lepidoptera). Biol. J. Linn. Soc. 23:375–380.

SCRIBER, J. M., M. T. S. HSIA, P. SUNARJO & R. LINDROTH. 1987. Allelochemicals as determinants of insect damage across the North American continent, pp. 439–448. *In* Waller, G. R. (ed.), Allelochemicals: Role in agriculture and forestry, A.C.S. Symp. Ser. 330. American Chemical Society, Washington, D.C.

TYLER, H. 1975. Swallowtails of North America. Naturegraph Press, Healdsburg, California. 192 pp.

WIKLUND, C. & T. JAERVI. 1982. Survival of distasteful insects after being attacked by naive birds: A reappraisal of the theory of aposematic coloration evolving through individual selection. Evolution 36:998–1002.

WIKLUND, C. & B. SILLEN-TULLBERG. 1985. Why distasteful butterflies have aposematic larvae and adults, but cryptic pupae: Evidence from predation experiments on the monarch and the European swallowtail. Evol. 39:1155–1158.

Received for publication 11 January 1990; revised and accepted 14 September 1990.

Journal of the Lepidopterists' Society
44(4), 1990, 252–256

A NEW SPECIES OF *MOMPHA* (MOMPHIDAE) FROM THE QUEEN CHARLOTTE ISLANDS, BRITISH COLUMBIA

J. F. GATES CLARKE[1]

National Museum of Natural History, Department of Entomology,
Smithsonian Institution, Washington, D.C. 20560

ABSTRACT. *Mompha nancyae* is described, figured, and compared with *M. terminella* (Westwood).

Additional key words: Canada, *M. nancyae, M. terminella,* distribution, endemic species.

A considerable body of literature exists on the geology, endemism, and the possibility of a refugium in the Queen Charlotte Islands, British Columbia, Canada, but very little has been written on the lepidopterous fauna. Specifically, Holland (1930) described *Chrysophanus charlottensis* (currently known as *Lycaena mariposa charlottensis*) (Lycaenidae). Subsequently, Freeman (1966) described *Zeiraphera pacifica* (Tortricidae) from Sandspit and later Mutuura and Freeman (1966) treated this species in more detail. Then Prentice (1966) listed eight species as indicated on his distribution maps. These were *Polychrosis piceana* Freeman (currently *Endopiza piceana*), *Griselda radicana* Heinrich, *Choristoneura fumiferana* (Clemens), *Argyrotaenia pinatubana* (Kearfott), *Acleris fishiana* (Fernald) (a synonym of *A. maccana* (Treitschke)), *Acleris variana* Fernald, *Acleris senescens* (Zeller) (Tortricidae), and *Martyrhilda sciadopa* (Meyrick) (a synonym of *Agonopterix canadensis* (Busck)) (Oecophoridae). Ferguson (1987) then described *Xanthorhoe clarkeata* (Geometridae).

One species, *X. clarkeata*, is an alpine endemic. *Lycaena mariposa charlottensis* is a bog insect found at low evaluation. *Zeiraphera pacifica* is apparently endemic; the others are forest insects found primarily at low elevations.

There may be other references to the Lepidoptera of these islands which I have missed, but Anderson (1904) and Blackmore (1927) listed nothing.

The *Mompha* described here is also a low elevation species, which we found along the main road on the east side of Sandspit. Between the road and the beach there is a long strip of native herbaceous plants and shrubs with some weed species mixed in. There is a surprising number of microlepidoptera in this area.

---

[1] J. F. Gates Clarke, an Honorary Life Member of the Lepidopterists' Society, died 17 September 1990.

FIG. 1. *Mompha nancyae* Clarke, new species. Holotype male.

Mompha nancyae, new species
(Figs. 1, 2)

Description. Labial palpus grayish fuscous on outer surface; inner surface sordid white. Antenna black; thicker in male than in female. Head dull leaden color. Thorax fuscous dorsally, with posterior tuft leaden metallic; tegula leaden metallic; laterally shining leaden metallic. Alar expanse 10–11 mm. Forewing ground color ochraceous tawny; base of forewing silver; on costa at one-third, a rectangular shining silver patch extending across wing to fold; at middle of costa a small white spot bordered inwardly by a small cluster of shining silver scales; at outer third of costa a subquadrate patch of shining silver scales; beyond this a large triangular white spot followed by black scaling before apex; at one-third of dorsum a quadrate patch of shining silver scales, joining the coastal patch, and followed by a raised tuft of black scales; on middle of dorsum a small group of shining silver scales; before tornus, a raised tuft of black scales at the base of which are shining silver scales; beyond this tuft a longitudinal line of shining silver scales terminating in an expanded group of shining silver scales at apex; cilia fuscous. Hindwing blackish fuscous; cilia somewhat lighter. Foreleg black; tibia white inwardly; tarsi annulated white, midleg black; tarsi annulated white; hindleg lustrous black; tibia with silver scales at base of spurs; tarsi with silver annulations. Abdomen blackish fuscous dorsally; lustrous ventrally; anal tuft blackish fuscous dorsally, whitish ventrally.

Male genitalia (Fig. 2a) (slides USNM 27270, USNM 69785). Harpe divided; coastal part tapering to a bluntly pointed cucullus; sacculus strongly sclerotized and very broad basally, tapering to a long point, and reaching or exceeding the costal part in length. Uncus a slender, curved process. Vinculum broadly rounded with a ventral median point. Tegumen rather strongly sclerotized, broader anteriorly than posteriorly. Anellus fused with aedeagus, terminating in two widely separated, slender lobes. Aedeagus stout, short, lightly sclerotized; vesica armed with a single cornutus.

Female genitalia (Fig. 2b) (slides USNM 69782, USNM 69786). Ostium oval. Antrum moderately sclerotized. Inception of ductus seminalis at about junction of antrum and ductus bursae. Ductus bursae coiled; moderately sclerotized posteriorly, membranous anteriorly. Bursa copulatrix membranous. Signa two lighty sclerotized discs, each with a strongly sclerotized hook from near center. Lamella antevaginalis broad, subrectangular. Lamella postvaginalis triangular with a club-shaped sclerite on each side.

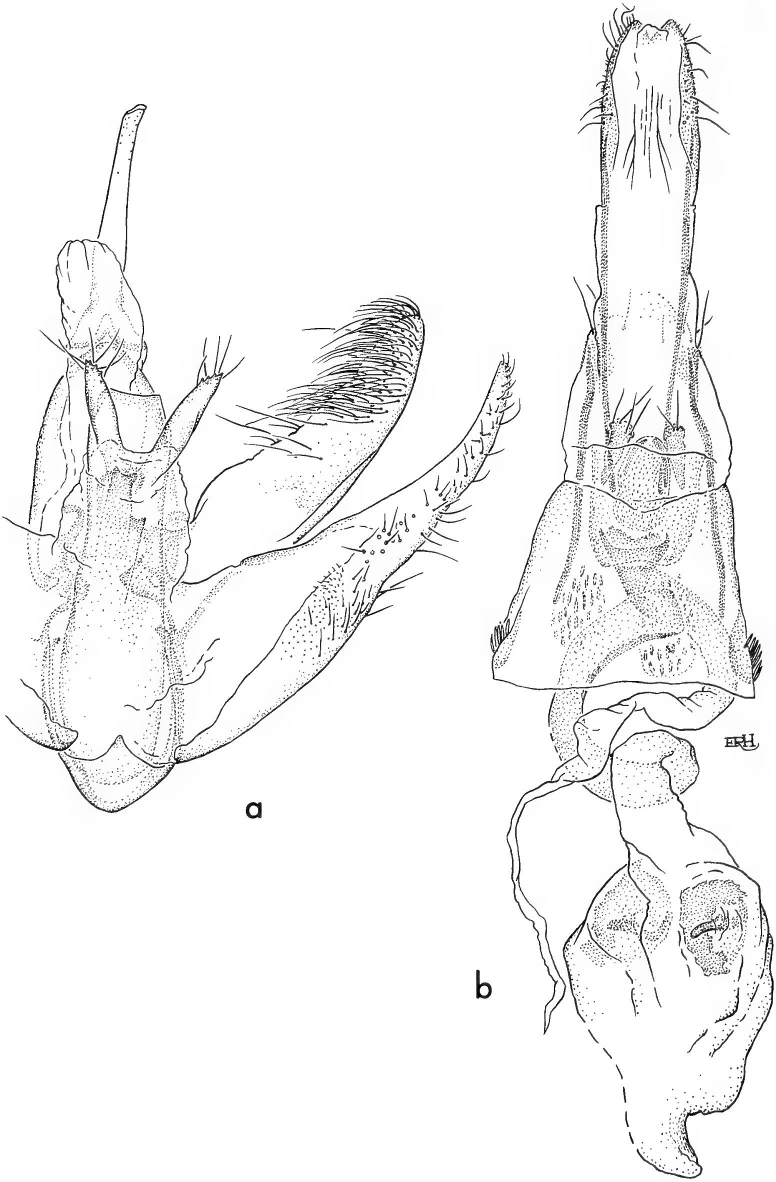


FIG. 2. *Mompha nancyae* Clarke, new species. a, Male genitalia (left harpe not shown); b, ventral view of female genitalia.

Types. Described from the male holotype, six male and two female paratypes all from the type locality, on 21 July 1987 and from 9 to 23 August 1988, collected by my wife and me. One paratype will be placed in the Canadian National Collection, Ottawa, one in the Provincial Museum, Victoria, British Columbia and the remainder in the U.S. National Museum.

The holotype is in the United States National Museum of Natural History.

Type locality: Canada, British Columbia, Queen Charlotte Islands, Sandspit.

Distribution: Known only from the Queen Charlotte Islands.

Food plant: Unknown.

Etymology. I am very pleased to name this species for my wife, Nancy, who has accompanied me and has endured many cold and wet days and nights in the Queen Charlottes; who has not only helped me collecting but has assumed many tasks incident to our expeditions.

DISCUSSION

This species is closely related to the European *Mompha terminella* (Westwood) but differs from it in several respects. *Mompha terminella* is native to Europe, but has been introduced to North America (see Riedl 1969: 674 for illustrations). First, *nancyae* is larger, measuring 10 to 11 mm in alar expanse, whereas European specimens of *terminella* measure 9–10 mm. We have a substantial series of *terminella* in the USNM from Illinois, Michigan, Iowa, Ohio, and Pennsylvania, and these measure 7–9 mm, although one U.S. specimen exists that measures 10 mm, an exception. In addition, the antenna of *terminella* displays a conspicuous terminal white band that is absent in *nancyae,* although the two female paratypes of *nancyae* show an indication of this band. On the middle of the forewing costa of *nancyae* there is a conspicuous white spot, totally absent in our large series of both the European and U.S. specimens of *terminella.*

The male genitalia are similar, but those of *nancyae* are proportionately larger than those of *terminella.* The prolonged sacculus of *nancyae* reaches, or slightly exceeds, the dorsal part of the harpe, but in *terminella* the sacculus is considerably shorter. In the female genitalia of *nancyae,* the club-shaped sclerite on each side of the lamella postvaginalis is absent in *terminella.*

ACKNOWLEDGMENTS

The drawings were made by Elaine R. Snyder Hodges and the photograph was made by Victor Krantz, both on the Smithsonian staff. I thank my wife Nancy L. duPre Clarke for typing the manuscript.

LITERATURE CITED

ANDERSON, E. M. 1904. Catalog of British Columbia Lepidoptera. Provincial Museum of Natural History, Victoria, British Columbia, pp. 1–56.

BLACKMORE, E. H. 1927. Check-list of the Macrolepidoptera of British Columbia (butterflies and moths). Provincial Museum of Natural History, Victoria, British Columbia, pp. 1–47.

FERGUSON, DOUGLAS C. 1987. *Xanthorhoe clarkeata* (Geometridae), a new species and possible endemic of the Queen Charlotte Islands, British Columbia. J. Lepid. Soc. 41: 98–102.

FREEMAN, T. N. 1966. A new species of *Zeiraphera* Treitschke from British Columbia (Lepidoptera: Tortricidae). Can. Entomol. 98:588–589.

HOLLAND, W. J. 1930. Two new North America butterflies. Ann. Carnegie Mus. 20: 5–7.

MUTUURA, A. & T. N. FREEMAN. 1966. The North American species of the genus *Zeiraphera* Treitschke (Olethreutidae). J. Res. Lepid. 5:153–176.

PRENTICE, R. M. 1966. Forest Lepidoptera of Canada. Recorded by the Forest Insect Survey, 4:545–840. Dept. of Forestry of Canada, Ottawa, Publ. 1142.

RIEDL, T. 1969. Matériaux pour la connaissance des Momphidae paléarctiques (Lepidoptera). Partie IX. Revue des Momphidae européennes, y comprìs quelques espèces d'Afrique du Nord et du Proche-Orient. Polskie Pismo Entomologìczne 39:635–919.

Received for publication 26 April 1990; accepted 27 August 1990.

Journal of the Lepidopterists' Society
44(4), 1990, 257-272

SYSTEMATIC REVISION OF *PARAPTILA* MEYRICK (TORTRICIDAE)

JOHN W. BROWN
10 East Sierra Way, Chula Vista, California 91911

ABSTRACT. *Paraptila* Meyrick is a neotropical tortricid genus distributed from central Mexico to northern South America. Three previously described species [i.e., *P. argocosma* Meyrick, *P. gamma* (Walsingham), and *P. cornucopis* (Walsingham)] and five new species (i.e., *P. pseudogamma, P. bloomfieldi, P. biserrata, P. symmetricana,* and *P. equadora*) are recognized. Descriptions, or redescriptions, and illustrations of the genitalia are presented for each species. *Paraptila hydrochoa* Meyrick is transferred to *Popayanita* Razowski (**new combination**). The synonymy of *Paraptila infusoria* Meyrick and *P. gamma* is proposed (**new synonymy**). The presence of a male foreleg hairpencil from the base of the femur appears to represent a synapomorphy supporting the tribal assignment of *Paraptila* to Euliini.

Additional key words: Euliini, hairpencil, neotropical, new species.

The genus *Paraptila* was described by Meyrick (1912) to accommodate the single species *P. argocosma*. Meyrick later described two additional species in the genus, *P. infusoria* (Meyrick 1926) and *P. hydrochoa* (Meyrick 1930). The latter is neither superficially nor morphologically similar to *P. argocosma* and *P. infusoria,* and is transferred to *Popayanita* Razowski (new combination), with which it shares facies and a similar configuration of the valva, uncus, and gnathos.

Two species described by Walsingham (1914), *Enarmonia cornucopis* and *Tortrix gamma,* are congeneric with *P. argocosma* and *P. infusoria*. The holotype male of "*T.*" *gamma* is apparently conspecific with *P. infusoria,* while the single paratype appears to be conspecific with "*E.*" *cornucopis*. Five previously undescribed species of *Paraptila* were discovered in the collections of the National Museum of Natural History, Washington, D.C. (USNM); Essig Museum of Entomology, University of California, Berkeley (UCB); San Diego Natural History Museum, San Diego, California (SDNHM); and British Museum (Natural History), London, England (BMNH).

In this paper I redescribe the genus *Paraptila* and all correctly associated, previously described species (i.e., *P. argocosma, P. gamma,* and *P. cornucopis),* propose the synonymy of *P. infusoria* and *P. gamma,* transfer *P. hydrochoa* to *Popayanita,* and describe five species as new: *P. pseudogamma, P. bloomfieldi, P. biserrata, P. symmetricana,* and *P. equadora*.

Dissection methodology followed Powell (1964). Terminology and homology of wing venation and genitalic structures follows Horak (1984); FW = forewing; HW = hindwing; DC = discal cell.

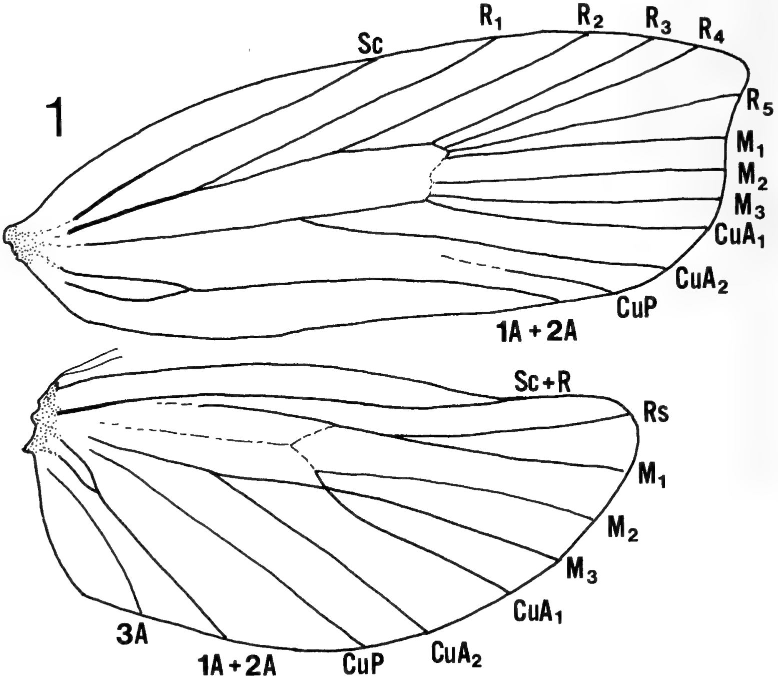


FIG. 1. Wing venation of *Paraptila argocosma*.

PARAPTILA MEYRICK, 1912

Paraptila Meyrick (1912:677), Meyrick (1926:259), Clarke (1958:167), Razowski (1986: 21), Powell (1986:374).

Type species. *Paraptila argocosma* Meyrick (1912), by monotypy.

Head: Antennal setae in male ca. 1.25 × flagellar segment width. Labial palpus slightly upturned, moderately broad; segment II expanded distally by scales to ca. 1.8 × its basal diameter, slightly curved; segment III ca. 0.25 as long as II. Maxillary palpus longer than pilifer. Frons scaling with overhanging crown tuft; smooth and sparse below mid level of eye. Ocelli well developed. Chaetosema present. Periorbital strip scaled. **Thorax:** With upraised scale tuft situated posteriorly. Male foreleg with hairpencil consisting of a fascicle of elongate setae arising from base of femur, extending to base of coxa; hairpencil absent in female. **Forewing:** Venation as in Fig. 1. Length 2.5–2.6 × width; length of DC ca. 0.55 × FW length; width of DC ca. 0.15 its length; CuA_2 originating ca. 0.65 along length of DC; R_4 and R_5 connate or very short-stalked; M_3 and CuA_1 separate; CuP present; chorda absent; M-stem absent. **Hindwing:** Venation as in Fig. 1. Sc+R and Rs separate; Rs and M_1 stalked; M_3 and CuA_1 connate; CuP vestigial; M-stem absent. **Abdomen:** Dorsal pits absent. **Male genitalia:** Uncus extremely long, thin, drawn out to fine apex (except in *P. equadora*). Socii strongly arched basally, large, pendant, with dense, elongate scales, the largest of which originate from distinct sockets; usually divided longitudinally into scaled and naked portions. Gnathos arms narrow, smooth, from lateral margin of tegumen, joined distally into slender mesal process, usually with a minute hook distally. Transtilla usually constricted mesally; large spur-like projection(s) subbasally; shallow cone-like depression at base. Valva simple, long rectangular, rounded apically; sacculus a narrow ridge, usually attenuate within basal 0.5. Aedeagus large, stout, with broad, rounded phallobase; usually with single, large cornutus. **Female genitalia:** Papillae anales elongate, flattened, nearly parallel-sided. Apophyses posteriores broad, inflated, sack-like (except in *P. argocosma*); apophyses anteriores long, slightly broadened in basal 0.75. Sterigma irregularly rectangular, weakly sclerotized; usually with lateral band and patches of sclerotization near ostium. Ductus and corpus bursae not distinctly differentiated; ductus bursae usually with sclerotized region near ostium. Corpus bursae simple, without accessory bursa; spiculae variable from faint and indistinct to large and dense; signum absent. Ductus seminalis from near middle of corpus bursae.

Distribution and biology. *Paraptila* is distributed from Colima to Veracruz, Mexico, south to Bolivia. The early stages are unknown.

Diagnosis. *Paraptila* is characterized superfically by a reddish or purplish brown forewing featuring a distinctive silver-white, cornucopia-shaped patch bordering the costa. This forewing pattern is unlike any other genus in the Euliini. The most conspicuous synapomorphies for the genus include 1) narrow, nearly lateral, mesally joined arms of the gnathos, bearing a fine, hooked tip, 2) long, complex, strongly curved socii with a narrow longitudinal line of sclerotization, and 3) broad, inflated, sack-like apophyses posteriores (unmodified in the presumably most plesiomorphic species, *P. argocosma*). The presence of a male foreleg hairpencil remarkably consistent with that of other genera in the Euliini (Brown 1990) confirms the tribal assignment of *Paraptila* (Powell 1986). The genus is uniform in external facies, and genitalic preparations are required for accurate species determination.

Males of all species but *P. biserrata* have a single, large, basally attached cornutus. The absence of cornuti in bursae of dissected females (n = 15) indicates that the structure is almost certainly non-deciduous, consistent with other genera in the Euliini, and in contrast to the condition found in Sparganothini and Atteriini.

On the basis of the unusual modification of the socii and the general configuration of the female genitalia, *Paraptila* appears to represent the sister group to *Terinebrica* Razowski.

1. *Paraptila argocosma* Meyrick
(Figs. 1, 8)
(Illustrated in Clarke 1958:166)

Paraptila argocosma Meyrick (1912:677), Clarke (1958:167).

Male. Unknown.

Female. FW length 11.5 mm (n = 2). **Head:** Frons and vertex dark red-brown. Labial palpus concolorous with head. Antenna concolorous with head. **Thorax:** Dark red-brown. **Forewing:** Dark red-brown in basal 0.15, narrowly bordered by white distally; light purple-gray lateral band, with diffuse, transverse, light tan-orange striae, from costa 0.15–0.35 from base, expanding distally along dorsum; cornucopia-shaped, silver-white patch bordering costa 0.55–0.70 from base; broad, dark red-brown band bordering costal patch basally, 0.40–0.50 from base, attenuate before dorsum; region apicad of costal patch orange mixed with red-brown and streaks of white; small, round, dark red-brown spot faintly bordered by white near middle of DC; irregular, wedge-shaped, silver-white patch from near apex to near mid point of termen. Fringe red-brown mixed with purple-gray.

Hindwing: White with uniform light gray-brown overscaling. Fringe pale gray to pale yellow with dark red-brown smudge at apex. **Genitalia:** As in Fig. 8 [drawn from JFGC slide no. 6361 (BMNH); n = 2]. Apophyses slender, unmodified. Sterigma rectangular, evenly sclerotized; transverse band situated ventro-anteriorly, with shallow U-shaped notch mesally near ostium. Corpus bursae irregular, oblong, with scultptured region ventrally immediately anterad of ostium; dense patches of long spicules; irregular, sclerotized patch near ostium.

Type material. Lectotype: female; W. Colombia, San Antonio, 5800' [1850 m], "11.07" [November 1907] (BMNH).

1F, paralectotype, same data as holotype (USNM).

Diagnosis. *P. argocosma* is known from two females from western Colombia. It can be distinguished superficially from other species of *Paraptila* by its greater forewing length and darker forewing ground color. The female genitalia lack the inflated apophyses posteriores present in all other species of *Paraptila,* and possess dense patches of large spicules, absent in other members of the genus.

2. *Paraptila gamma* (Walsingham), new combination

(Figs. 2, 9)

[Illustrated in Clarke 1958:166 (as *P. infusoria*)]

Tortrix gamma Walsingham (1914:287).
Paraptila infusoria Meyrick (1926:259), Clarke (1958:167). **NEW SYNONYMY.**

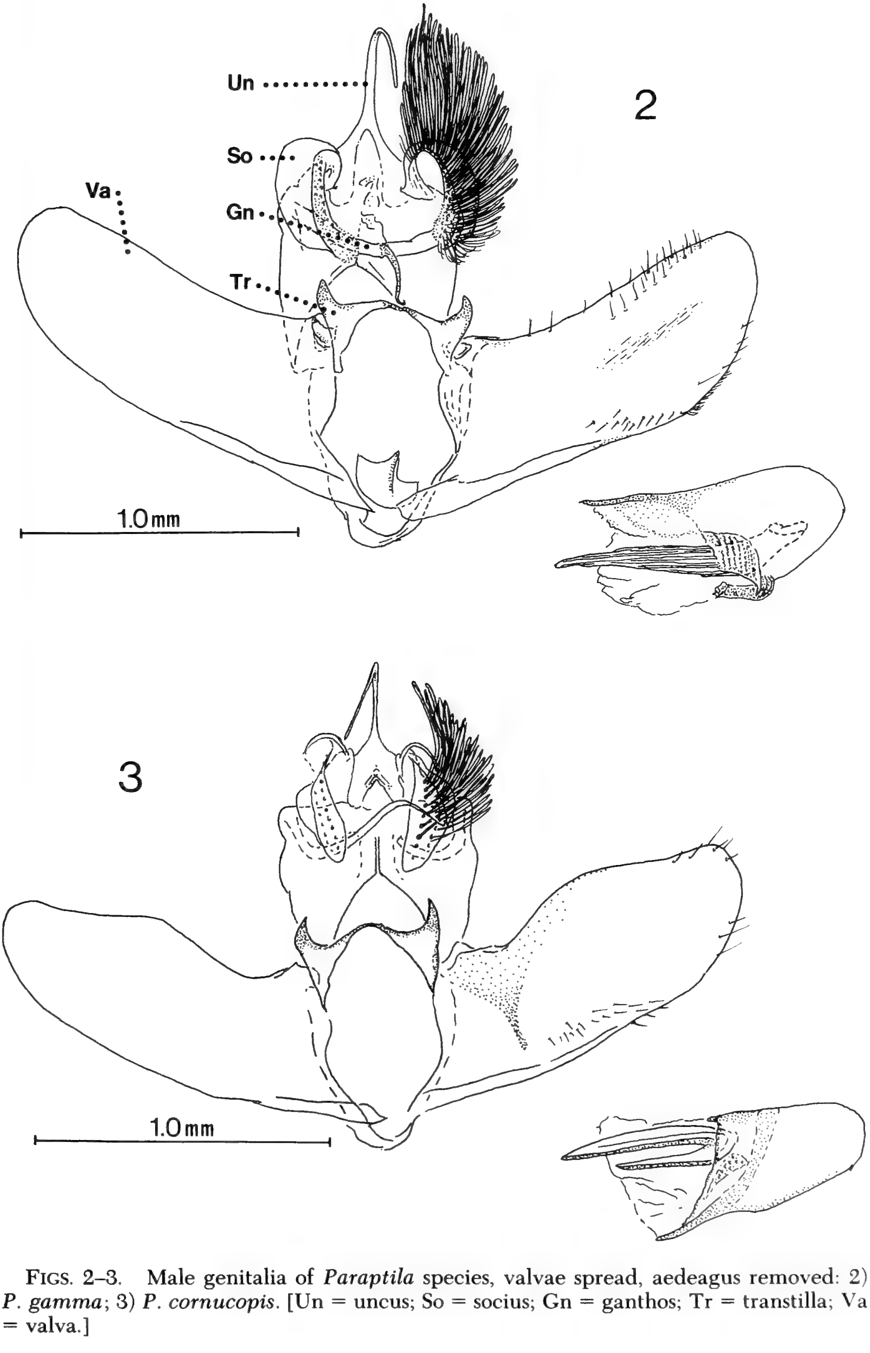
Male. FW length 6.5–7.0 mm ($\bar{x} = 6.7$; n = 3). **Head:** Frons and vertex light red-brown speckled with whitish yellow. Labial palpus pale yellow, red-brown laterally. Antenna red-brown. **Thorax:** Dark purple-gray with dark red-brown tegulae. **Forewing:** Dark red-brown in basal 0.15; broad, transverse, pale brown band from costa 0.15–0.50 from base, slightly expanded at dorsum; silver-white cornucopia-shaped patch bordering costa 0.60–0.75 from base, bordered distally and basally by darker red-brown; narrow brown band curving from near apex of DC to tornus, with lighter region immediately apicad; apical region brown with scattered red-brown scales. Fringe dark red-brown. **Hindwing:** White with uniform light gray-brown overscaling; dark red-brown smudge at apex. Fringe whitish yellow and gray. **Genitalia:** As in Fig. 2 (drawn from USNM slide no. 68836; n = 3). Uncus simple, extremely long, narrow. Socii strongly arched basally; divided longitudinally into narrow mesal strip bearing dense, long, fine setae, and broader lateral strip without setae. Gnathos narrow, arising well below bases of socii; united mesally into narrow, attenuate, ventrally-curving projection, with minute distal hook. Transtilla with a pair of large, stout, weakly hooked processes basally; narrowed mesally; base with shallow cone-like depression. Valva simple, long rectangular, rounded apically; sacculus weak, narrow. Aedeagus broad, stout, with single large cornutus.

Female. FW length 10.0 mm (n = 1). As described for male. **Genitalia:** As in Fig. 9 (drawn from BMNH slide no. 6370; n = 1). Apophyses posteriores greatly inflated; apophyses anteriores weakly broadened. Sterigma lightly sclerotized with strongly sclerotized band-like pouch on left lateral side (looking anteriorly). Corpus bursae with irregular folds and creases posteriorly, densely covered with small spicules.

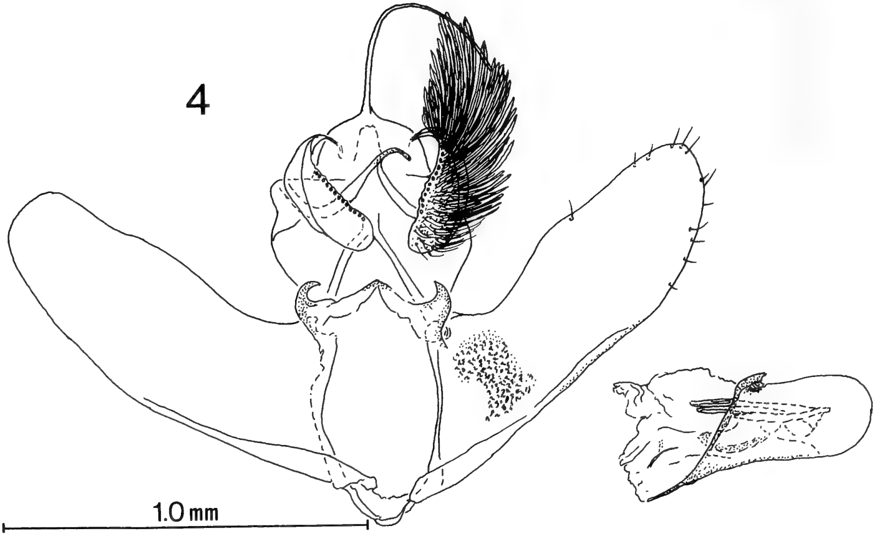
Type material: Holotype: male; Mexico, Tabasco, Teapa, ".III" [March], H. H. Smith (BMNH).

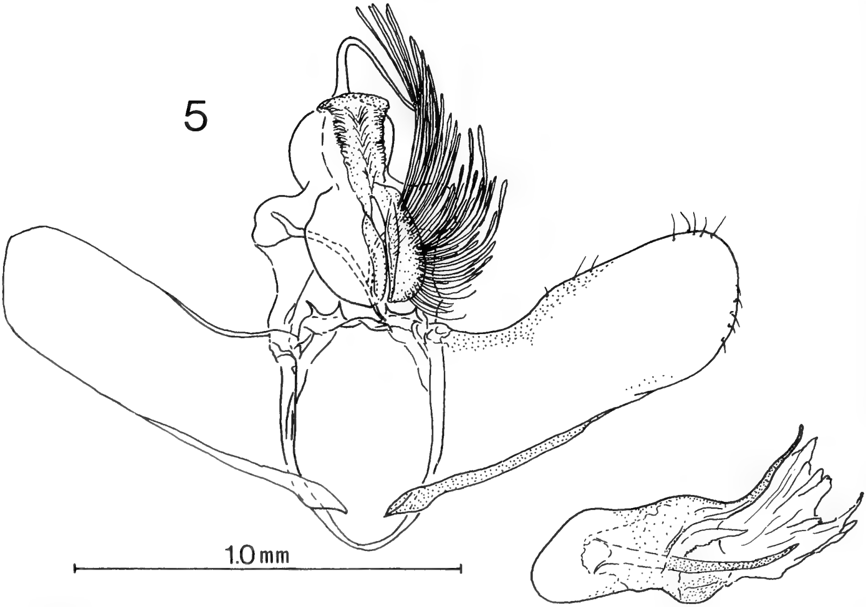
1M (lectotype of *P. infusoria*), Costa Rica, San Jose, ".22" [1922] (H. Schmidt, BMNH); 2F paralectotypes, same data as lectotype (BMNH), 1F paralectotype, same locality as lectotype, ".20" [1920] (BMNH).

Additional material: 1M, Costa Rica, Juan Vinas, June [no year], Coll. Wm. Schaus (USNM).

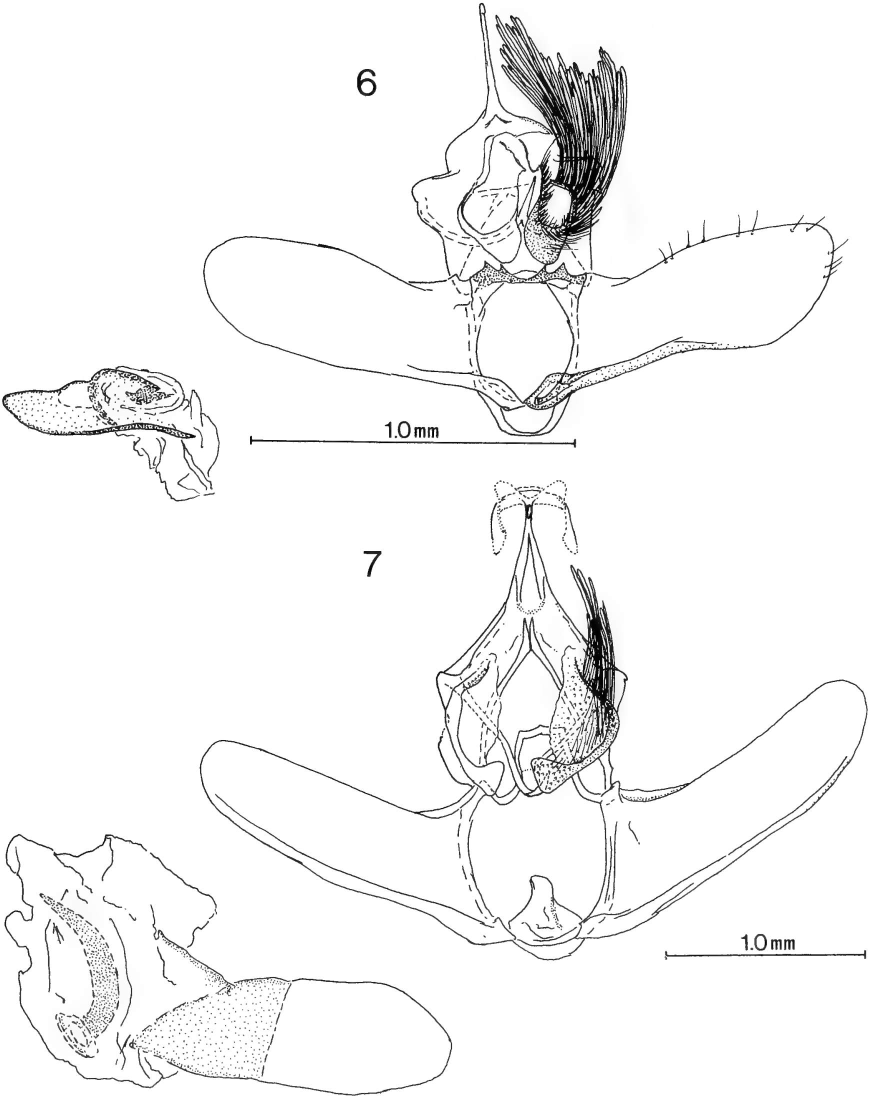


FIGS. 2–3. Male genitalia of *Paraptila* species, valvae spread, aedeagus removed: 2) *P. gamma*; 3) *P. cornucopis*. [Un = uncus; So = socius; Gn = ganthos; Tr = transtilla; Va = valva.]





FIGS. 4–5. Male genitalia of *Paraptila* species, valvae spread, aedeagus removed: 4) *P. pseudogamma*; 5) *P. bloomfieldi*.



FIGS. 6–7. Male genitalia of *Paraptila* species, valvae spread, aedeagus removed: 6) *P. biserrata*; 7) *P. equadora*.

Diagnosis: *Paraptila infusoria*, *P. gamma*, and *P. cornucopis* are identical in superficial facies, and it is possible that all represent a single species. The male genitalia of the holotypes of *P. gamma* and *P. infusoria* are indistinguishable, and on this basis the synonymy of the two is proposed. Females from Costa Rica associated with the male holotype of *P. infusoria* are weakly distinguished from the female holotype of *P. cornucopis* by the nearly smooth, narrow band of the ductus bursae immediately anterior of the ostium. The structure is more wrinkled and pocket-like in *P. cornucopis,* suggesting that this species is distinct from *P. gamma* and *P. infusoria.* The male genitalia of the paratype of *P. gamma* are unlike those of the holotype of *P. gamma* and *P. infusoria* because of the presence in the former of a digitate patch of sclerotization from the costa on the inner third of the face of the valva, and a slender process from the dorsum of the socii. Hence this male is provisionally assigned to *P. cornucopis* (see below).

3. ***Paraptila cornucopis*** **(Walsingham), new combination**
(Figs. 3, 10, 14)

Enarmonia cornucopis Walsingham (1914:240).

Male. FW length 6.9 mm (n = 1). **Head:** Frons and vertex light purple-brown. Labial palpus concolorous with head, slightly darker laterally. Antenna cinerous, chocolate brown at base. **Thorax:** Dark red-brown, with shiny copper tufts posteriorly. **Forewing:** Basal 0.15 dark red-brown; tawny gray band, with faint purplish suffusion and irregular dark striae, from costa 0.15–0.45 from base; cornucopia-shaped, silver-white patch bordering costa 0.60–0.75 from base, with 1–4 minute dark costal dots; broad, red-brown band bordering costal patch basally; red-brown area situated apically and immediately posterior to costal patch; narrow, pale yellow, crescent-shaped line from near apex to mid point of termen. Fringe dark red-brown along termen, gray near tornus. **Hindwing:** Dingy white with uniform light gray-brown overscaling; dark brown smudge at apex. Fringe light gray to brown, dark brown at apex. **Genitalia:** As in Fig. 3 (drawn from USNM slide no. 68835; n = 1). Uncus simple, long, slender. Socii large, broad, pendant, with slender digitate dorsal projection from near base. Gnathos narrow, joined distally into slender mesal process with weakly hooked tip. Transtilla constricted mesally; large spur-like process subbasally; shallow cone-like depression at base. Valva long, with narrow, digitate patch of sclerotization in basal 0.25; costa strongly undulate. Aedeagus broad with sclerotized distal process; a large compound cornutus joined basally to a second smaller cornutus.

Female. FW length 6.8–9.5 mm ($\bar{x}$ = 7.5; n = 7). As described for male. **Genitalia:** As in Fig. 10 (drawn from USNM slide no. 68832; n = 6). Apophyses posteriores broad, inflated, sack-like. Sterigma weakly sclerotized with irregular, transverse band posterad of ostium; large sclerotized pouch on left lateral side (looking anterad). Ductus bursae reduced. Corpus bursae lightly sclerotized posteriorly, with faint longitudinal creases.

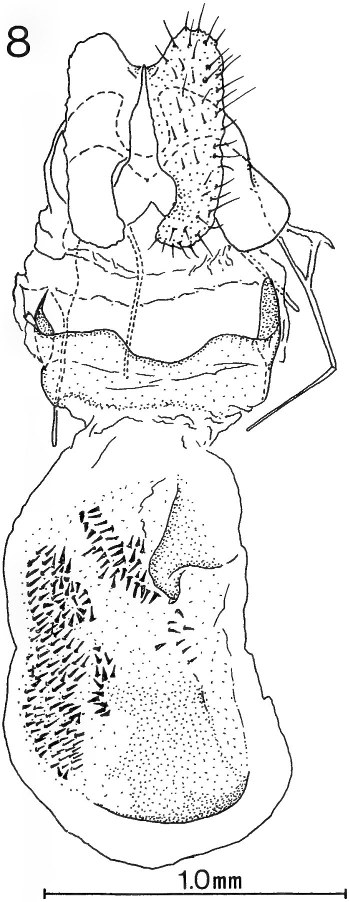
Type material: Holotype: female; Mexico, Oaxaca, Salina Cruz, 1906, Wm. Schaus (USNM).

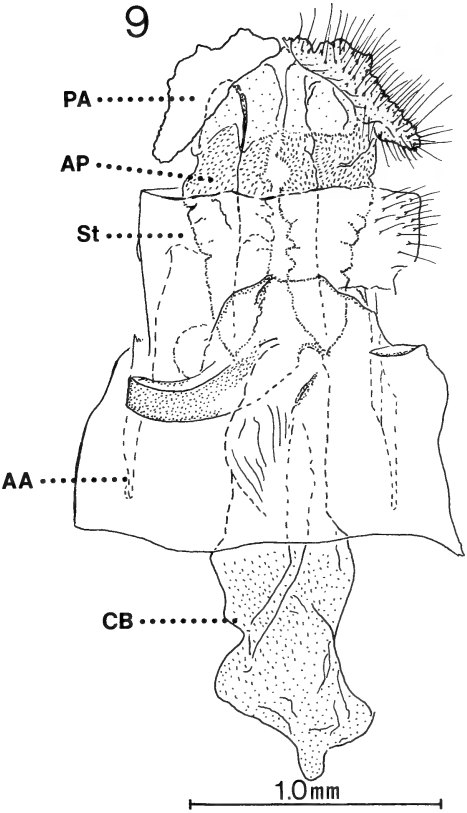
1F paratype, same data as holotype.

1M (paratype of *P. gamma*), Mexico, Veracruz, Jalapa, [no date], M. Trujillo (USNM).

Additional material: 6F as follows: MEXICO: Distrito Federal: 2F, Mizantla, July (T. Escalante, USNM). Colima: 2F, Colima, [no date], Condradt Coll. (USNM). San Luis Potosi: 1F, 4 mi S Tamazunchale, 27.vi.1965 (O. Flint, USNM). Veracruz: 1F, Cordoba, 2.vii.1965 (P. Spangler, USNM).

Diagnosis: As discussed in the diagnosis of *P. gamma, P. cornucopis* is nearly indistinguishable from the former. The two species appear to be allopatric: *Paraptila gamma* is known primarily from Costa Rica with a single record from southern Mexico; *P. cornucopis* occurs throughout much of central Mexico from Veracruz in the east to Colima





FIGS. 8–9. Female genitalia of *Paraptila* species: 8) *P. argocosma*; 9) *P. gamma*. [PA = papillae anales; AP = apophyses posteriores; St = sterigma; AA = apophyses anteriores; CB = corpus bursae.]

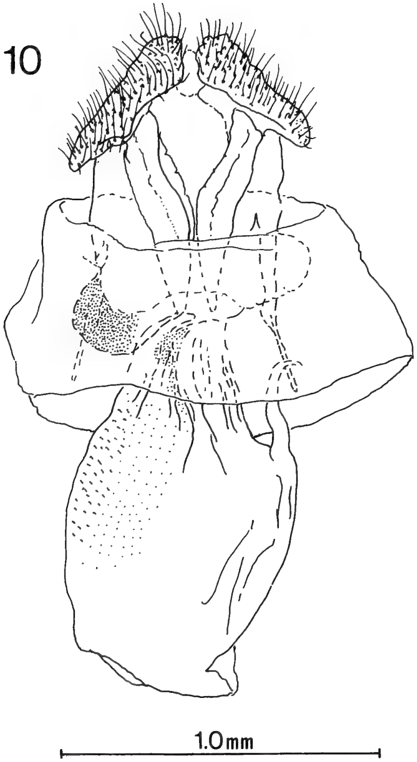
in the west. The association of the single male with the females of *P. cornucopis* is equivocal; this specimen was treated as a paratype of *Tortrix gamma* (see Diagonsis under *P. gamma*).

This species previously has not been illustrated elsewhere. It is one of several taxa described but not illustrated by Walsingham (1914) in the *Biologia Centrali-Americana*.

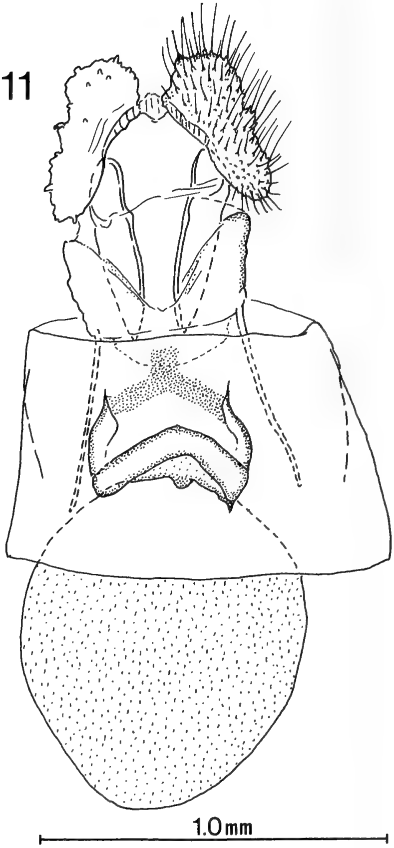
4. *Paraptila pseudogamma* Brown, new species
(Figs. 4, 12, 15)

Male. FW length 6.0 mm (n = 1). **Head:** Frons and vertex light purple-gray. Labial palpus concolorous with head, darker laterally. Antenna dark brown. **Thorax:** Dark brown

10



11



FIGS. 10–11. Female genitalia of *Paraptila* species: 10) *P. cornucopis*; 11) *P. bloomfieldi*.

with shiny posterior copper tufts. **Forewing:** Basal 0.15 dark brown with scattered red-copper scales; basal 0.15–0.40 slate gray with sparse, indistinct, dark brown striae; silver-white cornucopia-shaped patch bordering costa 0.60–0.75 from base; dark brown band bordering costal patch basally, extending to posterior edge of DC: region from costal patch to apex dark brown with scattered orange, copper, and red scales; faint, narrow V-shaped, white line in termen. Fringe red-brown. **Hindwing:** Whitish yellow with uniform light gray-brown overscaling. Fringe gray. **Genitalia:** As in Fig. 4 (drawn from USNM slide no. 68838; n = 1). Uncus simple, long, slender. Socii arched at base, long, pendant, with long dense scales. Gnathos narrow, joined distally into slender mesal process. Transtilla with stout, basal, hook-like projection, and shallow depression at bases. Valva long, simple; basal 0.25 with patch of fine scobination; costa slightly depressed in basal 0.25. Aedeagus broad, stout, with sclerotized distal perimeter; a single cornutus with several free apices.

Female. FW length 8.5 mm (n = 1). As described for male. **Genitalia:** As in Fig. 12 (drawn from USNM slide no. 68837; n = 1). Apophyses posteriores inflated. Sterigma weakly sclerotized, with narrow, lateral, slightly arched band above ostium. Corpus bursae weakly sclerotized near ostium; corpus with faint, reticulate pattern of minute spicules.

Type material: Holotype: male; El Salvador, Santa Tecia, 28–29.x.1967, E. L. Todd (USNM).

1F paratype as follows: EL SALVADOR: L. Ilopango, nr. Apulo, 4–5.vii.1966 (O. Flint & A. Ortiz, USNM).

Diagnosis: *Paraptila pseudogamma* is superficially most similar to *P. gamma* and *P. cornucopis*. The male genitalia of *P. pseudogamma* can be distinguished from those of the latter two species by the broader transtilla with more robust and strongly curved basal hook-like projections, and the scobinate region on the inner face near the base of the valva.

5. *Paraptila bloomfieldi* Brown, new species
(Figs. 5, 11, 16)

Male. FW length 4.9–5.9 mm (x̄ = 5.4; n = 3). **Head:** Frons and vertex gray-brown to purple-brown. Labial palpus concolorous with head. Antenna concolorous with head. **Thorax:** Dark brown with orange scale tufts posteriorly. **Forewing:** Basal 0.13 dark brown with scattered red-brown scales; broad, transverse, white to light tan band from costa 0.15–0.40 from base, extending to dorsum; silver-white, cornucopia-shaped patch bordering costa 0.60–0.75 from base; distal 0.60 of wing brown, lighter towards dorsum; red-brown band from near tornus to apex of silver-white patch. Fringe gray-brown. **Hindwing:** Gray-brown. Fringe gray-brown. **Genitalia:** As in Fig. 5 [drawn from JWB slide no. 277 (UCB); n = 3]. Uncus long, slender. Tegumen broadly expanded subdorsally. Socii large, broadly rounded, with membranous processes extending dorso-caudally from base of socius to base of uncus. Transtilla arched mesally, with short, pointed, paired, teeth-like subbasal processes. Valva simple, subrectrangular. Aedeagus stout, blunt, with narrow, pointed, sclerotized distal process; finely dentate ridge dorso-apically; single large cornutus.

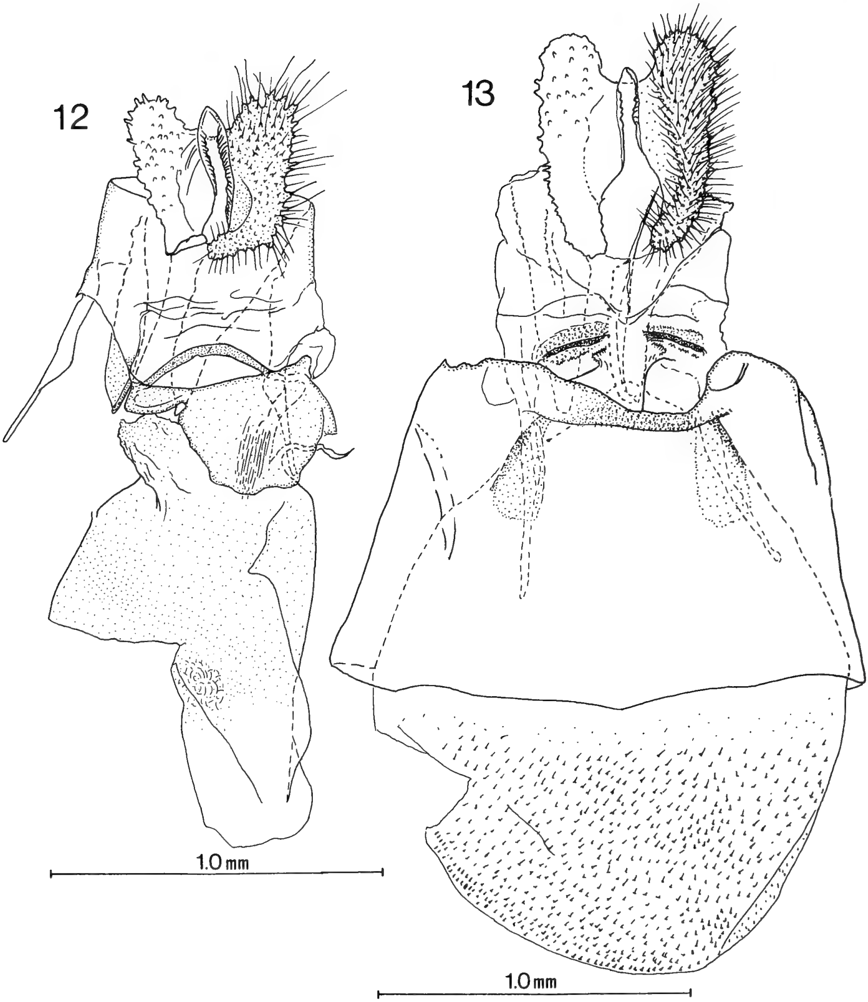
Female. FW length 5.5–6.5 mm (x̄ = 6.0; n = 5). As described for male. **Genitalia:** As in Fig. 11 [drawn from JWB slide no. 266 (UCB); n = 2]. Apophyses posteriores inflated; apophyses anteriores unmodified. Sterigma unsclerotized except for broad, transverse, U-shaped band with lightly sclerotized caudal arch mesally. Corpus bursae with minute spicules.

Type material: Holotype: male; Mexico, Jalisco, Estacion Biologia Chamela, 16–19.x.1987, J. Chemsak and J. Powell (UCB).

4M, 3F paratypes as follows: MEXICO: Colima: 1M, 13 mi N of Manzanillo, microondas Toro, 24–26.xii.1988 (N. Bloomfield, SDNHM). Jalisco: 1M, 1F, same locality as holotype, 21–22.x.1987, blacklight (J. Chemsak & J. Powell, UCB); 1F, 5 km N of El Tuito, 800 m, at light, 23.x.1987 (J. Chemsak & J. Powell, UCB); 1M, 1F, 10.8 mi N of Hwy 54, Nevado Colima [Volcano], 27–30.v.1989 (N. Bloomfield, SDNHM); 1M, 2.3 mi E of Durazno, 3899′, 6–8.vi.1989 (N. Bloomfield, SDNHM).

Additional material: MEXICO: Guerrero: 1M, 16 km NW of Iguala, 1160 m, 12–15.ix.1982 (J. Chemsak & J. Powell, UCB).

Diagnosis: *Paraptila bloomfieldi* can be distinguished from other species in the genus by the broad, well defined, light tan subbasal band of the forewing and the expanded silver-white costal patch. The male genitalia of *P. bloomfieldi* are most similar to *P. biserrata*. Those of *P. bloomfieldi* can be distinguished from those of *P. biserrata* by the unique configuration of the socii, which includes a membranous unscaled portion that extends from the dorsal base of the socius to the base of the uncus. Also, the aedeagus of *P. bloomfieldi* has a long slender



FIGS. 12–13. Female genitalia of *Paraptila* species: 12) *P. pseudogamma*; 13) *P. symmetricana*.

cornutus; cornuti are apparently absent in *P. biserrata*. *Paraptila bloomfieldi* is known from the states of Colima, Guerrero, and Jalisco, along the western coast of central Mexico; *P. biserrata* is known only from Costa Rica.

The single male from Guerrero deviates from the holotype in several respects: it is slightly larger, the forewing ground color is slightly darker, the dentate processes of the transtilla are slightly broader, and the valvae are shorter and broader basally. Consequently, this specimen is not included in the type series.

6. *Paraptila biserrata* Brown, new species
(Figs. 6, 18)

Male. FW length 5.0 mm (n = 1). **Head:** Frons and vertex dark purple-brown. Labial palpus concolorous with head, lighter mesally. Antenna dark purple-brown. **Thorax:** Dark purple-brown. **Forewing:** Basal 0.15 dark brown with sparse, scattered, red-brown scales; broad, transverse, tan band from costa 0.15–0.45 from base, extending to dorsum; short, transverse, dark brown band from costa 0.45–0.60 from base, terminating near posterior edge of DC; silver-white, hook-shaped patch from costa 0.60–0.70 from base, curving apically to near apex of DC; area between silver-white band and apex mottled with tan and dark brown, faint orange spot at apex of hooked tip of silver-white patch; diffuse, narrow, white transverse bar subapically; narrow brown band extending from near mid point of termen nearly to hooked tip of silver-white band. Fringe brown to tan, lighter near tornus. **Hindwing:** Light gray-brown. Fringe concolorous with wing. **Genitalia:** As in Fig. 6 (drawn from USNM slide no. 69311; n = 1). Uncus simple, slender. Tegumen greatly broadened subdorsally. Socii elongate, narrow basally, expanding distally, curving mesally; irregular, wrinkled, semi-sclerotized mesal flap immediately below uncus between bases of socii. Gnathos arms narrow, arising from broadest portion of tegumen, joined distally. Transtilla arched mesally, with short, pointed, paired, subbasal teeth-like processes. Valva elongate, narrow, parallel-sided. Aedeagus stout with slender sclerotized distal process; cornuti absent.

Female: Unknown.

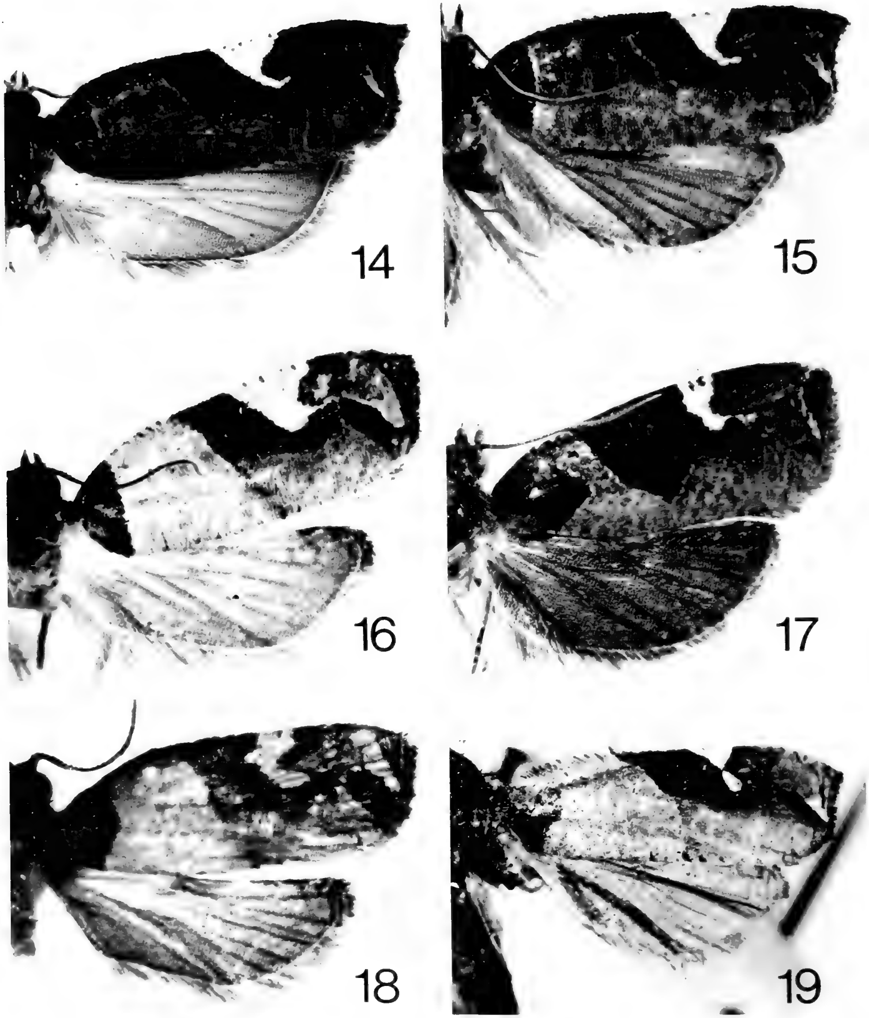
Type material: Holotype: male; Costa Rica, Turrialba, 22–28.ii.1965, S. S. and W. D. Duckworth (USNM).

Diagnosis: *Paraptila biserrata* can be distinguished superficially from other species of *Paraptila* by its broadly C-shaped silver-white costal patch. The genitalia are most similar to those of *P. bloomfieldi*, particularly in the paired, subbasal processes of the transtilla. However, the two can be separated easily by the shape and configuration of the socii and the aedeagus (see Diagnosis of *P. bloomfieldi*). In *P. biserrata* the phallobase is moderately attenuate and cornuti are absent; in *P. bloomfieldi* the phallobase is broadly rounded and there is a single large cornutus.

7. *Paraptila symmetricana* Brown, new species
(Figs. 13, 19)

Male. Unknown.

Female. FW length 9.0 mm (n = 1). **Head:** Frons and vertex dark red-brown. Labial palpus concolorous with head. Antenna concolorous with head. **Thorax:** Dark purple-brown. **Forewing:** Basal 0.15 dark brown; basal 0.15–0.40 gray-brown with faint, yellow-brown striae; broad, short, dark red-brown patch from costa 0.40–0.60 from base, extending to near posterior edge of DC; silver-white triangular patch bordering costa 0.60–0.70 from base, with silver-white oval spot below apex of triangular patch; costa with fine, transverse, brown striae between silver-white patch and apex; oblique brown dash from mid point of termen, bordered apically by narrow, silver-white wedge. Fringe light brown to pale yellow, lightest near tornus. **Hindwing:** Gray-brown. Fringe pale yellow. **Genitalia:** As in Fig. 13 (drawn from BMNH slide no. 23540; n = 1). Apophyses posteriores inflated. Sterigma unsclerotized with V-shaped depression mesally; irregular, transverse



FIGS. 14–19. Adults of *Paraptila* species: 14) *P. cornucopis,* female; 15) *P. pseudogamma,* holotype male; 16) *P. bloomfieldi,* holotype male; 17) *P. equadora,* holotype male; 18) *P. biserrata,* holotype male; 19) *P. symmetricana,* holotype female.

patch of sclerotization ventro-anterad, divided mesally by ostium. Ductus bursae extremely short, with narrow sclerotized ridges. Corpus bursae with sclerotized band at junction of ductus, curving anterior-laterally.

Type material: Holotype: female; Bolivia, Yungas de La Paz, 1908, Seebold, Rebel, "16565" (BMNH).

Diagnosis: The silver-white forewing patch of *P. symmetricana* is distinct from that of other species in the genus. It is narrowly divided into two parts: a small, triangular region along the costa, and a rounded, somewhat teardrop-shaped portion immediately posterior to the costal triangle. The female genitalia of *P. symmetricana* are unique in the possession of dense, fine, slender spicules in the anterior portion of the corpus, and the paired sclerotized ridges of the sterigma.

8. *Paraptila equadora* Brown, new species
(Figs. 7, 17)

Male. FW length 10.0 mm (n = 1). **Head:** Frons and vertex dark gray mixed with red-brown. Labial palpus white-ocherous, gray-brown laterally. Antenna gray, dark red-brown at scape. **Thorax:** Dark gray mixed with red-brown; red-copper tuft posteriorly. **Forewing:** Basal 0.25 with rectangular, red-brown patch, with distal angle directed toward termen; broad, similarly colored triangular patch in middle of wing, with base of triangle bordering costa 0.33–0.75 from base, and vertex attenuate 0.80 from costa to dorsum; latter patch poorly defined apically, bordered by narrow, sinuate, silver-white streak at costa 0.65 from base; diagonal gray band from costa 0.20–0.33 from base, broadening toward dorsum, becoming tan-orange, continuing to mid point of termen. Fringe pale orange. **Hindwing:** Uniform gray-brown. Fringe concolorous with wing. **Genitalia:** As in Fig. 7 (drawn from USNM slide no. 68839; n = 1). Uncus slender with broad apical dorsal hood. Socii long, narrow, enlarged apically; longitudinal ridge strongly sclerotized. Gnathos arms angulate, joined distally into slender mesal process. Transtilla narrow basally, with large, rectangular, mesal process. Valva moderately large, rectangular, nearly parallel-sided; sacculus extending to lower edge of apex. Aedeagus large, stout, broadly rounded basally; cornutus large, curved, basally attached.

Female. Unknown.

Type material: Holotype: male; Ecuador, [Pastaza Province], Shell-Mera, 18.iv.1958, R. W. Hodges (USNM).

Diagnosis: *Paraptila equadora* is fairly divergent from other members of the genus and may require separate generic assignment when the female is discovered. It can be distinguished from all other species of *Paraptila* by its greater forewing length, dark brown hindwing, and large hood-like process of the uncus. The aedeagus is also distinctive with an unusually large, curved cornutus.

ACKNOWLEDGMENTS

I thank the following for allowing me the use of material in their care: J. F. G. Clarke and R. W. Hodges (USNM); D. K. Faulkner (SDNHM); J. A. Powell (UCB); and K. R. Tuck (BMNH). Two anonymous reviewers provided numerous helpful suggestion for the improvement of the manuscript. I thank Norris Bloomfield (SDNHM) and Jerry Powell (UCB) for their collecting efforts in western Mexico. Photographs of adult moths were provided by Victor Krantz (USNM), Kevin Tuck (BMNH), and Don Meyer (Natural History Museum of Los Angeles County). This work was completed with the support of a Smithsonian Postdoctoral Fellowship (1988–1989).

LITERATURE CITED

BROWN, J. W. 1990. Taxonomic distribution and phylogenetic significance of the male foreleg hairpencil on the Tortricinae (Lepidoptera: Tortricidae). Entomol. News 101: 109–116.

CLARKE, J. F. G. 1958. Catalogue of the type specimens of Microlepidoptera in the

British Museum (Natural History) described by Edward Meyrick. Vol. 3. Trustees British Museum, London, England. 600 pp.

HORAK, M. 1984. Assessment of taxonomically significant structures in Tortricinae (Lep., Tortricidae). Mit. Schweiz. Entomol. Ges. 57:3–64.

MEYRICK, E. 1912. Descriptions of South American Micro-Lepidoptera. Trans. Entomol. Soc. London 1911:673–718.

——— 1926. Exotic Microlepidoptera 3(8–9):225–288, Marlborough.

POWELL, J. A. 1964. Biological and taxonomic studies on tortricine moths, with reference to the species in California. Univ. Calif. Pub. Entomol. 32:1–317.

——— 1986. Synopsis of the classification of the Neotropical Tortricinae, with descriptions of new genera and species (Lepidoptera: Torticidae). Pan-Pacif. Entomol. 62: 372–398.

RAZOWSKI, J. 1986. Descriptions of new Neotropical genera of Archipini and rectification of the *Deltinea* problem (Lepidoptera: Tortricidae). Bull. Soc. Sci. Nat. 52: 21–25.

WALSINGHAM, LORD T. DE GREY. 1914. Lepidoptera-Heterocera. Vol. 4. Tineina, Pterophorina, Orueodina, Pyralidina and Hepialidina (part). *In* Godman, F. du C. & O. Salvin (eds.), Biologia Centrali-Americana. Insecta. London. 482 pp.

Received for publication 12 June 1989; revised and accepted 18 August 1990.

PROFILES

Journal of the Lepidopterists' Society
44(4), 1990, 273–284

HARTFORD H. KEIFER—PIONEER CALIFORNIA MICROLEPIDOPTERIST

JERRY A. POWELL

Department of Entomological Sciences, University of California,
Berkeley, California 94720

ABSTRACT. H. H. Keifer was the first person to study Microlepidoptera extensively in California, but after a series of excellent papers in 1927–37, he decided at the age of 35 to devote the remainder of his career to eriophyid mites. Keifer's early career and Lepidoptera work is summarized. He described 46 new taxa (1 genus, 44 species, 1 race), primarily Gelechioidea, all but one from California, 87% from specimens that he reared from larval collections. He characterized larvae and often pupae of about 40 additional species and for others he reported occurrences in California or hostplants or both. A bibliographic list of the total of about 150 species is presented.

Additional key words: Gelechiidae, larval hostplants, bibliography, biography.

The first person to study Microlepidoptera extensively in California was Hartford Hammond Keifer, who published a series of papers in 1927–37. His approach emphasized biologies and immature stages, his techniques were superb, and his analysis of systematic placements was far ahead of his time, employing hostplant and ecological specificity as well as morphological features of larvae, pupae and adults, which he illustrated in great detail. His work has served as a beacon for standards of quality for those of us who were familiar with it. However, at the age of 35, Keifer decided to study eriophyid mites, and he terminated his work on the taxonomy of Lepidoptera.

Hartford Keifer was born in 1902 in Oroville, California, where an interest in natural history and insects, especially butterflies, was encouraged by his aunt, Dr. Cordelia Burt Leggett. He attended the University of California, Berkeley in 1920–24 and earned a B.S. degree in entomology. After working for the Forest Service for a few months, Keifer took a position as Assistant to the Curator, E. P. Van Duzee, at the California Academy of Sciences, San Francisco, mounting and labeling accumulated material. He was the entomologist on the Academy's expedition to the Revillegigedo and Tres Marias Islands, Mexico, in April–June 1925, returning with more than 10,000 specimens (Keifer 1926).

We do not know why Keifer decided to study Microlepidoptera—there was no lepidopterist at the University or the Academy—but it seems likely it was because nobody else in California was interested in them. He is described by his wife, Mary, as a kind of loner who liked to branch out and work on his own. This interest was evident already in 1925 by a large number of spread micros among his collections from the Revillegigedos expedition, an effort that general collectors do not make. Van Duzee, although a hemipterist, had worked with A. R. Grote in New York, and was an industrious moth collector who made considerable progress in building up the Academy's collection by exchange and identifications from Barnes and McDunnough. He helped and encouraged Keifer to build the micro collection at the Academy (Keifer 1935a:197), although much of the work was carried out during weekends and evenings (Van Duzee 1927).

The first species that Keifer described, *Recurvaria bacchariella,* was reared from larvae, and from the beginning his approach emphasized life histories (Keifer 1927). In a letter to Annette Braun (October 1926), he noted that San Francisco was a place for the person wishing to do life history work because net collecting usually is poor and light collecting out of the question most of the time due to the fog and cool winds.

The situation that Keifer faced, beginning a study of Microlepidoptera in California in the 1920's, is almost unimaginable. There was no collection, and the literature consisted largely of isolated descriptions without illustrations of genitalia. In a letter to Braun in February 1927, two years after Keifer began his studies, he enthused over a gift of specimens representing 58 eastern species, which "more than double our number of named species"! Evidently, he attempted taxonomic placements primarily using *Genera Insectorum* by Meyrick, and Forbes' *Lepidoptera of New York,* which were based on wing venation.

In early 1928, Keifer returned to the University of California and began taking classes towards a higher degree. However, his father became ill and died, which upset Hartford's plans. He then stayed at the family home in Oroville for a few months, during which he made collections in the foothills of the Sierra Nevada and Sutter Buttes (which had not been sampled for Microlepidoptera before and have not since). After returning to the Academy for a brief time, Keifer was appointed as the first laboratory assistant in charge of the collection and identifications for the California State Department of Agriculture (Mackie 1928), and, newly married, he moved with his wife, Mary, to Sacramento, in August 1928.

There he again started with no collection, inadequate library facilities, and isolated from professional colleagues. Again, the lack of comparative material is impossible to comprehend: in February 1931, more than two years later, Keifer responded to a return of Tortricidae that August Busck identified, "This is the largest number of named tortricids I have yet had the opportunity to examine." The lot contained *eight* species of the 80+ Tortricinae that we now recognize in California! He remained at Sacramento for the duration of his career, at first as the only systematic entomologist and ultimately becoming Program Supervisor of the Insect Identification Laboratory, until his retirement in 1967.

The scope of administrative responsibilities at Sacramento grew staggeringly during Keifer's 39-year tenure, yet he continued a productive research career through nearly all of that period. Insect identifications provided by the lab increased in concert with California's growth as the richest agricultural State. In the early years (1928–42), IDs averaged 2300/year, all recorded in log books in longhand by Keifer; discovery of the Oriental Fruit Moth in California late in 1942 resulted in extensive trapping programs and an increase in IDs to 45,000/year during 1943–52; another quantum jump resulted from Khapra Beetle and fruit fly surveys in the late 1950's, increasing the load to 146,000/year and the taxonomists under Keifer's direction to five, an average of 87 IDs per taxonomist per day! (Harper 1963). With the spread of Pink Bollworm to California, a massive light trapping program was carried out, and identifications averaged 188,000/year in the 1960's, handled by eight taxonomists (Harper 1965).

Keifer's expertise extended over all orders of insects, and his early reports in the *Bulletin of The California Department of Agriculture* treated larvae of Diptera, weevils, and other insects in addition to Lepidoptera. He recorded biologies, geographical distributions, or first occurrences in California of hundreds of insect species, including many moths, in the annual reports published in the *Bulletin* between 1935 and 1953 (Appendix 1). After R. W. Harper became Bureau Chief in 1955, however, the sections of the Annual Report no longer credited Program Supervisors with authorship, and after 1962 records of insect species ceased to be included in the reports of the Insect Identification Laboratory.

In addition to his other duties, Keifer served for 30 years as Secretary to the California Entomology Club, producing the minutes of meetings, which appeared in the *Bulletin*, and he was its president in 1964. In 1943 he served as president of The Pacific Coast Entomological Society, and in 1972 he was presented the C. W. Woodworth Award by the Pacific Branch of the Entomological Society of America (Carter 1972).

His fieldwork, which was done primarily on weekends and vacations, did not extend beyond Los Angeles, and much of it was in the nearby Sierra Nevada. He returned occasionally for family visits to San Francisco and made additional collections, although by early 1934, he noted in a letter to Busck that "These San Francisco collecting grounds, which have yielded so many new species, are rapidly being destroyed."

During 1927–37 Keifer published a series, "California Microlepidoptera" in parts I–XII, in which he described 46 new taxa (1 genus, 44 species, 1 race) (Appendix 2) in painstaking detail and increasingly profusely illustrated. All but two of the species are Gelechioidea, mainly Gelechiidae, all but one from California, and 39 of them (87%) had been reared from larval collections. In addition, he characterized the larvae and often pupae of more than 40 previously described species that he reared. More than half of the new taxa were described in the last three years (1935–37), and during this time he emphasized analysis of relationships among the groups of "*Gelechia*," "*Gnorimoschema*," and the higher taxa of Gelechioidea. Based on larval and pupal characters, he was the first to point out the gelechioid relationships of the Scythridae and confirmed them for the ethmiids, which were considered to be Yponomeutoidea by Meyrick and others. Hence, his work was increasing in breadth as well as quantity, rather than waning, when he abruptly terminated it. After 1937, Keifer's contributions to Lepidoptera knowledge were limited to reports of newly discovered occurrences and foodplants in California, in connection with his work in the Department of Agriculture. Altogether, he published on more than 150 species of moths representing virtually all superfamilies (Appendix 2).

It is a tribute to the meticulous care with which he worked that despite the handicaps of isolation from collections and type specimens, literature and contemporary specialists, Keifer described only five species that are now considered to be subjective synonyms of names that he did not recognize. One of these, *Keiferia elmorei*, is questionably synonymous.

Throughout the Microlepidoptera period, Keifer maintained an active correspondence with colleagues, particularly Braun and Busck. Both were extremely responsive to requests for identifications and confirmation of his suspected new species, as well as in exchanging specimens. Both repeatedly encouraged his requests, stating that it was a pleasure to work with his excellent, reared material, and both encouraged him to describe his species, welcoming "the good work based on reared material such as you are doing" (Busck, May 1932) and complimented him, e.g., "your descriptions of new species are much ahead of most of those made by the last generation, including my own, due to your rearing notes and to your genitalia figures" (Busck, January 1934, which was prior to most of Keifer's descriptions and more detailed larval and pupal diagnoses). Keifer noted that without their help, work on micros in the West would be impossible (Keifer 1932:73).

Ultimately, I suspect that it was this dependence upon the collections and specialists in the East that caused Keifer to give up the study of Microlepidoptera. He wanted to work on his own, and this simply was impossible in an era when travel was too costly and time-consuming to permit visits to the major museums of the world to which we are now accustomed.

The primary types representing Lepidoptera names proposed by H. H. Keifer are nearly all at the California Academy of Sciences, San Francisco, along with most of the specimens from his early years of fieldwork. Paratypes of many of his species are in the Braun collection at the Academy of Natural Sciences, Philadelphia, and in the National Museum of Natural History, Washington, D.C. His private collection of Microlepidoptera, which was assembled mostly between 1928 and 1936 and is estimated to have contained 5–6000 specimens, was donated to the California State Department of Agriculture, Sacramento, in 1974.

In 1937, when an outbreak of Citrus Bud Mite occurred in southern California, Keifer was assigned to the identification of eriophyid mites. Soon he perceived that little was known and there were no other "experts" on which he would need to depend. All the literature was available at the University of California, and he turned his limitless energy to a wide open field that lay before him. Starting in 1938 he began extensive descriptive taxonomy of this economically important group of mites, and he became the world authority. A similarity in approach carried over from his work with the micros—host plant specificity as a key to discovery of species, coupled with detailed and profusely illustrated descriptions. Because his descriptive work on Eriophyidae spanned more than 30 years and produced more than 630 new taxa, in 56 publications including comprehensive works (Arnaud & Blanc 1988), we can only speculate on the impact Keifer might have had on our knowledge of western Nearctic Microlepidoptera had his decision in 1937 been otherwise.

Although he was not directly associated with students, Keifer assisted in the early interests of them in the 1930's, including W. H. Lange Jr. and J. W. Tilden (whose fine early work on life histories of micros was terminated for the same reason, I believe), and later Keifer encouraged G. T. Okumura's larval studies and my early efforts. Throughout, as in his own work, he urged the broadening of the basis of taxonomy to include as many character sets as possible: larval, pupal, adult, and biological features. Ultimately, this philosophy has been inherited by more recent students: P. A. Opler, D. L. Wagner, J. A. De Benedictis, and others. It is no coincidence that the knowledge of biology of California Microlepidoptera is advanced over that of almost any other region of the New World.

ACKNOWLEDGMENTS

I thank the following, who provided information on various aspects of Hartford Keifer's career: P. H. Arnaud Jr., California Academy of Sciences, San Francisco; Martin Barnes, University of California, Riverside; T. D. Eichlin, California Department of Food and Agriculture, Sacramento, and especially Mary Keifer, Sacramento, and John Keifer, San Jose, California.

LITERATURE CITED

ARNAUD, P. H. JR. & F. L. BLANC. 1988. Hartford Hammond Keifer, 1902–1986. Bull. Entomol. Soc. Amer. 34:46.

CARTER, R. D. 1972. Proceedings of the Fifty-sixth Annual Meeting, Pacific Branch—Entomological Society of America. Bull. Entomol. Soc. Amer. 18:185–186.

HARPER, R. W. 1963. Annual Report of the Bureau of Entomology (1962). Calif. Dept. Agric., Bull. 52:98–109.

——— 1965. Annual Report of the Bureau of Entomology (1964). Calif. Dept. Agric., Bull. 54:81–89.

KEIFER, H. H. 1926. Report on the California Academy of Sciences Expedition to the Revillegigedo Islands, Mexico, in 1925. Proc. Pacific Coast Entomol. Soc. 2(5):67–69.

——— 1927. California Microlepidoptera. Pan-Pacific Entomol. 3:136–138.

——— 1932. California Microlepidoptera V. (Gelechiidae). Pan-Pacific Entomol. 8:61–74 (1931).

——— 1935. California Microlepidoptera VII. Calif. Dept. Agric., Mo. Bull. 24:195–218.

MACKIE, D. B. 1928. Entomological services. *In* Jacobsen, W. C. (ed.), Annual Report of the Bureau of Plant Quarantine and Pest Control. Calif. Dept. Agric., Mo. Bull. 17:672–683.

VAN DUZEE, E. P. 1927. Department of Entomology, Report for 1926:3–4. Calif. Acad. Sci., San Francisco [unpublished].

APPENDIX 1

Annotated Bibliography of Publications on Lepidoptera by H. H. Keifer[1]

KEIFER, H. H. 1925. *Coloradia pandora* in Oregon. Pan-Pacific Entomol. 1:143.

——— 1926. Report on the California Academy of Sciences Expedition to the Revillegigedo Islands, Mexico in 1925. *In* Blaisdell, Minutes of 100th Meeting, Aug. 29, 1925. Proc. Pacific Coast Entomol. Soc. 2(5):67–69. [Itinerary with notes on the insects taken; 10,700 specimens were collected including many Lepidoptera from Clarion, Socorro, and the Tres Marias Islands]

——— 1927a. California Microlepidoptera. Pan-Pacific Entomol. 3:136–138. [New species of Gelechiidae and life history notes on *Gelechia occidentella*, *Gnorimoschema chenopodiella* and *Mnemonica cyanosparsella* (=*auricyanea*)]

——— 1927b. California Microlepidoptera II. Pan-Pacific Entomol. 3:160. [Life history of *Aristotelia argentifera*]

——— 1927c. [Note that Keifer had collected Microlepidoptera, to build up the collection of the Academy, and to work up the life histories of the species.] *In* Blaisdell, Minutes of 105th Meeting, Sept. 11, 1926. Proc. Pacific Coast Entomol. Soc. 2(6):90.

——— 1928a. California Microlepidoptera III. Pan-Pacific Entomol. 4:129–132. [New species of Gelechiidae]

——— 1928b. [Observations on *Mnemonica cyanosparsella* (=*auricyanea*)]. *In* Martin, Minutes of 110th Meeting, Sept. 3, 1927. Proc. Pacific Coast Entomol. Soc. 2(7):101–103.

——— 1929. [Report on studies of life histories of Microlepidoptera]. *In* Martin, Minutes of 114th Meeting, Sept. 15, 1928. Proc. Pacific Coast Entomol. Soc. 2(8):114.

——— 1930a. California Microlepidoptera IV. Pan-Pacific Entomol. 7:27–34. [New species of Ericaceae-feeding Gelechiidae, with comparison of adult and larvae to *Gelechia panella*]

---

[1] Nomenclatural changes reflecting current use are given for species (in parentheses) but not genera.

——— 1930b. Argyresthias found in Golden Gate Park, San Francisco. Pan-Pacific Entomol. 7:76. [Synopsis of adults and larval biologies of four pine- and cypress-feeding species]

——— 1931a. Notes on some California Lepidoptera of economic interest. Calif. Dept. Agric., Mo. Bull. 20:613–626. [Photos of adults, larval biologies, and geographic occurrence of 4 Noctuidae, 7 Pyralidae, 1 Tortricidae, 4 Gelechiidae]

——— 1931b. *Gelechia versutella* Zell. Pan-Pacific Entomol. 8:54. [First record in California]

——— 1932a. California Microlepidoptera V (Gelechiidae). Pan-Pacific Entomol. 8: 61–74 (1931). [New species and biological notes on *Gelechia sistrella*]

——— 1932b. *Ephestia kuehniella fuscofasciella* Rag. in California. Pan-Pacific Entomol. 8:156. [Reared from woodpecker-stored acorns in the foothills of the Sierra Nevada]

ESSIG, E. O. & H. H. KEIFER. 1933. A pest of Sierra plums. Calif. Dept. Agric., Mo. Bull. 22:153–155. [*Mineola scitulella* (=*Acrobasis tricolorella*) reared, with comparisons of larval characters to *A. indigenella* and *Ambesa mirabella*]

KEIFER, H. H. 1933a. Insect notes. Pan-Pacific Entomol. 9:62. [*Paraneura simulella* (=*Lindera tessalatella*) and *Homeosoma electellum* common in California, rearing records]

——— 1933b. California Microlepidoptera VI. Calif. Dept. Agric., Mo. Bull. 22:351–365. [*Clepsis busckana* n. sp. (=*fucana* Wlsm.) and first report of *Batodes angustiorana* in California; new species of Gelechiidae and biological records of 8 others]

——— 1933c. The lesser apple worm (*Grapholitha prunivora* Walsh) in California. J. Econ. Entomol. 26:509.

KEIFER, H. H. & L. S. JONES. 1933. Some parasites of *Anarsia lineatella* Zell. in California. Calif. Dept. Agric., Mo. Bull. 22:387–388.

KEIFER, H. H. 1935a. California Microlepidoptera VII. Calif. Dept. Agric., Mo. Bull. 24:195–218. [New species of Gelechiidae and "Borkhausenia" (*Anoncia*); relationships of Gelechioid taxa based on larval setae; foodplant of *Gelechia scabrella*; first report of *Aristotelia elegantella* in California]

——— 1935b. Systematic entomology. *In* Mackie, Ann. Rept. of Bur. Entomol. & Plant Quar., Calif. Dept. Agric., Bull. 24:427–430. [First report of *Paraleucoptera albella* in California; status of 3 phycitine Pyralidae, as well as *Celerio lineata*, *Xylomiges curialis*, and *Vanessa cardui* populations in California]

——— 1936a. California Microlepidoptera VIII. Bull. So. Calif. Acad. Sci. 35:9–29. [Descriptions of new *Agonopteryx*, *Pyramidobela*, and Gelechiidae; relationships of oecophorids, ethmiids, based on larval and pupal characters]

——— 1936b. California Microlepidoptera IX. Calif. Dept. Agric., Bull. 25:235–259. [Description of *Argyrolacia*, new genus, and species of several genera of Gelechiidae; relationships within "Gnorimoschema" (*s. lat.*) and the enigmatic systematic placement of *Deoclona*, based on larval and pupal characters]

——— 1936c. California Microlepidoptera X. Calif. Dept. Agric., Bull. 25:349–359. [New species and relationships of the *Gnorimoschema lycopersicella* group (=*Keiferia* Busck, 1939); redescription and larval description of *Setiostoma fernaldella*]

——— 1937a. California Microlepidoptera XI. Calif. Dept. Agric., Bull. 26:177–203. [New species and relationships in *Gnorimoschema* (*s. lat.*); new *Scythris* and evidence for relationship of scythrids to Gelechioidea; biology, larval and pupal descriptions of *Lineodes integra*]

——— 1937b. California Microlepidoptera XII. Calif. Dept. Agric., Bull. 26:334–338. [New species including larval and pupal descriptions of *Antaeotricha* and *Choreutis*]

——— 1937c. Systematic entomology. *In* Mackie, Ann. Rept. of Entomol. Service. Calif. Dept. Agric., Bull. 26:433–435. [First reports of *Gracilaria azaleella*, *Ephestia elutella*, *Callopistria floridensis* in California; distribution of *Synanthedon exitiosa* and *Gnorimoschema lycopersicella*]

——— 1938. Systematic entomology. *In* Mackie, Ann. Rept. of Bur. Entomol. & Plant Quar., Calif. Dept. Agric., Bull. 27:661–664. [Interceptions of introduced *Grapholita molesta*, *Laspeyresia caryana*, and *Pyrausta nubilalis*]

——— 1939. Systematic entomology. *In* Mackie, Ann. Rept. of Bur. Entomol. & Plant Quar., Calif. Dept. Agric., Bull. 28:538–539. [First report of *Spilonota ocellana* in California]

——— 1940. Systematic entomology. *In* Mackie, Ann. Rept. of Bur. Entomol. & Plant Quar., Calif. Dept. Agric., Bull. 29:241–245. [Discovery of a parthenogenetic psychid; *Ancylis comptana* intercepted]

——— 1941. Systematic entomology. *In* Mackie, Ann. Rept. of Bur. Entomol. & Plant Quar., Calif. Dept. Agric., Bull. 30:352–354. [First report of *Aphomia gularis* in California]

——— 1942. Systematic entomology. *In* Mackie, Ann. Rept. of Bur. Entomol. & Plant Quar., Calif. Dept. Agric., Bull. 31:175–178. [First reports of *Grapholita molesta* and *Symmoca signatella* in California; distribution and larval hosts of *Paraneura simulella* (=*Lindera tessellatella*), *Pyramidobela angelarum* Keif., *Pyroderces rileyi, Myelois venipars* (=*Amyelois transitella*), and *Grapholita prunivora*]

——— 1943a. Discovery of *Grapholitha molesta* (Busck) in Orange Co., Calif. *In* Linsley, Minutes 176th Meeting Pacific Coast Entomol. Soc. Pan-Pacific Entomol. 19:40.

——— 1943b. Systematic entomology. *In* Mackie, Ann. Rept. of Bur. Entomol. & Plant Quar., Calif. Dept. Agric., Bull. 32:256–260. [Report on the Oriental Fruit Moth Survey: more than 60,000 identifications of 50+ species of Lepidoptera from ca. 600,000 specimens based mainly on dimalt bait traps; flight periods given for *Tinea fuscipunctella* (=*Niditinea spretella*), *Bondia comonana,* 8 Tortricidae, 3 phycitine Pyralidae]

——— 1944a. Applied entomological taxonomy. Pan-Pacific Entomol. 20:1–6. [Presidential address: Oriental Fruit Moth as an example of the importance of accurate taxonomic identification in pest detection leading to survey and control]

——— 1944b. Systematic entomology. *In* Armitage, Ann. Rept. of Bur. Entomol. & Plant Quar., Calif. Dept. Agric., Bull. 33:248–252. [More than 80,000 identifications, 85% from the Oriental Fruit Moth Survey, yielded the first California record of *Anthophila pariana*; *Apterona crenulella* (=*A. helix*) identified]

——— 1945. Systematic entomology. *In* Armitage, Ann. Rept. of Bur. Entomol. & Plant Quar., Calif. Dept. Agric., Bull. 34:186–191. [Over 30,000 identifications from the Oriental Fruit Moth Survey yielded 41 records of *G. molesta*; *Chilo loftini* first record in California; biology of *Hepialus behrensi* (=*californicus*) and *Litoprosopis coachella*]

——— 1946. Systematic entomology. *In* Armitage, Ann. Rept. of Bur. Entomol. & Plant Quar., Calif. Dept. Agric., Bull. 35:208–210. [*Aristotelia urbaurea* defoliating blue oaks; *L. coachella* in Central Valley]

——— 1947. Systematic entomology. *In* Armitage, Ann. Rept. of Bur. Entomol. & Plant Quar., Calif. Dept. Agric., Bull. 36:168–173. [Spread of *Apterona crenulella* to Placer Co.; *Myelois venipars* (=*Amyelois transitella*) in walnut packing houses; *Argyrotaenia citrana* in economic levels]

——— 1948. Systematic entomology. *In* Armitage, Ann. Rept. of Bur. Entomol. & Plant Quar., Calif. Dept. Agric., Bull. 37:205–209. [*Apterona crenulella* biology and spread; first report of *Cnephasia longana* in California; *Zale lunata* reported as a pest of berries in widely scattered localities]

——— 1949. Systematic entomology. *In* Armitage, Ann. Rept. of Bur. Entomol. & Plant Quar., Calif. Dept. Agric., Bull. 38:166–170. [Range extensions of *Cnephasia longana* and *Myelois venipars* (=*Amyelois transitella*)]

——— 1950. Systematic entomology. *In* Armitage, Ann. Rept. of Bur. Entomol. & Plant Quar., Calif. Dept. Agric., Bull. 39:181–186. [Biology and county records of *Myelois venipars* (=*Amyelois transitella*)]

——— 1952. Systematic entomology. *In* Armitage, Ann. Rept. of Bur. Entomol. & Plant Quar., Calif. Dept. Agric., Bull. 41:238–241. [First report of *Coleophora spissicornis* (Haw.) in California; spread of *Apterona crenulella*]

——— 1953. Systematic entomology. *In* Armitage, Ann. Rept. Bur. Entomol. & Plant Quar., Calif. Dept. Agric., Bull. 42:227–230. [First report of *Pyrausta* (=*Ostrinia*) *penitalis* in California (but it is recorded at Buena Vista Lk., Kern Co., in 1920 by Munroe 1976)]

——— 1954. Systematic entomology. *In* Armitage, Ann. Rept. of Bur. Entomol. & Plant Quar., Calif. Dept. Agric., Bull. 43:190–192. [First report of *Thyridopteryx ephemeraeformis* in California; *Melissopus latiferreanus* principal species doing damage to walnuts; spread of *Coleophora spissicornis* into San Joaquin Valley]

APPENDIX 2

Lepidoptera Described and Recorded by and Named in Honor of H. H. Keifer

New genus:

Argyrolacia (1933b) (Type species, *bifida* Keifer, 1933)

New species (present generic assignment, status given in parentheses):

acrina, Gelechia (1933b) (*Chionodes*)
adceanotha, Aristotelia (1935a) (*Aristotelia*)
adenostomae, Aristotelia (1933b) (*Aristotelia*)
altisierrae, Scythris (1937a) (n. genus, Landry ms)
altisolani, Gnorimoschema (1937a) (*Tildenia*)
angelarum, Pyramidobela (1936a; 1942 geogr. distr.) (*Pyramidobela*)
arbutina, Gelechia (1930a) (*Pseudochelaria*)
bacchariella, Recurvaria (1927a; 1933b larva & genitalia figd.) (*Recurvaria*)
bifida, Argyrolacia (1933b) (*Argyrolacia*)
braunella, Gelechia (1932a) (*Chionodes*)
burkei, Exoteleia (1932a) (*Exoteleia*)
busckana, Clepsis (1933b) (*Clepsis*, subjective syn. of *fucana* Wlsm.)
californica, Epithectis (1930a; 1935a genitalia figd.) (*Leucogoniella*)
chrysopyla, Gelechia (1935a) (*Chionodes*)
clarkei, Agonopteryx (1936a) (*Agonopterix*)
crinella, Agnippe (1927a) (*Agnippe*)
dammersi, "Gelechia" (1936b) (*Chionodes*)
demissae, Gelechia (1932a; 1936b larva) (*Filatima*)
distincta, Leucogonia (1935a) (*Leucogoniella*)
eldorada, Aristotelia (1936a) (*Aristotelia*)
eldorada, "Gelechia" (1936b) (*Aroga*)
elmorei, Gnorimoschema (1936c) (*Keiferia*, doubtful subjective syn. of *lycopersicella* Wlsm.)
ericameriae, Gnorimoschema (1933b) (*Gnorimoschema*)
francisca, Recurvaria (1928a; 1936a pupa) (*Recurvaria*)
huntella, Eucordylea (1936a) (*Coleotechnites*)
langei, Gelechia (1936a) (*Chionodes*, subjective syn. of *retiniella* Barnes & Bsk.)
mackiei, Eucordylea (1932a) (*Coleotechnites*)
manzanitae, Antaeotricha (1937b) (*Antaeotricha*)
manzanitae, Gelechia (1930a; 1937a larva) (*Pseudochelaria*)
marinensis, Gelechia (1935a) (*Chionodes*, subjective syn. of *ceanothiella* Braun)
marinensis, "Borkhausenia" (1935a) (*Anoncia*)
melanifera, Choreutis (1937b) (*Caloreas*, subjective syn. of *multimarginata* Braun)
neopetrella, Gnorimoschema (1936b) (*Exceptia*)
ontariensis, Xenolechia (1933b) (*Xenolechia*)
pasadenae, Duvita (1935a) (*Battaristis*)
potentella, Gnorimoschema (1936b) (*Scrobipalpula*)
querciphaga, Xenolechia (1933b) (*Xenolechia*)
rhamnina, Aristotelia (1933b) (*Aristotelia*)
sacramenta, Anacampsis (1933b) (*Anacampsis*)
saliciphaga, "Gelechia" (1937a) (*Filatima*)
sphacelina, "Borkhausenia" (1935a) (*Anoncia*)
stanfordia, Recurvaria (1933b) (*Coleotechnites*)

urbaurea, Aristotelia (1933b; 1946 biol., geogr. distr.) (*Aristotelia*)
vanduzeei, Gelechia (1935a) (*Chionodes*)

New race:

arborei, Gelechia braunella (1932a) (*Chionodes,* subsp. of *braunella* Keif.)

Reports on previously named species (current generic assignments):

aesculana Riley, *Proteoteras* (1940, biol., geogr. distr.)
agyrtodes Meyr., *Pyramidobela* (1936a, genitalia figd.)
albella (Chamb.), *Paraleucoptera* (1935b, geogr. distr.)
albitogata Wlsm., *Ethmia* (1936a, pupa figd.; 1937b, compared)
algidella (Wlk.), *Antaeotricha* (1937b, larva)
angustiorana (Haw.), *Ditula* (1933b, biol., geogr. distr.)
arctostaphylella (Wlsm.), *Ethmia* (1936a, larva)
argentifera Bsk., *Aristotelia* (1927b, larva, pupa; 1935a, figd.)
argyllacea (Hbn.), *Alabama* (1945, intercepted in California)
argyrospilus (Wlk.), *Archips* (1943b, phenology)
azaleae (missp.) = *azaleella* (Brants), *Caloptilia* (1937c, geogr. distr.)
baldiana (B. & Bsk.), *Teleiopsis* (1933b, geogr. distr.)
behrensi Stretch, *Hepialus* (1945, biol., geogr. distr.)
bibionipennis (Bvd.), *Synanthedon* ("strawberry crown moth") (1946, biol.)
bonifatella (Hlst.), *Tehama* (1931a, geogr. distr.)
brillians B. & McD., *Harrisina* (1942, biol., geogr. distr.)
cardui (L.), *Vanessa* (1935b, biol., geogr. distr.)
caryana (Fitch), *Cydia* (1937c, 1938, 1941, 1943b, 1944b, 1945, intercepted in California)
caryanae (missp.) = *caryana, Cydia* (1937c)
cautella Wlk., *Ephestia* (1931a, adult figd., larva)
ceanothiella Braun, *Recurvaria* (1928a, larva, pupa)
cecropia (L.), *Hyalophora* (1944b, 1945, intercepted in California)
chenopodiella Bsk., (=*atriplicella* Roesl.) *Scrobipalpa* (1927a, biol.; 1937a, larva, pupa)
citrana (Fern.), *Argyrotaenia* (1947, biol., geogr. distr.)
coachelli, coachellae (missp.) = *coachella* Hill, *Litoprosopis* (1945, 1946, biol., geogr. distr.)
comonana Kft., *Bondia* (1943b, biol., geogr. distr., phenology)
comptana (Froh.), *Ancylis* (1940, intercepted in California)
crenulella Brouard (=*helix* Siebold), *Apterona* (1940, discovery in California, biol.; 1944b, biol., geogr. distr.; 1947, 1948, 1952, geogr. distr.)
cupressana Kft., *Cydia* (1943b, biol.)
cupressella Wlsm., *Argyresthia* (1930b, biol.)
curialis (Grt.), *Egira* (1935b, geogr. distr.)
cyanosparsella (Williams) (=*auricyanea* Wlsm.), *Dyseriocrania* (1927a, 1928b, biol.)
desiliens Meyr., *Gelechia* (1931a, adult figd., biol.)
discostrigella (Chamb.), *Ethmia* (1936a, larva)
diversella (Bsk.), *Arla* (1936b, larva, pupa, systematic relationships)
electellum Hlst., *Homoeosoma* (1933a, 1935b, biol., geogr. distr.)
elegantella Chamb., *Aristotelia* (1935a, geogr. distr.)
elutella (Hbn.), *Ephestia* (1937c, 1941, 1943b, biol., geogr. distr.)
ephemeraeformis (Haw.), *Thyridopteryx* (1954, geogr. distr.)
exigua (Hbn.), *Spodoptera* (1931a, adult figd., biol.)
farinalis L., *Pyralis* (1942, biol.)
fernaldella Riley, *Setiostoma* (1936c, adult, larva, pupa)
figulilella Gregson, *Ephestia* (1931a, adult figd., biol., geogr. distr.; 1935b, geogr. distr.; 1943b, phenology, abundance)
floridensis (Gn.), *Callopistria* (1937c, geogr. distr.)
franciscella Bsk., *Argyresthia* (1930b, biol.)
frugiperda (Smith), *Spodoptera* (1931a, adult figd., biol., geogr. distr.)

fuscipunctella Haw. (=*spretella* (D. & S.)), *Niditinea* (1943b, geogr. distr., phenology)
gallicola (Bsk.), *Coleotechnites* (1936a, biol., larva)
glandiferella (Z.), *Deltophora* (1933b, geogr. distr.)
gossypiella (Saunders), *Pectinophora* (1945, intercepted in California, larval survey)
gracilalis (Hlst.), *Palpita* (1931a, biol., geogr. distr.)
gularis (Z.), *Paralipsa* (1941, geogr. distr.)
iceryaeella (Riley) (?), *Holcocera* (1937a, larva, pupa)
indiginella (Z.), *Acrobasis* (Essig & Keifer, 1933, larva; 1935b, geogr. distr.)
integra Z., *Lineodes* (1937a, adult, larva, pupa)
interpunctella Hbn., *Plodia* (1931a, adult, larva)
kuehniella Rag., *Anagasta* (1932b, biol.)
latiferreanus (Wlsm.), *Cydia* (1931a, adult figd., biol.; 1943b, 1954, biol.)
leachellus, not *Zincken* (=*sperryellus* Klots, 1940), *Crambus* (1931a, adult figd., geogr. distr.)
lineata (F.), *Hyles* (1935b, geogr. distr.)
lineatella Z., *Anarsia* (1935a, larva; 1931a, abundance; Keifer & Jones, 1933, parasites)
loftini (Dyar), *Eoreuma* (1945, geogr. distr.)
longana (Haw.), *Cnephasia* (1948, 1949, biol., geogr. distr.)
lunata (Drury), *Zale* (1948, biol., geogr. distr.)
lycopersicella (Bsk.), *Keiferia* (1936b, larva, tax. relationships, geogr. distr.)
marginata (Harris), *Pennisetia* ("raspberry root borer") (1946, biol., geogr. distr.)
marginella (F.), *Dichomeris* (1944b, biol., geogr. distr.)
metadesma (Meyr.), *Syncopacma* (1933b, larva)
mirabella Dyar, *Ambesa walsinghami* (Essig & Keifer, 1933, larva)
molesta (Bsk.), *Grapholita* (1937c, 1938, 1941, 1944b, intercepted in California; 1942, 1943b, 1944b, 1945, geogr. distr.; 1943b, 1944b, biol.)
nigrella (Hlst.) (=*gilvescentella* Rag.), *Ephestiodes* (1931a, adult figd., larva)
niveopulvella (Chamb.), *Anacampsis* (1933b, biol.)
nubilalis (Hbn.), *Ostrinia* (1938, intercepted in California; 1944b, 1945)
obsoleta (F.), (=*zea* Boddie), *Heliothis* (1931a, adult figd., abundance; 1936b, larva)
obsoletella (Roesl.), *Scrobipalpa* (1931a, adult figd., biol.; 1937a, larva, pupa) (=*psiliella* H.-S. sensu Povolny?)
occidentella, not Chamb. (=*vanduzeei* Keifer), *Chionodes* (1927a, biology; 1933b, biol., larva)
occidentella (Chamb.), *Chionodes* (1935a, larva)
ocellana (D. & S.), *Spilonota* (1939, 1943b, geogr. distr., phenology)
ochreistrigella (Chamb.), *Chionodes* (1933b, larva)
opalescens (H. Edw.) (=*exitiosa* Say), *Synanthedon* (1937c, geogr. distr.)
operculella (Z.), *Phthorimaea* (1936b, adult, larva)
panella Bsk., *Gelechia* (1928a, larva; 1930a, geogr. distr.)
pariana (Clerck), *Choreutis* (1944b, geogr. distr.)
penitalis (Grt.), *Ostrinia* (1953, biol., geogr. distr.)
pilatella Braun, *Argyresthia* (1930b, biol.)
plaesiosema (Turner) (=*tangolias* Gyen), *Symmetrischema* (1936b, adult, larva; 1937a, adult, larva, pupa figd., biology, geogr. distr.)
prunivora (Walsh), *Cydia* (1942, 1943b, biol., geogr. distr.)
pyrusana Kft., *Pandemis* (1943b, phenology)
quinquecristata (Braun), *Pyramidobela* (1936a, genitalia figd.)
reversalis (Gn.), *Uresiphita* (1931a, adult figd., larva, biol.)
rileyi (Wlsm.), *Pyroderces* (1942, biol., geogr. distr.)
rosaceana (Harris), *Choristoneura* (1943b, phenology)
scabrella (Bsk.), *Pseudochelaria* (1933b, geogr. distr.; 1935a, biol.)
scitulella (Hlst.) (=*tricolorella* Grt.), *Acrobasis* (Essig & Keifer, 1933, biol., larva)
semifuneralis (Wlk), *Euzophera* (1931a, adult figd., biol.)
serratilineella Rag., *Vitula edmansae* (1943b, geogr. distr.)
signatella (H.-S.), *Symmoca* (1942, geogr. distr.)
simulella Dietz (=*tessalatella* Blanch.), *Lindera* (1933a, 1942, biol., geogr. distr.)

sistrella (Bsk.), *Chionodes* (1932a, larva)
sororia (Z.), *Anadesmus* (1937b, larva)
spissicornis (Haw.), *Coleophora* (1952, 1954, geogr. distr.)
striatella (Murtf.), *Symmetrischema* (1936b, adult, larva; 1937a, genitalia, larva, pupa figd.)
subsimella (Chamb.), *Leucogoniella* (1935a, genitalia char.)
testulalis (Geyer), *Maruca* (1945, intercepted in California)
trichostola (Meyr.), *Chionodes* (1931a, adult figd., biol., larva)
trifasciae Braun, *Argyresthia* (1930b, biol.)
venipars Dyar (=*transitella* Wlk.), *Amyelois* (1942, 1947, 1949, 1950, biol., geogr. distr.)
vernella Murtf. (=*formosella* Murtf.), *Chionodes* (1933b, larva)
versutella Z., *Gelechia* (1931b, geogr. distr.)
vitrana (Wlsm.), *Grapholita* (1943b, biol., geogr. distr.)
yuccasella Bsk., *Deoclona* (1936b, biol., larva, pupa)

Patronyms in Lepidoptera named for H. H. Keifer:

Keiferia Busck, (Type species: *Gnorimoschema lycopersicella*), 1939, Proc. U.S. Natl. Museum 86:571.
keiferana Lange, *Epinotia*, 1937, Pan-Pacific Entomol. 13:118.
keiferi Benjamin, *Amphipoea*, 1935, Pan-Pacific Entomol. 11:55.
keiferi Powell, *Acleris*, 1964, Univ. Calif. Publ. Entomol. 32:83.

Received for publication 5 February 1990; revised and accepted 14 September 1990.

GENERAL NOTES

Journal of the Lepidopterists' Society
44(4), 1990, 285–288

THE STRIDULATORY ORGAN IN *HAMADRYAS* (NYMPHALIDAE): PRELIMINARY OBSERVATIONS

Additional key words: Wing morphology, sound production, discal cell, *Hamadryas feronia, Hamadryas februa.*

Sound production in *Hamadryas* has long been a subject of speculation regarding the location and functional mechanism of the stridulatory organ. Several possible explanations have been proposed, such as noise being produced by a membranous sac in the base of the forewing (E. Doubleday, *in* Darwin, C. 1871, The descent of man and selection in relation to sex, Vol. I, John Murray, London, vii + 423 pp.), by a stridulatory comb (Swinton, A. H., 1877, Entomol. Month. Mag. 13:207–208), by coupling and sudden release of chitinized structures in the bases of wings (Hampson, G. F., 1892, Proc. Zool. Soc. London XIV:188–193; Jenkins, D. W., 1983, Bull. Allyn Mus., No. 81, 146 pp.), scutum movements during flight (Swihart, S. L., 1967, J. Insect Physiol. 13:469–476), and by friction of two lateral distad-extending projections of the eighth abdominal sternum of males (J. L. Reverdin, *in* Fruhstorfer, H., 1916, *Ageronia,* pp. 537–545, *in* Seitz, A. (ed.), Macrolepidoptera of the world, Vol. 5, The American Rhopalocera, Alfred Kernen, Stuttgart, viii + 1139 pp.; Scott, J. A., 1986, The butterflies of North America, Stanford Univ. Press, Stanford, California, xiii + 583 pp.). A common feature of all these propositions is the lack of any experimental evidence other than observation of butterflies in free flight or morphological studies of dissected specimens.

Contrary to what has been accepted in the past (e.g., Swihart *op. cit.*), it is possible to have *Hamadryas* stridulate while being hand-held, by the following manipulations: switching their hindwings from their normal position to an upper position with respect to forewings, holding the hindwings with tweezers in the sagittal plane, and stimulating the movement of the free forewings, which in this position can move through their complete wing-beat cycle (Fig. 1). By manipulating hand-held individuals of *H. feronia* in this way and observing wing morphology, I obtained some preliminary data about the topographic location and functional mechanism of the stridulatory organ.

In *H. feronia,* only the male produces the loud sounds so characteristic of this and other species of the genus. If the forewings of male and female *H. feronia* are compared,

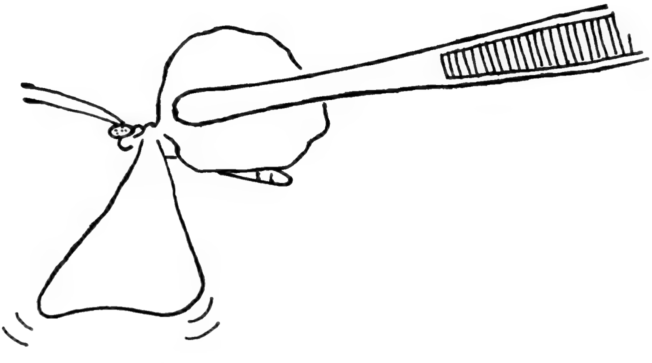


FIG. 1. Manipulation of individual *H. feronia* butterflies to allow free movement of the forewings.

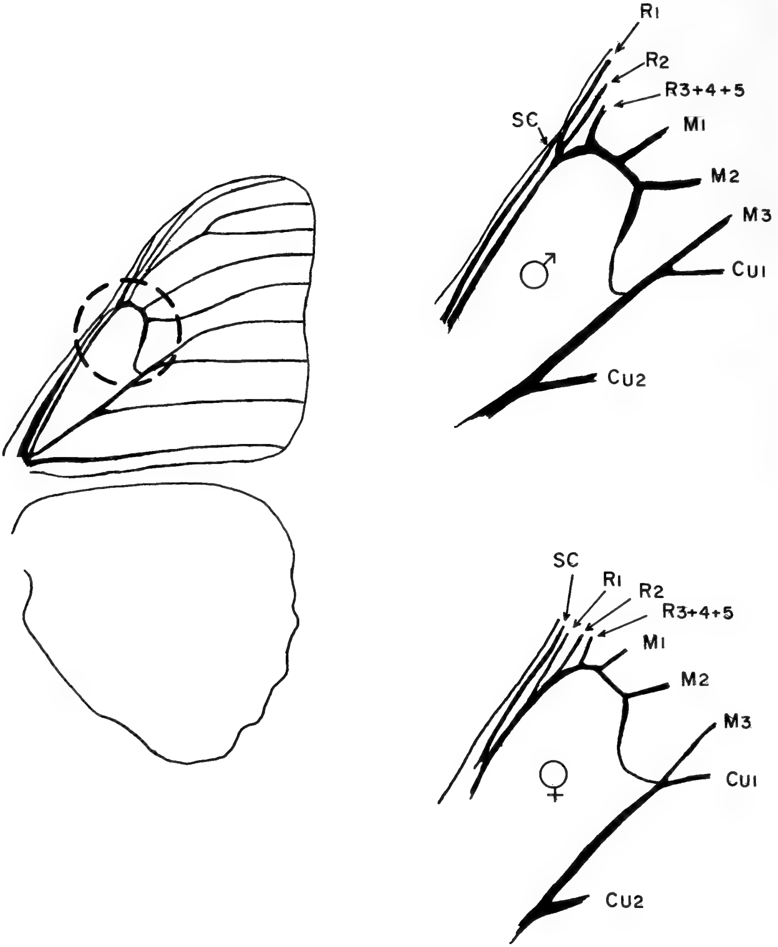


FIG. 2. Venation differences in forewings of male and female *H. feronia*. Vein nomenclature conforms to the Comstock and Needham system (Miller, L.D., 1969, J. Res. Lepid. 8:37–48).

obvious differences in venation can be observed (Fig. 2). These differences, and the fact that the sound is produced during the superior half of the upstroke of the wing beat, led me to perform a series of ablation experiments on male forewings. Ablations were made with a razor blade while the butterfly's wing to be operated on was held against a flat surface. The results of these treatments may be summarized as follows:

1. When the apical portions of both wings were removed by cutting beyond the discal cell (Fig. 3a′), the butterfly was still able to stridulate, but when the cut was made below the apex of the discal cell (Fig. 3a″), the butterfly was unable to stridulate.
2. Removal of the thickened transverse wing veins in the apex of the discal cell, including the proximal portion of M_2–M_3 (Fig. 3b, n = 5), or removal of only the portion between the insertion of R_{3+4+5} and M_2 (Fig. 3c, n = 4), suppressed stridulation

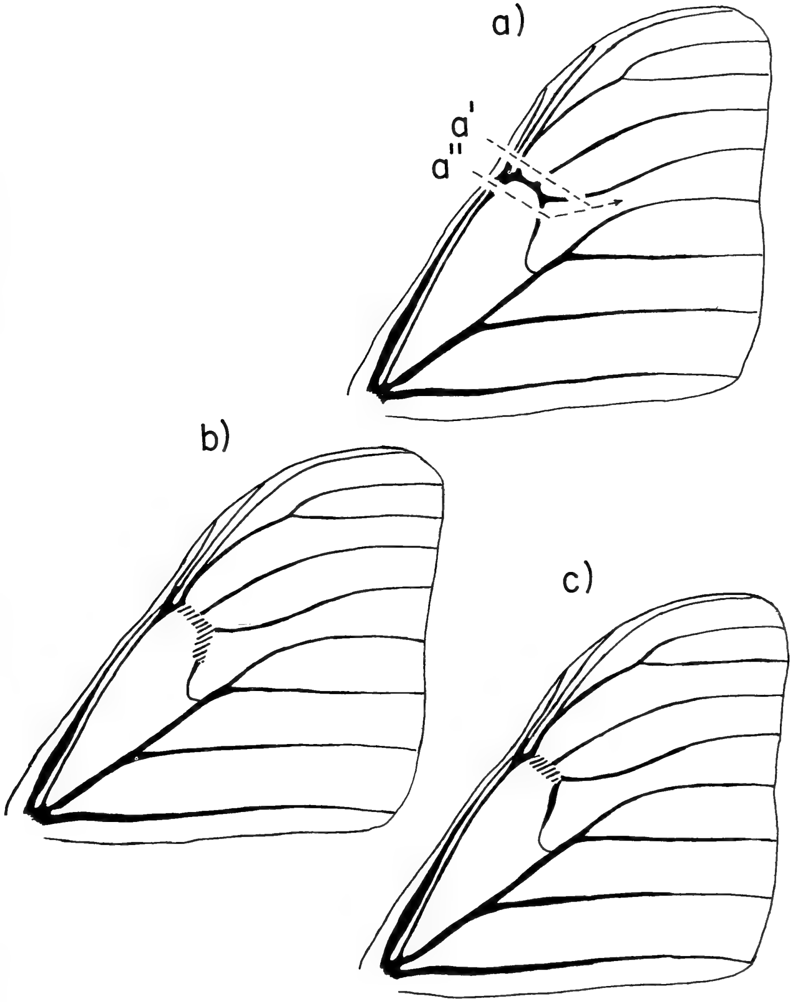


FIG. 3. Ablation experiments on the forewing of male *H. feronia* (see text for explanation).

when the cut was made on both wings. Curiously, when such cuts were made on only one of the wings, stridulatory ability persisted, but when the apical part of one of the wings was removed by cutting below the apex of the discal cell, the stridulatory ability was cancelled even if the other wing remained intact.

These results suggest that the stridulatory mechanism is associated with the thickened veins that close the discal cell at its apex. Even though these observations do not elucidate the functional mechanism, the strike of both wings at the end of the upstroke, with the sudden deformation of chitinized structures at the apex of the discal cell, seems to be the probable cause of sound production.

The male wing-vein characteristics referred to above seem to be a common feature in all species that have been reported as stridulators, except *H. februa*, which exhibits a venation similar to that of female *H. feronia* in both sexes. Even though *H. februa* is commonly cited as a stridulating species, behavioral studies revealed that males of this species in northern Venezuela populations do not produce the characteristic loud clicking sounds of several species of the genus (Otero, L. D. 1988, Contribución a la historia natural del genero *Hamadryas* (Lepidoptera: Nymphalidae), Tesis doctoral, Universidad Central de Venezuela, Facultad de Agronomía, Instituto de Zoología Agrícola, Maracay, viii + 108 pp.). This leaves open the question of whether this absence of stridulation is a particular feature of Venezuelan populations or if previous reports of stridulation in *H. februa* are due to field misidentifications, a likely possibility considering the similarity of *H. februa* with other species when seen from a distance.

I thank Dr. Dale Jenkins, Dr. Thomas Emmel, Dr. James Scott, and John Lattke for reviewing the manuscript.

L. DANIEL OTERO, *Instituto de Zoología Agrícola, Facultad de Agronomía, U.C.V., Maracay 2101, Edo Aragua, Venezuela.*

Received for publication 6 April 1989; revised and accepted 12 October 1990.

Journal of the Lepidopterists' Society
44(4), 1990, 288–289

DIFFERENCES BETWEEN NEARCTIC *PAMMENE PERSTRUCTANA* AND ITS MOST SIMILAR PALEARCTIC RELATIVES (TORTRICIDAE)

Additional key words: Olethreutinae, Grapholitini, taxonomy.

Pammene is distinguished from other genera of Grapholitini, subfamily Olethreutinae, by the presence in males of dorsal hair tufts beneath scales on tergites 6, 6 and 7, or 6–8 (illustrated in the following two sources: Kuznetsov, V.I., 1987, Family Tortricidae . . . , pp. 279–967, *in* Medvedev, G.S., [ed.], Keys to the insects of the European part of the USSR, vol. 4, pt. 1, Tech. Transl. 81-52013, U.S. Dept. Comm.; Miller, W. E., 1987, U.S. Dept. Agr., Agr. Handb. 660, 104 pp.). In the Nearctic, *Pammene* is also distinguished from other genera by veins Sc and Rs in the male being united beyond the discal cell (illustrated by Heinrich, C., 1926, U.S. Natl. Mus. Bull. 132, 216 pp.). The known *Pammene* larvae feed in fruits, catkins, and beneath bark of woody plants (Danilevsky, A. S., & V. I. Kuznetsov, 1968, Fauna USSR, Lepidopterous insects, vol. 5, pt. 1, U.S.S.R. Academy of Sciences, Leningrad, 635 pp. [Russian]).

The *Pammene obscurana* (Stephens) species group, long a problem taxonomically in the Palearctic because of indistinct species limits, was resolved into four species by V. I. Kuznetsov (1961, Entomol. Rev. [Entomol. Obozr. in English transl.] 40:506–513). This group is represented in the Nearctic only by *P. perstructana* (Walker), which I identified after it had eluded proper generic placement for more than a century (Miller, W. E., 1985, Great Lakes Entomol. 18:145–147). In reporting this belated identification, I noted a strong resemblance between *P. perstructana* and Palearctic *P. clanculana* (Tengstrom).

Here I compare *P. perstructana* with *P. clanculana* and *P. obscurana*, its most similar Palearctic relatives. I measured dimensions with an ocular micrometer at magnifications of 10 to 45×, and counted vesical cornuti at 200×. The main findings are shown in Table 1.

One structural difference among the three taxa involves cornuti: *P. perstructana* and *clanculana* have only developed ones, the latter the fewest; whereas *P. obscurana* has both developed and rudimentary ones (Table 1).

Another structural difference involves valval length. Valval length and forewing length appear independent of one another in the three taxa (Table 1). Valvae are shortest in *P.*

TABLE 1. Values for four male characters of three species of the *Pammene obscurana* group. Numbers in the same column followed by different letters differ significantly (F-test, $P < 0.05$). Ranges are shown in brackets.

Pammene species	N	Mean fore-wing length (mm)	Mean number vesical cornuti		Mean length of valva (mm)	Hue of hind-wing sex scaling
			Developed	Rudimentary		
perstructana	6	6.1a [6.0–6.4]	15.5a [10–24]	0	1.00a [0.95–1.02]	off-white
clanculana	6	6.3a [5.8–6.6]	9.5b [6–14]	0	0.91b [0.86–0.93]	off-white
obscurana	5	6.4a [5.9–6.9]	14.8a [10–21]	3.8 [0–6]	1.00a [0.94–1.11]	black

clanculana, and this departure is thus absolute, not relative to forewing length which reflects overall body size (Miller, W. E., 1977, Ann. Entomol. Soc. Amer. 70:253–256). Not tabulated here is the difference in valval shape between *P. obscurana* and the other two taxa. This difference results from the longer valval neck in *P. obscurana,* well illustrated by Kuznetsov (1961, *op. cit.*) who used it with body size, color of sex scaling, and other characters to distinguish *P. obscurana* and *P. clanculana.*

Melanic sex scaling of *P. obscurana* differs from its off-white homologs in both *P. perstructana* and *P. clanculana* (Table 1). This scaling occupies the hindwing area between costa and subcosta from the wing base to slightly beyond the discal cell.

Based on the foregoing differences, I conclude that *P. perstructana* is distinct from both *P. clanculana* and *P. obscurana.* The differences, which I assume to be specific, are slight but typical of the seemingly small divergence among species of the *P. obscurana* group.

For specimen loans and other assistance, I thank L. Aarvik, Ås, Norway (LA); P. J. Clausen, University of Minnesota, St. Paul (UM); P. T. Dang, Canadian National Collection of Arthropods, Ottawa (CNC); O. Karsholt, Zoological Museum, Copenhagen (ZMC); and V. Varis, Zoological Museum, Helsinki (ZMH).

Material examined. *P. perstructana*: Minnesota: Ely, 12.VII.65, genit. prep. DH716816; 13.VII.65, genit. prep. DH902804; Cass Lake, 20.VI.72, genit. prep. DH326813 (UM); Ontario: Thunder Bay, 2.VII.81, genit. prep. WEM1911872; Toronto, 30.VI.27, genit. prep. WEM196901; Quebec: Norway Bay, 18.VI.39, genit. prep. WEM1911871 (CNC). *P. obscurana*: Denmark: Asserbo, 14.VI.52, genit. prep. NLW1621; 1.VI.74, genit. prep. WEM85903; Ølene, 12.VI.60, genit. prep. WEM196902; Favrsted, 14.VI.80, genit. prep. WEM85901; Onsbaek, 16.VI.58, genit. prep. WEM85902 (ZMC). *P. clanculana*: Norway: Damtjerm, 21.V.80, genit. prep. LA551; 1.VI.80, genit. prep. LA554 (LA); Finland: Saanaw, 14.VII.38, genit. prep. WEM196903; P. Malla, 9.VII.38, genit. prep. WEM196904; Kilpisjärvi, no date, genit. prep. WEM196905; Palastunturit, 1.VIII.51, genit. prep. WEM196906 (ZMH).

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

Received for publication 26 June 1990; revised and accepted 21 September 1990.

Journal of the Lepidopterists' Society
44(4), 1990, 290–291

BATTUS POLYDAMAS (PAPILIONIDAE) ON BARBADOS, WEST INDIES

Additional key words: distribution, deforestation.

Of the 22 species of Papilionidae reported from the West Indies, *Battus polydamas* (L.) is the most widespread and the most subspecifically diverse. The species also occurs on the mainland from North America to northern Argentina (J. F. Emmel, 1975, p. 391, *in* Howe, W. H. (ed.), The butterflies of North America, Doubleday and Co., New York, 633 pp.) and in southern Florida. In the Antilles, there are (or were) 13 endemic subspecies: one on each of the Greater Antilles, one in the Bahama Islands, and the remaining eight from Antigua to Grenada in the Lesser Antilles (Riley, N. D., 1975, A field guide to the butterflies of the West Indies, New York Times Book Co., Boston, MA, 224 pp.).

Battus polydamas has also been reported from the island of Barbados. E. J. Pearce (1970, An attempted re-appraisal of the butterflies of Barbados, with reference to certain weather phenomena, J. Barbados Mus. & Hist. Soc. 33:76–84) noted that he had never seen *B. polydamas* on Barbados but commented that it had been included in R. H. Schomburgk's *History of Barbados* (1848), was considered quite rare by H. A. Ballou (1937, Notes upon insects mentioned in Schomburgk's history, J. Barbados Mus. & Hist. Soc. 4:1–4), and was listed by R. W. E. Tucker (1953, Insects of Barbados, J. Barbados Mus. & Hist. Soc. 20:155–181). Pearce (*op. cit.*) also noted that there were no Barbadian specimens in the British Museum (Natural History), a collection where one might logically assume such specimens would be stored.

More recently, R. Pinchon and P. Enrico (1969, Faune des Antilles françaises les Papillons, MM. Ozanne et Cie., Caen, pp. 39–47) had not examined specimens from Barbados but (p. 42) suggested that [translated] they were uncertain as to which subspecies the Barbadian material should be assigned. Riley (*op. cit.*:140) stated that typical *B. polydamas* is "confined to the American mainland, and does not now occur on any of the islands, although it seems to have been present earlier on the island of Barbados." Pinchon and Enrico (*op. cit.*) had studied examples of all of the living Lesser Antillean subspecies of *B. polydamas* (from the islands of Guadeloupe, Dominica, Martinique, St. Vincent, and Grenada) but none from Barbados, even though they had spent four days on that island and collected 17 species of butterflies (p. 33). Thus, the status (extant or extinct) and subspecific designation of the Barbadian population remained equivocal.

Donald W. Buden, while studying birds on Barbados on 15–18 July 1988 generously agreed to make a collection of butterflies on my behalf, as his own research allowed. His collection, numbering 112 specimens, contained one *B. polydamas*. The specimen was taken on 17 July 1988 at Turner's Hall Woods, St. Andrew Parish, Barbados. One other individual was seen at the same locality but not collected. The butterflies were at the margin of and within the woods. Thus, *B. polydamas* does occur on Barbados, although it is probably present only locally and thus easily overlooked. Since the birds that Buden was studying are forest-dwelling, he travelled the island looking for the appropriate habitat (woods) for them. Coincidentally, such wooded areas are favored by local *B. polydamas*.

The localization of *B. polydamas* probably is due to the immense deforestation of Barbados, first settled in 1627; sugarcane is the primary cultivation. Except for areas that cannot be cultivated conveniently (such as some of the ravines and steep or rocky slopes, which retain woods or woods-remnants), the vista on Barbados is of endless waving fields of sugarcane.

The Barbados female (forewing length 51 mm) does not agree in appearance with specimens of any of the Lesser Antillean or Greater Antillean subspecies. The only remaining subspecies is the South American *B. p. polydamas*, with which the Barbados individual does agree in detail. The fresh condition of the Barbados female precludes the possibility of its having been blown or having flown to the island from the mainland (a distance of about 280 km). Thus, I consider the resident population to be *Battus polydamas polydamas* (L.).

I thank Frederick H. Rindge, Dept. of Entomology, American Museum of Natural History, for his assistance with finding pertinent literature, Susan Borkin and Allen M. Young, Milwaukee Public Museum, for the loan of specimens, and Donald W. Buden for collecting specimens on Barbados.

ALBERT SCHWARTZ, *10000 S.W. 84 St., Miami, Florida 33173.*

Received for publication 29 November 1988; revised and accepted 10 September 1990.

Journal of the Lepidopterists' Society
44(4), 1990, 292–293

BOOK REVIEWS

BUTTERFLIES OF EUROPE, Vol. 2: INTRODUCTION TO LEPIDOPTEROLOGY, by Otakar Kudrna, Editor. 1990. AULA-Verlag GmbH, Postfach 1366, D-6200 Wiesbaden, Germany. 557 pp. + list of contributors, with 4 color plates containing 32 photographs, 93 figures, 25 tables, and 2 diagrams. Hard cover, 16 × 23.5 cm, ISBN 3-89104-033-4; DM 197 ($125 U.S.).[1]

Review by Clifford D. Ferris

Because of the nature of this volume, it is difficult for one individual to review the entire book in detail. To do it justice, several specialists should comment upon the individual technical chapters that are related to their areas of expertise. Consequently, my comments will be of a general nature.

Volume 2 is the third to be issued in a projected eight-volume series (previously published were Vol. 1: *Concise Bibliography of European Butterflies,* 1985; Vol. 8: *Aspects of Conservation of Butterflies in Europe,* 1986). In addition to the editor, there are twelve authors from Germany, The Netherlands, Switzerland, United States, United Kingdom, and Yugoslavia. The 14 chapters are titled: General introduction; Lepidopterology in Europe; Morphology: Early stages; Morphology: Adult structure and function; Butterfly phylogeny and fossils; Origins and phylogeny of butterflies; Genetics of European butterflies; Case studies in ecological genetics; The butterfly chromosomes and their application in systematics and phylogeny; Enzyme electrophoretic methods in studies of systematics and evolutionary biology of butterflies; Experimental breeding of butterflies; Parasitoids of European butterflies and their study; Behaviour of butterflies; The movements of butterflies. The book concludes with an index of butterfly scientific names, followed by a general index. All four of the color plates depict either hybrids or various color forms of European pierids. References are provided at the end of each chapter, but only those not included in Vol. 1 of this series. Consequently, the reader who wishes to follow up on text citations must have this volume available. Butterfly nomenclature generally follows that of Higgins and Riley: *A Field Guide to the Butterflies of Britain and Europe* (Houghton Mifflin, Boston, 1970).

Introduction to Lepidopterology is very thorough and by far the longest of the three volumes published to date. Although the book is directed toward a European audience, 9 of the 14 chapters apply to butterflies in general and contain a wealth of information about physiology, genetics, breeding, behavior, movement, and dispersal. Although many of the chapters address butterflies in general, all of the species cited as examples are European, as the book's title implies.

Chapter 1 is simply a two-page introduction written by the editor. Chapter 2, by the editor and M. Wiemers, presents a list of European institutions, societies, and periodicals that are devoted to Lepidoptera. It is useful to have this information compiled in one place, since many American collectors seem to a large degree to be unaware of European organizations and periodicals. There are five listings for the U.S.A., including three museums and two societies. Unfortunately, the book states that the Allyn Museum of Entomology (AME) is a former name, and does not point out that AME has retained its individual identity even though it is now part of the Florida Museum of Natural History. Forty-six pages of this chapter are devoted to very brief biographical entries for "selected past [deceased] personalities" of the European lepidopterological community. For those individuals who maintained collections, the current locations of extant collections are listed. This in itself is very useful information for taxonomists. Where applicable, citations are provided to more extensive biographies of the individuals.

---

[1] Editor's note: Volume 1, *Concise Bibliography of European Butterflies,* was reviewed by Oakley Shields in JLS 40(2):123; Volume 8, *Aspects of the Conservation of Butterflies in Europe,* was reviewed by Clifford D. Ferris in JLS 41(2):128–129.

Chapters 3 and 4, authored respectively by J. P. Brock and J. A. Scott, on morphology and physiology cover these subjects in depth. Many well executed line drawings are provided to explain points made in the associated text. Both chapters contain extensive glossaries of terms. Chapter 5, by J. A. Scott and D. M. Wright, treats butterfly phylogeny and fossils. Actually there is only very brief mention (less than a page) of butterfly fossils *per se*, and I feel that this is an unfortunate omission. Although a few literature citations are included, the papers by Scudder, Cockerell, F. M. Brown, J. Y. Miller and F. M. Brown, and others are not cited. The majority of this chapter is devoted to a list that delineates shared derived traits arranged by butterfly family/subfamily/tribe. I suspect that many specialists will find controversial certain aspects of this presentation. The chapter concludes with a phylogeny of butterflies as presented in Fig. 5/1. The relatively short Chapter 6, by J. P. Brock, presents another viewpoint about the origins and phylogeny of butterflies. Various conflicting theories are explored, and the later sections of the chapter assess various evolutionary scenarios.

In Chapter 7, R. Robinson presents a broad coverage of Lepidopteran genetics, including mechanisms of inheritance, polymorphism, electrophoretic variation, and cytogenetics. Specific species examples are discussed. A comprehensive glossary and extensive bibliography conclude this chapter. The difference between genetic and non-genetic variation (such as seasonal, thermal or photo-variation) is clearly differentiated. Chapter 8, by P. M. Brakefield, treats case studies in ecological genetics using several European satyrids as examples. The discussion is generally directed toward wing-spot characters of adult butterflies. Chapter 9, by Z. Lorkovic, on chromosomes and their application in systematics, and the following chapter, by H. Geiger on enzyme electrophoretic methods, present many practical details and methods for conducting such studies. Both are extensive treatments.

S. R. Boden, in the short Chapter 11, presents much useful information with regard to pairing and rearing butterflies. His comments apply to any region of the world in which butterflies occur. In Chapter 12, M. R. Shaw presents a broad overview of the study of lepidopteran parasitoids. General biology of parasitoids is discussed along with collecting and rearing methods. Various families of dipteran and hymenopteran parasitoids are outlined. A brief glossary and extensive bibliography conclude this chapter.

Chapters 13 and 14, by T. G. Shreeve, explore butterfly behavior, movement, and dispersal. Such matters as thermoregulation, mate location, communication, mate recognition, feeding behavior, oviposition behavior, and migration are addressed.

The high quality of publication of the two previous volumes is maintained in Vol. 2. The book is in English, but I did note occasional lapses into Germanic spelling, such as "Amerika," "Republik," and "Finnland."

It is difficult to assess the audience to which this work is directed. In the introductory chapter, the editor has stated that the book is aimed toward "lepidopterists and the mere users of Lepidoptera." He also noted that it deals in a somewhat unbalanced manner with only some aspects of lepidopterology. There is virtually no treatment of ecology, for example, but all of Vol. 7 is to be devoted to this subject. Volumes 3–6 will be the taxonomic treatments, and will probably generate the most interest among readers. For the most part, this book presents in-depth coverage; more so than is necessary or even understandable to the casual butterfly collector. On the other hand, the serious lepidopterist should find much that is of interest. Volume 2 also serves as the reference/backup for some of the sections of the previously published Vol. 8. The associated bibliographies provide sources for detailed information not included in the individual chapters. The market potential of this work is somewhat limited because of the restriction to European species, although as noted above, much of the content is of general applicability.

This is the type of book that should be available in institutional libraries, but its high cost will probably discourage many private individuals from buying a copy. On balance, I feel that it would be a worthwhile addition to the libraries of those lepidopterists who can afford it.

CLIFFORD D. FERRIS, *Bioengineering Program, University of Wyoming, P.O. Box 3295 University Station, Laramie, Wyoming 82071-3295.*

Journal of the Lepidopterists' Society
44(4), 1990, 294–297

BUTTERFLIES OF EUROPE, Vol. 2: INTRODUCTION TO LEPIDOPTEROLOGY, by Otakar Kudrna, Editor. 1990. AULA-Verlag GmbH, Postfach 1366, D-6200 Wiesbaden, Germany. 557 pp. + list of contributors, with 4 color plates containing 32 photographs, 93 figures, 25 tables, and 2 diagrams. Hard cover, 16 × 23.5 cm, ISBN 3-89104-033-4; DM 197 ($125 U.S.).

Review by Thomas C. Emmel

The 1945 edition of E. B. Ford's book, *Butterflies* (Collins, London), was the first general book on the biology of butterflies published in the English language. It had been preceded by a comprehensive technical treatise authored by Martin Hering, *Biologie der Schmetterlinge* (Julius Springer, Berlin, 1926), which unfortunately was never translated into English from the original German. Then in 1984, Philip Ackery and Richard Vane-Wright edited an outstanding volume of collected papers, *The Biology of Butterflies* (Academic Press, London), which has recently been reissued (Princeton University Press, Princeton, NJ, 1989) in a paperback version with an updated introduction and additional bibliography. Using a group of authorities invited to a symposium held in England in September 1981, more than thirty excellent contributions were prepared for that volume, covering most of the modern areas of the study of butterflies. Matthew Douglas followed that volume in 1986 with his own book, *The Lives of Butterflies* (Univ. Michigan Press, Ann Arbor), written from a more popular viewpoint. These four books represent those works devoted specifically to a general survey of the biology of butterflies, excluding the rest of the Lepidoptera.

Now in 1990, Otakar Kudrna has provided the scientific community and amateur naturalist with another comprehensive introduction to the biology of butterflies, emphasizing a European perspective. Thirteen European and American authors have contributed chapters of greatly varying length and comprehensiveness to this volume. Most of the literature cited in each chapter is dated earlier than 1986, but several authors have provided literature references up to 1988.

The book opens with a two-page general introduction by the editor which is actually a foreward, describing the intent of the book as a textbook and reference book alike. As the editor points out, the book deals with only some aspects of lepidopterology "and it treats them in an unequal, indeed to some degree unfair, manner." Since the editor blames himself at length here for failing to find a competent ecologist to write a timely chapter on this subject, we need not do so here. Kudrna does promise that ecology will be dealt with comprehensively in the seventh volume of this series. (Volume 1, a bibliography of European literature on butterflies, and Volume 8, a volume on the conservation of butterflies, were previously published in 1985 and 1986, respectively, by the same editor and publisher.) As the editor also points out, all the chapters of this present volume are aimed at advanced students of butterflies, and though highly unequal in coverage, they do indeed direct themselves toward that relatively limited audience. With these omissions and reservations stated, let us proceed to look at the merits of each of the contributed chapters in more detail.

Chapter 2 deals with "Lepidopterology in Europe." Kudrna and Martin Wiemers provide a guide to European lepidopterological institutions, societies, and periodicals. They also treat a selected list of past personalities among the hundreds of well-known European lepidopterists. These treatments are admittedly short and terse, expressing in only several lines the basic biography, but normally also providing a literature reference to a more thorough published treatment of that person's biography. A list of acronyms of major museums relevant to lepidopterology is included for easy reference, and may be useful to those wishing to employ standard abbreviations in their own publications (such as in lists of specimens examined for taxonomic revisions).

Chapter 3 deals with the morphology of early stages of butterflies, and is authored by

Jim P. Brock, of Glascow, Scotland. Brock provides a short but very competent overview of the terminology and structure pertaining to the description of the egg, the larva, and pupa. And the chapter is reasonably well illustrated. The keys to the larvae and pupae of the early stages of the various higher groups of butterflies are excellent. There is also a short section on methods for preserving early stages, and a glossary of terms pertaining to early stages. Most entomologists in North America would be able to obtain the same information in greater detail in their copies of James A. Scott's book, *The Butterflies of North America* (Stanford University Press, Stanford, California, 1986), referring to his excellent introductory section on the same subjects.

Chapter 4 is devoted to a discussion of adult structure and function, by James A. Scott of Colorado. In a series of succinct text sections and detailed figures, Scott covers the body segments, appendages, muscular system, reproductive system, breathing and blood circulation, feeding, digestion and excretion, nervous and sensory systems, and the endocrine system of adult butterflies. He closes his chapter with a glossary of morphological terms pertaining to the adult. One nice feature of this chapter is its emphasis on functional morphology, that is, how each of these structures actually works in the living butterfly. This chapter is excellent, but again a North American reader could obtain the same information in perhaps greater detail from Scott's 1986 book.

In Chapter 5, entitled "Butterfly phylogeny and fossils," James A. Scott and David M. Wright of the United States first present an interesting summary of methods for the study of phylogeny, including chemical/genetic methods, intuition, phenetics, and phylogenetics, or cladistics. The rest of the chapter employs cladistic methods to deduce the branching sequence in phylogenetic trees of butterflies. A brief discussion of the ancestors of butterflies is followed by detailed specification of characters for each major group of Lepidoptera (superfamilies). A very short discussion on butterfly fossils is then followed by detailed specification of shared derived traits between the major superfamilies of butterflies, families, and subfamilies, even down to tribal level. This very thorough discussion culminates in a single figure for this chapter, showing the phylogeny of butterflies obtained by these two authors using these procedures.

Chapter 6, by J. P. Brock, also deals with the origins and phylogeny of butterflies. Using the characters of eggs, larvae, and pupae, and various adult structures, Brock looks at various evolutionary scenarios as to the phylogeny of butterflies, and finally to families within Rhopalocera. A comparison of these two chapters (5 and 6) will provide many hours of stimulating mental exercise in considering the evidence from various phylogenetic approaches to relationships among the butterfly groups. The worldwide coverage in both chapters will provide innovative ideas and food for thought to the interested lepidopterist.

The genetics of European butterflies is surveyed by Roy Robinson in Chapter 7. This is a very generalized discussion of the principles of inheritance, looking first at Mendelian ratios and then discussing some of the other basic genetic concepts. Almost all of the literature cited stops with Robinson's book in 1971, and few specific examples are offered for each phenomenon discussed. Robinson then goes on to treat the topic of cytogenetics in the rest of the chapter. He has compiled a list of the haploid chromosome numbers of European Rhopalocera, and compares the numerical modes for the European families with the worldwide distribution of chromosome numbers among families surveyed in his 1971 book. Robinson also reviews the traditional hypotheses for variation in chromosome number and then presents an interesting discussion on sex chromosomes, supernumerary chromosomes, and other topics; in all of these areas, the work as described is primarily based on material already in his 1971 book, *Lepidoptera Genetics* (Pergamon Press, Oxford). Finally, Robinson treats the genetics of various European species of butterflies, listing the genetic variations that have been found in each. This section cites both old and new references (post-1971) in considerable detail. In a very real sense, this is a modern-day treatment of the genetics of British and other European species that is similar to what Ford first did in 1945, in his book *Butterflies*. Lepidopterists interested in breeding these species or in trying their hand at genetic work will find this section quite valuable. This chapter closes with a glossary of genetic and evolutionary terms authored jointly by Paul M. Brakefield and Roy Robinson.

Chapter 8 deals with case studies in ecological genetics and is by Paul M. Brakefield, one of the leading ecological geneticists in England today. Although relatively short, this chapter covers the basic methodology of ecological genetics and then discusses and illustrates work with *Maniola jurtina,* including the heritability of hindwing spotting, the expression of spotting, and types of selection operating on these other spot characters, along with discussion of the extensive field survey data for hindwing spot number in the species. Since Brakefield has been a prolific worker in the field and is incapable of writing a dull paper, this chapter is one of the most interesting in the book and offers much food for thought for those interested in evolutionary phenomena in butterflies. He even treats variation in the *genitalia* from the viewpoint of an ecological geneticist. In the final portion of his chapter, he applies some of the lessons learned from *Maniola jurtina* to *Coenonympha tullia* populations. A model presented by R. L. H. Dennis regarding the selective influences of climate and predation on butterfly variation is discussed with special emphasis. These authors found a close positive association between type of spotting pattern and the duration of bright sunshine in the adult flight period in particular areas. The relationship with sunshine is consistent with geographic changes in increased levels of adult activity, which apparently could shift the balance of selection on wing pattern towards an emphasis on more highly developed spotting, which in turn would function primarily to deflect attacks by predators.

The following chapter is also among the best in the book. Zdravko Lorkovic covers butterfly chromosomes and their application to systematics and phylogeny in Chapter 9. This 65-page chapter provides a brilliant synthesis of our knowledge of chromosomes, spermatogenesis, and oogenesis in butterflies. He shows in great detail how to prepare material for the examination of chromosomes and covers recently introduced methods, including their advantages and disadvantages. He points out that of the 500 or so European species of butterflies and skippers, the karyotypes of approximately 272 species (about 60%) are known. Yet only about 23% of closely related species can be distinguished by their chromosome sets; most species in every family have such constant chromosome numbers that chromosome number is of little utility as a taxonomically differentiating character. Lorkovic then goes on to discuss, in much more detail than Robinson's earlier chapter, the topics of supernumerary chromosomes, variable chromosome numbers, subspecific differences in chromosome numbers, and the behavior of chromosomes in hybrids, where Lorkovic's work has provided distinguished leadership in the field. He illustrates his discussion not only with outstanding text figures, but also with two color plates of 16 figures. The chapter closes with a discussion of the distribution of chromosome numbers among the various families worldwide. This chapter is really an outstanding contribution to the literature on evolution of butterflies and their chromosomes.

Another outstanding chapter follows Lorkovic's. In Chapter 10, Hansjurg Geiger treats the subject of enzyme electrophoretic methods and their impact on studies of the systematics and evolutionary biology of butterflies. Geiger, like Lorkovic with chromosomes, presents some 40 pages of outstanding step-by-step discussion of the utility of enzyme electrophoretic methods in such studies. He includes detailed step-by-step interpretations of the genetics of zymograms (staining of enzyme bands on a gel) and explains how to calculate allelic frequencies from such data. Even more usefully, he discusses in a step-by-step manner the various ways of calculating genetic identity and distance based on enzyme electrophoretic data. This allows even a novice in the field to understand how to quantify the degree of genetic correspondence between populations or taxa, using several different methods. This chapter provides an excellent entry into the literature and methodology of enzyme electrophoresis, and its utility in systematics.

Chapter 11 is by Sydney R. Bowden of West Sussex, Great Britain, and deals with the experimental breeding of butterflies. Beginning with a treatment of the usefulness of experimental cross-breeding in determining taxonomic relationships, he proceeds to discuss in short sections such elementary topics as larval housekeeping, size of cages needed, the recording of data, and how to work out breeding scenarios. Although this short introduction to the problem of experimental breeding of butterflies is interesting, a great many additional topics ought to be covered in a thorough treatment of the subject.

In Chapter 12, the parasitoids of European butterflies are surveyed by Martin R. Chaw, of the Royal Museum of Scotland's Natural History Department. Chaw provides a useful summary of the topics of population ecology (such as estimating percentage of parasitism), host associations and general parasitoid biology, before describing techniques for collecting, rearing, and handling adult parasitoids. He then provides an outline of the principal groups and families of parasitoids attacking European butterflies. The short paragraph for each family includes one or several literature references to monographs on the European or world genera and species. The chapter concludes with a short glossary.

The penultimate chapter in the book deals with the behavior of butterflies and is authored by Timothy G. Shreeve of Great Britain. With only one figure (basking postures adopted by individuals engaged in temperature regulation), Shreeve nevertheless provides a carefully written summary of thermoregulation, mate location, mate recognition, egg laying behavior, and feeding behavior as "the five major components" of adult butterfly behavior. In each section, Shreeve treats a few examples and cites a fair number of references on European and American species. The chapter concludes with a brief discussion (of several pages) on methods that can be used in behavioral research on each of these five components of adult butterfly behavior.

The final chapter (14), also by Timothy G. Shreeve, deals with the movements of butterflies—migration, dispersal, and within-habitat movements. The treatment begins by defining the various types of movement, and then examines variation in movement, range, sex, timing, and so forth. Local movements are treated at length, and factors underlying dispersal are discussed over several pages, with a modest number of references cited. The topic of directionality in dispersal and migration is treated with a single figure (showing peak flight directions of *Pieris rapae* recorded in western Europe during late summer 1987, though the data are said to be from Baker 1969!). The final pages of this chapter describe methods of measuring dispersal and migration, but the information provided is so sparse as to merely tantalize the reader, who must refer to the original papers for very significant details, such as specific marking methods or the utility of each procedure.

Each of the chapters in this book concludes with a more or less detailed list of references, not necessarily restricted to the European fauna and European studies. There is no central bibliography. There is, however, a terminal index to the scientific names of Lepidoptera mentioned in the text, and a general index to topics.

It is clear that this *Introduction to Lepidopterology* is not really a comprehensive introduction to the biology of butterflies, but instead represents a group of papers on selected topics that are developed with highly uneven thoroughness by their respective authors. As such, this volume cannot equal in coverage the outstanding *Biology of Butterflies* volume edited by Ackery and Vane-Wright (1984, 1989). Nor is it as highly readable as Matthews' *The Lives of Butterflies* (1986). However, the outstanding nature of several of these chapters makes this new work an important reference for those interested in cytogenetics, ecological genetics, or the genetics of European butterflies, especially for researchers employing techniques of enzyme electrophoresis in studies of the systematics and evolutionary biology of butterflies. Taxonomists may find the chapter on European museums and other institutions to be of interest as well. The high price of this book insures that it will be sold mostly to institutional libraries, where it could serve as a useful reference for the above purposes. A well-illustrated introduction to the biology of butterflies, with detailed modern treatment of all areas in this rapidly advancing field of study, is still in the future.

THOMAS C. EMMEL, *Division of Lepidoptera Research, Department of Zoology, University of Florida, Gainesville, Florida 32611.*

Journal of the Lepidopterists' Society
44(4), 1990, 298–302

INDEX TO VOLUME 44

(New names in **boldface**)

Date of Issue (Vol. 44, No. 4): 16 May 1991

NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of Lepidoptera study. Categories are Articles, Profiles, 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 111 in Volume 44(2). *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 submit manuscripts in *triplicate*, typewritten, *entirely double-spaced*, with wide margins, on one side only of white, letter-sized paper. Prepare manuscripts according to the following instructions, and submit them flat, not folded.

Abstract: An informative abstract should precede the text of Articles and Profiles.

Key Words: Up to five key words or terms not in the title should accompany Articles, Profiles, General Notes, and Technical Comments.

Text: Contributors should write with precision, clarity, and economy, and should use the active voice and first person whenever appropriate. Titles should be explicit, descriptive, and as short as possible. The first mention of a plant or animal in the text should include the *full scientific name* with *author*, and *family*. Measurements should be given in metric units; times in terms of the 24-hour clock (0930 h, not 9:30 AM). Underline only where *italics* are intended.

Literature Cited: References in the text of Articles and Profiles should be given as Sheppard (1959) or (Sheppard 1959, 1961a, 1961b) and listed alphabetically under the heading LITERATURE CITED, in the following format without underlining:

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

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

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

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.

Tables: Tables should be numbered consecutively in Arabic numerals. Headings for tables should not be capitalized. Tabular material must be typed *on separate sheets*, and placed following the main text, with the approximate desired position indicated in the text. Vertical lines as well as vertical writing should be avoided.

Voucher specimens: When appropriate, manuscripts must name a public repository where specimens documenting identity of organisms can be found. Kinds of reports that require vouchering include life histories, host associations, immature morphology, and experimental enquiries.

Proofs: The edited manuscript and galley proofs will be mailed to the author for correction of printer's errors. Excessive author's changes at this time will be charged to authors at the rate of $2 per line. A purchase order for reprints will accompany proofs.

Page charges: For authors affiliated with institutions, page charges are $20 per *Journal* page. For unaffiliated authors, page charges are $10 per *Journal* page with a $50 maximum. Authors of Book Reviews and Obituaries are exempt from page charges. Authors unable to pay page charges for reasons such as difficulties with foreign exchange should apply to the editor for free publication.

Correspondence: Address all matters relating to the *Journal* to the editor.

PRINTED BY THE ALLEN PRESS, INC., LAWRENCE, KANSAS 66044 U.S.A.

CONTENTS

PROFILES

GENERAL NOTES

BOOK REVIEWS

FEATURE PHOTOGRAPH

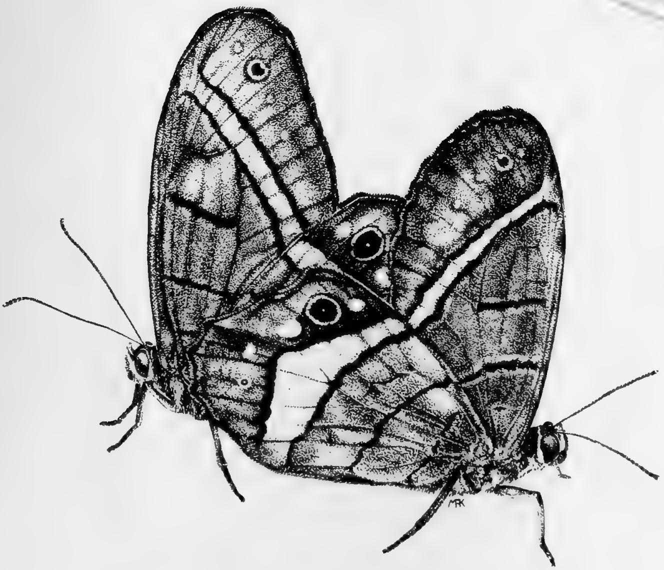
THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

ne 45 1991 Number 1

ISSN 0024-0966

JOURNAL
of the
LEPIDOPTERISTS' SOCIETY

Published quarterly by THE LEPIDOPTERISTS' SOCIETY
Publié par LA SOCIÉTÉ DES LÉPIDOPTÉRISTES
Herausgegeben von DER GESELLSCHAFT DER LEPIDOPTEROLOGEN
Publicado por LA SOCIEDAD DE LOS LEPIDOPTERISTAS



14 August 1991

THE LEPIDOPTERISTS' SOCIETY

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.

Active members—annual dues $25.00
Student members—annual dues $15.00
Sustaining members—annual dues $35.00
Life members—single sum $500.00
Institutional subscriptions—annual $40.00

Send remittances, payable to *The Lepidopterists' Society*, to: Fay H. Karpuleon, Treasurer, 1521 Blanchard, Mishawaka, Indiana 46544, U.S.A.; and address changes to: Julian P. Donahue, Natural History Museum, 900 Exposition Blvd., Los Angeles, California 90007-4057 U.S.A. For information about the Society, contact: William D. Winter, Secretary, 257 Common St., Dedham, Massachusetts 02026-4020, U.S.A. (617-326-2634). To order back issues of the *Journal, News,* and *Memoirs,* write for availability and prices to the Publications Coordinator: Ronald Leuschner, 1900 John St., Manhattan Beach, California 90266-2608, U.S.A.

Journal of the Lepidopterists' Society (ISSN 0024-0966) is published quarterly for $40.00 (institutional subscription) and $25.00 (active member rate) by the Lepidopterists' Society, % Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, California 90007-4057. Second-class postage paid at Los Angeles, California and additional mailing offices. POSTMASTER: Send address changes to the Lepidopterists' Society, % Natural History Museum, 900 Exposition Blvd., Los Angeles, California 90007-4057.

Cover illustration: Mating pair of the Costa Rican satyrid, *Pierella helvetia incanescens* Godman & Salvin (Nymphalidae: Satyrinae). Original drawing by Mark A. Klingler, Scientific Preparator, Section of Invertebrate Zoology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213.

JOURNAL OF
THE LEPIDOPTERISTS' SOCIETY

Volume 45 1991 Number 1

Journal of the Lepidopterists' Society
45(1), 1991, 1–10

PRESIDENTIAL ADDRESS, 1990: THE AGE OF DISCOVERY—LEPIDOPTERA IN THE WEST INDIES[1]

JACQUELINE Y. MILLER
Allyn Museum of Entomology, Florida Museum of Natural History,
3621 Bay Shore Road, Sarasota, Florida 34234

Additional key words: history, exploration, biogeography, biodiversity, ecology.

As we enter the decade of the 90's and approach the quinque-centennial anniversary of the discovery of the New World in 1992, perhaps this is a time to reflect on the progress—or lack thereof—that we have made in the study of Lepidoptera. While the study of the West Indian fauna may not appear to have contributed significantly to our general knowledge of North America or other continental fauna, these indeed share a parallel history in many ways. In this abbreviated space I will present a brief history of the study on the Lepidoptera of the West Indies, post some questions, and discuss the problem areas that remain to be addressed. Similar queries are applicable to continental faunas; all lepidopterists can play a significant role in resolving many questions.

Consider how our geographical horizons have expanded in the last 500 years. Despite the voyages of Leif Erickson and the Vikings to the coast of Newfoundland, the Western Hemisphere was unknown to most Europeans prior to the voyages of Columbus. The Ptolemaic map illustrated only two major land masses (Europe and Africa) and about a dozen islands; little was known about the relative positions or dimensions of even the recognized continents. On 3 August 1492, Columbus and his crew set sail from Spain to the Canary Islands, where they stopped for provisions and repairs. After 37 days crossing the Atlantic, Columbus arrived by 12 October on the eastern side of the Central Bahamian islands. Most historians agree that he made landfall on Guanahani, also

---

[1] Delivered to the Annual Meeting of the Lepidopterist's Society in Milwaukee, Wisconsin, on 16 June 1990.

known as Watling or San Salvador, but the meandering path of his explorations through the islands and the West Indies is still in dispute. Ironically, the discovery of "America" actually occurred in the Bahamas.

Biogeography of the West Indian Lepidoptera

The West Indies encompass an area of 600,000 square miles, about the size of the United States. The area is comprised of four major island groups: the Bahama Islands, the Greater Antilles (Cuba, Haiti, Dominican Republic, Puerto Rico, Jamaica), the Virgin Islands, and the Lesser Antilles (Leeward and Windward Islands). Geologically, the proto-Greater Antilles date from the late Cretaceous to the Paleocene (approximately 80–60 million years before present), with the subsequent break up of the individual islands sometime during the late Eocene, and reaccretion of some islands, such as Hispaniola, during early Oligocene to Miocene. The Lesser Antilles arose as a volcanic arc (the Aves Arc) with land emergent during most of the Tertiary.

Although limited in land area, a wide variety of habitats is extant throughout the Western Antilles. The topography and geographical position of islands with respect to the trade winds play a significant role in the distribution of fauna and flora. Habitats range from tropical rain forests, such as the Caribbean National Forest near Loquillo in eastern Puerto Rico, parts of Dominica, and northwestern St. Vincent in the Lesser Antilles, to desert scrub near Guanica in southwestern Puerto Rico and on the island of Barbuda. There are picturesque beaches edged by crystalline, aquamarine waters, but these may be bordered by salt flats, especially in the Bahamas. However, observing and collecting Lepidoptera in this tropical paradise are not without some problems.

With the exception, perhaps, of the Greater Antilles, the West Indies are not self-sustaining, and most goods are transported to these islands. Accommodations and restaurants may be sparse and expensive on some islands. In addition, available habitat is restricted either due to human encroachment or floristic diversity, and road access may be quite limited. I might also add that, for whatever islands you sample, you will work exceedingly hard for the observations made and the specimens collected. You will indeed find collecting a challenge in the West Indies.

With more than 322 described and a few undescribed species, the butterfly fauna of the West Indies is quite manageable. The number of moth species represented is obscure at this juncture, yet another problem area beset by the lack of appropriate study and little available literature. Specimens in museum collections generally have been provided by a few collectors, and there have been a few faunal surveys.

Most noteworthy are those of the Van Voast expedition during the late 1930's to the Bahamas and the Bredin-Archibold-Smithsonian on Dominica during the mid-1960's. Although the lepidopteran fauna may appear to be limited by the available geographical area, our knowledge of species diversity, host plant associations, and other aspects of life history is severely hampered by the paucity of studies completed and **published**.

In a recent address, one of our honorable Presidents analyzed the specialized interests of lepidopterists, their collecting habits, and their selection of habitats. Some people find it rather peculiar that Florida residents would leave home to study similar habitats and taxa in the Caribbean. While this point has some merit, there are some definite advantages in studying island fauna and flora. One is that the actual land area and the associated fauna and flora are rather limited, providing an ideal laboratory setting for study. The lepidopteran taxa present are subject to a number of variables. The climate is quite stable for most of the year, but unpredictable storms and hurricanes, coupled with the ever present trade winds, affect the geographic distribution of species. There are indeed turnover and fluctuation rates of butterfly and moth species on these islands similar to those proposed in the theory of island biogeography by MacArthur and Wilson (1967). However, common taxa such as *Vanessa cardui* (L.) and *Danaus plexippus* (L.) may be present in large numbers one year, as for example on Great Inagua in the southern Bahamas, and inexplicably absent the next (Simon & Miller 1986). In these cases, other factors such as available larval hostplant, parasitism, pesticide use, or even migratory patterns need to examined, but in many instances, these aspects do not adequately explain the complete absence of such species from one year to the next. In addition, there is a definite seasonal rain pattern, and emergence periods of species may be interlocked with the onset or end of the rainy season. Most of the material collected in the West Indies has been taken during the winter months, often by collectors seeking to avoid the northern winter, but the number of taxa represented during these periods is diminished, and unfortunately, many of the smaller islands have been omitted by such collectors.

Although our initial impetus was to survey the West Indian fauna and to determine the diversity of species present on these islands, it was also important that we glean the necessary rudiments about the conservation measures necessary to protect them. As mentioned previously, with the intervention of man, the loss of available habitats and associated host and nectar sources has diminished the areas available for collecting and observation. Limited land space on these islands means little arable land for cultivation and less potable water. For residents of the rapidly developing states of Florida and California, this has new meaning and rather permanent significance.

There are apparent similarities in collectors' perceptions of species diversity of Lepidoptera in the southern U.S., especially Florida and the West Indies. The stable climate, warm temperatures, and the presence of palm trees apparently triggers something in the human psyche that conjures up the idea of an increase in species numbers and population sizes, especially of Lepidoptera. Such impressions are not necessarily true even in some areas of the Amazon basin, let alone the Caribbean. Even Gosse (1851) in his exploration of Jamaica stated: "I had left England with high expectations of the richness of the West Indian entomology; large and gaily-coloured beetles, I supposed, would be crawling on almost every shrub, gorgeous butterflies befilling the air, moths be swarming about the forest-edge at night, and caterpillars be beaten from every bush. These expectations were far from being realized." Gosse discusses further the various butterfly species that are exceedingly common on the island and also decries the paucity of larvae present. For example, he collected 20 species in Newfoundland during an hour and half one afternoon, but scarcely saw 20 species during his whole stay on Jamaica. Similar observations on the species diversity of the West Indies and other areas of the neotropics have been made by Longstaff (1907).

History of Lepidopterology in the West Indies

There is little information about early collecting in the West Indies, and that available is largely devoted to the fauna of the Greater Antilles. Perhaps the best known source is the diary of Hans Sloane, who visited Jamaica in 1687 as a physician to the Duke of Albemarle. Sloan recorded observations and collected on the island for 15 months. During this period he collected more than 3800 insects, including immature stages, most of which were illustrated and published in 1725. Sloane's notes and illustrations were of significant interest to Linnaeus in his compilation of butterflies in 1758, the official starting point for zoological nomenclature. Many of the butterflies described were endemic Jamaican species, but others such as *Phoebis sennae* (L.) have associated subspecies on the continent. Many of these New World taxa were described by Linnaeus (1758), Fabricius (1775), Cramer (1775–80), Drury (1770–73), and other early authors who depended on other collectors to obtain specimens and who relied on the accuracy of their data. There are still some definite concerns about the precision of the locality data associated with these species. In some cases the distributional ranges were extended by thousands of miles and sometimes by entire continents!

TABLE 1. Faunal Studies in the West Indies.

- General
  - Clench (1964)
  - Comstock and Huntington (1943)
  - Godman and Salvin (1879–1901)
  - Scott (1971)
  - Riley (1975)
  - Walsingham (1897)
- Specific
  - Bahama Islands
    - Clench (1977a, 1977b)
    - Clench and Bjorndahl (1980)
    - Rindge (1955)
    - Simon and Miller (1986)
  - Greater Antilles
    - Alayo and Hernandez (1981)
    - Avinoff and Shoumatoff (1946)
    - Bates (1935)
    - Brown and Heineman (1972)
    - Carpenter, Hale, and Lewis (1943)
    - Comstock (1944)
    - Gundlach (1881)
    - Hall (1925)
    - Holland (1916)
    - Poey (1832)
    - Ramos (1982)
    - Schwartz (1983; 1989)
    - Smith et al. (1988)
    - Torre y Callejas (1954)
    - Wolcott (1927)
  - Lesser Antilles
    - Godman and Salvin (1884; 1896)
    - Hall (1936)
    - Pearce (1969)
    - Pinchon and Enrico (1969)

The major faunal studies in the West Indies have been devoted to the larger islands, especially those of the Greater Antilles (Table 1). These surveys include the works of Gundlach (1881), Poey (1832), Bates (1935) in Cuba, Darlington (1934, 1939) and Schwartz (1983, 1989) in Hispaniola, Comstock (1944), Ramos (1982), and Wolcott (1927) in Puerto Rico, and a long list of collectors and researchers in Jamaica summarized in the invaluable *Jamaica and its Butterflies* by Brown and Heineman (1972). The references in Table 1 are restricted to faunal surveys and do not include individual revisionary treatments. While time does not permit me to discuss the merits of each work in detail, I would like to mention a couple of these and other studies briefly and note some of their major contributions.

W. J. Kaye, an engineer by profession, first visited the West Indies about 1918. While he worked for the British government, especially on Jamaica and Trinidad, his spare time was spent studying the Lepidoptera. Perhaps his favorite tropical genus was *Heliconius* Kluk, but his scientific contributions included comparative analyses between the Greater Antillean and Central American faunas, noting, for example, the absence of mimicry complexes in the Ithomiidae on Jamaica as compared with the genera and families represented in Central and South America. Kaye willingly shared his field notes and observations on endemic taxa with Holland, Bell, and Rothschild, among others. In addition, he described a number of species, including *Thecla burdi* (=*Electrostrymon angerona*), *Leptotes perkinsae*, *Phocides perkinsae*, and *Rhinthon thermae*. He also began to delve into the geographical and geological separation of these islands, noting differences in sea depths long before plate tectonic theory and vicariance biogeography came into the fore. Some of these latter observations were presented in an address to the Royal Entomological Society in 1925 by this learned entomologist who considered himself to be amateur! For more than 40 years, Kaye traveled throughout the Caribbean collecting, and he was an active member of the Royal Entomological Society of London for 63 years.

Another avid lepidopterist interested in the West Indies was Harry Clench, a co-founder of the Lepidopterists' Society. Harry served as an Associate Curator at the Carnegie Museum of Natural History, and was best known for his keen interest in and work on the Lycaenidae, especially the Central American fauna. From about 1967 onward his interests changed somewhat to include the comparative study of the butterfly faunas of Florida and the Bahamas, especially of the islands of Andros and Great and Little Inagua. In 1978, Harry and his wife, Mary, a prominent ornithologist, completed a major faunal survey of many of the Bahamian islands previously or rarely collected, making notes and observations on foodplant associations and perching behavior. Although some of these observations and new taxa were published, a great deal of unpublished knowledge was lost with Harry's untimely death in 1979. However, his legacy lives on in the new discoveries shared and the uncanny enthusiasm that he generated through correspondence with other researchers and collectors, particularly Don Harvey, Al Schwartz, and the Millers, among others.

The Future: Where Do We Go From Here?

Since that momentous discovery of the Western Hemisphere in 1492, man has continued to explore the world and record its natural phenomena. However, in these almost 500 years, how much of this information concerning the fauna and flora has been actually documented and published? Are there some new discoveries and observations to be made on Lepidoptera in the West Indies, the United States, and elsewhere? The fact that this Society meets each year indicates that there is indeed new knowledge and information to be shared. In preparation for the forthcoming volume on the butterflies of the West Indies and southern Florida, we have learned how incomplete our knowledge of the area is. Although Norman D. Riley produced a superlative volume in 1975 (*A Field Guide to the Butterflies of the West Indies*), additional field work, study of collection records, and some limited life history work have expanded our knowledge about the butterfly taxa in the area.

In conducting faunal surveys, we need to continue to pose what appear to be rather ordinary questions. First, what taxa are present and what time of the year are these species observed? Are these derived from or associated with the current continental fauna, or are they part of the endemic fauna of the West Indies? It is generally not difficult to obtain the appropriate identification of endemic taxa to the generic level such as the satyrid, *Calisto* Hüebner, or the hesperiid, *Ephyriades* Hüebner, or with such distinctive species as *Electrostrymon angerona* (Godman & Salvin), *Polites dictynna* (Godman & Salvin), *Wallengrenia ophites* (Mabille), and *Chiodes vintra* Evans. However, exploring the phylogenetic relationships of continental and West Indian taxa can be a stimulating mental exercise, particularly with some Hesperiidae such as *Pyrgus* Hüebner, *Astraptes* Hüebner, and *Rhinthon* Godman. Among the Heterocera, consider the dilemma of the origin of *Ircila hecate* (Herrich-Schaeffer), the only endemic castniid species in the West Indies and recorded from Hispaniola. The wing maculation is similar to the Mexican species, *Athis inca inca* (Walker), but other characteristics closely align this species with the Brazilian genus *Synpalamides* Hüebner. This evidence would appear to indicate that the ancestral stock is relatively old and dates from the late Cretaceous or early Paleocene.

Other questions that should be addressed include: What are the current distributional ranges of these Lepidoptera, and Where are they found (ecological associations)? The literature is replete with broad assumptions about geographic distribution of taxa, and the West Indies presents some rather interesting puzzles on occasion. For example, on Puerto Rico, the lycaenid *Strymon columella cybira* (Hewitson), a distinctive subspecies, occurs; however, just on the offshore on Culebra Island, less than eight miles to the east, the nominate species, *S. c. columella* (Fabricius) is found. Other curious distributional patterns include those of *Hemiargus thomasi* Clench, a species that is widely distributed throughout the West Indies, with nominate *thomasi* Clench on Long Island, and *H. thomasi bahamensis* Clench from Crooked Island, 70 miles to the south. On Mayaguana Island, another subspecies of *H. thomasi* is being described (Miller, Simon & Harvey in press). Finally, on the Virgin Island of Tortola, we find *H. t. watsoni* Comstock & Huntington. What is the evolutionary history of these subspecies? How did these taxa arrive here: was it through dispersal or vicariance or both?

To explain their present distribution, we need to analyze the present and previous distributions of other groups with fossil records in conjunction with the geological evidence. For example, the current geological evidence indicates that the fauna of the southern Bahamian islands is most closely related to the Greater Antilles, and, curiously enough, another subspecies of *H. thomasi, H. t. noeli* Comstock & Huntington, has been described from Hispaniola. The latter has not been recorded from Cuba, Jamaica, or Puerto Rico in the Greater Antilles.

All of the above questions need to be addressed if we are to analyze the biodiversity of an area properly. Obviously, thorough systematic and taxonomic revisions are required to make the appropriate identifications and evaluate phylogenetic relationships. However, this is only a minute portion of the problem. Unfortunately, the Heterocera and a number of other insect orders have been inadequately sampled or totally ignored.

Although Gundlach, Poey, Perkins, Kaye, and Turner have made some considerable contributions to our knowledge of the life histories of West Indian Lepidoptera, there have been few studies **published** since the mid-sixties. Of the above, Lilly Perkins, for whom Kaye named *Phocides perkinsae* and *Leptotes perkinsae,* is an unsung heroine and was an excellent correspondent, researcher, and collector from Jamaica. Like Kaye, she provided information, specimens, and logistical support to a number of collectors and researchers who frequented Jamaica. Perkins' major contribution was the study of immatures and she kept detailed records of their associated larval food plants. Although a number of collectors have subsequently published on the Jamaican fauna, her observations on life histories are the only information available on many species. These descriptions often were documented in her correspondence and published by other authors.

What about the behavior of Lepidoptera in the field? These studies should include a variety of parameters, including observations of flight and mating behavior. In 1844–46, Philip Gosse, the British zoologist, made observations on flight behavior of different lepidopteran species in the West Indies, noting, for example, the crypsis of *Phoebis sennae* in association with yellowish flowers, in addition to the seasonality of

Lepidoptera. These were unparalleled contributions to the general study of the Lepidoptera and are some of the earliest studies published. Likewise Schwartz (1989), in his notable *Butterflies of Hispaniola*, recorded adult behavior and ecological associations of butterflies. Other behavioral observations that are rarely noted but that should be recorded include perching (where does "x" or "y" prefer to perch, its position, and preferred substrate), flight levels (how far above nectar sources does the butterfly normally fly?), and feeding (a record of the identified preferred nectar sources). Other information to record might include the main emergence periods for particular species and the number of broods each year.

How about other discoveries in the West Indies? The age and geological picture of this area, especially of the Greater Antilles and the Bahamian and Virgin Islands, has always been cloaked in mystery and is constantly under review (Pindell & Dewey 1982, Case et al. 1984, Burke et al. 1984). We presented evidence in support of a vicariance/dispersal distribution and origin of the West Indian lepidopteran fauna (Miller & Miller 1989). Recent data confirm that there are proximal Cretaceous-Tertiary boundary impact deposits in the Caribbean to the south of Cuba (Hildebrand & Boynton 1990). Upon reevaluation of the present lepidopteran distributions, this evidence may affect our current concepts of the age and origin of certain Lepidoptera in the West Indies.

Finally, but not least, is conservation. It is absolutely essential that we address as many of the previous questions as possible before we can make the intelligent decisions concerning conservation management and protection of the remaining available habitat and its associated species. With the rapid disappearance of unique habitats, such as tropical rain forests or xeric broadleaf forests, our ability to document the species biodiversity throughout the tropics or in other critical habitats may have been diminished by other economic considerations. However, lepidopterists' concern for the environment and the protection of species is nothing new. Kaye, in a letter dated 13 May 1930, stated his concern for the habitat protection of *Papilio homerus* Fabricius and its possible association with water mahoe, *Hernandia catalpaefolia*, as the potential larval food plant. At that time the government saw no special reason to protect this disappearing habitat. Recently, through the efforts of Tom Turner, John Parnell, the World Wildlife Fund and others, some progress has been made. However, politics and human economic concerns are seemingly more important, and the future of *P. homerus* is uncertain. Again, man's impact on the environment in the West Indies has perhaps altered it forever, and definitely not for the better.

All of these critical questions that I have posed are applicable to other biogeographical areas, and for those of you more interested in

North American fauna, I would direct you to any of the major references, such as Scudder (1875), Holland (1898), Klots (1958), Howe (1975), Opler and Krizek (1984), and Scott (1986), and let you evaluate for yourself as to how incomplete our knowledge about North American butterflies actually is. You may have unknowingly made some significant observations on some these species but never published the information. Documenting what a lepidopteran species does for a living is really a formidable task, and one which is curiously neglected in the literature.

In this brief space, I have summarized an encapsulated history of the study of the West Indian lepidopteran fauna, discussed some of the major workers, and presented some of the areas which require further study. How much knowledge about the lepidopteran fauna or other insect orders have we documented since Columbus' discovery of the Western Hemisphere? The answer comes back resoundingly: *not nearly enough!* There is a lot of work ahead and a number of questions and problems remain to be resolved. The sands of time will wait for no one. The age of discovery in the study of Lepidoptera is now!

Received for publication 7 January 1991; accepted 7 January 1991.

Journal of the Lepidopterists' Society
45(1), 1991, 11–33

SYNOPSIS OF A NEW NEOTROPICAL HAIRSTREAK GENUS, *JANTHECLA*, AND DESCRIPTION OF A NEW SPECIES (LYCAENIDAE)

ROBERT K. ROBBINS
Entomology, NHB Stop 127, Smithsonian Institution, Washington, D.C. 20560

AND

B. ADRIENNE B. VENABLES
Department of Entomology, University of Maryland, College Park, Maryland 20742

ABSTRACT. We describe *Janthecla* Robbins and Venables in the Eumaeini with *Thecla janthina* Hewitson as type, transfer eight additional neotropical species from *Thecla* Fabricius to *Janthecla*, and name a new species, *J. leea* Venables & Robbins. The new species had been misidentified as *T. janthina*, but the two are sympatric in northern Venezuela. We give distribution, habitat, and distinguishing traits for each *Janthecla* species and present an identification key to males. New synonymies are *J. janthina* (Hewitson) = *J. venezuelae* (Lathy) and *J. rocena* (Hewitson) = *J. major* (Lathy); *J. janthodonia* (Dyar) is removed from the synonymy of *J. janthina*. We code 12 characters, from which we infer phylogenetic relationships among *Janthecla* species.

Additional key words: Theclinae, Eumaeini, androconia, cladogram, comparative morphology.

The current taxonomy of *Thecla janthina* Hewitson (Theclinae) is incorrect. Draudt (1921–22) recorded *T. janthina* from Guatemala to Brazil, but individuals from South America east of the Andes belong to an undescribed species that is sympatric with *T. janthina* in northern Venezuela. Similarly, *T. janthina* and *T. janthodonia* Dyar have been considered conspecific (Hoffmann 1940), but are distinct and sympatric. Lastly, *T. venezuelae* Lathy, which was described as a subspecies of *T. janthina*, is a synonym of *T. janthina*.

The original purpose of this paper was to correct the nomenclature for *T. janthina* and to describe the South American species that had been confused with it. However, we could not place the *T. janthina* complex in an existing eumaeine genus—*Thecla* Fabricius belongs to the Theclini, not the Eumaeini (Eliot 1973). In the process of determining those eumaeines that are closely related to *T. janthina*, we discovered enough information to expand upon our original purpose. Thus, in this paper, we (1) describe a new genus, *Janthecla*, for *T. janthina* and relatives, (2) name the new species that had been confused with *T. janthina*, (3) discuss the species that belong to *Janthecla*, with notes on their distribution, morphology (emphasizing androconia), and biology, (4) present an identification key to males, and (5) propose a preliminary cladogram of phylogenetic relationships among these species. A secondary reason for expanding the paper is that it allows us to assess the phylogenetic position of *T. rocena* Hewitson, a species that had been reported to have an aberrant male foreleg (Robbins 1987).

Abbreviations for museum collections are as follows: AME—Allyn Museum of Entomology, Sarasota; AMNH—American Museum of Natural History, New York; BMNH—The Natural History Museum (formerly British Museum), London; CMNH—Carnegie Museum of Natural History, Pittsburgh; MIZA—Instituto de Zoologia Agricola, Maracay; NMNH—National Museum of Natural History, Washington; MUSM—Museo de Historia Natural Universidad Nacional Mayor de San Marcos, Lima; and UFPC—Universidade Federal do Parana, Curitiba. Abbreviations for private collections are: CVC—Charles V. Covell Jr., Louisville, Kentucky, USA; JBS—J. Bolling Sullivan, Beaufort, North Carolina, USA; ROM—Romero family, Maracay, Venezuela.

Janthecla Robbins & Venables, new genus

Type species. *Thecla janthina* Hewitson 1867.

Systematic placement. *Janthecla* belongs to the Eumaeini (Lycaenidae: Theclinae) as characterized by Eliot (1973). It has ten forewing veins (Fig. 22), hairy eyes, a stubby-tipped male foreleg tarsus (Fig. 21), and "greyhound-shaped" male genitalia lacking a juxta (Figs. 23–26). The closest relatives of *Janthecla* within the Eumaeini are unknown. We discuss interspecific morphological variation in the Comparative Morphology section below.

Unique character state. The cervix of the female genitalia characterizes *Janthecla*. Attachment of the corpus bursae to the ductus bursae is more posterior ventrally than dorsally (Figs. 27–29). However, in *J. malvina* the anterior ductus bursae is sharply curved so that the points of attachment are ventral and dorsal (Fig. 28), rather than posterior and anterior. This cervical morphology has not been reported previously in the Eumaeini and appears to be unique.

Field identification. A conspicuous submarginal green spot in ventral hindwing cell Cu2-2A (Figs. 2, 4, 8, 9) coupled with either two ventral forewing white lines or a single disjoint white line distinguish *Janthecla* from all other eumaeines. Because the genus contains two ventral wing patterns, that typified by *J. leea* (Figs. 2, 4) and that of *J. rocena* (Figs. 8, 9), learning these two patterns is an easy means of field identification.

Specific identification. Most *Janthecla* species are not easy to identify. Males are distinguished by presence or absence of a dorsal forewing scent patch, and when present, its shape and placement. For this reason, we emphasize description and illustration (Figs. 12–20) of these patches. Other useful distinguishing characters are presented in the identification key. Although we examined antennae, labial palps, wing patterns, and abdomens, including genitalia, we cannot distinguish females of some sympatric species.

Biology. *Janthecla* species occur most often in wet (> 200 cm annual precipitation) lowland forests (they are uncommon above 1000 m) except that *J. flosculus* apparently is not found in the lowlands. Males of *J. rocena* are territorial in the mid-afternoon. No larval foodplants are recorded for the genus.

Etymology. *Janthecla* is an arbitrary combination of "*janthina*" and "*Thecla*." Its gender is feminine.

Key to Males

1. With a red spot at base of the ventral hindwing (Figs. 8, 9) .... *J. rocena*
– Without a red spot at base of the ventral hindwing 2

2. Dorsal forewing without androconia 3
– Dorsal forewing with androconia 4
3. Forewing costa tan .... *J. janthodonia*
– Forewing costa white .... *J. leea*
4. Dorsal forewing cell Cu2-2A black, without iridescent blue scales (Fig. 18) .... *J. cydonia*
– Dorsal forewing cell Cu2-2A with black and iridescent blue scales 5
5. With a small "v-shaped" scent patch along the bases of dorsal forewing veins M1 and Cu1 (Fig. 16) .... *J. janthina*
– Without a small "v-shaped" scent patch along the bases of dorsal forewing veins M1 and Cu1 6
6. Dorsal forewing scent patch does not cover vein ldc (Fig. 12) .... *J. malvina*
– Dorsal forewing scent patch does cover vein ldc (Figs. 13–15, 20) 7
7. Dorsal forewing scent patch small (<3 mm across) (Figs. 13, 20) 8
– Dorsal forewing scent patch large (>3 mm across) (Figs. 14, 15) 9
8. Dorsal forewing scent patch centered on base of wing cell M3-Cu1 (Fig. 20) .... *J. armilla*
– Dorsal forewing scent patch centered on veins mdc and ldc (Fig. 13) .... *J. flosculus*
9. Ventral cornutus wide (>0.16 mm). Coastal Brazil from Bahia to Santa Catarina and Misiones, Argentina .... *J. aurora*
– Ventral cornutus narrow (<0.16 mm). Guianas, Orinoco and Amazon Basins .... *J. sista*

Note: The forewing of *J. sista* is more falcate than that of *J. aurora* (see Comparative Morphology section), its scent pad is usually larger, and its apical border is wider on average, but width of the ventral cornutus is the most definitive character for separating these two species.

SYNOPSIS OF SPECIES

We use Comstock and Huntington (1959–64) and Bridges (1988) as nomenclatural references. They contain citations to original descriptions. Synonymies and combinations not noted in these works are designated as new.

1. *Janthecla rocena* (Hewitson 1867), new combination
(Figs. 5, 8, 9, 21, 23, 27)

= *Janthecla major* (Lathy 1926). **NEW SYNONYMY**

Male forewing length: 17.2 mm (s = 1.44, n = 89). **Distribution** (Fig. 5): Mexico (Chiapas) to southern Brazil (Parana), but not recorded from coastal Brazil. The type locality is the Amazon. **Habitat:** Wet lowlands to 1100 m. **Biology:** Robbins (unpubl.) observed territorial males landing 2–3 m high in a sunlit area along a trail through late secondary forest on Barro Colorado Island (Canal Area, Panama) on 24 and 25 July 1977 at 1430–1530 hours. **Geographical variation:** Three specimens from the southern extreme of the range (Parana, Brazil) differ from the others. Their dorsal wing borders are narrower. The ventral forewing submarginal white line, which is absent in other specimens of *J. rocena* is represented by a few spots (Figs. 8, 9). Since there are not enough specimens from intermediate areas with which to assess geographical variation, we cannot rule out the possibility that the Parana specimens represent a distinct species. Their genitalia, however, are indistinguishable from those of *J. rocena* elsewhere. **Identification:** Both sexes are distinguished by the red spot at the base of the ventral hindwing. **Androconia:** A cluster of black androconia occurs along the inner margin of the ventral forewing (Fig. 8). **Nomenclature:** Lathy (1926) differentiated *Thecla major* (type locality: Muzo, Co-

FIGS. 1–4. *Janthecla leea*. **1,** Upperside male (Peru). **2,** Underside male. **3,** Upperside female (Venezuela). **4,** Underside female.

lumbia) from *T. rocena* by wing pattern characters (size, extent of dorsal blue, underside color and markings) that vary similarly in all populations. **Other illustrations:** Adults (De La Maza 1987 as "*Thecla*" *minyia*), legs (Fig. 21), and genitalia (Figs. 23, 27). **Material examined:** 52 males and 4 females.

FIG. 5. Distribution of *J. rocena* (circles) and *J. malvina* (triangles).

2. *Janthecla malvina* (Hewitson 1867), new combination (Figs. 5, 12, 24, 28)

Male forewing length: 15.2 mm (s = 1.04, n = 8). **Distribution** (Fig. 5): Guianas, Amazon Basin, and coastal Brazil. The type locality is Rio de Janeiro, Brazil. **Habitat:** Lowlands to 700 m. **Identification:** Both sexes can be distinguished from other *Janthecla* by their more inclined postmedian line on the ventral forewing. This species and *J. armilla* are the rarest *Janthecla* species in collections. **Androconia:** A somewhat oval cluster of gray-brown androconia occurs at the upper end of the dorsal forewing discal

FIG. 6. Distribution of *J. janthodonia* (circles), *J. cydonia* (solid triangles), *J. leea* (squares), and *J. armilla* (hollow triangles).

cell (Fig. 12). **Other illustrations:** Adults (Lewis 1973 as *Thecla malvina*) and genitalia (Figs. 24, 28). **Material examined:** 13 males and 5 females.

3. *Janthecla janthodonia* (Dyar 1918), new combination
(Figs. 6, 17)

Male forewing length: 15.3 mm (s = 0.47, n = 8). **Distribution** (Fig. 6): Mexico (San Luis Potosi, Veracruz, Tabasco, Chiapas) and eastern Guatemala (Izabal). The type locality is Santa Rosa, Veracruz, Mexico. **Habitat:** Lowland forest. **Identification:** Hoffmann (1940) treated this taxon as a subspecies of *J. janthina,* but it differs by its lack of androconia, narrower ventral cornutus, lack of white scales on the forewing costal margin, lack of iridescent blue in the dorsal forewing discal cell, and darker dorsal forewing blue color. **Possible hybrid:** There is a Mexican male (Veracruz, Presidio) from the Hoffmann collection (AMNH) that we believe to be a hybrid between *J. janthodonia* and *J. janthina* and that may account for Hoffmann's failure to recognize these two taxa as distinct. This specimen has the dorsal blue color and ventral cornutus of *J. janthina,* but lacks white scales on the forewing costal margin, as in *J. janthodonia.* The part of the forewing discal cell that is blue in *J. janthina* and black in *J. janthodonia* is a mixture of blue and black scales. Where *J. janthina* has a scent patch, there are black scales shaped like regular wing scales, not reduced in size like the androconia of *J. janthina.* **Androconia:** None (Fig. 17). **Nomenclature:** Comstock and Huntington (1959–64) incorrectly gave 1919 as the date of publication. **Material examined:** 17 males and 5 females.

4. *Janthecla cydonia* (Druce 1890), new combination
(Figs. 6, 18)

Male forewing length: 15.0 mm (s = 1.03, n = 8). **Distribution** (Fig. 6): Costa Rica to northern Colombia (Magdalena) and western Ecuador (Pichincha). The type locality is the interior of Colombia. **Habitat:** Wet forest from sea level to about 700 m. **Identification:** Males are immediately recognizable by their almost all black dorsal forewings, but we cannot distinguish females from those of sympatric *J. janthina.* **Androconia:** A narrow band of iridescent gray or blue (depending upon the angle at which they are viewed) androconia occurs at the end of the dorsal forewing discal cell over veins mdc and ldc (Fig. 18). **Material examined:** 31 males. Also, 15 females that may be this species.

5. *Janthecla leea* Venables & Robbins, new species
(Figs. 1–4, 6, 19, 22, 26, 29)

Male forewing length: 14.4 mm (s = 0.56, n = 8). **Distribution** (Fig. 6): Northern Venezuela, the Guianas, and the Amazon Basin. **Habitat:** Wet forest to 1100 m. **Identification and distinguishing characters:** *Janthecla leea* has been misidentified as *J. janthina* (Draudt 1921–22). Male *J. janthina* have a scent patch at the base of dorsal forewing veins M3 and Cu1 whereas male *J. leea* lack androconia (Figs. 16, 19). Where *J. janthina* and *J. leea* are sympatric in Henry Pittier National Park (Aragua, Venezuela), the hindwings of both sexes of *J. janthina* have translucent patches that are lacking in *J. leea* (Figs. 1, 3, 11). The lack of androconia differentiates male *J. leea* from other *Janthecla* species except *J. janthodonia,* whose forewing costa lacks white scales. Also, the ventral cornutus of *J. leea* is significantly wider (Table 3) than that of *J. janthodonia* ($t = 3.910$, df = 14, $P < 0.01$). We cannot distinguish females of *J. leea* from those of sympatric *J. sista.* **Androconia:** None (Fig. 19). **Other illustrations:** Adults (Figs. 1–4), wing venation (Fig. 22), and genitalia (Figs. 26, 29).

Holotype. The holotype is a male labelled "PERU, 20 km SW Pto. Maldonado, 25 Oct. '83, S. S. Nicolay." We added a red label—"Holotype, *Janthecla leea* Venables and Robbins." The specimen is in excellent condition except that the left antenna is broken. It is deposited in NMNH. The locality is about 10 km from the Tambopata Reserve and is called Infierno by the local inhabitants.

Paratypes. We designate 48 male and 2 female paratypes and have labelled all except for 4 individuals for which we mailed the paratype labels, as noted. We cannot distinguish females of *J. leea* from those of *J. sista,* but can from females of *J. janthina* (as noted above) and thus recognize only two female paratypes from northern Venezuela, where *J. sista* does not occur. VENEZUELA: Aragua, Rancho Grande 1 ♂, 1 ♀ (NMNH), 1 ♂, 1 ♀ (MIZA, paratype labels sent), 2 ♂ (ROM, Maracay, paratype labels sent), 1 ♂ (JBS). GUYANA: Potaro River 1 ♂ (AME). FRENCH GUIANA: St. Jean, Maroni 2 ♂ (NMNH). COLOMBIA: Meta, Rio Ariari 1 ♂ (NMNH), Villavicencio 1 ♂ (AME); Vaupes, Mitu 1 ♂ (NMNH); Amazonas, Leticia 1 ♂ (NMNH). ECUADOR: Rio Napo, Limoncocha 1 ♂ (NMNH); Napo, Puerto Napo 1 ♂ (CVC), Napo, Rio Tiputine 1 ♂ (JBS). PERU: Madre

FIG. 7. Distribution of *J. janthina* (hollow triangles), *J. sista* (squares), *J. aurora* (solid triangles), and *J. flosculus* (circles).

de Dios, 30 km SW Pto. Maldonado = Boca Rio La Torre = Tambopata 3 ♂, 4 ♂ (MUSM), 2 ♂ (CVC); Huanuco, Tingo Maria 1 ♂ (NMNH); Loreto, Yanamono, 80 km E Iquitos 1 ♂ (MUSM), Iquitos 1 ♂ (AME); San Martin, Bonilla, Km 75 Tarapoto-Yurimaguas 1 ♂ (MUSM). BOLIVIA: Cochabamba, Chapare 1 ♂ (NMNH); Santa Cruz, 17°46–55′S Lat. 63°5–34′ Long. 2 ♂ (NMNH), Buena Vista 1 ♂ (CMNH), Rio Surutu 1 ♂ (CMNH). BRAZIL: Para, Belem 1 ♂ (AME), Obidos 1 ♂ (AME); Amazonas, 75–85 km N Manaus 1 ♂ (UFPC), Dist. Agr. da Suframa 1 ♂ (JBS), Manaus 2 ♂ (AME), Mancapuru 13 ♂ (CMNH), S. Paulo de Olivenca 1 ♂ (NMNH); Rondonia, Ariquemas 2 ♂ (NMNH); Mato Grosso, Diamantino, Alto Rio Arinos 1 ♂ (NMNH), 1 ♂ (UFPC); Goias, Tower, 10 km N Goiania 1 ♂ (NMNH).

Etymology. In Middle English, "lee" means "a calm and sheltered place." It is also the first name of Lee Venables, an avid entomologist who has provided support during this project. We consider "leea" to be an indeclinable, non-latinized name.

6. *Janthecla armilla* (Druce 1907), new combination
(Figs. 6, 20)

Male forewing length: 14.4 mm (s = 1.17, n = 8). **Distribution** (Fig. 6): Coastal Brazil from Minas Gerais and Espirito Santo to Santa Catarina. The type locality is Rio de Janeiro, Brazil. **Habitat:** Lowlands. **Identification:** We cannot distinguish females of *J. armilla* from those of *J. aurora*, but males can be separated by the wider dorsal forewing border of *J. armilla* as well as by the smaller scent patch. **Androconia:** Iridescent scales are mostly covered by regular blue wing scales, such that the scent patch appears to change when viewed at different angles. The androconia cover dorsal forewing vein ldc and the basal end of cell M3-Cu1 (Fig. 20). **Material examined:** 9 males. Also, 7 females that may be this species.

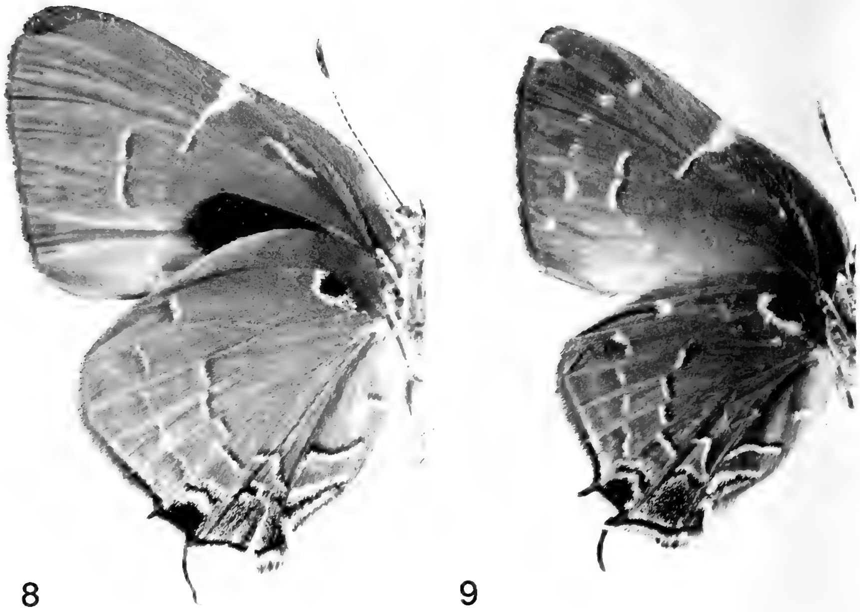
7. *Janthecla janthina* (Hewitson 1867), new combination
(Figs. 7, 10, 11, 16, 21, 25)

= *Janthecla venezuelae* (Lathy 1930). **NEW SYNONYMY**

Male forewing length: 15.1 mm (s = 1.25, n = 8). **Distribution** (Fig. 7): Mexico (Veracruz) to western Ecuador (Pichincha) and east to northern Venezuela (Aragua). The type locality is Vera Paz, Guatemala. **Habitat:** Wet forest from sea level to 1250 m. In Panama, individuals fly in small clearings and edges of late secondary forest, often in the shade. **Geographical variation:** Scale density in the basal half of the hindwing is lower—so that the hindwing appears translucent—in both sexes from northern Venezuela than in those from Central America (Figs. 10, 11), but individuals from northern and western Colombia (Santander, Caldas, Valle, Choco) are phenotypically intermediate, as noted by Lathy (1930), indicating that this variation is clinal. **Identification:** Both sexes have white scales on the forewing costal margin whereas these white scales are lacking in *J. janthodonia*. Where *J. janthina* and *J. leea* overlap in northern Venezuela, both sexes can be distinguished by the translucent patch at the base of the hindwing in *J. janthina*. We cannot distinguish females of *J. janthina* and *J. cydonia*. **Androconia:** The scent patch is composed of small iridescent scales, similar to those in *J. armilla*, but restricted to the base of dorsal forewing veins M3 and Cu1 (Fig. 16). **Nomenclature:** The type series of Lathy's (1930) *Thecla venezuelae* includes several Venezuelan specimens in the BMNH, "others" in the NMNH (actually one Venezuelan specimen), and a male in the Fournier Collection in Paris of unknown locality. This taxon represents the translucent phenotype. Since it is a clinal geographical form of *J. janthina*, as noted by Lathy, it is a synonym. **Other illustrations:** Legs (Fig. 21) and genitalia (Fig. 25). **Material examined:** 54 males and 3 females. Also, 15 females that may be this species.

8. *Janthecla sista* (Hewitson 1867), new combination
(Figs. 7, 14)

Male forewing length: 13.5 mm (s = 0.67, n = 8). **Distribution** (Fig. 7): Guianas, eastern Venezuela, and Amazon Basin. The type locality is the Amazon (mistakenly listed as Mexico in Bridges 1988). **Habitat:** Wet forest from sea level to about 1000 m (eastern slope of the Andes). **Identification:** Generally the most common *Janthecla* species where it occurs. We are unable to distinguish females of *J. sista* from sympatric females of *J. leea*. **Androconia:** The scent patch is complex. There is a large patch of brown or gray scales covering the distal half of the dorsal forewing discal cell and the area beyond the

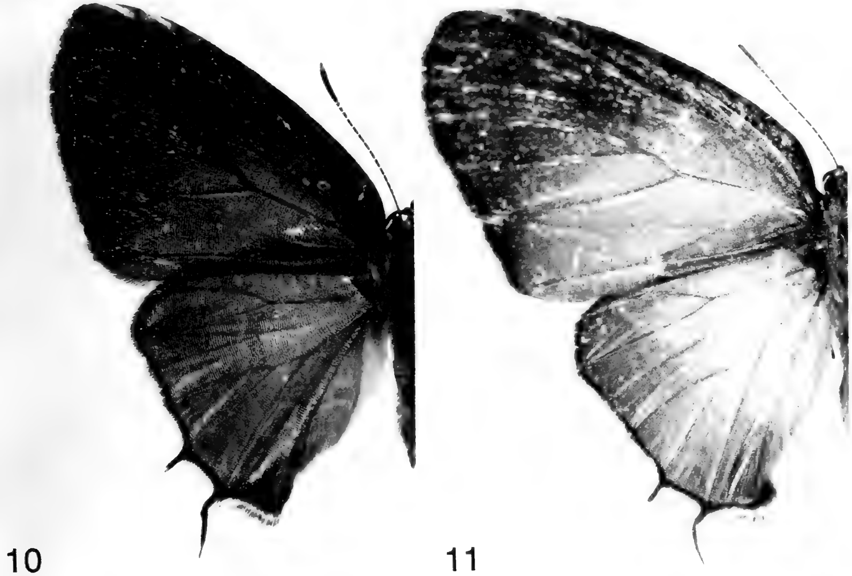


FIGS. 8, 9. Underside of *J. rocena* showing geographical variation in presence of forewing submarginal row of white dots. **8,** Male from Panama without white dots. **9,** Female from Brazil (Parana) with white dots.

discal cell to the wing border. The wing veins in this patch are covered with small iridescent gray-blue-green scales, similar to those in *J. janthina* (Fig. 14). **Material examined:** 164 males. Also, 22 females that may be this species.

9. *Janthecla aurora* (Druce 1907), new combination (Figs. 7, 15)

Male forewing length: 14.3 mm (s = 0.95, n = 8). **Distribution** (Fig. 7): Coastal Brazil (Bahia to Santa Catarina and Rio Grande do Sul—Druce 1907), west to Argentina (Misiones). The type localities are Espiritu [sic] Santo and Rio Grande, Brazil. **Habitat:** Lowland forest up to 800 m. **Geographical variation:** The dorsal forewing scent patch of males is separated from the distal black border by blue scaling in specimens from Santa Catarina (Brazil), but this trait is variable in individuals from Bahia, Minas Gerais, and Espirito Santo. The extent of white scales on the forewing costa is often reduced in specimens from Rio de Janeiro and south. **Identification:** We are unable to distinguish females of *J. aurora* from sympatric females of *J. armilla*. **Androconia:** The scent patch is the same as in *J. sista* except slightly smaller (Fig. 15). **Material examined:** 37 males. Also, 7 females that may be this species.



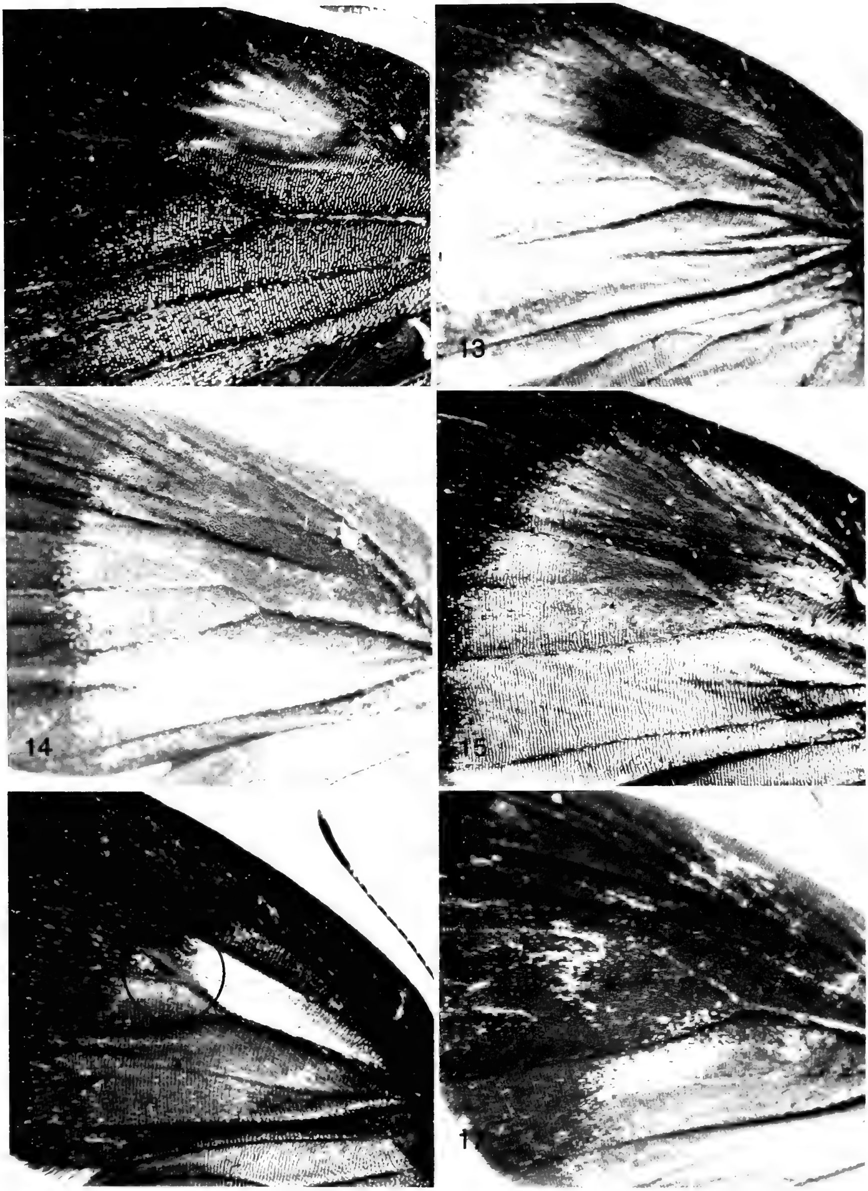
FIGS. 10, 11. Upperside of *J. janthina* showing geographical variation. **10,** Male from Panama. **11,** Male from northern Colombia (Victoria, Caldas) with translucent patches.

10. *Janthecla flosculus* (Druce 1907), new combination
(Figs. 7, 13)

Male forewing length: 14.1 mm (s = 0.70, n = 8). **Distribution** (Fig. 7): Espirito Santo to Santa Catarina (Brazil). The type locality is Espiritu [sic] Santo, Brazil. **Habitat:** Coastal mountains, usually above 500 m, possibly restricted to moist forests. It is not known from lowlands and does not appear to be sympatric with *J. aurora*. **Identification:** Both sexes are distinguished from *J. aurora* and *J. armilla* by a lack of white scales on the forewing costal margin. **Androconia:** A cluster of small iridescent gray-green scales covering the distal end of the dorsal forewing discal cell and extending beyond the discal cell between veins R3 and M3 (Fig. 13). **Material examined:** 12 males and 3 females.

COMPARATIVE MORPHOLOGY

We describe and code characters in *Janthecla* and summarize character state distributions in Table 1. We use a dash to indicate situations in which information is lacking. The remainder of the Eumaeini is our outgroup because we have not been able to narrow the outgroup to a portion of the tribe. For characters in which each of the states occurs in other eumaeines, we code the outgroup with a dash and usually list two representative eumaeine taxa with each state.



FIGS. 12–17. Upperside male forewing showing androconial cluster (circled). **12,** *J. malvina.* **13,** *J. flosculus.* **14,** *J. sista.* **15,** *J. aurora.* **16,** *J. janthina.* **17,** *J. janthodonia.*

FIGS. 18–20. Upperside male forewing showing androconial cluster (circled). **18,** *J. cydonia*. **19,** *J. leea*. **20,** *J. armilla*.

TABLE 1. Data matrix for *Janthecla*. Characters and their states are discussed in text. A dash means that information is missing or ambiguous.

Taxon	Characters											
	1	2	3	4	5	6	7	8	9	10	11	12
J. rocena	1	1	2	0	0	0	1	0	0	—	1	0
J. malvina	0	0	2	1	1	1	1	1	1	—	1	1
J. janthodonia	0	0	3	1	1	1	0	0	2	0	1	1
J. cydonia	0	0	3	1	1	1	0	0	2	1	1	1
J. leea	0	0	3	1	1	1	0	0	2	1	1	1
J. armilla	0	0	1	1	1	1	0	0	2	1	1	1
J. janthina	0	0	3	1	1	1	0	0	2	1	1	1
J. sista	0	0	2	1	1	1	0	0	2	1	1	1
J. aurora	0	0	1	1	1	1	0	0	2	2	1	1
J. flosculus	0	0	0	1	1	1	0	0	2	2	1	1
Other Eumaeini	0	0	—	—	—	0	—	0	—	—	0	0

Antennae. The antennae of *Janthecla* are comprised of 29–36 segments. The nudum occurs on the last 12–16 segments and is confined to the club in both sexes. There is little interspecific variation except that the average number of segments in *J. rocena* is about 2 more than the other species.

Legs. The unusual male foreleg of *J. rocena* differs from other lycaenids (Robbins 1988) (Fig. 21). The coxa and femur are elongated while the tibia is shortened. The distal femur is bulbous, and the inner surface of it and the tibia have a scale brush (not evident in the figure). The scale brush may be rubbed against the ventral forewing androconia and used during courtship.

Character 1. Length of male foreleg femur (0) shorter than length of tibia plus tarsus (Fig. 21), (1) longer than length of tibia plus tarsus (Fig. 21). Comment: Among the Eumaeini, character state 1 is restricted to *J. rocena*.

Character 2. Male foreleg femur (0) without a scale brush, (1) with a scale brush. Comment: Although some pierids have a scale brush on the foreleg tibia (Robbins 1990), the brush on the foreleg femur in *J. rocena* is unique among the Papilionoidea.

Wing venation, shape, and pattern. The wing venation of *J. leea* (Fig. 22) is typical of the genus. However, male forewing shape varies markedly in the degree to which the apex is produced, and we quantified this variation. All species except *J. rocena* share the same ventral wing pattern. Whether the forewing costa is white or tan varies within the genus, but we did not code it because it is geographically variable within *J. aurora*.

Character 3. Ratio of the length of male forewing vein 2A divided by length from the base of vein 2A to the forewing apex (0) >0.827, (1) <0.827 and >0.803, (2) <0.803 and >0.759, (3) <0.759 (see Table 2 for means and standard deviations). Comment: We measured these distances under a microscope at 15× using a digitizing

FIG. 21. Male forelegs of *J. rocena* (right) and *J. janthina* from Panama. The tarsus is at bottom and coxa at top.

pad and calculated a *t*-statistic between pairs of means on arcsine transformed ratios (Sokal & Rohlf 1969). We then assigned means to different character states (Table 2) if the distance between them was "significant" at the 0.05 level using a 2-tailed *t*-test. Because we chose pairs a posteriori, this gap criterion does not mean that the differences were significant in the usual statistical sense. Rather, we simply used this difference as a gap criterion. Farris (1990) is a recent reference that provides citations to the literature on coding continuously varying characters. Among other eumaeines, male forewing shape varies from *Pseudolycaena* Wallengren, with falcate wings, to *Trichonis* Hewitson, with almost rectangular wings (Robbins 1987).

Character 4. Base of ventral hindwing (0) with a red spot (Figs. 8, 9), (1) with no red scales (Figs. 2, 4). Comment: Character state (0) occurs in eumaeines such as *Atlides inachus* (Cramer) and *Olynthus narbal* (Stoll) (Nicolay 1982) and state (1) in *Arcas imperialis* (Cramer) (Nicolay 1971b) and *Symbiopsis lenitas* (Druce) (Nicolay 1971a).

Androconia. Robbins (1991) differentiated scent pads (androconia underlain by a chamber between the wing membranes, see Thomas 1893 for histology) from scent patches, which lack the chamber. We dissected the wings of *J. janthina* and *J. sista*, and their androconial clusters are scent patches. As noted under the species accounts, all but

TABLE 2. Ratio of length from forewing apex to base of vein 2A divided by length from base of vein 2A to terminus of vein 2A (Character 3). The gap criterion (see text) is exceeded between *J. flosculus* and *J. aurora* ($t = 2.258$, df = 14), between *J. armilla* and *J. malvina* ($t = 2.872$, df = 14), and between *J. rocena* and *J. leea* ($t = 2.530$, df = 14).

Taxon	Mean	SD	N	State
J. flosculus	0.852	0.0166	8	0
J. aurora	0.822	0.0334	8	1
J. armilla	0.817	0.0173	8	1
J. malvina	0.789	0.0222	8	2
J. sista	0.780	0.0155	8	2
J. rocena	0.768	0.0166	8	2
J. leea	0.752	0.0072	8	3
J. janthodonia	0.749	0.0202	8	3
J. janthina	0.745	0.0260	8	3
J. cydonia	0.732	0.0114	8	3

three *Janthecla* species have an androconial cluster on the dorsal forewing, but it differs in each species (except *J. sista* and *J. aurora*), and there is no unambiguous way to code it. As a result, we code only presence or absence of a ventral forewing scent patch.

Character 5. Ventral forewing (0) with black androconia (Fig. 8), (1) without black androconia (Fig. 2). Comment: Character state (0) occurs in eumaeines such as "*Thecla*" *falerina* Hewitson and *Arawacus leucogyna* (Felder & Felder) and state (1) in *Parrhasius m-album* (Boisduval & LeConte) and *Michaelus hecate* (Godman & Salvin) (Nicolay 1979).

Male genitalia. *Janthecla* species, except for *J. rocena* and *J. malvina,* had nearly identical male genitalia. Because cornuti seemed to vary interspecifically, we everted the vesica at the penis tip. Although the position of the cornuti on the everted vesica was invariant in *Janthecla,* it facilitated measurement of the ventral cornutus and may help solve homology problems among other eumaeines in the future.

Character 6. Ventro-lateral edge of tegumen with (0) no processes (Fig. 23), (1) with horizontal processes that lie above the valves (Figs. 24–26). Comment: The size and shape of the ventro-lateral processes vary greatly (Figs. 24–26), but most of this variation is intraspecific. Although many eumaeines have ventro-lateral processes of the tegumen that lie under the valves, such as *Pseudolycaena* (Clench 1964) and *Arcas* Swainson (Nicolay 1971b), the dorsal position of the processes in *Janthecla* is shared only with "*Thecla*" *eronos* Druce and "*T.*" *aepea* Hewitson. These two species have nearly identical genitalia, and their processes are rectangular and massive in contrast to the delicate, triangular ones in *Janthecla*. The "*T.*" *eronos* group shares no other character state with *Janthecla,* indicating a lack of close relationship with *Janthecla,* but appears to be a close relative of *Micandra* Schatz (Robbins 1987). On the basis of this evidence, we conclude that similarity in position of the processes in this group and in *Janthecla* is convergent.

Character 7. Elbow of gnathos (0) with a keel-shaped ridge (not illustrated), (1) without a keel-shaped ridge. Comment: Examples of state (0) among other eumaeines

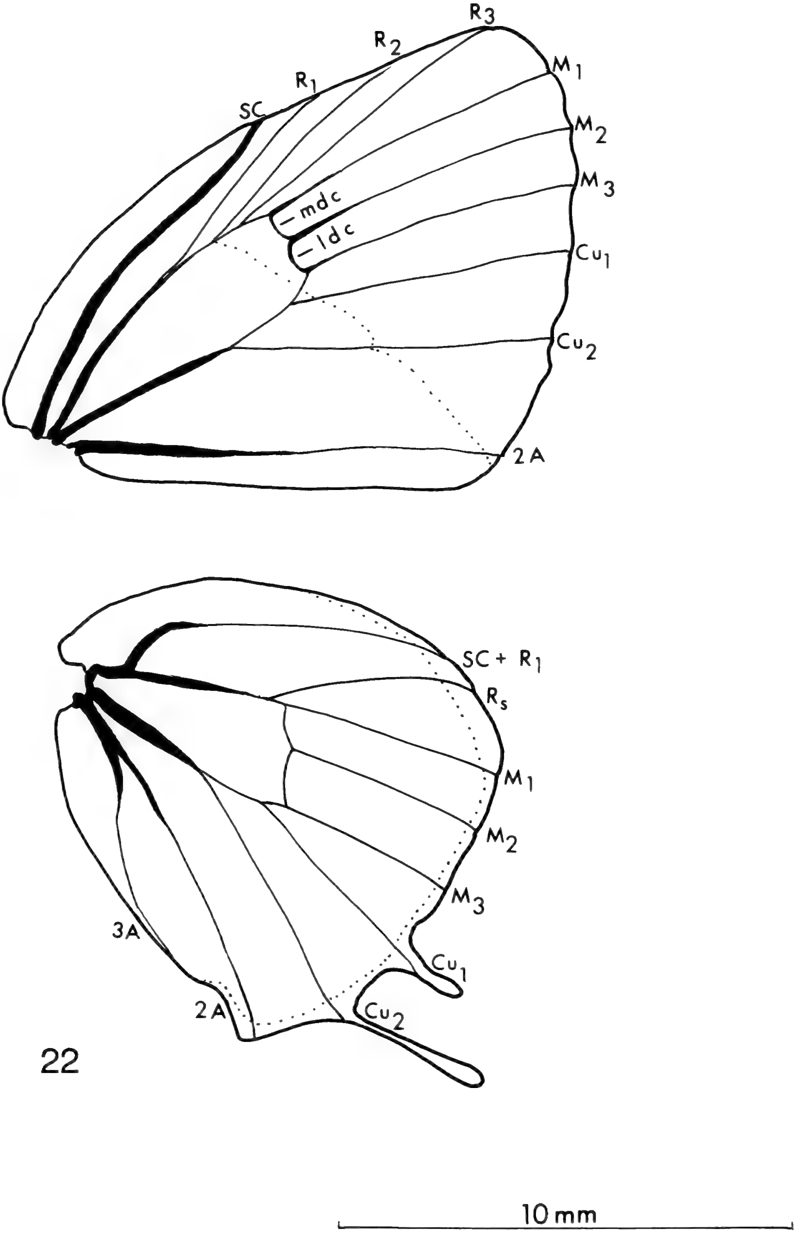


FIG. 22. Wing venation of *J. leea* with wing veins labelled.

TABLE 3. Width in mm of ventral cornutus (Character 10). The gap criterion (see text) is exceeded between *J. janthodonia* and *J. cydonia* ($t = 2.459$, df = 13) and between *J. sista* and *J. flosculus* ($t = 6.857$, df = 14).

Taxon	Mean	SD	N	State
J. janthodonia	0.050	0.0153	8	0
J. cydonia	0.067	0.0111	7	1
J. armilla	0.077	0.0157	8	1
J. leea	0.084	0.0191	8	1
J. janthina	0.091	0.0112	8	1
J. sista	0.101	0.0101	8	1
J. flosculus	0.215	0.0457	8	2
J. aurora	0.236	0.0270	8	2

are genera *Eumaeus* (Clench 1961) and *Symbiopsis* (Nicolay 1971a) and of state (1) are genera *Arcas* (Nicolay 1971b) and *Magnastigma* (Nicolay 1977).

Character 8. Setae on valves (0) extend continuously to valve tips (Figs. 23, 25, 26), (1) occur at the valve tips and on the middle of the ventro-lateral surface of the valves, but not in between (Fig. 24). Comment: State (1) occurs in no other eumaeines.

Character 9. Ventral cornutus (0) absent (Fig. 23), (1) shaped like an arrowhead (Fig. 24), (2) shaped like a tongue-depressor—the sides of the cornutus are parallel (Figs. 25, 26). Comment: Most eumaeines have 0–2 cornuti, but homology is unclear except among closely related species. Position of cornuti after being everted may be one solution to this problem.

Character 10. Average width of the ventral cornutus (0) <0.06 mm, (1) >0.06 mm and <0.16 mm, (2) >0.16 mm (Table 3). Comment: The ventral cornutus has small teeth at its ventro-distal end, and we measured width, after everting the vesica, just anterior to the teeth using a binocular microscope at 125×, a drawing tube, and a digitizing pad. We coded *J. rocena* and *J. malvina* with a dash because the former lacks this cornutus and the latter has a cornutus differently shaped than the other species. Our gap criterion for recognizing different character states was significance at the 0.05 level using a two-tailed t-test, but as noted for Character 3, this coding does not mean that the differences were statistically significant.

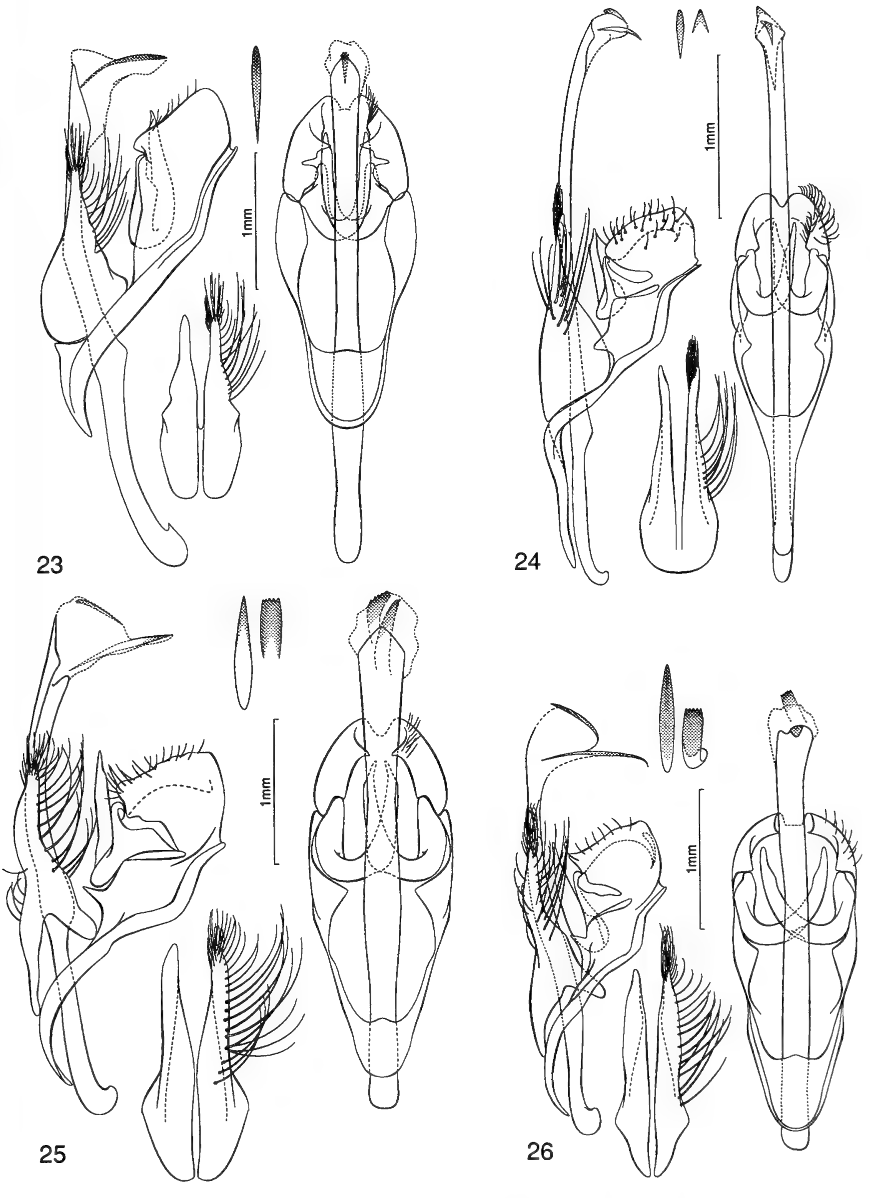
Female genitalia. As noted in the species accounts, we cannot distinguish females of some species.

Character 11. Ventral surfaces of the corpus bursae (0) directly below the dorsal surface attachment to the ductus bursae, (1) 0.25 mm or more posterior than the dorsal surface attachment to the ductus bursae (Figs. 27–29). Comment: Character state 1 characterizes *Janthecla,* although as noted, the ductus bursae of *J. malvina* curves sharply so that the points of attachment are ventral and dorsal, not posterior and anterior (Fig. 28).

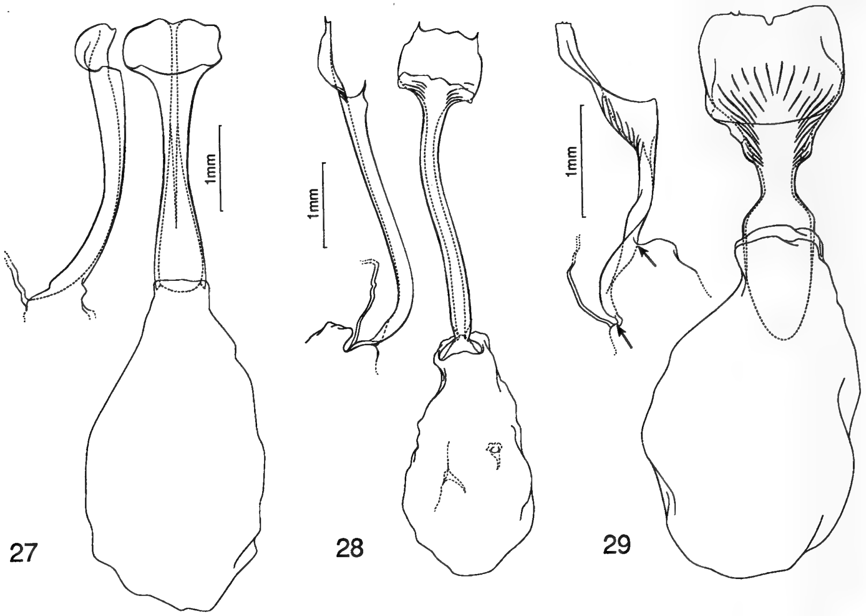
Character 12. Anterior lamella postvaginalis (0) without dorsal and ventral longitudinal striations (Fig. 27), (1) with dorsal and ventral longitudinal striations (Figs. 28, 29). Comment: Character state 1, which occurs in all *Janthecla* species other than *J. rocena,* appears to be unique among Eumaeini.

DISCUSSION

We derived a most parsimonious cladogram for *Janthecla* species (Fig. 30) using Hennig86 phylogenetic software (Farris 1988), but had



FIGS. 23–26. Lateral, ventral (valves separate), and posterior (of cornuti) aspects of male genitalia. **23,** *J. rocena.* **24,** *J. malvina.* **25,** *J. janthina.* **26,** *J. leea.*



FIGS. 27–29. Lateral and ventral aspects of female genitalia. **27,** *J. rocena*. **28,** *J. malvina*. **29,** *J. leea*. The arrow on the top of the lateral view shows where the ventral surface of the corpus bursae attaches to the ductus bursae whereas the one on the bottom shows where the dorsal surface of the corpus bursae attaches to the ductus bursae.

little success resolving relationships. Although no characters are homoplastic, there is a trichotomy and a quadrichotomy, and most nodes are supported by only one or two character state changes. Character numbers are indicated on the cladogram where changes in character state took place. Although these changes could be assigned in different, equally parsimonious ways, they support the same tree topology. *Janthecla janthodonia, J. cydonia, J. leea, J. armilla, J. janthina, J. sista, J. aurora,* and *J. flosculus* are morphologically very similar species, and we found few informative characters among them.

At the outset of this study, on the basis of geographical distributions (Figs. 6, 7), we hypothesized that *J. janthodonia, J. cydonia, J. leea,* and *J. armilla* formed a superspecies (a monophyletic group of non-overlapping species) and that *J. janthina, J. sista, J. aurora,* and *J. flosculus* were a second superspecies. Although none of the species comprising either proposed superspecies are sympatric, the cladogram is inconsistent with our hypothesis.

Structure of the male foreleg has been used in the higher classification of the Eumaeini (Eliot 1973). Because the unusual male foreleg of *J.*

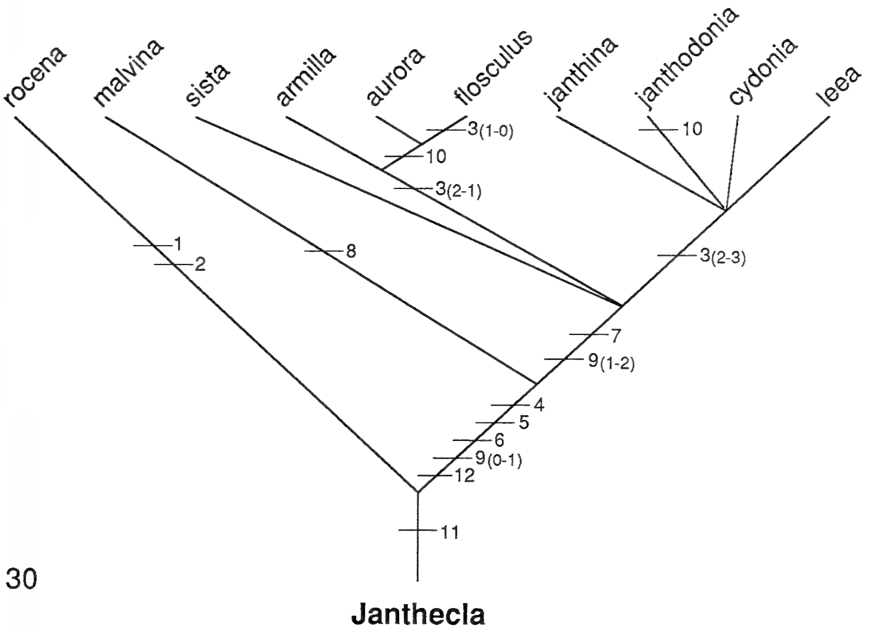


FIG. 30. Phylogeny of *Janthecla* species. Numbers designate where changes in character state occurred, as described in the text. For multi-state characters, the transformed states are added in parentheses: for example 3(2-1) is where state 2 of character 3 changed to state 1.

rocena (Fig. 21) does not occur in other *Janthecla* species, it appears to have evolved in the lineage leading only to it. Thus, it has no systematic importance at higher levels. This result is similar to that concerning the unusual male forelegs of *Trichonis hyacinthus* (Cramer), *Micandra platyptera* Felder & Felder, and "*Thecla*" *myrtusa* Hewitson (Robbins 1987).

ACKNOWLEDGMENTS

For allowing us to examine specimens in collections under their care, we thank Jacqueline Miller and Lee Miller (AME), Fred Rindge and Jim Miller (AMNH), Phil Ackery and Dick Vane-Wright (BMNH), John Rawlins (CMNH), Jürg de Marmels and the late Francisco Fernandez-Yepez (MIZA), Gerardo Lamas (MUSM), and Olaf Mielke (UFPC). For loaning us specimens from their private collections, we thank Jim Adams, Bob Busby, George Busby, Charles Covell, the Francisco Romero family, and Bo Sullivan. We are grateful to George Venable and Vic Krantz for illustrative and photographic aid. For reading and commenting upon the manuscript, we thank Keith Brown, Bob Busby, George Busby, Charles Covell, Larry Gall, Don Harvey, Gerardo Lamas, Mike McInnis, Dug Miller, Jacqueline Miller, Lee Miller, Charles Mitter, Stan Nicolay, Brian Wiegmann, and Ben Ziegler.

Note: After this manuscript was in review, Robbins collected a male of a new *Janthecla* species at Pakitza, Manu National Park, Madre de Dios, Peru on 12 Oct. 1990. On the ventral forewing, this species shares a disjointed postmedian line (apparently unique in the Eumaeini) and a black androconia patch with *J. rocena* and thus appears to be its sister species. Its ventral pattern and foreleg are otherwise like the other *Janthecla* species. We refrain from describing this species because it is known from only one specimen. However, field-work is planned at the same locality for the next three years, and we hope more specimens will be found. It is deposited in MUSM.

LITERATURE CITED

BRIDGES, C. 1988. Catalogue of Lycaenidae & Riodinidae (Lepidoptera: Rhopalocera). Published by the author, Urbana, Illinois. 788 pp.

CLENCH, H. K. 1961. Tribe Theclini, pp. 177–200. *In* Ehrlich, P. R. and A. H. Ehrlich, How to know the butterflies. Brown Company, Dubuque, Iowa. 262 pp., 525 figs.

——— 1964. A synopsis of the West Indian Lycaenidae, with remarks on their zoogeography. J. Res. Lepid. 2:247–270.

COMSTOCK, W. P. & E. I. HUNTINGTON. 1959–64. An annotated list of the Lycaenidae (Lepidoptera: Rhopalocera) of the Western Hemisphere. J. N.Y. Entomol. Soc. 66: 103–118; 67:59–95, 163–212; 68:105–122, 176–186, 232–240; 69:54–58, 105–118, 157–176, 191–200; 70:39–46, 100–118, 177–179; 71:45–57, 115–119, 189–197, 262–264; 72:120–130, 173–192.

DE LA MAZA R., R. 1987. Mariposas Mexicanas. Fondo de Cultura Economica, Mexico City. 302 pp.

DRAUDT, M. 1921–22. Theclini F., pp. 744–812. *In* Seitz, A. (ed.), Macrolepidoptera of the world. Vol. V. The American Rhopalocera. Alfred Kernen Verlag, Stuttgart. 1140 pp., 194 pl.

DRUCE, H. H. 1907. On neotropical Lycaenidae, with descriptions of new species. Proc. Zool. Soc. Lond. 1907:566–632, 6 pl.

ELIOT, J. N. 1973. The higher classification of the Lycaenidae (Lepidoptera): A tentative arrangement. Bull. Brit. Mus. (Nat. Hist.) Entomol. 28:371–505.

FARRIS, J. S. 1988. Hennig86, version 1.5. Published by the author, Port Jefferson, New York, 18 pp.

——— 1990. Phenetics in camouflage. Cladistics 6:91–100.

HOFFMANN, C. C. 1940. Catálogo sistemático y zoogeográfico de los lepidópteros Mexicanos, Primera parte, Papilionoidea. An. Inst. Biol. Univ. Nal. Auton. Mexico 11:639–739.

LATHY, P. I. 1926. Notes on the American Theclinae (Lepidoptera). Ann. Mag. Nat. Hist., series 9, 17:35–47.

——— 1930. Notes on South American Lycaenidae, with descriptions of new species. Trans. Entomol. Soc. Lond. 78:133–137.

LEWIS, H. L. 1973. Butterflies of the world. Follett Publ. Co., Chicago. 311 pp.

NICOLAY, S. S. 1971a. A new genus of hairstreak from Central and South America (Lycaenidae, Theclinae). J. Lepid. Soc. 25 (Suppl. 1):39 pp.

——— 1971b. A review of the genus *Arcas* with descriptions of new species (Lycaenidae, Strymonini). J. Lepid. Soc. 25:87–108.

——— 1977. Studies in the genera of American hairstreaks. 4. A new genus of hairstreak from Central and South America (Lycaenidae: Eumaeini). Bull. Allyn Mus. 44:1–24.

——— 1979. Studies in the genera of American hairstreaks. 5. A review of the Hübnerian genus *Parrhasius* and description of a new genus *Michaelus* (Lycaenidae: Eumaeini). Bull. Allyn Mus. 56:1–52.

——— 1982. Studies in the genera of American hairstreaks. 6. A review of the Hübnerian genus *Olynthus* (Lycaenidae: Eumaeini). Bull. Allyn Mus. 74:1–30.

ROBBINS, R. K. 1987. Evolution and identification of the New World hairstreak butterflies (Lycaenidae: Eumaeini): Eliot's *Trichonis* Section and *Trichonis* Hewitson. J. Lepid. Soc. 40:138–157.

——— 1988. Male foretarsal variation in Lycaenidae and Riodinidae, and the systematic placement of *Styx infernalis* (Lepidoptera). Proc. Wash. Entomol. Soc. 90:356–368.

——— 1990. Systematic implications of butterfly leg structures that clean the antennae. Psyche 96:209–222.

——— 1991. Evolution, comparative morphology, and identification of the eumaeine butterfly genus *Rekoa* Kaye (Lycaenidae: Theclinae). Smith. Contr. Zool. No. 498: 1–64.

SOKAL, R. R. & F. J. ROHLF. 1969. Biometry. W. H. Freeman & Co., San Francisco. 776 pp.

THOMAS, M. B. 1893. The androconia of Lepidoptera. Amer. Nat. 27:1018–1021.

Received for publication 23 July 1990; revised and accepted 22 February 1991.

Journal of the Lepidopterists' Society
45(1), 1991, 34–41

A REVIEW OF FOUR SPECIES NAMES OF *PAECTES* FROM NORTH AMERICA (NOCTUIDAE: EUTELIINAE)

Eric H. Metzler

Ohio Department of Natural Resources, Fountain Square, Columbus, Ohio 43224

AND

John G. Franclemont

Department of Entomology, Cornell University, Ithaca, New York 14853

ABSTRACT. The status of *Paectes pygmaea* Hübner, *P. abrostolella* (Walker), *P. praepilata* (Grote), and *P. flabella* (Grote) is discussed. *Paectes abrostolella* is the prior name for the species previously misidentified as *P. flabella*. *Paectes praepilata* is a junior synonym of *P. abrostolella*. *Paectes flabella* is a junior synonym of *P. pygmaea*. Type specimens for all available names are illustrated. The male and female genitalia of *P. pygmaea* and *P. abrostolella* are illustrated. *Paectes pygmaea* occurs in the eastern U.S. and *P. abrostolella* occurs in the western U.S. The ranges of the two species overlap in the midwest from Michigan and Ohio through Kansas, and both species occur in Florida.

Additional key words: *pygmaea, abrostolella, flabella, praepilata,* Ohio, Kentucky.

In Ohio and Kentucky, two species of *Paectes* have long been treated by collectors as a single taxon, *P. pygmaea* Hübner. Although similar, these two species can be distinguished morphologically, and one is restricted to remnant prairies. After examining photographs of the types of *P. abrostolella* (Walker 1866), *P. praepilata* (Grote 1875), *P. flabella* (Grote 1879), and photographs of the pattern plate of the type (i.e., the original plate illustrating the type, hand-painted by Hübner himself) of *P. pygmaea* Hübner 1818, we determined that the senior name for the widespread species is *P. pygmaea*, and that *P. abrostolella* is the valid name for the species from remnant prairies.

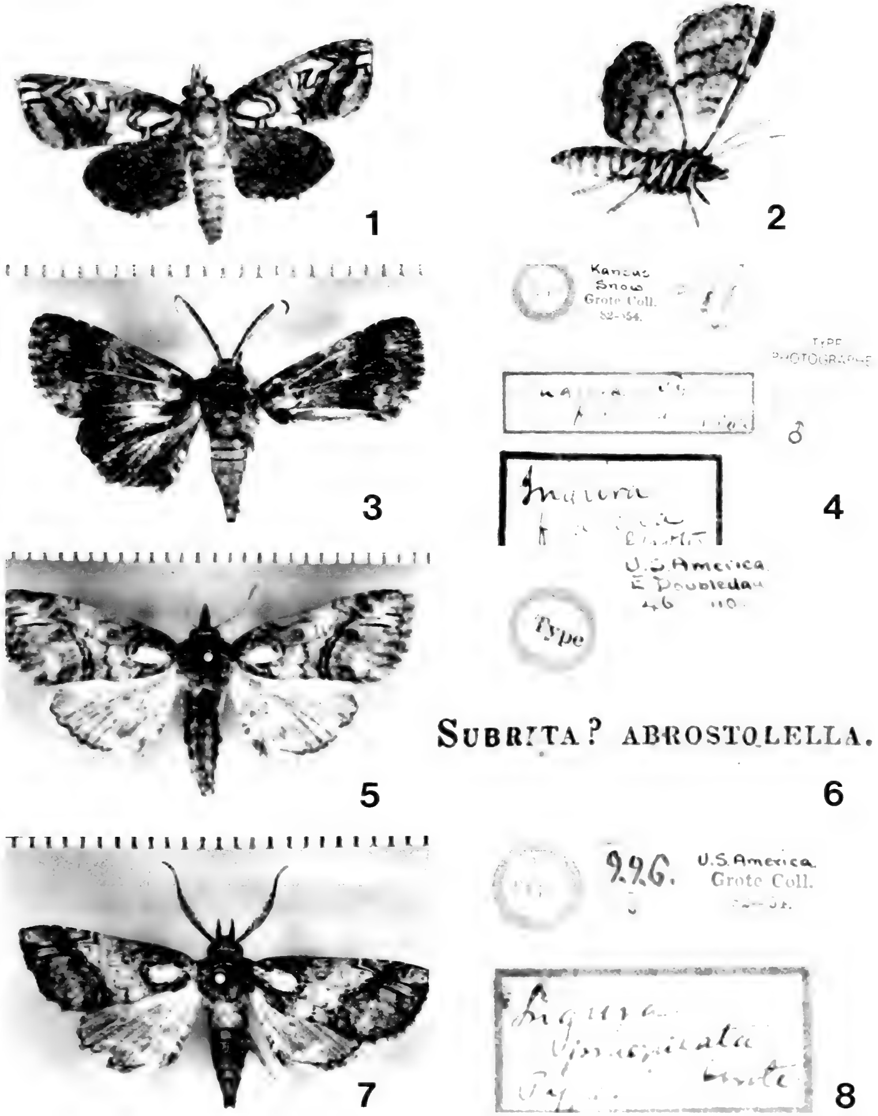
Paectes abrostolella was previously considered a synonym of *P. pygmaea* and misidentified as *P. flabella*. *Paectes praepilata*, previously considered a synonym of *P. pygmaea*, is a junior synonym of *P. abrostolella*. *Paectes flabella*, previously thought to be a distinct species, is a junior synonym of *P. pygmaea*. *Paectes pygmaea* and *P. abrostolella* occur sympatrically over much of their ranges in the midwest and in Florida.

Paectes pygmaea Hübner
(Figs. 1–4, 9, 11)

Paectes pygmaea Hübner 1818:21, plate [19], figures 109 & 110. Type locality: "Aus Georgien in Florida."

Ingura flabella Grote 1879:208. Type locality: Kansas. Revised Synonymy.

Paectes pygmaea is distinguished by its small size (19–24 mm wingspan) and very dark hindwing with contrasting white fringe. The forewing is dark brown with some lighter areas. Some specimens show a contrastingly pale basal area in the fold of the forewing.



FIGS. 1–8. **1,** Type of *Paectes pygmaea*, upper side; **2,** Type of *Paectes pygmaea*, under side; **3,** Type of *Ingura flabella*. Scale bar in mm; **4,** Labels for type of *Ingura flabella*; **5,** Type of *Subrita? abrostolella*. Scale bar in mm; **6,** Labels for type of *Subrita? abrostolella*; **7,** Type of *Ingura praepilata*. Scale bar in mm; **8,** Labels for type of *Ingura praepilata*.

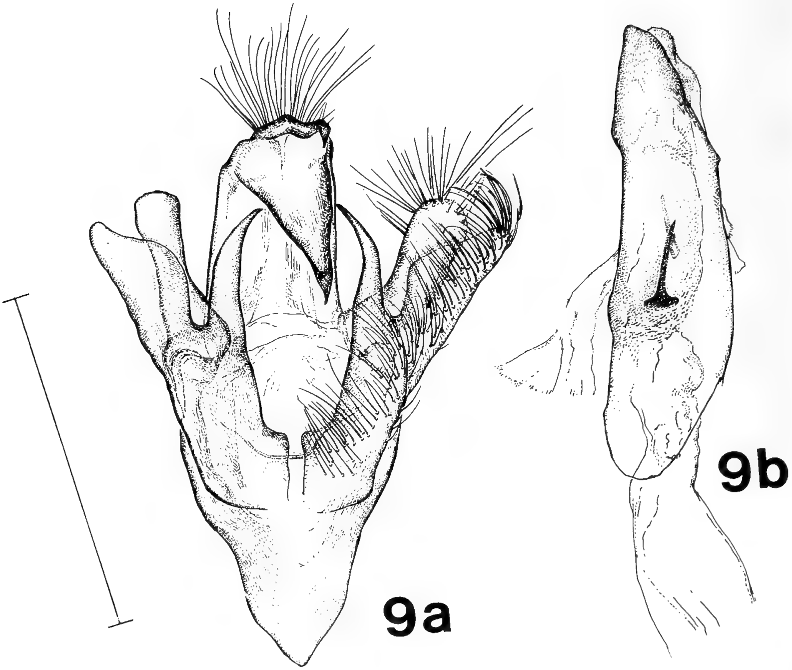


FIG. 9. *Paectes pygmaea:* male genitalia with aedoeagus removed; b aedoeagus. Slide JGF 2501. Ozark, Dale Co., Alabama. Scale bar = 1 mm.

There is practically no bluish-gray as in *P. abrostolella*. Males and females have similar maculation. The male antennae are pectinated to more than $3/5$ the length. Female antennae are simple.

Figs. 1 and 2 (type of *P. pygmaea*), and 3 (type of *P. flabella*) are diagnostic for this species. The type of *P. pygmaea* is lost, but Hübner's illustrations, which we reproduce, are adequate. His rendering of the forewing is rather stylized but the darker area along the postmedial line and the black hindwing with white fringe are sufficient to diagnose this species. *Paectes pygmaea* was illustrated by Covell (1984), plate 30 (20).

The male genitalia of *P. pygmaea* are distinguished by the long saccular process (Fig. 9). The genitalia of *P. abrostolella* have a shorter saccular process (Fig. 10). Overall, the male genitalia of *P. pygmaea* are about 17% smaller than the genitalia of *P. abrostolella*.

The female genitalia of *P. pygmaea* (Fig. 11) differ from those of *P. abrostolella* (Fig. 12) in the shape and positions of the two sacs of the corpus bursae. The junction of the two sacs is "Y" shaped in *P. pygmaea*. In *P. abrostolella*, the junction of the two sacs is broadly "U" shaped. Overall, the female genitalia of *P. pygmaea* are about 17% smaller than the genitalia of *P. abrostolella*.

Paectes pygmaea is widespread in the eastern U.S. from Massachusetts to Florida and west to Michigan, Kansas, and eastern Texas (Fig. 13). In the south it flies from February (in the Florida Keys) to April–June and August (in the Florida panhandle) and in May–early July (Louisiana). In the vicinity of Washington, D.C., it flies in mid June–early July and late July–mid August. In Ohio it flies in late May–mid June and again in mid July–early August. In Michigan it flies in late May–early July and late July–late August.

The larva was described by Edwards and Elliot (1883): "Larva. (Full grown.) Yellowish apple green. Second segment with yellow line in front. All the segments have about 15 to 18 yellow spots irregularly disposed. Most of these spots are lozenge-shaped; those of

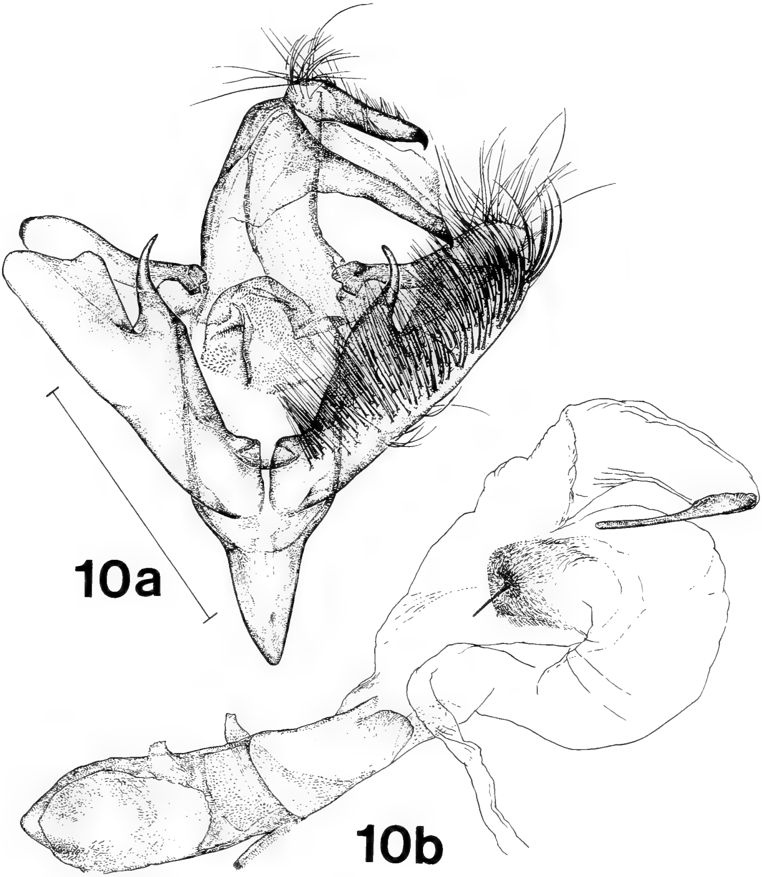


FIG. 10. *Paectes abrostolella*: male genitalia with aedoeagus removed; b aedoeagus. Slide JGF 7518. Madera Canyon, Santa Rita Mts., Santa Cruz Co., Arizona. Scale bar = 1 mm.

the subdorsal region being somewhat linear. Spiracles dull orange, with bright lemon-yellow stigmatal line. Length: 16 mm. Food plant *Liquidamber* [sic] *ptyraciflua* [sic] L." *Liquidambar styraciflua* is Sweet Gum (Hamamelidaceae).

Paectes abrostolella (Walker)
(Figs. 5–8, 10, 12)

Subrita? abrostolella Walker 1866:1744. Type locality: United States. Revised status.
Ingura praepilata Grote 1875:311. Type locality: Texas (Bosque County)? Revised synonymy

Paectes abrostolella is distinguished from *P. pygmaea* by its slightly larger size (22–27 mm wingspan), blue-gray appearance, and paler hindwings. Whereas *P. pygmaea* is dark brown, *P. abrostolella* is a bluish gray species that varies from pale to dark gray. The black markings are thinner and finer. The fringe of the hindwing is gray or only partially white.

FIGS. 11, 12. **11,** *Paectes pygmaea*: Female genitalia. Slide JGF 3558. Ozark, Dale Co., Alabama. Scale bar = 1 mm; **12,** *Paectes abrostolella*: Female genitalia. Slide JGF 7519. Madera Canyon, Santa Rita Mts., Santa Cruz Co., Arizona. Scale bar = 1 mm.

Figs. 5 and 7 illustrate adults of this species. The oval basal area of the forewing is not contrastingly pale on all specimens. The hindwings are light gray at the inner margin where they are crossed with dark lines. The adult moth resembles a diminutive *P. abrostoloides*, but *P. abrostoloides* tends to be a brownish moth whereas *P. abrostolella*

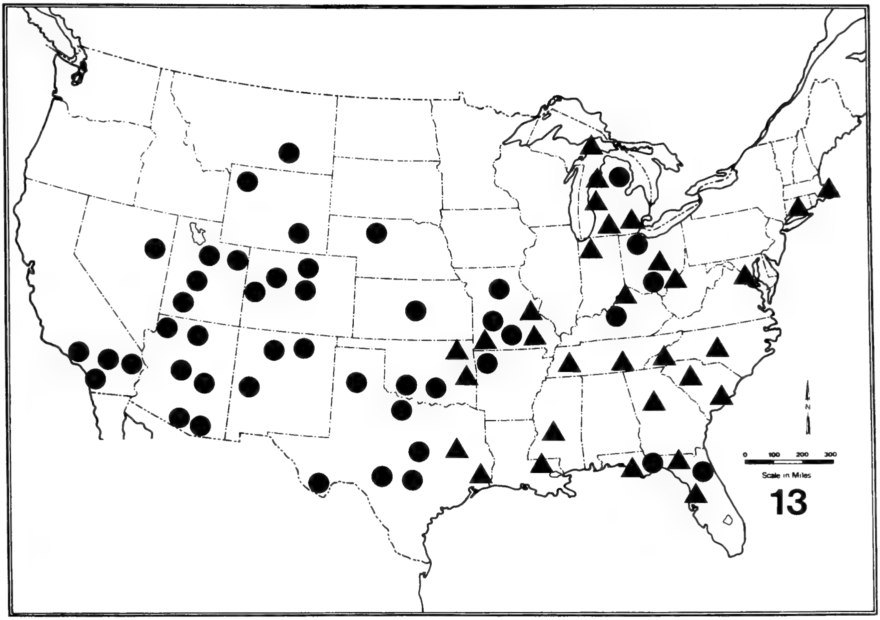


FIG. 13. Geographical ranges of *Paectes* species in the United States. Triangles = *Paectes pygmaea*. Circles = *Paectes abrostolella*.

tends to be a grayish moth. The maculation of the males and females are similar. The antennae are similar to *P. pygmaea* for each sex, respectively. This species, misidentified as *Paectes pygmaea,* was illustrated by Holland (1903) plate 29 (2).

Paectes abrostolella was described from a single female specimen from the "United States. Presented by E. Doubleday, Esq." (Walker 1866). The specimen may have been collected on Doubleday's trip from Pittsburgh, Pennsylvania down the Ohio River to St. Louis, Missouri (Doubleday 1838).

Paectes abrostolella has often been misspelled as *P. abrostella* (Smith 1893, Dyar 1902[3]). *Paectes abrostolella* (as a synonym of *P. pygmaea*) was misspelled as *P. abrostoloides* in Hodges et al. (1983).

Figs. 10 and 12 show the male and female genitalia of *P. abrostolella*. The differences between *P. abrostolella* and *P. pygmaea* were described under *P. pygmaea*.

Paectes abrostolella is widespread in the western U.S. from California east to Texas and north to Montana (Fig. 13). Populations also occur in Florida, Kentucky, Ohio, and Michigan. It occurs in remnant prairies in Kentucky (mid May and July), southern Ohio (mid-July), and northern Ohio (late June). It occurs in Putnam and Gadsden counties, Florida (March–April and September), and Oscoda County, Michigan (mid-June). In the west it occurs from Texas (March through October), Arizona (April through September), and California (May through September) north to Missouri (May–mid August), Nebraska, Montana, and Utah (June–August). If Doubleday collected the type on his trip down the Ohio River, it would have been collected in mid-September.

DISCUSSION

Paectes pygmaea was variously misidentified by early authors working on North American Noctuidae. It was not included on North American lists until 1882 (Grote), after which it was associated with several other species including *P. fuscescens* (Walker 1855), *P. abrostolella*, and *P. praepilata*. *Paectes abrostolella* was even less well understood by earlier authors. It was not included on North American lists until 1893 (Smith), after which it was associated with *P. fuscescens* and *P. praepilata*. Nearly all workers have agreed that *P. abrostolella* and *P. praepilata* are synonyms. Forbes (1954) separated *P. praepilata* from *P. pygmaea*, but he omitted *P. abrostolella*. None of the early workers considered *P. flabella* to be a synonym of *P. pygmaea*.

The corrected list of species should be:

Paectes Hübner, 1818
  pygmaea Hübner 1818
    abrostolella authors, not (Walker 1866); misidentification
    praepilata authors, not (Grote 1875); misidentification
    flabella (Grote 1879); revised synonymy
  abrostolella (Walker 1866); revised status
    praepilata (Grote 1875); revised synonymy
    flabella authors, not (Grote 1879); misidentification

Subrita? abrostolella, *Ingura praepilata*, and *Ingura flabella* are represented by single type specimens in the Natural History Museum, London. Hübner's pattern plate for *Paectes pygmaea* is also in the Natural History Museum, London.

ACKNOWLEDGMENTS

The discovery of *Paectes abrostolella* in Ohio and publication of this paper are part of The Comprehensive Survey of Ohio Butterflies and Moths sponsored by The Ohio Lepidopterists and funded by The Ohio Department of Natural Resources (ODNR) Division of Wildlife. The ODNR Division of Natural Areas and Preserves granted permission to collect at Chaparral Prairie State Nature Preserve in Adams County, Ohio. The Metropolitan Park District of the Toledo Area granted permission to collect at Oak Openings Metropolitan Park in Lucas County, Ohio.

The first author thanks J. Donald Lafontaine for assisting with the initial literature search and for contacts with the Natural History Museum (London) to obtain photographs of the types. We thank Martin Honey for supplying the photographs of the types and additional information about the type series. H. David Baggett, Charles V. Covell, Jr., Julian P. Donahue, Loran D. Gibson, J. Richard Heitzman, J. Donald Lafontaine, Ronald H. Leuschner, Robert W. Poole, Eric L. Quinter, and Donald J. Wright provided specimens under their care. James S. Ashe facilitated an examination of collections in the Snow Museum of Entomology at the University of Kansas in Lawrence. The drawings of the genitalia were skillfully prepared by Amy Louise Trabka. Douglas C. Ferguson, John E. Rawlins, and Dale F. Schweitzer reviewed the manuscript.

LITERATURE CITED

COVELL, CHARLES V., JR. 1984. A field guide to the moths of eastern North America. Houghton Mifflin Company, Boston. 496 pp.

DOUBLEDAY, E. 1838. Communications on the natural history of North America. The Entomol. Magazine 5(20):199–206.

DYAR, H. G. 1902[03]. A list of North American Lepidoptera and key to the literature of this order of Insects. Bull. U.S. Natl. Mus. No. 52. 723 pp.
EDWARDS, H. & S. L. ELLIOT. 1883. On the transformations of some species of Lepidoptera. Papilio 3(7–10):125–136.
FORBES, W. T. M. 1954. Lepidoptera of New York and neighboring states. Part III. Noctuidae. Cornell Univ. Agric. Exper. Station Memoir 329. 433 pp.
GROTE, A. R. 1875. On the genus *Agrotis* with additions to the "List of North American Noctuidae." Bull. Buffalo Soc. Nat. Sci. 2:301–312.
——— 1879. Identifications and descriptions of Noctuidae, with a new *Heterocampa*, and notes on *Nemeophila*. Canad. Entomol. 11:205–210.
——— 1882. New check list of North American moths. New York. 73 pp.
HODGES, R. W., ET AL. 1983. Check list of the Lepidoptera of America north of Mexico. E. W. Classey Limited and The Wedge Entomological Research Foundation, London. 284 pp.
HOLLAND, W. J. 1903. The moth book. Doubleday, Page & Company, New York. 479 pp.
HÜBNER, J. 1818. Zuträge zur Sammlung exotischer Schmettlinge [sic]. Vol. 1. Augsburg. [40] pp.
SMITH, J. B. 1893. A catalogue, bibliographical and synonymical, of the species of moths of the lepidopterous superfamily Noctuidae, found in Boreal America. Bull. U.S. Natl. Mus. No. 44. 424 pp.
WALKER, F. 1855. List of the specimens of lepidopterous insects in the collection of the British Museum. Part 5. British Museum (Natural History), London. Pp. 977–1257.
——— 1866. List of the specimens of lepidopterous insects in the collection of the British Museum. Part 35 Supplement. Part 5. British Museum (Natural History), London. 505 pp.

Received for publication 24 February 1990; revised 18 January 1991; accepted 27 February 1991.

Journal of the Lepidopterists' Society
45(1), 1991, 42–45

A NEW SPECIES OF *PIRUNA* FROM OAXACA, MEXICO (HESPERIIDAE)

HUGH AVERY FREEMAN
1605 Lewis Drive, Garland, Texas 75041

ABSTRACT. *Piruna mullinsi* is described from Oaxaca, Mexico, the type series consisting of 76 males and 2 females collected by John Kemner. The new species is differentiated from its closest ally *P. sina* Freeman 1970 by morphological and genitalic characters. Holotype and genitalia of a paratype are illustrated.

Additional key words: *Piruna mullinsi, Piruna sina,* genitalia.

While in the process of collecting Lepidoptera in Mexico, John Kemner located a grassy area near a ravine on highway 175, 8 km north of the city of Oaxaca, Oaxaca, Mexico, ca. 1800 m elevation, where six species of *Piruna* (Evans 1955) were flying. What was perhaps the most common species there turned out to be undescribed.

Piruna mullinsi Freeman, new species
(Figs. 1–3)

Male upper side. Primaries dark brown, overscaled entirely with lighter bronzy scales except over the veins so as to produce a streaked appearance. There are usually six, light tan, hyaline spots: the largest in the middle of space 2 beyond a small spot near the base of space 2; small roundish spots in spaces 3, 6, and 8; and a well developed upper cell spot, almost directly over the basal spot in space 2. Rarely, a minute dot appears in the lower cell; in space lb, outward from the spot in space 2; and in space 7. Outer margin dark brown from apex to anal angle. Fringe light brown, uncheckered. Secondaries dark brown overscaled submarginally with lighter bronzy scales that again shun the veins, leaving them dark. There are two, light tan, opaque spots at the end of the cell and another near the base of space 2, which may be absent in some specimens. Fringe light brown, uncheckered.

Male under side. Primaries lighter brown than above, with the submarginal area and apex ferruginous. All spots are better defined than above. Usually there is a sordid white spot in space lb, directly below the larger spot in space 2, and another in space 10, directly above the cell spot. Space 1 lighter in coloration than rest of wing. Veins dark at base of fringe. Secondaries uniform light ferruginous becoming darker basad. The two spots at the end of the cell are barely visible and absent in some specimens. Rarely will the spot near the base of space 2 be visible. There may also be a faint suggestion of a row of submarginal spots. Veins dark at base of fringe.

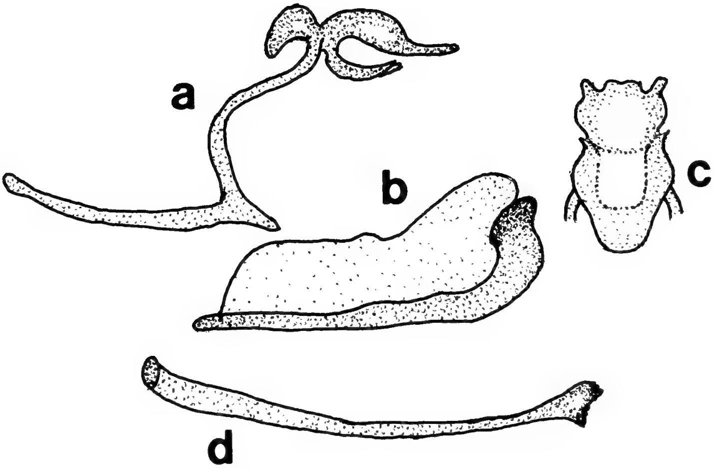
Body: Palpi, head, thorax, and abdomen darker above, lighter beneath. Legs mostly bronzy. Antennae: shaft blackish brown and checkered with cream above, creamy below; club blackish brown above, creamy below, with the nudum yellowish brown.

Wing measurements: Holotype. Primaries: base to apex, 12 mm; apex to outer angle, 8 mm; outer angle to base, 10 mm. Secondaries: base to end of vein 3, 10.5 mm, center of costa to anal angle, 8 mm. Total expanse: 24 mm. Average total expanse of paratypes: 24 mm (n = 77).

Female. Very similar to the males but with the spots slightly larger; both specimens have a lower cell spot.

Types. Holotype, male, Mexico: Oaxaca; 8 km north of Oaxaca, Hwy. 175, ca. 1800 m elev., 17 August 1988 (leg. John Kemner) in the American Museum of Natural History, New York. There are 75 male and 2 female paratypes all from the type locality except

1 2



3

FIGS. 1–3. **1, 2,** Upper side (1) and under side (2) of *Piruna mullinsi* Freeman, holotype, male, Mexico: Oaxaca, 8 km north of the city of Oaxaca, ca. 1800 m elev., 17 August 1988 (leg. John Kemner); **3,** *Piruna mullinsi*, male genitalia of paratype (Genitalia Vial H-904), same location and collector as holotype, 16 July 1988: a) tegumen, uncus, gnathos, vinculum, and saccus in lateral view; b) right valva, inner surface; c) tegumen and uncus in dorsal view; d) aedeagus in lateral view.

one male from Oaxaca: 27 km east of Mitla, San Lorenzo, 16 June 1989, all specimens collected by John Kemner during July and August 1987–89. Three paratypes will be placed in the following collections: American Museum of Natural History, New York; National Museum of Natural History, Washington, D.C.; The Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; Allyn Museum of Entomology, Sarasota, Florida; private collections of Douglas Mullins and Jim Brock of Tucson, Arizona.

Etymology. I take pleasure in naming this new species for Douglas Mullins, Tucson, Arizona, who has collected many fine skippers in Mexico and has been of great help in my study of *Piruna*.

Diagnosis

The species most closely related to *Piruna mullinsi* is *P. sina* Freeman (Freeman 1970), from which it is differentiated by the following characters:

(1) In both *mullinsi* and *sina* the ground color of the upper side of both primaries and secondaries is dark brown; paler overscaling is sparse in *sina* but relatively heavy in *mullinsi*, where it occurs all over the primaries and submarginally over about 40% of the secondaries on both wings, but not on the veins and spots. Thus does *mullinsi* appear "streaked" whereas *sina* does not.

(2) The primary spots look bright white in *sina* because the white scales that form them lie flat on the wing, creating an opaque spot that reflects light well, whereas in *mullinsi* some of these white scales are relatively colorless and rise from the plane of the wing, letting light through the wing membrane and creating a semihyaline-to-hyaline spot that actually looks a little duller (light tan).

(3) On the lower side of the primaries of *sina* the ground color is dull brown, with the subapical area slightly ferruginous and space 1 being only slightly lighter than the rest of the wing, whereas in *mullinsi* the ground color is warm brown and the submarginal area is ferruginous from the apex to the outer angle and space 1 is much lighter than the rest of the wing.

(4) On the lower side of the secondaries of *sina* the ground color is uniform light chocolate brown, with a distinct white cell spot, a light brown discal spot in space 2, two similar spots at the end of the cell, and an indistinct spot in space 7 directly over the spots at the end of the cell; and there is usually a submarginal row of 4 to 5 sordid white spots in spaces 1 to 5, whereas in *mullinsi* the ground color is ferruginous becoming slightly darker over the discal and basal areas and the spots are not as well defined as usually the two spots at the end of the cell are the only ones that are well defined. Of the 78 specimens of *mullinsi* examined none had a distinct cell spot, whereas of the 30 specimens of *sina* examined all had a cell spot.

(5) Ten male paratypes were dissected and their genitalia compared with three dissections of *sina* with the following observations: (a) tegu-

men, uncus, gnathos, vinculum, and saccus were very similar; (b) lower distal division of the valva much broader at its upturned and finely dentate distal end in *mullinsi* than in *sina*. Moreover, in *mullinsi*, the distal end of the lower distal division of the valva not entirely medial to the upper distal division as it is in *sina*; (c) the distal end of the aedeagus is broader and blunter in *sina* than in *mullinsi*, and the aedeagus is somewhat longer in *mullinsi* than in *sina*.

ACKNOWLEDGMENTS

I thank Dr. Frederick H. Rindge of the American Museum of Natural History, New York, for making the photographs of the holotype used in this article, and Dr. John M. Burns of The National Museum of Natural History, Washington, DC, for helpful comments on the manuscript. I also thank Douglas Mullins and Jim Brock of Tucson, Arizona, for furnishing specimens of *Piruna sina* and John Kemner, Dripping Springs, Texas, for collecting the type series.

LITERATURE CITED

EVANS, W. H. 1955. A catalogue of the American Hesperiidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part IV. Hesperiinae and Megathyminae. British Museum, London. 499 pp., pls. 54–88.

FREEMAN, H. A. 1970. A new genus and eight new species of Mexican Hesperiidae. J. N.Y. Entomol. Soc. 78:88–99.

Received for publication 21 April 1990; revised and accepted 16 March 1991.

Journal of the Lepidopterists' Society
45(1), 1991, 46–57

THREE BIOTYPES OF *APODEMIA MORMO* (RIODINIDAE) IN THE MOJAVE DESERT

GORDON F. PRATT

Entomology and Applied Ecology Department, University of Delaware,
Newark, Delaware 19716

AND

GREGORY R. BALLMER

Department of Entomology, University of California, Riverside, California 92521

ABSTRACT: Along the western edge of the Mojave Desert and southeastern Sierra Nevada there occur three sympatric biotypes of *Apodemia mormo* (Felder & Felder) (Riodinidae). One is multivoltine and uses a wide variety of larval food plants, but most often selects and feeds on *Eriogonum inflatum* Torr. & Frem. (Polygonaceae). The other two are univoltine; one flies in the spring and feeds on *Eriogonum fasciculatum* Benth.; the other flies in late summer and eats various late-blooming, perennial *Eriogonum* species. These biotypes maintain different developmental patterns when reared under laboratory conditions. Various populations of the univoltine biotypes differ independently in adult wing patterns. The multivoltine biotype varies little throughout this area. These three biotypes may comprise distinct species.

Additional key words: *Eriogonum*, Polygonaceae, diapause, California, food plants.

Apodemia mormo ranges throughout western North America from northern Mexico to southern Canada (Scott 1986). Throughout its range, there is pronounced geographic variation in adult wing pattern such that five allopatric species were once thought to exist (Opler & Powell 1961). Stichell (1911), however, reduced these to subspecies rank and since then four new subspecies have been recognized (Opler & Powell 1961).

We have found that three biotypes of *A. mormo* occur in an area bordering the western Mojave Desert and southeastern Sierra Nevada in California. This area includes the Little San Bernardino Mts., the northern slopes of the San Bernardino and San Gabriel Mts., and the southeastern slopes of the Sierra Nevada. Characteristics of the three biotypes are: (Type 1) multivoltine and most often ovipositing and feeding on *Eriogonum inflatum* Torr. & Frem. and various annual *Eriogonum* species (Polygonaceae); (Type 2) univoltine, spring-flying, and with *E. fasciculatum* Benth. as the sole larval food plant; (Type 3) univoltine, late-summer-flying, and with various late-blooming, perennial *Eriogonum* species as larval food plant. Although the two univoltine biotypes display geographic variation in wing characters, they can be distinguished wherever they are sympatric. The late-summer population (Fig. 1b, d) has either more dorsal orange or smaller white

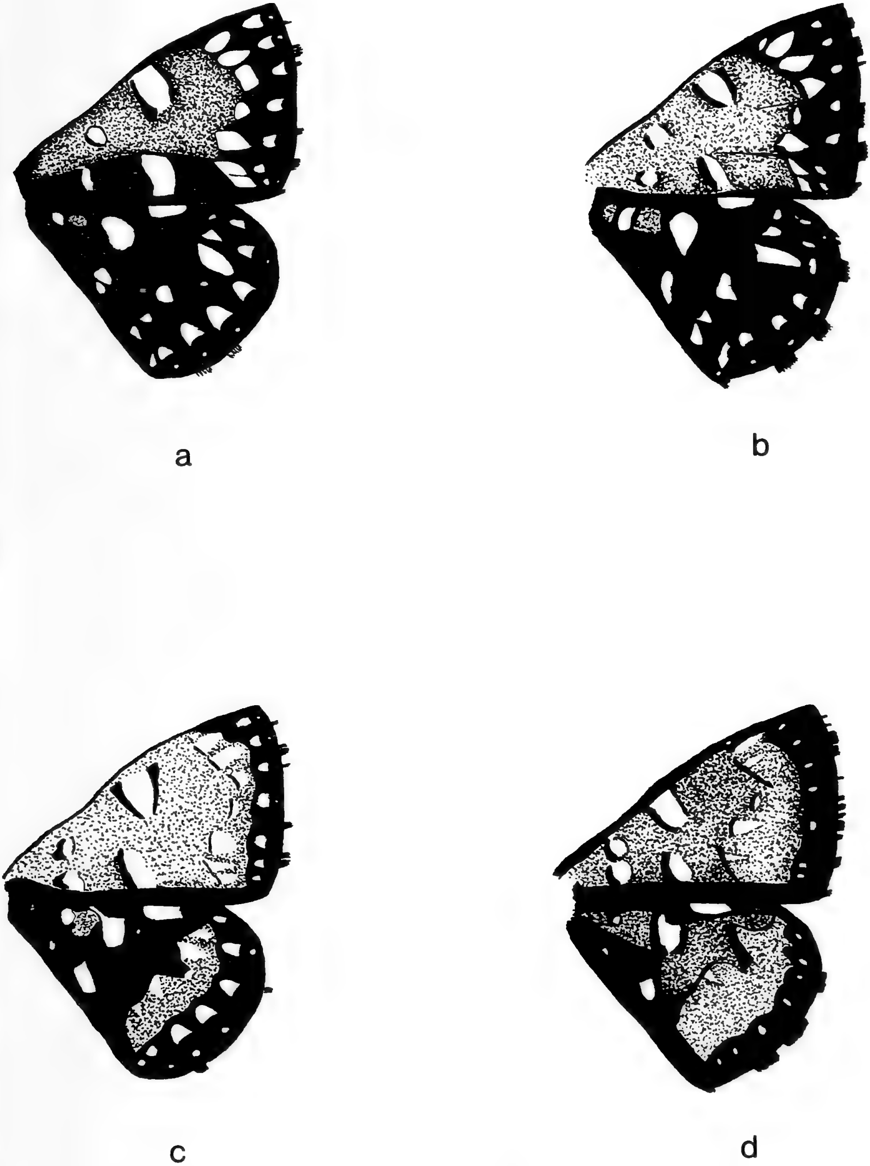


FIG. 1. Adult 'phenotypes' of the various *Apodemia mormo* populations found in the Mojave Desert. Basically, there are three colors on the dorsal wing surface: black, white, and orange (stippled area). The phenotypes are as follows: the near *dialeuca* phenotype (a) from Eureka Peak (Joshua Tree National Monument) (Type 2); the subspecies *mormo* (b) from Covington Flat (Joshua Tree National Monument) (Type 3); the near *virgulti* phenotype (c) from Pinyon Mt. (Type 2); and the subspecies *cythera* (d) from Mojave River Forks (Type 3).

macules than the spring population (Fig. 1a, c). The multivoltine biotype shows little variability throughout the area and resembles the late summer population of Covington Flat (Fig. 1b).

To determine whether these different biotypes are due to seasonal or host-related factors or to genetic differences, we reared a number of populations under similar laboratory conditions.

MATERIALS AND METHODS

Larvae of *A. mormo* representing five populations from southern California (localities numbered 1–5 as shown in Figs. 2 & 4) were reared in the laboratory in screened 1-liter plastic containers (two 25 cm^2 screened windows on the sides and complete screening on the top) on fresh *E. fasciculatum* (with branches set in water) at ca. 25°C. The *E. fasciculatum* was changed every 4–5 days or when needed. Egg and larval stage durations were recorded. Statistical differences in development times between the populations were determined by Duncan's Multiple-Range Test. The stages of development at various times of year for most subspecies of *A. mormo* were determined from field observations of adults, pupae, larvae, and ova. The eggs were measured to the nearest 0.01 mm using a dissecting scope with an ocular micrometer that was calibrated with a ruler.

Apodemia mormo females from the following populations were allowed to oviposit in screened 1-liter plastic containers on their *Eriogonum* larval food plant (host) or on *E. fasciculatum*: Eureka Peak, Little San Bernardino Mts., Riverside Co., California (Fig. 2, site 1) (adults mid-May)—host: *E. fasciculatum*; Juniper Flat, northwest slopes of the San Bernardino Mts., San Bernardino Co., California (Fig. 2, site 2) (adults mid-May)—host: *E. fasciculatum*; Pinyon Mt., southeast slopes of the Sierra Nevada, Kern Co., California (Fig. 2, site 3) (adults late-May)—host: *E. fasciculatum*; Mojave River Forks, northwest slopes of the San Bernardino Mts., San Bernardino Co., California (Fig. 4, site 4) (adults mid-August)—hosts: *E. fasciculatum* and *E. wrightii*; Old Woman Mts., San Bernardino Co., California (Fig. 4, site 5) (adults late-September)—host: *E. heermannii* Dur. & Hilg. All of the hosts were determined by adult association. Adult association was determined by observing adults (particularly females) land on the plants and wander through the branches and by correlating the distributions of the butterflies to the distributions of the plant (many *Eriogonum* species have patchy distributions as do the butterflies). These same plant species have been identified as larval hosts (by presence of larvae or eggs) of other neighboring populations of the same subspecies or phenotype of *A. mormo* (Pratt & Ballmer unpubl. data).

RESULTS

Among Type 2 populations along the southwestern margin of the Mojave Desert, there is a southeast-northwest clinal gradient in adult characters (Fig. 2). At the southeast end of this cline (Eureka Peak in the Little San Bernardino Mts.) adults have wings that have a dark black ground color with the dorsal orange restricted to a small area of the forewing and with large white macules (Fig. 1a). These populations resemble *Apodemia mormo dialeuca* Opler & Powell and the near *dialeuca* from above 2400 m on Sugarloaf Mt. in the San Bernardino Mts. (Stanford 1973). At Pinyon Mt., Nine Mile Canyon, and Walker Pass (>100 miles northwest of Eureka Peak), other Type 2 populations are lighter, with orange extending through much of the forewing and into the hindwing, and resemble *A. m. virgulti* (Fig. 1c). Between these areas, along the north slope of the San Gabriel Mts. and the northwest slope of the San Bernardino Mts. (examples: Juniper Flat and Cajon Pass), Type 2 populations are variable, exhibiting both the eastern and western extremes in wing pattern as well as various intermediates. Probably this is a blend zone between *dialeuca* and *virgulti* phenotypes, rather than blend zone between a dark *A. m. mormo* phenotype and *A. m. virgulti* as proposed by Opler and Powell (1961).

The phenotypes of the adult *A. mormo* reared from ova or larvae collected from *Eriogonum inflatum* at various sites (Kern Co.: Jawbone Canyon and El Paso Mts.; San Bernardino Co.: Danby, Granite Mts. near Victorville, Kramer Hills, Morongo Valley, Queen Mt. in Joshua Tree National Monument, and Yucca Valley) exhibited little variability and resembled Fig. 1b. In these adults the dorsal orange was restricted to the basal two thirds of the forewings and the white macules tended to be larger than in *cythera*, but smaller than in the near *dialeuca* phenotype from the Little San Bernardino Mts. Additional localities of this Type 1 *A. mormo* are shown in Fig. 3.

The phenotype of the Type 3 populations (from the southeastern slopes of the Sierra Nevada down to the northern slope of the San Gabriel Mts. and east to the north slopes of the San Bernardino Mts.; Fig. 4) is very orange dorsally, with orange extending beyond the basal two thirds of the forewing as well as into the hindwing (subspecies *A. m. cythera*—Fig. 1d). This orange tends to be browner and the dorsal white macules tend to be smaller than that of the sympatric spring-flying *A. mormo* nr. *virgulti* Type 2 populations (Fig. 1c). To the east (starting from Cactus Flat just north of Baldwin Lake) along the northeast slopes of the San Bernardino Mts., the phenotype of the Type 3 populations (Fig. 1b) is darker, with the dorsal orange usually restricted to the basal two thirds of the forewing, much like *A. m. deserti* (some

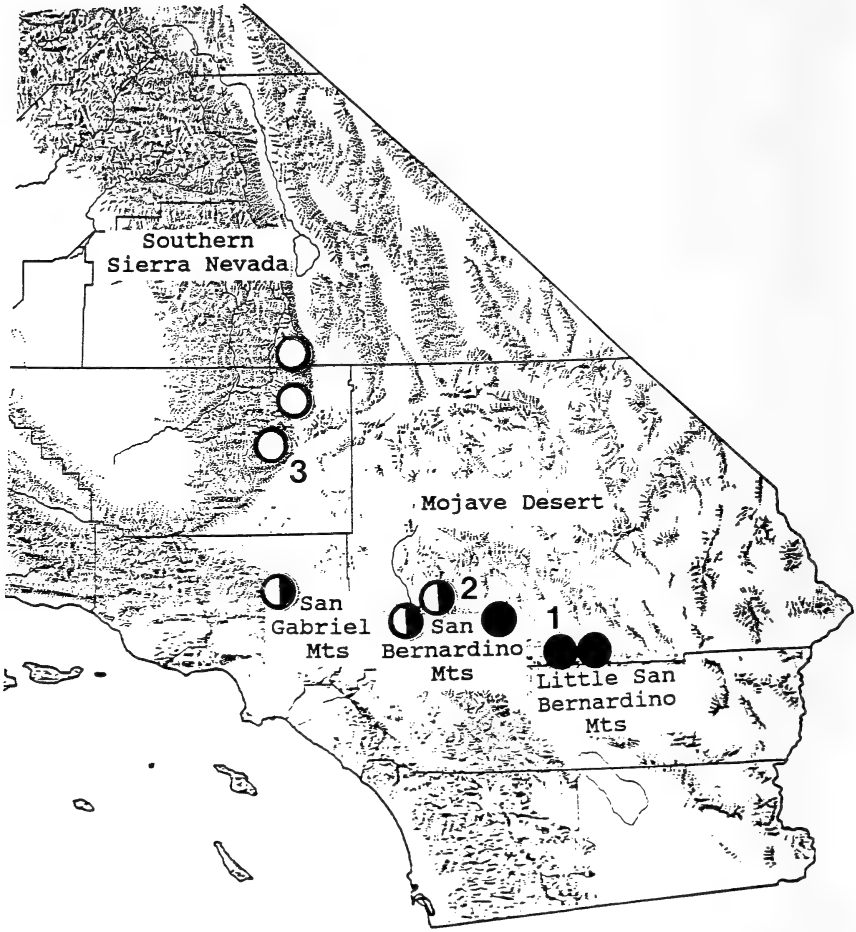


FIG. 2. Map of southern California showing locations of Type 2 populations found along the edge of the Mojave Desert. The closed circles are localities where the near *dialeuca* phenotype (a in Fig. 1) is found, the open circles are localities where the near *virgulti* phenotype (c in Fig. 1) is found, and the half closed circles denote populations with various intermediates between these two phenotypes. The localities in Table 1 are as follows: 1 is Eureka Peak, 2 is Juniper Flat, and 3 is Pinyon Mt.

individuals exhibit more extensive orange scaling that extends weakly into the hindwing).

The three biotypes had different development times under identical laboratory conditions. Populations from the western Mojave Desert reared from ova, collected from *E. inflatum*, exhibited a Type 1 life history with ova hatching 10 days after oviposition and larval durations of approximately 70 days. These populations (*Apodemia mormo deserti*

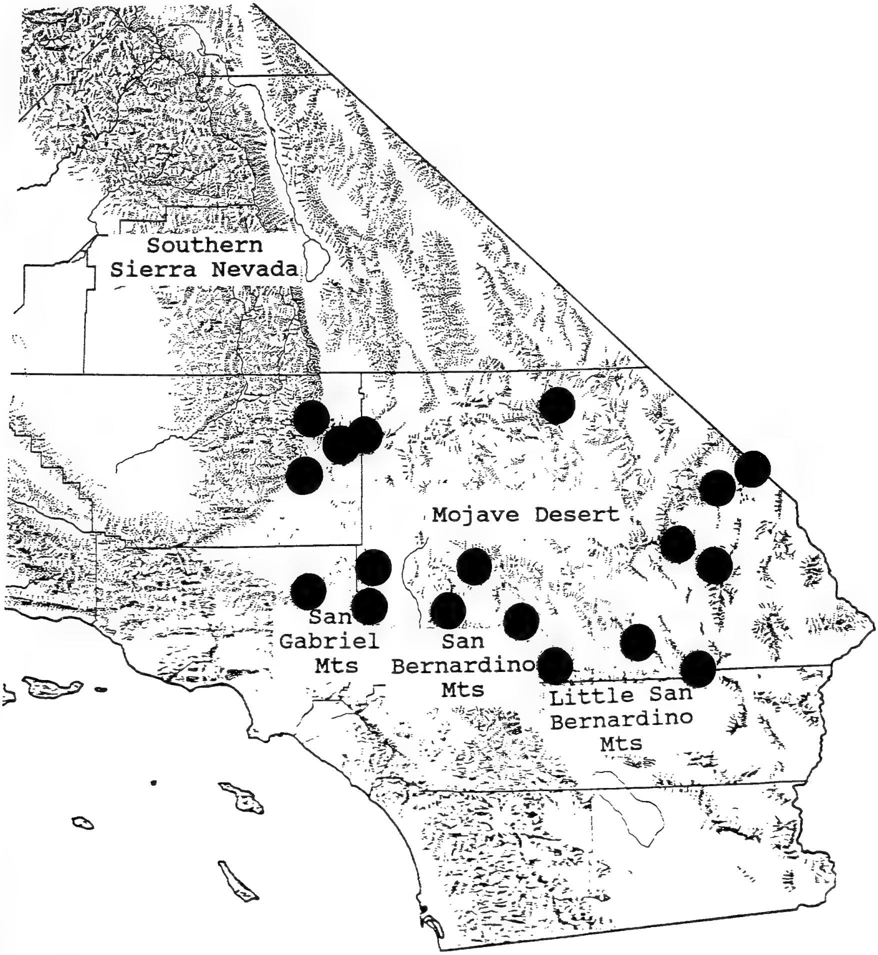


FIG. 3. Map of southern California showing locations of Type 1 populations (*A. m. deserti*) in the Mojave Desert. The phenotype of this subspecies is much like b in Fig. 1.

Barnes & McDunnough) were found at the following locations: Kern Co., California, El Paso Mts.; San Bernardino Co., California, Danby, Kramer Hills, and Sheephole Pass.

Type 2 populations exhibited long larval development times in the laboratory. Populations from Eureka Peak, Juniper Flat, and Pinyon Mt. (Table 1) had mean larval stage durations of 182, 231, and 156 days, respectively. We have observed similar long development times (>150 days) under laboratory conditions for populations of *A. mormo* from Holcolmb Valley, San Bernardino Co., California (host—*E. wrightii*

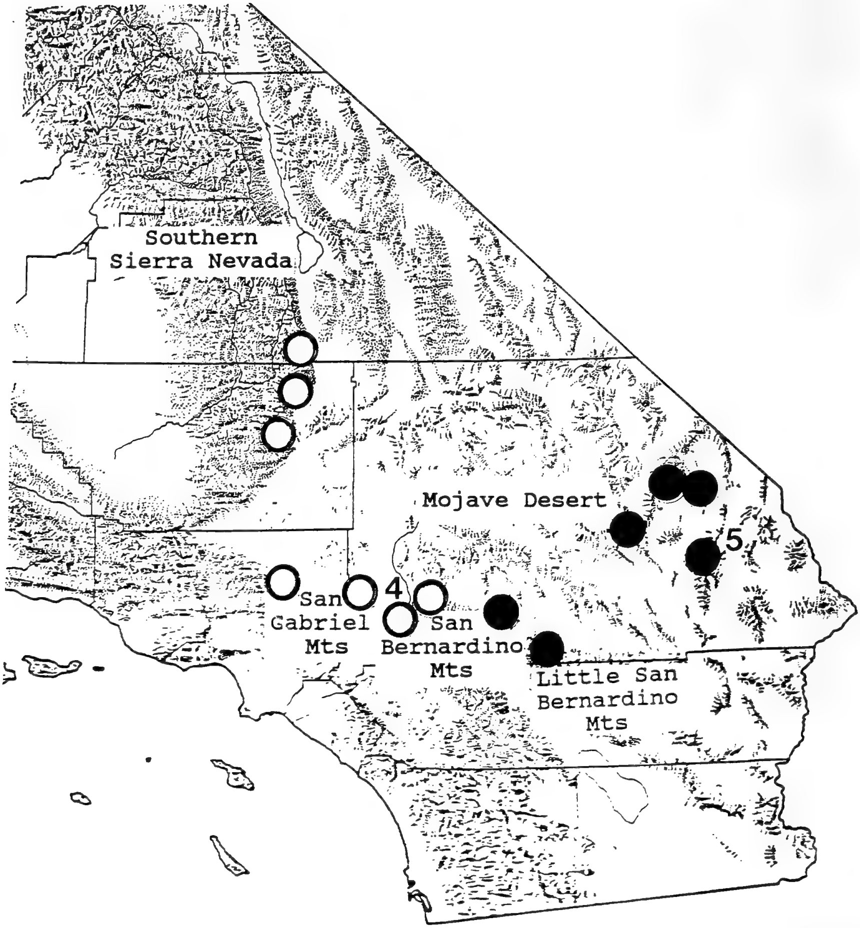


FIG. 4. Map of southern California showing locations of Type 3 populations in the Mojave Desert. The open circles indicate populations of the subspecies *cythera* (d in Fig. 1) and the closed circles denote populations of the subspecies *mormo* (b in Fig. 1). The localities used in Table 1 are as follows: 4 is Mojave River Forks and 5 is Covington Flat.

& *E. kennedyi* Porter ex Wats.); Dome Spring (*A. m.* nr. *virgulti*), Ventura Co., California (host—*E. fasciculatum*); and Nine Mile Canyon (*A. m.* nr. *virgulti*), Inyo Co., California (host—*E. fasciculatum*). All of the above larval host plants were determined by adult association (as described in the Materials and Methods), except for *E. kennedyi* from Holcolmb Valley, which was also determined from a collected larva (Table 2).

Type 3 populations differed from those of Types 1 and 2 by having a longer and more variable egg stage, and from Type 2 by having a

TABLE 1. Egg size and development times of *A. mormo* populations from the western Mojave Desert and southeastern Sierra Nevada.

Locality	Size mm	Eclos. mean (days)	Range	n	Dev. mean (days)	SD	Range	n	Life history type
Eureka Pk.	<0.90	10 C*	10	28	182	41 B*	111–253	28	2
Juniper Ft.	<0.90	10 C	10	10	231	42 A	151–290	10	2
Pinyon Mt.	<0.90	10 C	10	13	156	17 C	123–180	13	2
Mojave R F	>0.95	19 B	16–33	146	52	7 E	42–70	52	3
Old W. Mts.	>0.95	34 A	20–64	51	75	18 D	52–104	27	3

The development times for *A. mormo* populations are described in Materials and Methods in days at 25°C. All larvae were reared on fresh shoots of *Eriogonum fasciculatum*.

* The development times of those populations followed by a different letter were significantly different ($P > 0.001$) according to Duncan's Multiple-Range Test.

[Note: J. F. Emmel (pers. comm.) has reared the Type 3 biotype under outdoor conditions at Hemet (elev. 600 m), Riverside Co., California, where they take 130 to 150 days to hatch. Thus under natural conditions Type 3 ova do not hatch until February to June of the following year, depending on elevation and local climatic conditions.]

relatively short larval stage. The mean egg stage durations of Type 3 populations from Mojave River Forks (*Apodemia mormo cythera*) and Old Woman Mts. (*A. m. mormo*), were 19 and 34 days, respectively (Table 1).

The ova of most Type 3 populations are larger than those of the other two biotypes, a characteristic useful in discriminating fall-flying multivoltine populations of *A. m. deserti* (eggs < 0.9 mm, Type 1) from *A. m. mormo* (eggs > 0.95 mm, Type 3), which are phenetically very similar as adults, but often use different *Eriogonum* hosts. Differences in the three life history types are summarized in Fig. 5.

The larval food plants of the various *Apodemia mormo* subspecies and their localities in the Mojave Desert and along its western edge are presented in Table 2. Some taxa (*A. m.* nr. *dialeuca* and *A. m. virgulti*) appear to feed on only one species of *Eriogonum*, whereas others (*A. m. cythera* and *A. m. mormo*) utilize various late-summer blooming, perennial *Eriogonum* species, and one (*A. m. deserti*) feeds on many plant species. Although *A. m. deserti* was not observed to oviposit on *Krameria* (Krameriaceae), several females at Sheephole Pass were seen wandering through *Krameria* plants as though searching to oviposit. Larvae from Sheephole Pass have been reared to adults on the *Krameria* that occurs there. *Krameria* is recorded as a larval host for *A. m. mejicanus* (Behr) in Texas (Kendall 1976) and is a suspected host for *A. m. duryi* (Edwards) in New Mexico (G. S. Forbes pers. comm.).

DISCUSSION

The population that flies synchronically with both Type 2 and Type 3 populations along the northwest slopes of the San Bernardino Mts. and the northern slopes of the San Gabriel Mts. is *A. m. deserti*. If blending between *A. m. deserti* and the two other biotypes were oc-

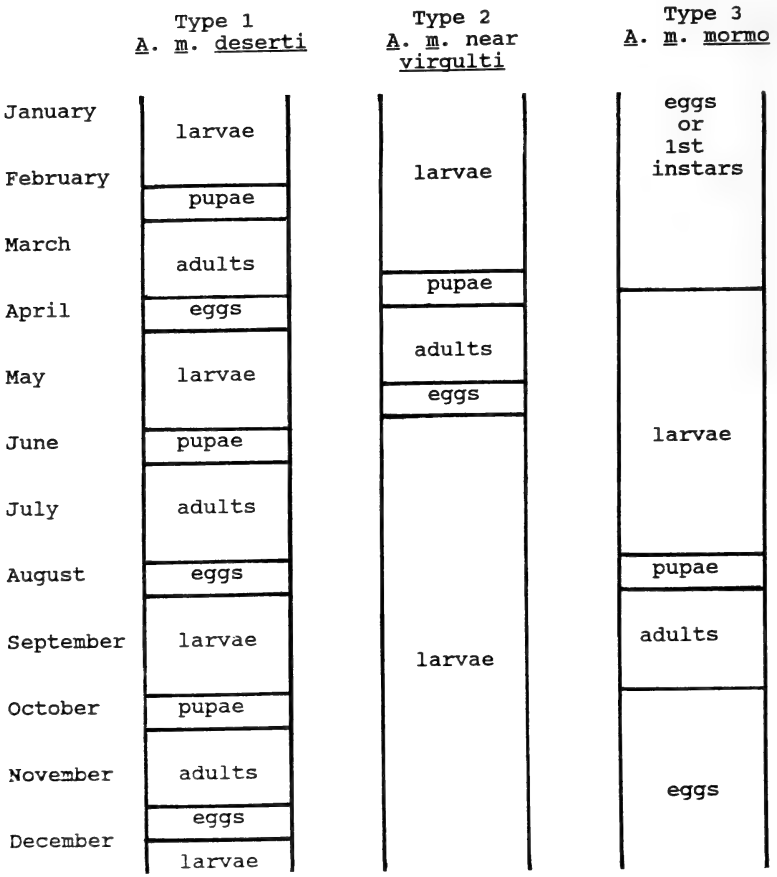


FIG. 5. Life history types showing distribution of stages throughout the year.

curring, one would expect a continuous blend zone, or a gradation of both extremes in pattern, throughout the desert edge (not one limited to the Cajon Pass area and areas just east and west of the pass as occurs with Type 2 populations), because both Types 2 and 3 come into contact with *deserti* mainly along the desert's edge (Figs. 2–4). *Apodemia mormo deserti* seems to be restricted to the lowland areas below 1500 m in the Mojave Desert, whereas both Types 2 and 3 populations of *mormo* seem to be largely restricted to above 900 meters along the desert edge (Figs. 2–4). Only populations of Type 3 can be found away from the desert's edge, on the slopes of the moister higher mountains where their late-summer blooming perennial hosts are found (Little San Bernardino Mts., Old Woman Mts., Granite Mts. southwest of Kelso, New York Mts., Providence Mts., Hackberry Mt., and Westgard Pass

TABLE 2. Life histories and host plants of *A. mormo* populations from the western Mojave Desert.

Taxon	†Life history type	*Larval host plant	Localities
cythera (Edwards) 1873	3	*Eriogonum microthecum* Nutt.	Kern Co.: Pinyon Mt.
		E. umbellatum Torr.	Mono Co.: Sherwin Summit
		E. wrightii Torr. ex Benth. in DC.	San Bernardino Co.: Big Pines Flat
deserti Barnes & McDunnough 1918	1	*E. inflatum* Toff. & Frem.	Kern Co.: El Paso Mts., Randsburg, Jawbone Canyon; Los Angeles Co.: Pearblossom; San Bernardino Co.: Danby, Sheephole Pass, Queen Mt, Morongo Canyon, Pinyon Hills, Granite Mts. near Victorville.
		E. nudum Dougl. ex Benth.	Kern Co.: El Paso Mts., Randsburg
		E. deflexum Torr. in Ives	San Bernardino Co.: Danby dry lake
		E. insigne S. Wats.	San Bernardino Co.: 7.5 miles east of Ludlow
		Oxytheca perfoliata Torr. & Gray	Kern Co.: El Paso Mts.
nr. *dialeuca*	2	*E. kennedyi* Porter ex Wats.	San Bernardino Co.: Holcolmb Valley
nr. *virgulti*	2	*E. fasciculatum* Benth.	San Bernardino Co.: Pinyon Hills
mormo (Felder & Felder) 1859	3	*E. wrightii* Torr. ex Benth. in DC.	San Bernardino Co.: Covington Flat, Joshua Tree National Monument
		E. heermannii Dur. & Hilg.	Inyo Co.: Westgard Pass

† Types of life histories are shown in Figure 5.
* The host plants were determined by field collection of larvae or eggs.

for the *mormo* phenotype; Hunter Mt., Coso Mts., and Inyo Mts. for the *cythera* phenotype). There appear to be no Type 2 populations feeding on *E. fasciculatum* in the Mojave Desert (even though the plant is present), except in the Little San Bernardino Mts., along the northern slopes of the San Bernardino and San Gabriel Mts., and the southeastern slopes of the Sierra Nevada (Fig. 2).

There is another reason that a north slope blend zone between *A. m. virgulti* and *A. m. deserti* is unlikely. Both taxa are multivoltine with Type 1 life histories. It would be surprising if a blend zone between these two taxa would yield a population that is univoltine with a Type 2 life history. Instead, it seems probable that this blend zone is between the *dialeuca* and near *virgulti* phenotypes, both of which have a Type 2 life history.

The phenotypes of these three biotypes are the most distinctive along the northwest slopes of the San Bernardino Mts. Under laboratory conditions the spring population (Juniper Flat) can be made to complete development in the fall. Normally the host plant, *E. fasciculatum*, becomes dormant during the summer, so in nature these larvae probably can not complete development until spring. When reared on plants allowed to desiccate, before being replaced with fresh branches, larvae often go into dormancy and will not readily feed when subsequently given fresh branches. The adults that emerge under laboratory conditions are different from the late-summer-flying populations and are identical to the parent spring brood. The late-summer-flying population from Mojave River Forks, only a few miles west of Juniper Flat, has more dorsal orange than does the spring phenotype (which resembles the Type 2 Juniper Flat population). When this late-summer population was reared in the laboratory on *E. fasciculatum*, adults that emerged in late-winter and early-spring were identical to *A. m. cythera*, rather than to the spring population. These results suggest that these phenotypes in the field are not seasonally or host plant induced.

These three biotypes are biologically adapted to their larval food plants' phenology. Type 1 populations, which feed on various annuals as well as the short-lived *E. inflatum*, are adapted to the variable and often short growing season of the desert by developing rapidly from oviposition to pupation. Type 2 populations, which are adapted to *E. fasciculatum* along the desert edge, exhibit a long larval development period, probably because the food plant usually goes dormant during the summer and doesn't resume growth until late-fall or early-winter rains. On the other hand, the food plants of the Type 3 populations do not bloom until late summer, so that food plant is available for larval development throughout the summer. Also, because these plants bloom in late-summer, they are nectar sources for the adults in areas where nectar can be unreliable at that season.

Although the eggs of the Type 3 populations had mean eclosion times of 19 and 34 days, these were obtained under a constant temperature of 25°C. In the field these ova would be exposed to lower temperatures and remain in diapause longer (J. F. Emmel pers. comm.). The larvae probably benefit from the ova remaining in diapause, because most of these late blooming food plants go dormant shortly after blooming or just after the females finish ovipositing.

Apodemia mormo is a complex species with nine described subspecies. Some populations (particularly in southern Arizona) are extremely variable in wing pattern, yet do not follow the "blend zone" concept as postulated by Opler and Powell (1961) (Forbes 1979). This suggests that morphology, particularly wing pattern, may be of little value in organizing the relationships of the different *A. mormo* taxa. Perhaps these three biotypes, which occur sympatrically, are distinct species. Their differences as described here, along with other characters such as enzyme polymorphisms, may help sort out the taxonomy of *Apodemia mormo* outside the Mojave Desert. For instance, *A. m. duryi* and *A. m. mejicanus* share with *A. m. deserti* a Type 1 life history (as probably does *A. m. maxima*); both are multivoltine with a short egg and larval development period and may be more closely related to each other than to other taxa of *A. mormo*. *Apodemia m. langei* has a Type 3 life history (eggs take more than 30 days to eclose), which may place it with *A. m. mormo* and *A. m. cythera*. Although *A. m. virgulti* is multivoltine and therefore does not have a Type 2 life history, it does share with Type 2 the same larval food plant not used by the other biotypes. Those populations of *A. mormo* that occur on the northern slopes of the San Bernardino Mts. and further north may have evolved in response to the shorter growing season experienced by desert populations of *Eriogonum fasciculatum*.

ACKNOWLEDGMENTS

We thank Art Shapiro and John Emmel for their suggestions and ideas. Thanks also to David Wright, Oakley Shields, John Emmel, and two anonymous reviewers for reviewing the manuscript.

LITERATURE CITED

FORBES, G. S. 1979. Description and taxonomic implications of an unusual Arizona population of *Apodemia mormo* (Riodinidae). J. Res. Lepid. 18:201–207.

KENDALL, R. O. 1976. Larval foodplants and life history notes for some metalmarks (Lepidoptera: Riodinidae) from Mexico and Texas. Bull. Allyn Mus. 32:1–12.

OPLER, P. A. & J. A. POWELL. 1961. Taxonomic and distributional studies on the western components of the *Apodemia mormo* complex (Riodinidae). J. Lepid. Soc. 15:145–171.

SCOTT, J. A. 1986. The butterflies of North America: A natural history and field guide. Stanford Univ. Press, Stanford, California. 583 pp.

STANFORD, R. E. 1973. *Apodemia mormo* near *dialeuca* (Riodinidae) from montane southern California: New for U.S.A. J. Lepid. Soc. 27:304–305.

STICHELL, H. 1911. Family Riodinidae, Allgemeines, subfamily Riodininae. Genera Insectorum Fasc. 112:452 pp.

Received for publication 10 April 1989; revised 30 July 1990 and 1 November 1990; revised and accepted 25 April 1991.

GENERAL NOTES

Journal of the Lepidopterists' Society
45(1), 1991, 58–62

A REVIEW OF THE STATUS OF *EUREMA DAIRA PALMIRA* (POEY) (PIERIDAE) IN FLORIDA, INCLUDING ADDITIONAL RECORDS FROM THE LOWER FLORIDA KEYS

Additional key words: *Eurema daira daira,* West Indies, subspecies.

The "barred" group of New World taxa within the genus *Eurema* Hübner has long confounded researchers. Similarities between species and confusion concerning the status of seasonal polyphenisms have led to misconceptions of species biology and distribution (Klots, A. B. 1928, J. N.Y. Entomol. Soc. 36:61–78; Klots, A. B. 1929, Entomol. Amer. 9: 99–171; Brown, F. M. & B. Heineman 1972, Jamaica and its butterflies, E. W. Classey, Ltd., London, 478 pp.). Most males of this group are bicolored, possessing a dorsal ground color of yellow (forewings) and white (hindwings). Females are predominantly white. An exception to this rule is the widespread North American *Eurema daira daira* (Godart) which is usually unicolored (yellow) in both sexes.

The bicolored Neotropical subspecies, *Eurema daira palmira* (Poey 1853), occurs throughout much of the West Indies, including Cuba (the type locality) and the Bahamas, where it is apparently rare (Riley, N. D. 1975, A field guide to the butterflies of the West Indies, Demeter Press, Boston, Massachusetts, 224 pp.; Leston, D. & D. S. Smith 1980, Florida Entomol. 63:509–510). Since the mid-nineteenth century, this taxon has been attributed to Florida and Georgia (Morris, J. G. 1862, Smiths. Misc. Coll., Washington, D.C., 358 pp.; Weidemeyer, J. W. 1863–64, Proc. Entomol. Soc. Phil. 2:143–154, 513–542; Edwards, W. H. 1872, Synopsis of North American butterflies, Amer. Entomol. Soc, Philadelphia, Pennsylvania, 52 pp.). Although W. H. Edwards (1877, Trans. Amer. Entomol. Soc. 6:1–68) dismissed the occurrence of *E. d. palmira* in North America, authors continued to associate North American butterflies with this taxon (Röber, J. 1907, Family Pieridae, pp. 53–111 *in* A. Seitz (ed.), Macrolepidoptera of the world, Vol. 5, A. Kernan, Stuttgart; Wood, W. C. 1939, Entomol. News 50:131; Klots, A. B. 1948, Lepid. News 2: 51–53; Klots, A. B. 1951, A field guide to the butterflies of North America, east of the Great Plains, Houghton Mifflin Co., Boston, Massachusetts, 349 pp.; Young, F. N. 1955, Lepid. News 9:204–212; Ehrlich, P. R. & A. H. Ehrlich 1961, How to know the butterflies, W. C. Brown Co., Dubuque, Iowa; Kimball, C. P. 1965, Lepidoptera of Florida, Div. of Plant Industry, Gainesville, Florida, 363 pp.).

H. K. Clench (1970, J. Lepid. Soc. 24:240–244) subsequently reported the capture in southern Florida of several *E. d. palmira,* together with *E. d. daira,* and discussed facies differences between the two subspecies based on Cuban and Floridian material. He noted that males of *E. d. daira* in southern Florida occasionally possess white dorsal hindwings, but they should not be confused with *E. d. palmira.* Nevertheless, the status of bicolored *E. daira* in Florida remained uncertain and misunderstood and authors persisted in referring all bicolored individuals to *E. d. palmira* (e.g., Howe, W. H. 1975, The butterflies of North America, Doubleday & Co., Inc., Garden City, New York, 633 pp.; Brewer, J. 1982, A butterfly watchers guide to the butterflies of Sanibel and Captiva, Sanibel-Captiva Conservation Foundation, Sanibel Island, Florida, 41 pp.). L. D. Miller and F. M. Brown (1981, Lepid. Soc. Memoir No. 2:1–280) unintentionally contributed to the confusion by mistakenly synonymizing *E. d. daira* fm. 'delioides' Haskin (type locality, Auburndale, Florida) under *E. d. palmira,* an error perpetrated earlier by C. F. dos Passos (1964, Lepid. Soc. Memoir No. 1:1–145). Miller and Brown (*op. cit.*) ultimately cast doubt on the validity of *E. d. palmira* in North America and tentatively listed the subspecies pending additional research.

To help clarify the status of bicolored *E. daira* in Florida, D. S. Smith et al. (Smith, D. S., D. Leston & B. Lenczewski 1982, Bull. Allyn Museum 70:1–8) collected a large series of this species from a variety of locations in southern Florida. They concluded that males of *E. d. daira* show a balanced polymorphism for dorsal hindwing ground color and most, if not all, reports of Floridian *E. d. palmira* are referable to *E. d. daira*. Smith et al. further concluded that Cuban *E. d. palmira* may occasionally reach Florida, but that evidence of their establishment is lacking. These findings have been misconstrued (e.g., Schwartz, A. 1987, Milwaukee Public Museum Contrib. in Biol. & Geol. 73:1–34) as testimony to the total absence of *E. d. palmira* in southern Florida. Although Smith et al. (*op. cit.*) did not reject the occurrence of *E. d. palmira* in Florida, they were clearly unaware of valid records and did not attempt to verify published reports of this subspecies.

More recently, P. A. Opler and G. O. Krizek (1984, Butterflies east of the Great Plains, Johns Hopkins Univ. Press, Baltimore, Maryland, 294 pp.) defined bicolored individuals of *E. daira* from southern Florida as indicating "genetic influx from the Antilles" without reference to *E. d. palmira*. Conversely, J. A. Scott (1986, The butterflies of North America, Stanford Univ. Press, Stanford, California, 583 pp.) and C. D. Ferris (1989, Lepid. Soc. Memoir No. 3:1–103) recognized the occurrence of *E. d. palmira* in North America. M. C. Minno and T. C. Emmel (1988, 39th Ann. Mtg. of the Lepid. Soc. Abstracts, p. 13) reported the capture of females of *E. d. palmira* on Big Pine Key (Monroe Co.), Florida. Four previously unreported bicolored specimens provide further evidence of the occurrence of *E. d. palmira* in southern Florida.

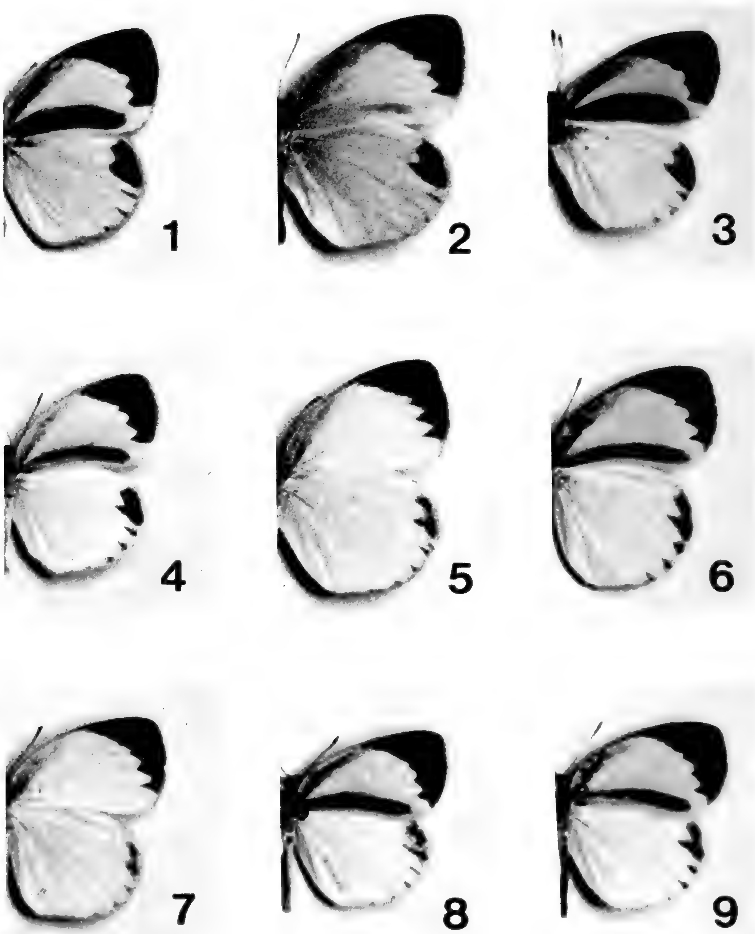
On 26 November 1972, the junior author collected one bicolored *E. daira* on Sugarloaf Key, Monroe Co., Florida and three additional males 20–28 December 1972 on Key West, Monroe Co., Florida. These specimens (Figs. 8, 9) are in good condition and morphologically consistent with *E. d. palmira* fm. 'ebriola' (Figs. 4, 5). The three individuals from Key West were visiting flowers of *Bidens alba* (L.) DC. (=*pilosa* L.) (Asteraceae) in an open, weedy vacant lot. Several others of this phenotype were seen but not collected. Typical *E. d. daira* were also present at this location. No additional information is available for the single individual from Sugarloaf Key.

The 1972 captures in the Lower Florida Keys prompted us to re-examine the Floridian specimens purported by Clench (*op. cit.*) to be *E. d. palmira*. These specimens (four males, four females), collected 22 and 31 December 1967 from two sites at Chokoloskee, Monroe Co., Florida, are also morphologically consistent with *E. d. palmira* fm. 'ebriola'. Despite an abundance of typical *E. d. daira*, Clench noted a lack of what he believed would represent "intermediates" among the adults he observed. The specimens (Figs. 6, 7) are generally in good condition.

It is our belief that additional Floridian *E. d. palmira* are harbored in collections among specimens of the nominate subspecies. These subspecies are superficially very similar and their identification is complicated by great seasonal and individual variation. The following comparisons (based on material from Florida, Cuba and Jamaica) are intended to illustrate morphological trends useful in discriminating these taxa in Florida. For convenience, these subspecies are defined in terms of "wet-season" and "dry-season" forms. These forms represent extremes; intermediates are common. The most conspicuous facies character of male *E. d. palmira* is the relatively narrow gray posterior forewing bar that is often subtended by a prominent orange inner margin. In both dry- and wet-season forms of *E. d. daira*, the forewing bar is wide, broadly reaching the discal cell and vein CU_2 and the orange inner margin is narrow and indistinct. The bar of *E. d. palmira* may possess much basal white scaling. In 'ebriola', these scales can be very numerous, occasionally obliterating the basal portion of the bar. This basal scaling is usually minimal and more yellow when present in *E. d. daira*.

The dorsal hindwing ground color of male *E. d. palmira* is white, whereas that of male *E. d. daira* varies continuously from yellow to white (see Smith et al., *op. cit.*). The dorsal ground color of female *E. d. palmira* is white and frequently has a yellow flush on the costal and apical regions of the forewing and apical region of the hindwing. The dorsal ground color of female *E. d. daira* is highly variable, ranging from nearly white to yellow. Although some females of *E. d. daira* may be very pale (reminiscent of *E. d. palmira*), they often possess much gray scaling, particularly those of the wet-season form 'jucunda' (Boisduval & LeConte) which frequently bear a distinct posterior forewing bar.

The dorsal hindwing apical black patch of both sexes of dry-season *E. d. palmira* is



FIGS. 1–9. *Eurema daira*: 1, 2, *E. d. daira* fm. 'daira'; 4–9, *E. d. palmira* fm. 'ebriola'. **1,** Male, 7 Oct. 1973, Key West, Florida (R. Anderson); **2,** Female, 9 Jan. 1986, Lee Co., Florida (J. Calhoun); **3,** Male, bicolored original specimen for Holland Plate XXXVII, fig. 12; **4,** Male, 24 Nov. 1929, Sierra Maistra East, Cuba (O. Querci); **5,** Female, 16 Feb. 1930, Sierra Maistra East, Cuba (O. Querci); **6,** Male, 31 Dec. 1967, Chokoloskee, Florida (H. & M. Clench); **7,** Female, 31 Dec. 1967, Chokoloskee, Florida (H. & M. Clench); **8,** Male, 26 Nov. 1972, Sugarloaf Key, Florida (R. Anderson); **9,** Male, 28 Dec. 1972, Key West, Florida (R. Anderson).

more poorly developed than in dry-season *E. d. daira* form 'daira' (Godart) (Figs. 1, 2). The black patch of *E. d. palmira* is often reduced to a series of vague marginal spots, the largest being two triangular spots at the end of veins Rs and M_1. The apical black patch of dry-season *E. d. daira* is typically prominent; dark spots at the ends of veins Rs and M_1 are fused, forming one large and distinctive pattern element. A series of additional marginal spots may be obvious or virtually absent. Males of wet-season *E. d. palmira* form 'palmira' (Poey) possess a dorsal hindwing black border that tapers toward the anal angle and has a fairly well defined and scalloped inner margin. Wet-season females have a black border that is similar to the male or reduced and only slightly more developed than in the dry-season form. The size and clarity of this black border is variable in both sexes of wet-season *E. d. daira,* ranging from a configuration similar to that of *E. d. palmira,* to a wide, poorly defined and less tapering band that becomes more diffuse toward the inner margin. Wet-season males of the two subspecies can be difficult to distinguish; the width of the posterior forewing bar can be a decisive character.

The fact that *E. d. daira* regularly produces bicolored phenotypes in Florida provides insight into the status of an old and controversial bicolored male specimen figured by W. J. Holland (1898, The butterfly book, Doubleday, Page & Co., New York, New York, 382 pp.: Plate XXXVII, fig. 12). Holland identified the specimen as *Eurema elathea* (Poey), a Neotropical species often confused with *E. d. palmira* and not reliably recorded in North America. Holland (1915, The butterfly guide, Doubleday, Page & Co., Garden City, New York, 237 pp.) alluded to a Floridian origin of this specimen by again figuring it (Plate CIX, fig. 2) and employing the common name "the Florida yellow" in his corresponding text discussion. Klots (1948, 1951, *op. cit.*) argued that the specimen is actually a misidentified *E. d. palmira* fm. 'ebriola' (Poey) and doubted a North American origin, retorting "apparently, Holland not only had a specimen with inaccurate data but also figured it under the wrong name". It is obvious that Klots never saw the original specimen. The senior author examined this specimen (in the Carnegie Mus. Nat. Hist.) (Fig. 3) and found it to lack locality data. Rather, it has a crude pencilled label reading "*elathea*" in Holland's handwriting and another small and very old label bearing only the handwritten number "6", possibly affixed by the collector in reference to a personal journal notation. The specimen (now without an abdomen) resembles Mexican and Central American populations of the *E. daira* complex, but the lack of data and phenotypic similarity to a bicolored dry-season *E. d. daira* do not rule out a Floridian origin.

Although all the specimens of Floridian *E. d. palmira* we examined are of the dry-season form, a specimen figured by Howe (*op. cit.*: Plate 72, fig. 14) presents a male, collected 22 October 1965 at Coral Gables (Dade Co.), Florida, that exhibits facies characteristics of the wet-season form. These records raise questions regarding the apparent sympatric occurrence of two subspecies of *E. daira* in southern Florida.

Although Clench and the junior author encountered a number of relatively unworn *E. d. palmira* at four separate locations, there is no evidence to suggest that a sympatric population of this taxon is, or ever was, established in Florida. This is true despite the misleading comment by Klots (1951, *op. cit.*) proposing that *E. d. palmira* in Florida is a "comparatively recent introduction" which "may die out". The long-term sympatric occurrence of two subspecies is, of course, improbable.

The presence of *E. d. palmira* in Florida is likely the result of emigrations from the West Indies, especially Cuba. This subspecies is an effective vagrant throughout its range (L. D. Miller pers. comm.) and Brown and Heineman (*op. cit.*) suspected that this is the reason that no island strains have developed distinctive forms in the Greater Antilles. In addition, a Central American member of the *E. daira* complex has been observed participating in at least one mass migration (Williams, C. B. 1930, The migration of butterflies, Oliver & Boyd, Edinburgh, Scotland, 473 pp.). Gravid immigrant females or immigrant pairs that manage to locate one another may produce offspring in Florida, conceivably accounting for the good condition of the specimens we examined. During the early 1970's, West Indian species of Pieridae, Lycaenidae and Nymphalidae were collected in southern Florida (Anderson, R. A. 1973, J. Lepid. Soc. 28:354–358; Fisher, M. S. 1973, J. Lepid. Soc. 28:305; Bennett, R. & E. C. Knudson 1976, J. Lepid. Soc. 30:234–235). The factors responsible for the immigration of these species into southern Florida (e.g., tropical storms, density-dependent emigration) also may have been responsible for the occurrence of *E. d. palmira* on Key West and Sugarloaf Key in 1972. Bicolored individuals of *E. d. daira* in southern Florida may be due to the introgression of alleles from *E. d. palmira* (Minno & Emmel, *op. cit.*), thus such immigrations may be frequent but overlooked.

Clench (*op. cit.*) discussed the controversial possibility that *E. d. palmira* and *E. d. daira* are two separate species. To a limited extent, this concept was previously endorsed (albeit hesitantly) by Klots (1938, 1939, *op. cit.*). Clench based this conclusion on the many phenotypic differences between these subspecies and the absence of "intermediates" among the specimens he collected at Chokoloskee. If this hypothesis is correct, *E. d. palmira* could be a rarely encountered (or overlooked) resident species in Florida or an irregular immigrant capable of establishing temporary breeding populations. Clench's failure to find additional *E. d. palmira* at Chokoloskee, two years after his initial visit, may be indicative of temporary residency.

A lack of "intermediates" does not necessarily imply that *E. d. palmira* is worthy of species-level status. If the *E. d. palmira* phenotype is recessive to that of *E. d. daira,* and differences between the subspecies are the result of a single genetic locus under simple dominant-recessive allelic expression, hybrids would possess facies characteristics of the nominate subspecies and recessive phenotypes would resemble *E. d. palmira.* In this genetic scenario, the "many intermediates" discussed and figured by Howe (*op. cit.*) would not be expected to occur. Smith et al. (*op. cit.*) dismissed such "intermediates" as within the range of variation of *E. d. daira.* The recessiveness or genetic swamping (or both) of the *E. d. palmira* phenotype also offer alternative explanations for the temporary occurrence of this taxon at Chokoloskee (Clench, *op. cit.*). The conventional subspecific status of *E. d. palmira* would be challenged by the discovery of a sympatric population of this taxon that is capable of retaining its genetic integrity in the presence of *E. d. daira.*

Finally, one should not preclude the possibility that supposed Floridian *E. d. palmira* are simply extreme examples of *E. d. daira.* This notion is perhaps supported by the paucity of known records. However, records consisting of more than one butterfly resembling *E. d. palmira,* especially males *and* females collected simultaneously within a limited area, suggest more than mere individual variation.

Bicolored males and pale females of *E. daira* encountered in southern Florida should be closely examined. Detailed electrophoretic experiments, breeding, and field studies would help resolve the enduring problematic ecological and taxonomic status of Floridian *Eurema daira palmira.*

The Florida Keys specimens of *E. d. palmira* are deposited in the collections of the authors and The Allyn Museum of Entomology, Florida Museum of Natural History. Thanks are extended to L. D. Miller and T. W. Turner for their opinions regarding the identity of the Florida Keys specimens, and to T. W. Turner, S. J. Ramos and an anonymous reviewer for helpful comments on the manuscript. We also wish to thank J. E. Rawlins of the Carnegie Museum of Natural History for the loan of specimens.

JOHN V. CALHOUN, *3524 Old Village Way, Oldsmar, Florida 34677,* AND RICHARD A. ANDERSON, *836 Amelia Court, NE, St. Petersburg, Florida 33702.*

Received for publication 11 September 1990; revised and accepted 16 February 1991.

Journal of the Lepidopterists' Society
45(1), 1991, 62–63

THE CAPTURE AND RELEASE OF A MONARCH BUTTERFLY (NYMPHALIDAE: DANAINAE) BY A BARN SWALLOW

Additional key words: aposematic, predation, Pennsylvania.

The monarch butterfly, *Danaus plexippus* (Linnaeus) (Nymphalidae: Danainae) is among the best studied of aposematic insects. The monarch's bright orange and black coloration warns predators of its cardenolide chemical defense (Brower, L. P. 1969, Sci. Am. 220:22–29; Brower, L. P. & S. C. Glazier 1975, Science 188:19–25). Although a few predators are able to circumvent the monarch's chemical defense (Brower, L. P. & W. H. Calvert 1985, Evolution 39:852–868; Calvert, W. H., L. E. Hedrick & L. P. Brower

1979, Science 204:847–851; Glendinning, J. I., A. Alonso Mejia & L. P. Brower 1988, Oecologia 75:222–227), this defense is thought to provide the monarch with protection from most vertebrate predators (Brower, L. P. 1984, pp. 109–134 *in* Vane-Wright, R. I. & P. R. Ackery (eds.), The biology of butterflies, Academic Press, London). Although birds do not appear to prey regularly on monarch butterflies, except at the Mexican overwintering sites (Brower & Calvert, *op. cit.*), there is little direct evidence to suggest that wild birds find monarchs aversive (Jeffords, M. R., J. G. Sternburg & G. P. Waldbauer 1979, Evolution 33:275–286). Beak marks found on the wings of monarchs are thought to result from predatory birds capturing and then rejecting the butterflies as unpalatable (Jeffords et al., *op. cit.*). Although Calvert et al. (*op. cit.*) and L. S. Fink and L. P. Brower (1981, Nature 291:67–70) report such behavior, no other accounts are available. I offer here an additional account.

On 25 August 1982 I witnessed a barn swallow, *Hirundo rustica* Linnaeus (Hirundinidae) capture and release a monarch butterfly at the top of a hill on a small farm in Butler County, Pennsylvania. It was late afternoon, on a partly cloudy, calm day (NNW wind at 3–6 m/sec). Mixed hay and fallow fields covered the hilltop. Monarchs, as well as other species of butterflies, foraged at the tips of goldenrod (*Solidago* sp., Asteraceae), Queen Anne's lace (*Daucus carota* (Linnaeus), Umbelliferae), and bull thistle (*Cirsuim vulgare* (Savi), Asteraceae) in the fallow field. An occasional monarch was seen migrating WSW, flying 12–15 m above the ground.

I first saw the barn swallow streaking up away from the earth about 20 m away from me. By the time I had fixed my eyes on the swallow it already had the monarch in its beak and was flying rapidly almost straight upward. A fraction of a second later the swallow dropped the monarch, turned abruptly down, and flew off. I could not tell whether the swallow had released the monarch or if the monarch had struggled free. If the monarch had escaped from the barn swallow, however, the swallow would have had no trouble recapturing it, as the monarch was 15 m above the ground and flying weakly. Yet the swallow made no effort at recapture.

Within moments of release the monarch started flying again. Flying slowly and seemingly insecurely at first, the butterfly flew SW. Gradually it flew with greater vigor, although not as robustly as the other migrating monarchs. Still flying high above the ground the monarch vanished from my view after two or three minutes, as I watched with 10 × 50 power binoculars.

I thank my wife Nancy Englund McIsaac for her editorial assistance.

HUGH P. MCISAAC, *Department of Biology, Frostburg State University, Frostburg, Maryland 21532.*

Received for publication 26 March 1990; revised and accepted 19 April 1991.

Journal of the Lepidopterists' Society
45(1), 1991, 63–65

ZYGAENIDAE TRAPPED WITH ENANTIOMERS OF 2-BUTYL(Z)-7-TETRADECENOATE

Additional key words: pheromones, attraction, isomers, Texas, Florida, Guatemala.

Enantiomers, or optical isomers, of 2-butyl(Z)-7-tetradecenoate (BTDO) have been found to be sex pheromones or sex attractants for three species of Zygaenidae in the United States. This compound was identified as a sex pheromone of the western grapeleaf skeletonizer *Harrisina brillians* (Barnes & McDunnough) by J. Myerson, W. F. Hadden, and E. L. Soderstrom (1982, Tetrahedron Lett. 23:2757–2760). E. L. Soderstrom, D. G.

TABLE 1. Numbers of males of species of Zygaenidae caught in traps baited with the R-/-(−) or S-/−(+) enantiomers of 2-butyl(Z)-7-tetradecenoate, or a 50:50 racemic mix (Guatemala only), at different geographic locations.

Location	Species	No. captured R-/−(−)	S-/−(+)	Racemic
Waco, Texas	*H. americana*	33	4	—
	H. coracina	2	26	—
Retalhuleu, Guatemala	*H. guatemalena*	1	12	13
Gainesville, Florida	*A. falsarius*	14	0	—
	A. novaricus	2	79	—
	H. americana	*	*	—
Key Largo, Florida	*H. americana*	4	0	—

* Numbers not recorded.

Brandl, J. Myerson, R. G. Buttery, and B. E. Mackey (1985, J. Econ. Entomol. 78:799–801) showed that the S-(+) enantiomer of this compound was active in field trapping tests and the R-(−) enantiomer was not. Subsequently, P. J. Landolt, R. R. Health, P. E. Sonnet, and K. Matsumoto (1986, Environ. Entomol. 15:959–962) found that male *Harrisina americana* (Guerin) and *Acoloithus falsarius* Clemens are attracted principally to the R-(−) enantiomer, with very little response to the S-(+) enantiomer.

G. Tarmann (1984, Entomofauna Zeitschrift fur Entomologie, Suppl. 2, Vol. I, Linz, Austria) listed 134 species of American Zygaenidae in 24 genera. They occur throughout the tropics and subtropics with few species in temperate North America. Only two, *Harrisina americana* and *Harrisina brillians*, are recorded as pests of agricultural crops.

Trapping efforts have been continued to determine if other species of Zygaenidae are also attracted to this compound, and if Zygaenidae attracted are specific to an enantiomer of BTDO. We report here the trapping of additional species attracted to enantiomers of BTDO as well as new distribution records obtained during these studies.

The enantiomers of BTDO were synthesized, purified, and formulated as described by Landolt et al. (*op. cit.*). All tests were conducted using plastic bucket traps, the Unitrap® of International Pheromones Limited (Merseyside, England). A rubber septum formulated with 500 μg pheromone was pinned to the inside top of each trap. Small pieces of No-Pest Strip (Texize, Greenfield, South Carolina) (1/16 of a strip/trap) were placed inside the buckets to kill captured moths. Generally, pairs of traps were placed at sites, baited with each of the two enantiomers of BTDO. Sites were selected near *Vitis* species (Vitaceae) where possible, but were determined largely by travel arrangements made for other studies. Traps were placed ca. 2 m above ground with a minimum of 10 m between traps. Pairs of traps were placed in the field at four sites reported here. Traps were hung in shrubs along a stream near Waco (McLennan Co.), Texas, 4–10 June 1986, along an abandoned roadway in upper Key Largo (Munroe Co.), Florida, 21–23 July 1986, in a mixed papaya, pineapple, and citrus planting near Retalhuleu, Guatemala, 20–23 June 1986, and in understory grapevines in a mesic hardwood forest near Gainesville (Alachua Co.), Florida, 20 April to 10 July 1989. At the Retalhuleu, Guatemala site, an additional trap baited with 1 mg of racemic 2-butyl(Z)-7-tetradecenoate was included.

Harrisina guatemalena (Druce) males were caught at Retalhuleu, Guatemala, primarily in traps baited with the S-(+) enantiomer or racemic material (Table 1). Moths were observed in flight at traps near dusk. Moths of an undescribed species of *Neofelderia* (Zygaenidae) collected at this site during the same time period were not caught in traps. Near Waco, Texas, *Harrisina coracina* (Clemens) males were captured in the trap baited with the S-(+) enantiomer, whereas most *H. americana* were in the trap baited with the R-(−) enantiomer. Both species are known to feed on grape (*Vitis* sp.), which was abundant in the study area. Three species of Zygaenidae were captured in traps placed in Alachua County, Florida: *H. americana*, *A. falsarius*, and *Acoloithus novaricus* (Barnes &

McDunnough) (Table 1). Catches of *H. americana* were not recorded. Most *A. falsarius* were in the trap baited with the R-(−)-enantiomer of BTDO, whereas nearly all *A. novaricus* were captured in the S-(+) baited trap.

This is the first documentation of attraction of *H. guatemalena, H. coracina,* and *A. novaricus* to BTDO and the first record of *A. novaricus* in the State of Florida (Kimball, C. P. 1965, Lepidoptera of Florida, Fla. Dept. Agric., Division of Plant Industry, Gainesville, Florida). Four male *H. americana* were caught in the R-(−)-BTDO trap in upper Key Largo (Table 1), which is a first record for this species in Munroe County, Florida (C. P. Kimball 1965, *op. cit.*).

Six species of Zygaenidae are now known to be attracted to 2-butyl(Z)-7-tetradecenoate, and all six appear to be fairly specific to either the R-(−) (*H. brillians, A. falsarius*) or S-(+) (*H. brillians, H. coracina, H. guatemalena, A. novaricus*) enantiomers. Although such specificity to optical isomers of a pheromone compound is known for other insects, it is uncommon (Silverstein, R. M. 1979, Chemical ecology: Odour communication in animals, pp. 133–146, Elsevier Press, Amsterdam).

We gratefully acknowledge the assistance of S. Roman, J. Lopez, and K. Vick with trapping tests.

PETER J. LANDOLT AND ROBERT R. HEATH, *Insect Attractants, Behavior, and Basic Biology Research Laboratory, Agricultural Research Service, U.S. Department of Agriculture, Gainesville, Florida 32604;* GERHARD TARMANN, *Tiroler Landesmuseum Ferdinandeum, A6020 Innsbruck, Museumstrasse 15, Austria.*

Received for publication 24 November 1989; revised and accepted 19 April 1991.

Journal of the Lepidopterists' Society
45(1), 1991, 65–66

FIRST RECORD OF *SATURNIA ALBOFASCIATA* JOHNSON (SATURNIIDAE) FROM MEXICO

Additional key words: Baja California Norte, chaparral.

Saturnia albofasciata Johnson is widely distributed throughout much of California. It is recorded from Los Angeles, Riverside, San Diego, Ventura, and Kern counties in Southern California and from El Dorado, Lake, Mariposa, Tulare, Glenn, and Tehama counties in Northern California (Johnson, J. W. 1938, Bull. Brooklyn Entomol. Soc. 33: 128–130; Hogue, C. L. et al. 1965, J. Res. Lepid. 4:173–184; Ferguson, D. C. 1972, Bombycoidea (in part), Saturniidae, *in* Dominick, R. B. et al. (eds.), The moths of America north of Mexico, fasc. 20.2B:155–275, E. W. Classey, London; Lemaire, C. 1978, The Attacidae of America. Attacinae. Edition C. Lemaire, Neuilly-sur-Seine, France, 238 pp.; 1990 Field Seasonal Summary NEWS Lepid. Soc., 1991, No. 3, p. 18). Like many elements of the Californian fauna, *S. albofasciata* is suspected to occur in adjacent Baja California Norte; however, it previously was unreported from this or any other Mexican state.

On 28 October 1989, I caged four unmated, reared females of *S. albofasciata* at a site 11.5 km (7.1 mi) SW of Parque Nacional Constitucion de 1857 on the Laguna Hanson road in the Sierra de Júarez, Baja California Norte, Mexico (elev. ca. 1525 m). The site is 68 km south of the international border and 80 km south of the nearest known United States locality for *S. albofasciata* at Kitchen Creek, San Diego County, California. With sunny conditions between 1610 and 1700 h PST, 37 wild males were attracted to the virgin females, all of which were captured.

The Sierra de Júarez site is characterized by a mixed chaparral community, a habitat known to support *S. albofasciata* populations (Ferguson, *op. cit.*). Dominant plants include

Ceanothus greggii A. Gray (Rhamnaceae), *Adenostoma sparsifolium* Torr. (Rosaceae), *Arctostaphylos peninsularis* Wells (Ericaceae), *Artemisia tridentata* Nutt. (Asteraceae), *Quercus chrysolepis* Liebm. and *Q. dumosa* Nutt. (Fagaceae), and *Pinus jefferyi* Grev. & Balf. (Pinaceae).

On 27 and 29 October 1989 the unmated females were caged at a site in the vicinity of Mike's Sky Ranch in the Sierra San Pedro Mártir, approximately 170 km south of the international border. Despite sunny weather and at a similar elevation and floral community, no males were attracted.

Two males were deposited as voucher specimens in both of the following institutions: Universidad Autonoma de Baja California Norte, Ensenada, Mexico, and the Essig Museum of Entomology, University of California, Berkeley. Eleven specimens are in the private collection of John Noble, Anaheim Hills, California; the remaining 22 specimens are in the collection of the author.

RALPH E. WELLS, *303-B Hoffman Street, Jackson, California 95642.*

Received for publication 10 February 1990; revised and accepted 15 March 1991.

Journal of the Lepidopterists' Society
45(1), 1991, 66–67

POSITIVE RELATION BETWEEN BODY SIZE AND ALTITUDE OF CAPTURE SITE IN TORTRICID MOTHS (TORTRICIDAE)

Additional key words: North America, biometrics, ecology.

Earlier I reported a positive correlation between forewing length and altitude of capture site in the Nearctic tortricid *Eucosma agricolana* (Walsingham) (Miller, W. E. 1974, Ann. Entomol. Soc. Amer. 67:601–604). The all-male sample was transcontinental, with site altitudes ranging from near sea level on east and west coasts to more than 2700 m in the Rocky Mountains. Altitudes of capture came from labels of some specimens, and from topographic maps for others. Forewing length increased 0.33 mm through each 500 m of site altitude. Forewing length is a reliable indicator of dry body weight, hence of body size (Miller, W. E. 1977, Ann. Entomol. Soc. Amer. 70:253–256).

More recently, I noticed at the American Museum of Natural History several series of other tortricid species with altitude labels. These numbered 34 or more specimens per sex or per species, and had been collected during the 1970's in New Mexico, Utah, Colorado, Wyoming, Idaho, Nevada, and Montana by the F. H. Rindge family. To extend the earlier work, I analyzed forewing length of these series with respect to altitude of capture site. Here forewing length is the maximum distance between wing base (excluding tegula) and tip (including fringe). The present study differs from the earlier one in three ways that are noteworthy: it involves three species, the data represent a smaller geographic area, and all altitudes are taken from labels.

I investigated each sex independently in *Choristoneura occidentalis* Freeman and *Pseudosciaphila duplex* (Walsingham), but combined the sexes in *Hystricophora asphodelana* (Kearfott), which does not exhibit marked sexual size dimorphism. In testing for correlation, I used Kendall's tau, a distribution-free, nonparametric rank-order statistic, as well as the more familiar Pearson product-moment correlation coefficient, r.

All five samples show evidence of positive correlation between forewing length and altitude of capture site (Table 1). Tau values for all five are positive, and three tau values are significantly ($P < 0.05$) greater than 0; r values for four samples are positive, and two r values are significantly ($P < 0.05$) greater than 0. I ruled out latitude as a hidden factor in the correlation because north and south partitions of the samples differed negligibly

TABLE 1. Relation between forewing length and altitude of capture site in five samples of three tortricid species.

Species		Range in:		Test statistics				Mean change in forewing length/500 m altitude (mm)[a]
Sex	N	Altitude (A) (m)	Forewing length (F) (mm)	tau	P	r	P	
Choristoneura occidentalis								
Female	36	1890–2896	10.0–14.0	0.30	<0.05	0.13	>0.10	0.05
Male	55	1798–3277	9.6–14.0	0.24	<0.05	0.16	>0.10	0.08
Pseudosciaphila duplex								
Female	34	1798–2896	10.0–14.0	0.19	≃0.10	−0.04	>0.10	−0.02
Male	53	1798–2804	9.5–13.0	0.07	≃0.10	0.37	<0.01	0.09
Hystricophora asphodelana								
Mixed	45	1219–3048	9.5–15.0	0.27	<0.05	0.45	<0.01	0.13

[a] Rounded slope (b) values of regressions of the form $F = a + bA$.

in mean forewing length, the largest difference in any sample being only 6%. Mean increase in forewing length per 500 m of altitude (Table 1) is 0.07 mm for the five samples.

These results, together with the earlier report, bring to four the number of tortricid species showing evidence of the correlation; no tortricid species checked so far has shown a clear absence of it. I know of no other reports concerning body size and altitude in Tortricidae.

For other lepidopterans, negative correlations between body size and altitude have been reported for *Occidryas chalcedona* (Doubleday) (Nymphalidae) (Hovanitz, W. 1942, Ecology 23:175–188), *Parnassius phoebus* (Fabricius) (Papilionidae) (Guppy, C. S. 1986, Can. J. Zool. 64:956–962), and *Polites draco* (Edwards) (Hesperiidae) (Brown, F. M. 1962, J. Lepid. Soc. 16:239–242). All of these are diurnal species. In diurnal lepidopterans, body sizes converge in alpine environments in accordance with body heat capacity (Douglas, M. 1986, The lives of butterflies, Univ. Michigan Press, Ann Arbor, 214 pp.). Thus positive as well as negative correlations with altitude are theoretically possible in butterflies.

In tortricids, which are crepuscular, the correlation may have a different explanation. It doubtless involves one or more of the well-known altitudinal gradients in temperature, solar radiation, and barometric pressure, with these factors acting directly, or indirectly through food plants. One likely indirect effect concerns nitrogen, which may be more abundant in plants at high altitudes (Körner, C. 1989, Oecologia 81:379–391). Nitrogen content of food is well known as a determinant of insect body size (Mattson, W. J. & J. M. Scriber 1987, pp. 105–146, *in* Slansky, F. & J. G. Rodriguez [eds.], Nutritional ecology of insects, mites, and spiders, Wiley, New York, 1016 pp.). In a phytophagous hymenopteran, positive correlations have been demonstrated in the same study among all three variables—altitude, pupal weight, and food-plant nitrogen content (Niemelä, P., M. Rousi & H. Saarenmaa 1987, J. Appl. Entomol. 103:84–91).

I thank C. S. Guppy, F. H. Rindge, J. M. Burns, and an anonymous reviewer for useful comments on the manuscript.

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

Received for publication 7 April 1990; revised and accepted 10 October 1990.

Journal of the Lepidopterists' Society
45(1), 1991, 68

A POPULATION OF *ANAEA RYPHEA* (NYMPHALIDAE) AND ITS LARVAL FOOD PLANT AT CAMPINAS, BRAZIL

Additional key words: *Croton floribundus,* Euphorbiaceae, *Hypna clytemnestra,* São Paulo.

The butterfly *Anaea ryphea* (Cramer 1775) (Nymphalidae) occurs from Mexico to subtropical South America, although its host plant is unknown (De Vries, P. 1987, The butterflies of Costa Rica and their natural history, Princeton Univ. Press, Princeton, New Jersey, 327 pp.). From September 1988 to March 1990 I studied a population of *Anaea ryphea* in a small reserve at Campinas, São Paulo State, Brazil (22°54'S and 47°05'W, elevation 650 m, annual rainfall 1500 mm, mean annual temperature 22°C) where it uses *Croton floribundus* Spreng (Euphorbiaceae) as its larval food plant.

Other species of *Anaea* are known to feed on Euphorbiaceae, such as *Anaea andria* Scudder which uses *Croton capitatus* Michx. as its primary host plant in the southern United States (Riley, T. J. 1988, J. Lepid. Soc. 42:263–268). Feeding on *Croton* may be a common feature of the genus, since *Croton* has a wide distribution in the tropics (Schnell, R. 1971, Introduction a la phytogeographie des pays tropicaux, Gauthier-Villars, Paris, 951 pp.), but other families are also used. Muyshondt found immatures of *Anaea* (*Zaretis*) *itys* Cramer on a species of Flaucortiaceae (also known as Samydaceae) (Muyshondt, A. 1973, J. Lepid. Soc. 27:294–302) and eggs and larvae of *Anaea* (*Consul*) *fabius* Cramer on three species of Piperaceae (Muyshondt, A. 1974, J. Lepid. Soc. 28:81–89). W. P. Comstock (1961, Butterflies of the American tropics: The genus *Anaea,* American Museum of Natural History, New York, 214 pp., 30 pls.) lists food plant records from seven plant families, with Euphorbiaceae (especially *Croton*) and Piperaceae being the most frequently used.

A species of *Anaea* can use more than one plant species as larval food plant (Muyshondt 1973, 1974, *op. cit.*). At Campinas I observed *A. ryphea* feeding on a second plant species (an unidentified Euphorbiaceae) at times when *C. floribundus* plants were completely defoliated or when they had only old leaves at the end of the wet season. At this time the larval population was decreasing rapidly from its maximum peak of 136 larvae on 186 plants in the study area.

Another species of Nymphalidae, *Hypna clytemnestra* (Cramer 1777) also was observed feeding on *Croton floribundus.* Its larvae and those of *A. ryphea* were sometimes found together on the same individual plant, but the number of *A. ryphea* immatures was always greater than that of *H. clytemnestra,* whose measured population density was never more than 10% of that of *A. ryphea.*

Larvae of *H. clytemnestra* are larger than *A. ryphea,* and in the laboratory they proved to be more voracious feeders; as a consequence, they cause heavy defoliation on *C. floribundus,* sometimes leading to starvation of *A. ryphea* larvae, which cannot move to other nearby plants.

I thank the faculty of the Botany Department of the Universidade Estadual de Campinas for identifying *Croton floribundus* and two anonymous reviewers for helpful comments on the manuscript. I also thank Dr. Woodruff W. Benson for suggesting the study organism.

ASTRID CALDAS, *Universidade do Estado do Rio de Janeiro, DBAV - IB, 20550 Rio de Janeiro, Rio de Janeiro, Brazil. Present address: Universidade Estadual de Campinas, Pós-Graduação em Ecologia, C.P. 6109, 13081 Campinas, São Paulo, Brazil.*

Received for publication 10 October 1990; revised and accepted 10 January 1991.

BOOK REVIEWS

Journal of the Lepidopterists' Society
45(1), 1991, 69

HETEROCERA SUMATRANA, Volume 6. Consisting of five chapters by various authors as described below. 1990. Text in English with German summaries. Heterocera Sumatrana Society e. V., Kreuzburger Strasse 6, W-3400 Göttingen, Germany. 204 pp., 16 color plates. by B. D'Abrera and others. Soft cover, 16 × 24 cm, ISBN 3-925055-02-9, DM 99, 80 (about $57).

I hope that this book, indeed this series, will receive the attention it deserves because of its relevance to studies on certain families of moths and lepidopteran phylogeny in general. I do not see how anyone with a serious interest in Limacodidae or Lasiocampidae can rationalize not buying this book. A team of Germans is the core of authors working on the abundant material being collected by E. W. Diehl, resident on the large Indonesian island of Sumatra. They are joined in this latest volume by Jeremy D. Holloway of The Natural History Museum (London), a well-known specialist of Indo-Australian Lepidoptera and author of *The Moths of Borneo* series. The text in the five chapters of this latest installment of the *Heterocera Sumatrana* series is thoroughly researched and well presented; with this volume there has been no rush to get something in print, as we sometimes see. Each chapter gives many details of morphology, figures of genitalia, and a comprehensive bibliography.

Below is a synopsis of the contents:

Chapter 1. *The Limacodidae of Sumatra*, by J. D. Holloway. Three new genera and 13 new species are described. Three color plates show 108 specimens. Holloway's working knowledge of the moth fauna of the Indo-Australian region is very evident as he draws comparisons between the Sumatran fauna and surrounding areas. Some of these limacodids are pests of coconut and oil palms.

Chapter 2. *The Ratardidae of Sumatra*, by L. W. R. Kobes and L. Ronkay. This is the most current and definitive treatment in existence for this small family of moths, which are exceedingly rare in collections. The authors used X-ray photography to show venation so as not to destroy specimens. One new genus and species are described in addition to the detailed overview of the family, which is probably the sister-group of the Callidulidae.

Chapter 3. *The Callidulidae of Sumatra*, by L. W. R. Kobes. These little diurnal moths are remarkable mimics of Lycaenidae. There are only 4 known species in Sumatra, but these are all described and figured in color, and phylogeny of the group is discussed. I suspect that some of these rarities are in collections mixed with lycaenids awaiting to be identified as moths.

Chapter 4. *The Brahmaeidae of Sumatra*, by W. A. Nässig and U. Paukstadt. Although only a single species is known for Sumatra, this chapter gives a fine overview of the morphology and phylogeny of this small Old World family (the "basket moths"), and illustrates in color the larval stages of the Sumatran species.

Chapter 5. *The Lasiocampidae of Sumatra*, by J. D. Holloway and R. Bender. Of the 69 known Sumatran species, 11 are described here as new. This lengthy chapter comprises about a third of the pages of the book and contains 9 color plates.

For individuals with an interest in moths of eastern Asia or specialists in the above families, I recommend the book highly. The other volumes in this series also will be worthwhile additions to the shelves of museum libraries where collections of tropical Asian moths are maintained. Any lepidopterist doing serious work on phylogeny of the families of Lepidoptera will find this book to be of particular value.

RICHARD S. PEIGLER, *Department of Zoology, Denver Museum of Natural History, 2001 Colorado Boulevard, Denver, Colorado 80205.*

Journal of the Lepidopterists' Society
45(1), 1991, 70–71

CARTOGRAPHIE DES RHOPALOCERA DE LA RÉGION AFROTROPICALE (INSECTA LEPIDOPTERA) I. PAPILIONIDAE, by Guy Mathot. 1990. Privately published (in French). Distributed by Guy Mathot, Pied Noir 7, Namur B5000, Belgium. 104 pp., 166 figs., 86 distribution maps. Soft cover, 21 × 30 cm, no ISBN number, $49.00 U.S. (postpaid).

This is the first atlas in a planned series on the distribution of butterflies of the Afrotropical zone (=Africa south of the Sahara to the Cape of Good Hope and including Ahaggar, Air, Tibesti, Yemen, Aden, Oman, Madagascar, and many of the smaller islands off the African mainland). It treats 86 species of Papilionidae in all. A second atlas covering 157 species of *Charaxes* is in press, and Pieridae and Nymphalidae (in part) are in preparation.

Each papilionid species has its distribution represented by individual dots denoting specific localities plotted onto a standard base map of the region with country outlines and major rivers. Although each dot encompasses 7500 km^2, the method is highly commendable for its accuracy, precision, and uniformity, qualities all too often lacking in zoogeographic studies of this scale. Distributions were compiled selectively from the rich collection of the Musee Royal de l'Afrique Centrale (Tervuren, Belgium), by consultation with, and publications from, the National Museum (Paris) and The Natural History Museum (London), and from information supplied by R. H. Carcasson, E. C. G. Pinhey, G. Van Son, and others from African institutions. The resulting 86 maps are thus provisional, but eliminate many published errors (such as *Graphium kirbyi* Hewitson of "Lagos," *G. leonidas* Fabricius of "Cape Horn," etc.). The distributions given here largely represent the current state of knowledge.

A number of taxonomic changes are proposed, such as including *Graphium pelopidas* Oberthur in *G. leonidas*, *Papilio teita* van Someren in *P. desmondi* van Someren (=*P. magdae* Gifford), and *P. chitondensis* de Sousa in *P. bromius* Doubleday, etc. *Papilio interjecta* (recte *interjectus*) van Someren and *P. horribilis* Butler are accepted as true species. *Druryia* and *Iterus* are given subgeneric status, and Hancock's resurrection of the genus *Princeps* is not accepted. For the most part, subspeciation is not delimited, although *Graphium pylades* Fabricius is tacitly considered a subspecies of *G. angolanus* Goeze.

The three-page Introduction also discusses methods and taxonomy of the forthcoming *Charaxes* atlas and briefly documents range expansions, contractions, and extinctions of key indicator species of papilionids and *Charaxes* of the great equatorial forest which, sadly, has deteriorated during this century because of cyclic aridity and man's activities.

Following the Introduction, the 86 species are listed alphabetically under each genus with synonyms, author names, and year of publication. Only three genera occur in the Afrotropical zone: *Atrophaneura* (1 sp.), *Graphium* (33 sp.), and *Papilio* (52 sp.). The Afrotropical zone has the lowest number of papilionid genera of the world's biogeographic regions. All but nine of the 86 high-quality distribution maps, also arranged alphabetically in a separate section, are accompanied by an accurate black-and-white drawing or photograph or both of at least one adult, displaying the upperside and sometimes the underside for that species. Sometimes the geographical and individual variation is remarkable. For example, *Papilio dardanus* Brown is illustrated by 43 figures from various localities, showing geographic variants, female variation, morphotypes, aberrants, a sexual mosaic, and a gynandromorph! A partial Bibliography (excluding Lycaenidae and Riodinidae) lists 61 selected references from A through L.

About half the species are tropical with the remainder about equally divided between savanna and montane forest habitats. Eleven of the species are endemic to Madagascar and five are endemic to small Indian Ocean islands. Fifteen montane species are found mainly along the Rift Valley system, six of these clustering in the vicinity of Lake Victoria. Three species are very widespread (*Papilio dardanus*, *P. demoleus* Linné, *P. nireus* Linné) and six species are confined to the African east coast. Only a few of the tropical species have very restricted distributions.

Some of the atlas's island distributions should be updated: *Graphium angolanus*, *G. evombar* Boisduval, and *Papilio epiphorbas* Boisduval are now known from the Comoro Islands (Turlin, B. 1984, Papilio International 1(4):86–88); *P. menestheus lormieri* Distant is found on Madagascar (Paulian, R. 1951, Papillons Communs de Madagascar, Publications de l'Institut de Recherche Scientifique, Tananarive-Tsimbazaza, 90 pp.); *P. bromius* occurs on Fernando Poo and Annobon, and *P. cypraeofila* Butler is known from Fernando Poo (Viejo, J. L. 1984, EOS Revista Espanola Entomol. 60:335–369). No papilionids have reached the Seychelles, although *P. phorbanta* Linné is recorded from there (a doubtful record). Sokotran *P. bennettei* Dixey was doubtless derived from mainland *P. demoleus* Linné (Ogilvie-Grant, W. R. 1903, pp. 310–311 *in* Forbes, H. O. (ed.), The natural history of Sokotra and Abd-el-Kuri, R. H. Porter, London, 598 pp.).

Mimicry in papilionids seems to be especially well-developed in the Afrotropical and Oriental regions. Afrotropical papilionids are likely derived from Southeast Asian ancestors and their dispersal to Madagascar was primarily from eastern Africa (Hancock, D. L. 1983, Smithersia 2:1–48). An isolated relic on Madagascar, *Atrophaneura antenor* Drury, is the only representative of Troidini in the entire Afrotropical zone and is directly related to Oriental *Atrophaneura* by facies, genitalia, larva, pupa, and pigments (Ford, E. B. 1944, Trans. R. Entomol. Soc. London 94:201–223; Corbet, A. S. 1948, Trans. R. Entomol. Soc. London 99:589–607; Munroe, E. 1960, Can. Entomol. Suppl. 17:1–51; Igarashi, S. 1984, Tyo to Ga 34:41–96). The Oriental to Afrotropical transfer of ancestral tropical papilionids likely occurred during, and not later than, Paleocene-Eocene times, based on evidence from paleobotany, the *Praepapilio* fossils, and seafloor spreading.

This book will be of particular interest to papilionid specialists, biogeographers, and conservationists.

OAKLEY SHIELDS, *6506 Jerseydale Road, Mariposa, California 95338.*

Journal of the Lepidopterists' Society
45(1), 1991, 71–72

BEAUTIFUL BUTTERFLIES, A COLOURFUL INTRODUCTION TO NEPAL'S MOST BEAUTIFUL INSECTS, by Colin Smith (edited by Dr. T. C. Najupuria). 1990. Craftsman Press, Tecpress Service Ltd., 487/42 Soi Wattanasilp, Pratunam, Bangkok, Thailand. 32 pp., 74 color figs. Soft cover, 14 × 22 cm, no ISBN, $10 U.S. (postpaid).

This fascinating little handbook, well-illustrated and with an English text, is an excellent introduction to the most attractive members of Nepal's butterfly fauna. It summarizes basic ecological information about Nepal and some of its most characteristic butterflies, information drawn from Smith's earlier book, *Butterflies of Nepal (Central Himilaya)* (Tecpress Service L.P., Bangkok, Thailand, 1989), which Oakley Shields and I reviewed in 1989 (J. Lepid. Soc. 43:255–257).

The author's stated purpose of this book is to "open the eyes of the reader to a wealth of hitherto unsuspected beauty to be found in nearly every corner of Nepal." This purpose the author definitely accomplishes. The introductory section divides the butterfly faunal regions of Nepal into three areas: below 1500 m (lowlands, including both grassland and jungle), between 1500 and 3000 m (mostly wooded Himilayan forest), and from 3000 to 5500 m (alpine pastures, mostly grassland). Over 5500 meters is land of perpetual snow. Butterflies of the lowest zone fly all year, but are in greatest abundance from February to November. The species in this zone are usually common and widespread; their primary zoogeographic relationships are with India and Malaysia. The butterflies of the middle zone fly mostly from March to September, and in many cases are endemic to the Himilayan region, with some being quite local in distribution. The butterflies of the highest zone (alpine pastures) fly principally from June to August, the height of the monsoon season, with a few spring species occurring in March to May. Although most alpine species are considered rare, many are locally abundant. In general, the butterflies of this highest zone are related to those groups found in Japan and other areas of northern Asia, Europe, and even North America.

The bulk of this fine booklet is devoted to abbreviated text descriptions of representative species of the various genera of Nepalese butterflies. At the top of each page are nicely produced color plates illustrating groups of species. Some of the species are also shown below, interspersed among the text paragraphs, in field photographs of live adults. All of these photographs are reproduced with remarkable fidelity and the book is well worth acquiring for these color photographs alone. Included in the text are fascinating comments about behavior, distinguishing features, and other interesting aspects of the biology of Nepalese butterflies; these offer considerable incitement for further study.

Anyone interested in the butterflies of the southeast Asian area, especially Nepal, would find this booklet to serve quite well as a mini-field guide and as an interesting but inexpensive reference to this fascinating part of the world.

THOMAS C. EMMEL, *Division of Lepidoptera Research, Department of Zoology, University of Florida, Gainesville, Florida 32611.*

Journal of the Lepidopterists' Society
45(1), 1991, 72–74

WHITE BUTTERFLIES, by Kenji Kohiyama (English translation by Jay W. Thomas; Design and layout by Motoko Naruse-Kenichi Suzuki). 1989. Graphic-sha Publishing Co., Ltd., Tokyo, Japan. Distributed by Books Nippan, 1123 Dominguez Street, Suite K, Carson, California 90746. 96 pp., 97 color photographs. Hard cover, 24.5 × 25.5 cm, ISBN-4-7661-0519-2, 2990 yen ($28.95 U.S.).

This slim volume depicts 23 species of Japanese Pieridae in 97 color photographs (99 if you count the photographs on the front and back of the book jacket). The text (in Japanese and English) is brief, consisting of a short introduction, a three-paragraph afterword, and a sentence or two to accompany each photograph. It is, therefore, the exact opposite of John Feltwell's *Large White Butterfly* (1981, W. Junk Publ., The Hague, 542 pp.), which profiled that well-studied pierid species by compiling almost everything known about it into a volume of dense, telegraphic prose, devoid of color plates. Art Shapiro, in his review of Feltwell's book (1983, J. Lepid. Soc. 37:259) pointed out that it was no coffee-table book and commented on the lack of color plates by asking "Why should there be, in a book about a black-and-white 'bug'?" By contrast, Kenji Kohiyama's volume *is* a coffee-table book, and his photographs explore the nuances of the delicate shades of white, yellow, and orange of these butterflies by framing them against the dark somber colors of their habitats in Japan.

In fact, it is this very emphasis on habitat in the photographs that gives the book its unusual quality. I say unusual because I have grown accustomed to picture books of live butterflies featuring mostly closeups that offer as much detail of the insect's body and wings as possible. Think, for example, of the lavish display of intimate close-up photographs in Tom Emmel's *Butterflies: Their World, Their Life Cycle, Their Behavior* (1975, Alfred A. Knopf, New York, 260 pp.) or Kjell Sanved's and Jo Brewer's *Butterflies* (1976, Henry N. Abrams, New York, 176 pp.). In these books the butterfly occupies 40–70% of the area of the photograph. In startling contrast, the butterflies in almost all of Kohiyama's photographs occupy less than one percent.

Why the difference? It is certainly not due to lack of proper photographic equipment. Photographers will appreciate the fact that full details of equipment, film, and exposure are given for every photograph at the back of the book. These notes show that Kohiyama used four different cameras, ranging from a Nikon F2 to a Hasselblad 500C, and at least eight different lenses, ranging in focal length from 28 mm to 210 mm. (Surprisingly, considering the range and quality of Japanese made transparency films, Kohiyama used Kodak film exclusively: Kodachrome Professional 25, 64 & 200 and Ektachrome Professional 64 & 200.)

Nor is the difference due to lack of experience. Mr. Kohiyama has photographed butterflies for more than a quarter of a century; *White Butterflies* is his fourth book. His first two books, *Nihon no Chō* (*The Butterflies of Japan*, Yama to Keikoku Sha, 1971 and 1972) record the entire range of butterfly species in Japan. His third book, *Agehachō* (*Papilionidae Butterflies of Japan*, Kodansha), was published in 1986.

Instead, the difference lies in the purpose of the book, which the author describes as a sort of visual haiku. Haiku, of course, is a traditional form of Japanese poetry, unrhymed and consisting of only three lines containing a total of seventeen syllables. Kohiyama quotes social anthropologist Tadao Umesao: "Photographs are like haiku—haiku that you can see with eyes, haiku with form. Japan is essentially a land of the arts. Through haiku it has become the land with the world's greatest number of poets. Through photography it may well become the land with the greatest number of visual artists." Girded with this explanation, Kohiyama writes: "As I took the photographs for this book, I felt that I was creating haiku from butterflies. I used time to cut out pieces of space and put butterflies as I saw them into that space."

The spaces occupied by Kohiyama's butterflies span the extraordinary length of his island country—some 3000 km from north to south, encompassing over 25 degrees in latitude. But those statistics are less important to the Japanese than the consequences such distances have on the arrival of the seasons: cherry trees, for example, bloom 40 days earlier in the south of the country than in the north. Kohiyama makes similar observations about the effects of latitude on seasonality and on the activity periods of different pierid species.

Japanese culture is closely tied to the changing seasons. Indeed, the patterns of Japanese kimonos, known the world over for their beauty, are abstractions of natural phenomena that change through the four seasons. Nature is also an important theme in classical Japanese literature, in which seasonal elements are incorporated as essential background. Of interest here is that words that indicate the seasons are indispensable components of haiku. This ancient appreciation for the four seasons in Japanese culture and the relatively new concept of photography as visual haiku combine to give *White Butterflies* its structure.

The photographs begin with spring butterfly species and progress through summer and fall to winter species. Yet, oddly enough, most photographs were taken during the summer months. This is possible because of the great latitudinal range already mentioned. In actuality, the photographs progress roughly from north to south over part of this latitudinal range, beginning in central Japan, near Tokyo on the great island of Honshu (about the latitude of Nashville, Tennessee), and extending southwest to the subtropical reaches of the country on the islands comprising the Okinawa Prefecture (about the latitude of central Florida). Superimposed on this latitudinal range is a diverse topography, which greatly increases the number of species that can be sampled at one time of year.

If this book is to be judged by its photographs, how good are they? In my opinion, they are of variable quality. Many are very good and a few are excellent, but the author's purpose must be kept in mind when evaluating them. They are designed to include a butterfly in a conceptual space that represents a poetical interpretation of season. If you are looking for spectacular close-ups you will be disappointed. Furthermore, almost all photographs were taken in natural light, which severely limits depth of field under low light conditions; although the butterflies are usually in sharp focus, the background and foreground often are not. Only rarely does the author intentionally flatten a picture to isolate a butterfly from its surroundings by using a wide aperture to narrow the depth of field (e.g., the Gray-veined White, *Pieris melete* Menetries, p. 39). Another problem is that several pictures are marred (in my view) by large pieces of blurred vegetation in the foreground. Finally, a great many photographs were taken with backlighting, which works to great advantage on translucent butterflies such as the Lessor Brimestone (*Go-*

nepteryx aspasia Menetries, p. 43), the Psyche (*Leptosia nina* Fabricius, p. 75), and especially the Common Grass Yellow (*Eurema hecabe* L., p. 86); but in most cases the butterfly is opaque and appears dark because we see its shadowed side.

In a few shots, special techniques were used to create dramatic effects. For example, a Yellow Tip (*Anthocaris scolymus* Butler, p. 13) nectaring in a sea of mustard flowers was photographed with backlighting and in soft focus, creating an image reminiscent of the famous meadow scene near the end of the film, *Elvira Madigan* (or of a Bob Guccione photograph in *Penthouse,* depending on the nature of your artistic experience). One of my favorites is a photograph of a flying Great Orange Tip (*Hebomoia glaucippe* L., p. 59), intentionally blurred by rapid horizontal camera movement to isolate the essence of flight against an impressionistic slur of dark and light green foliage.

I suspect that the sparse captions that accompany the photographs were intended to reinforce the poetic intent of the image rather than inform, because they are rarely factual, and are sometimes misleading. Occasionally they are wrong (the caption for the set of four photographs on pages 76 and 77 says that a Psyche butterfly is weaving through the grass, but actually it is flying through nettles, with no grasses in sight). A few captions seem to have suffered in translation: consider, for example, this inscrutable sentence "The male Chocolate Albatross is a braggart."

The physical production of the book is excellent, the color printing is superb, and the design and layout are pleasing to the eye. There are, of course, the inevitable (sometimes comical) errors of English to be found in text translated from Japanese; I found about three dozen, but all are minor. Publishing the brief text in both Japanese and English is certain to broaden the book's appeal, although I was disappointed to find the species descriptions in the back of the book to be in Japanese only. And, although each species is referred to by its Japanese name in the photo caption and in the appendix of species descriptions, English-speaking readers who wish to look up the date and equipment used for each photograph must struggle to associate the caption (which provides only the English common name) with the appropriate entry in the appendix (which gives only the scientific name).

Kenji Kohiyama has a doctorate in engineering and works as a researcher in a radio communications systems laboratory. But in this book he has revealed himself as an artist as well as a scientist, expressing his love of nature and butterflies through the medium of visual haiku.

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

Journal of the Lepidopterists' Society
45(1), 1991, 75–81

OBITUARY

JOHN F. GATES CLARKE (1905–1990)

John F. Gates Clarke (1905–1990), 'Jack' to nearly every one who knew him, died on 17 September 1990 of complications following a stroke earlier in the year. He was President of the Lepidopterists' Society in 1972–73. He is survived by his wife, Nancy duPre Clarke; a son, John F. Gates Clarke Jr.; a daughter, Carol Clarke Lewis; five grandchildren; and one greatgrandson. His wife of 59 years, Thelma M. Clarke died in 1988.

Jack was born in Victoria, British Columbia, and moved to Bellingham, Washington when he was 11. He became interested in natural history at an early age and soon focused on Lepidoptera and then more specifically on microlepidoptera. He collected avidly in the surrounding area as a youngster and gradually expanded his collecting sphere with the passage of time. He attended Washington State College (now University) at Pullman where he earned a bachelor's degree in zoology and pharmaceutical chemistry and a master's degree in entomology and pharmacology. He taught biology at Washington State College from 1931 to 1935. He worked in a drugstore as a helper, then as a pharmacist, nights and weekends during high school, college, and while he was an instructor. Subsequently, he matriculated at Cornell University but did not complete a full semester. In 1935 he moved to Washington, D.C. where he accepted a position, which became available when Foster H. Benjamin died, with the Systematic Entomology Laboratory, U.S. Department of Agriculture. He worked first on noctuoids, then on micros. During World War II he served in Europe in the Quartermaster Corps and was discharged with the rank of captain. Shortly after the war he was assigned to work at the British Museum (N.H.) on the Meyrick types of microlepidoptera. During these two years he completed requirements for the Ph.D. degree, which was awarded by the University of London. The results of his research became the monumental eight volume *Catalogue of the Type Specimens of Microlepidoptera in the British Museum (Natural History) Described by Edward Meyrick,* for which he received the Society's Karl Jordan Medal in 1979. He transferred to the Smithsonian Institution in 1954 as curator of insects and was the first chair of the new Department of Entomology from 1963 to 1965. He retired in 1975, and for a few weeks took a vacation and came to the office irregularly; but within two months, he returned to his regular work schedule of 6:00 am to 3:30/4:00 pm, five days a week. He worked in this fashion until a heart attack slowed his pace in April 1989. He remained in good spirits and continued to conduct research, curate the collection, and make progress on cleaning his office; a stroke left him disabled in June 1990.

Jack's publications reflect his interests and field work. The fauna of the Pacific Northwest was an early focal point, followed by a taxonomic revision of the North American Oecophoridae; illustration and taxonomic assignment of 5000+ Meyrick species; hosts and life histories of northwestern *Agonopterix* and *Depressaria*; Oecophoridae and Tortricidae of the Neotropics; and study of island faunas, particularly the Antilles and the South Pacific. Throughout, he published on individual species and other small projects, usually to solve taxonomic problems for others. During his later years he made four trips to the Queen Charlotte Islands, British Columbia, and was beginning to work up this material. *Xanthorhoe clarkeata* Ferguson (Geometridae), collected on one of these trips was named for him. His last written paper, recently published in this *Journal*, described a new species of *Mompha* (Momphidae) discovered on the Queen Charlotte Islands.

In 111 scientific and popular publications on moths he described 2 new families, 71 new genera, 547 new species, and 10 new subspecies. Five publications on pottery resulted from a long-term interest in 'Rebekah-at-the-Well' teapots.

Foreign travel was infrequent for a field biologist during the early phase of his career. However, after WW II he conducted field work in several South American countries, 30 Antillean islands, 33 Pacific islands, and many sites in North America. In later years he concentrated on collecting and curating butterflies while preparing and studying specimens collected on earlier trips. He appreciated warm weather and undoubtedly designed much field work with this in mind. His first wife, Thelma, accompanied and assisted him on extended field work in the South Pacific. Nancy Clarke, an enthusiastic field worker, ably assisted Jack on several field trips.

Jack was preeminently pro-Smithsonian and National Insect Collection. He actively pursued high quality collections with the paramount objective to have them become part of the National Collection, and he made every effort to ensure that all staff actively participated in such activity. Even though space and drawers never seemed adequate, his philosophy was "We can always stack drawers on the floor," and "We have always found room for new material; the important object is to get it." He used to point with pride, tempered with a tinge of sadness that Busck could not see them, to the 2180 drawers of microlepidoptera contrasted with the four schmitt boxes that Busck found when he arrived at the Museum in the late 1800's.

Organization, attention to detail, and good work habits enabled Jack to accomplish as much as he did. Once he indicated that he never had had benefit of technical assistance during this entire working career. He made innumerable genital and wing preparations, mounted and spread several thousand specimens, and curated many drawers of moths in addition to conducting research. He allotted a specific amount of time each day to each activity and made progress in each area; however, exceptions to the schedule were made for visitors.

Through the years Jack was extremely helpful to a great many of the individuals who sought his advice, particularly younger workers. He always responded to interest on an individual's part with encouragement. He identified many specimens, especially of New World species, for a worldwide array of colleagues and workers.

Beyond entomology he was extremely interested in postage stamps, particularly of the United States. He amassed a valuable collection and sold it in the 1950's. Immediately, he began work on another that emphasized plate blocks. The extraneous stamps were sold from Clarke's stamp box. He maintained a wide selection of stamps in many denominations that people throughout the Museum of Natural History could buy and thus be saved a trip to the post office.

He was very active in two social/professional organizations, the Cosmos Club and the Washington Biologists Field Club. For several years he, Karl Krombein, and Paul Hurd had lunch at the Cosmos Club each Friday. He became a member of the Field Club in 1958 and regularly participated in its functions, particularly the spring and fall work days and field days.

He was an enthusiastic gardener; however, he had one criterion for selection of materials: the plant should require no care during the middle of summer when he might be collecting. He had a small rock garden, a wide array of iris and chrysanthemums, and spring bulbs. Each year he would bring lots of daffodils and chrysanthemums to the office for others to enjoy. Periodically, many were beneficiaries of his lifting and dividing bulbs or rhizomes.

When Jack turned 80, his friends and colleagues gave him a surprise party. Because he had always declined any party in his honor, particular attention was paid to this detail. The pretext came as a carefully made, formal inivitation (in an edition of two) to a non-existent museum function. The event was highly successful, so much so, that he proposed and held his own party on reaching 85. Another small event 'happened' when Jack celebrated 50 years of work and association with the Smithsonian. Under the guise of discussing a problem in the hall, the lepidopterists entered his room and then presented him with a bottle of wine for the occasion.

He received an Alumni Achievement award from Washington State University in 1983 and a Special Recognition award from the National Museum of Natural History in 1985. Also in 1985 he was elected to Honorary Life Membership in the Lepidopterists' Society.

Jack Clarke had an infectious enthusiasm for insects, all aspects of his work, and life in general. He served as a role model for many. With his death the lepidopterists at the National Museum of Natural History have lost their remaining link with an earlier generation of workers—Busck, Heinrich, and Schaus—and one who was highly concerned about systematic entomology at the national level. His activities have touched a wide circle of friends and associates. Each of us has lost something valuable by his passing.

BIBLIOGRAPHY

1. 1930. Entomology. British Columbia, Rept. Prov. Mus. 1929:12–16 (ill.).
2. 1931. Entomology. British Columbia, Rept. Prov. Mus. 1930:14–15 (ill.).
3. 1932. New microlepidoptera from the Pacific Coast; (Gelechiidae). Can. Entomol. 64:63–69 (ill.).
4. 1933. Notes and new species of microlepidoptera from Washington State. Can. Entomol. 65:84–93 (ill.).
5. 1934a. Entomology. British Columbia, Rept. Prov. Mus. 1933:33–36 (ill.).
6. 1934b. Notes and new species of microlepidoptera from Washington State. Can. Entomol. 66:171–181 (ill.).
7. 1935. Notes and new species of microlepidoptera from Washington State. Can. Entomol. 67:244–254 (ill.).
8. 1937. A new species of *Azenia* from California (Noctuidae; Acronictinae). Bull. So. Calif. Acad. Sci. 36(2):65–67 (ill.).
9. ——— and F. H. Benjamin. 1938. A study of some North American moths allied to the thyatirid genus *Bombycia* Hübner. Bull. So. Calif. Acad. Sci. 37(2):55–73 (ill.).
10. 1939. A new geometrid genus from North America, with a discussion of its type (Lepidoptera). Proc. Entomol. Soc. Washington 41(3):73–74 (ill.).
11. 1940a. A study of the North American moths formerly referred to *Delta* Saalmüller, with two new species (Lepidoptera: Phalaenidae). Bull. So. Calif. Acad. Sci. 39:39–52 (ill.).
12. 1940b. A new species of *Utetheisa* from Newfoundland (Lepidoptera: Arctiidae). Proc. Entomol. Soc. Washington 42:42–44 (ill.).
13. 1940c. The European genus *Morophaga* Herrich-Schäffer in North America. Bull. So. Calif. Acad. Sci. 39(2):114–117 (ill.).
14. 1940d. United States records of tropical American Lepidoptera. Proc. Entomol. Soc. Washington 42(7):155–156.
15. 1941a. The preparation of slides of the genitalia of Lepidoptera. Bull. Brooklyn Entomol. Soc. 36(4):149–161 (ill.).
16. 1941b. A new subspecies of *Arachnis* from California. Bull. So. Calif. Acad. Sci. 39(3):187–188.
17. 1941c. Revision of the North American moths of the family Oecophoridae, with descriptions of new genera and species. Proc. U.S. Natl. Mus. 90(3107):33–286, i–viii, pl. 1–48 (ill.).
18. 1941d. The North American moths of the genus *Arachnis* with one new species. Proc. U.S. Natl. Mus. 91(3123):59–70, pl. 10–12 (ill.).
19. 1942a. A synopsis of the genus *Anoncia,* with one new species (Cosmopterygidae [sic]: Lepidoptera). Can. Entomol. 74:17–19 (ill.).
20. 1942b. Notes and new species of microlepidoptera from Washington State. Proc. U.S. Natl. Mus. 92(3149):267–276, pl. 27–32 (ill.).
21. 1943. A new pest of *Albizzia* in the District of Columbia (Lepidoptera: Glyphipterygidae [sic]). Proc. U.S. Natl. Mus. 93(3162):205–208, pl. 21–25 (ill.).
22. 1946. Synopsis of the genus *Nealyda* Dietz, with descriptions of new species (Gelechiidae: Lepidoptera). J. Washington Acad. Sci. 36(12):425–427 (ill.).
23. 1947a. Notes on Oecophoridae, with descriptions of new species. J. Washington Acad. Sci. 37(1):2–18 (ill.).
24. 1947b. A new *Eucosma* from the El Segundo sand dunes (Olethreutidae: Lepidoptera). Bull. So. Calif. Acad. Sci. 46:51–53 (ill.).
25. 1947c. A new *Dichomeris* from eastern United States (Lepidoptera: Gelechiidae). Proc. Entomol. Soc. Washington 49(7):187–189 (ill.).
26. 1947d. New North American species and new assignments in the genus *Chionodes* (Lepidoptera: Gelechiidae). J. Washington Acad. Sci. 37(7):243–254 (ill.).
27. 1947e. Notes on, and new species of, American moths of the genus *Filatima* Busck (Gelechiidae: Lepidoptera). J. Washington Acad. Sci. 37(8):263–275 (ill.).
28. 1949. Notes on South American "Tortricidae" (Lepidoptera) and descriptions of new species. Acta Zoologica Lilloana 7:579–588, pl. 1–3 (ill.).

29. 1950a. A new genus and three new species of microlepidoptera from California (Ethmiidae). J. Washington Acad. Sci. 40(5):161–163 (ill.).
30. 1950b. Two new genera and three new species of microlepidoptera from Argentina (Gelechiidae). J. Washington Acad. Sci. 40(9):285–289 (ill.).
31. 1950c. The date of "A list of North American Lepidoptera" by Harrison G. Dyar. Proc. Entomol. Soc. Washington 52(6):308.
32. 1951a. A new genus and species of North American Olethreutidae (Lepidoptera: Laspeyresiinae). J. Washington Acad. Sci. 41(1):46–47 (ill.).
33. 1951b. Grant no. 1259 (1950). [Report.] Year book of the American Philosophical Society 1950:136.
34. Field, W. D., J. F. G. Clarke & J. G. Franclemont. 1951c. On a recent proposal to correct an error committed by the International Commission on Zoological Nomenclature at the Paris 1948 meeting. Science 113(2925):68–70.
35. 1951d. New species of Gelechiidae from Argentina (Lepidoptera). J. Washington Acad. Sci. 41(4):140–142 (ill.).
36. 1951e. New species of Olethreutidae from Argentina (Lepidoptera). J. Washington Acad. Sci. 41(9):296–299 (ill.).
37. 1951f. Index to "Exotic microlepidoptera." Vol. 5. Taylor & Francis, London. 4 pp.
38. 1951g. The moths of the genus *Coptotelia* Zeller (Lepidoptera: Oecophoridae). Acta Zoologica Lilloana 11:335–352, pl. 1–5 (ill.).
39. 1952a. Host relationships of moths of the genera *Depressaria* and *Agonopterix*, with descriptions of new species. Smithsonian Misc. Coll. 117(7):1–20, pl. 1–6 (ill.).
40. 1952b. An unrecorded homonym in Gelechiidae. Proc. Entomol. Soc. Washington 54(2):99.
41. 1952c. A new carpenterworm from Florida (Lepidoptera: Cossidae). J. Washington Acad. Sci. 42(5):156–158 (ill.).
42. 1952d. A new heliodinid from Illinois. Proc. Entomol. Soc. Washington 54(3):138–139 (ill.).
43. 1952e. Two new species of Olethreutidae from California (Lepidoptera). Bull. So. Calif. Acad. Sci. 52(2):60–62 (ill.).
44. 1953a. New species of Olethreutidae from Illinois (Lepidoptera). J. Washington Acad. Sci. 43(7):226–231 (ill.).
45. 1953b. Notes, new synonymy, and new assignments in American Gelechiidae. J. Washington Acad. Sci. 43(10):317–320.
46. 1954a. The correct name for a pest of cacao (Lepidoptera, Stenomidae). Proc. Entomol. Soc. Washington 56(5):266–267.
47. 1954b. The correct name for a pest of legumes (Lepidoptera, Olethreutidae). Proc. Entomol. Soc. Washington 56(6):309–310.
48. 1954c. *Eustalodes anthivora* (Gelechiidae, Lepidoptera), a new pest of *Achras sapota* in the Philippines. Philippine Agriculturist 37(8):450–451, pl. 1 (ill.).
49. 1955a. Catalogue of the type specimens of microlepidoptera in the British Museum (National History) described by Edward Meyrick. Trustees of the British Museum, London. Vol. 1. [viii] + 332 pp., pl. 1–4, fig. 1.
50. 1955b. Catalogue of the type specimens of microlepidoptera in the British Museum (Natural History) described by Edward Meyrick. Trustees of the British Museum, London. Vol. 2. 531 pp. (ill.).
51. [1955c] 1953. A new *Porphyrosela* from Argentina (Gracilariidae [sic]; Lepidoptera). Acta Zoologica Lilloana 13:69–70.
52. [1955d] 1953. A new *Acrocercops* from Argentina (Lepidoptera: Gracilariidae [sic]). Acta Zoologica Lilloana 13:71–72.
53. Snyder, T. E., H. H. Shepard & J. F. G. Clarke. 1955e. Austin Hobart Clark. [Obituary]. Proc. Entomol. Soc. Washington 57(2):83–88 (ill.).
54. 1955f. Mann collection to Smithsonian Institution. Entomol. News 66(6):165.
55. 1955g. Insects of Micronesia. Vol. 1. [Book review.] Proc. Entomol. Soc. Washington 57:239.
56. 1955h. Smithsonian Institution receives Bromley collection. Entomol. News 66(9):238.

57. 1955i. Neotropical moths of the genus *Orthocomotis* Dognin (Lepidoptera: Tortricidae). Trans. Roy. Entomol. Soc. London 107:139–167 (ill.).
58. 1956a. Microlepidoptera of Argentina, VI (Oecophoridae). Entomol. News 67(10): 253–256 (ill.).
59. 1956b. Grant no. 1878 (1955). [Report.] Moths of the genera *Depressaria* and *Agonopterix* (Oecophoridae). Year Book of the American Philosophical Society 1955: 129.
60. 1956c. Outstanding collection to Smithsonian Institution. Entomol. News 67(8):217.
61. 1957. Nuevas especies de *Batrachedra* que atacan al *Agave* (Lepidoptera: Cosmopterygidae [sic]). Acta Zoologica Mexicana 2(1):1–4, pl. 1–2 (ill.).
62. 1958a. A new genus and two new species of microlepidoptera from Japan (Gelechiidae). Entomol. News 69(1):1–5 (ill.).
63. 1958b. The correct name for a pest of beans (Lepidoptera, Olethreutidae). Proc. Entomol. Soc. Washington 60(4):187.
64. 1958c. Catalogue of the type specimens of microlepidoptera in the British Museum (Natural History) described by Edward Meyrick. Trustees of the British Museum, London. Vol. 3. 600 pp. (ill.).
65. 1959. Recent Smithsonian Institution entomological accessions. Entomol. News 70(8): 220–222 (ill.).
66. 1960. A new species of moth injurious to pine (Lepidoptera: Blastobasidae). Florida Entomol. 43(3):115–117 (ill.).
67. 1962a. Neotropical microlepidoptera, I and II. Proc. U.S. Natl. Mus. 113(3457): 373–388 (ill.).
68. 1962b. New species of microlepidoptera from Japan. Entomol. News 73(4):91–102 (ill.).
69. 1962c. A new tortricid genus from South America. Proc. Biol. Soc. Washington 75: 293–294.
70. 1962d. A new species of *Trichotaphe* from Mexico and Hawaii (Lepidoptera: Gelechiidae). Proc. Hawaiian Entomol. Soc. 18(1):123–124 (ill.).
71. 1963a. Catalogue of the type specimens of microlepidoptera in the British Museum (Natural History) described by Edward Meyrick. Trustees of the British Museum, London. Vol. 4. 521 pp. (ill.).
72. 1963b. Butterflies. Golden Press, New York. 68 pp.
73. 1964a. Neotropical microlepidoptera, III. Restriction of *Gonionota melobaphes* Walsingham with descriptions of new species (Lepidoptera: Oecophoridae). Proc. U.S. Natl. Mus. 115(3480):61–83, pl. 1–3 (ill.).
74. 1964b. A new genus and species from the Juan Fernandez Islands (Lepidoptera: Blastodacnidae). Proc. Biol. Soc. Washington 77:125–126 (ill.).
75. 1964c. Neotropical microlepidoptera VI. Genera *Orsotricha* Meyrick and *Palinorsa* Meyrick (Gelechiidae, Oecophoridae). Proc. U.S. Natl. Mus. 116(3502):197–204, pl. 1 (ill.).
76. 1965a. Catalogue of the type specimens of microlepidoptera in the British Museum (Natural History) described by Edward Meyrick. Trustees of the British Museum, London. Vol. 5. 581 pp. (ill.).
77. 1965b. Microlepidoptera of Juan Fernandez Islands. Proc. U.S. Natl. Mus. 117(3508): 1–105, pl. 1 (ill.).
78. 1967. Neotropical microlepidoptera XIV. Chilean microlepidoptera described by Emilio Blanchard. Proc. U.S. Natl. Mus. 122(3591):1–8 (ill.).
79. 1968a. The correct name for the mimosa webworm (Lepidoptera: Glyphipterygidae [sic]). Ann. Entomol. Soc. America 61(1):228–229 (ill.).
80. 1968b. Neotropical microlepidoptera XVI. A new genus and two new species of Oecophoridae. Proc. U.S. Natl. Mus. 125(3654):1–8, pl. 1–2 (ill.).
81. 1968c. Neotropical microlepidoptera, XVII. Notes and new species of Phaloniidae. Proc. U.S. Natl. Mus. 125(3660):1–58, pl. 1–4 (ill.).
82. 1969a. Catalogue of the type specimens of microlepidoptera in the British Museum (Natural History) described by Edward Meyrick. Trustees of the British Museum, London. Vol. 6. 537 pp. (ill.).

83. 1969b. Catalogue of the type specimens of microlepidoptera in the British Museum (Natural History) described by Edward Meyrick. Trustees of the British Museum, London. Vol. 7. 531 pp. (ill.).
84. 1970. Catalogue of the type specimens of microlepidoptera in the British Museum (Natural History) described by Edward Meyrick. Trustees of the British Museum, London. Vol. 8. 261 pp. (ill.).
85. 1971a. The Lepidoptera of Rapa Island. Smithsonian Contrib. Zool. 56:iv + 1–282 (ill.).
86. 1971b. Neotropical microlepidoptera XIX. Notes on and new species of Oecophoridae (Lepidoptera). Smithsonian Contrib. Zool. 95:1–39 (ill.).
87. 1972a. Two pests of beans from tropical America (Lepidoptera: Olethreutidae). Proc. Entomol. Soc. Washington 74(4):467–471 (ill.).
88. 1972b. The moths of America north of Mexico. [Book review.] Smithsonian 3(2):64.
89. 1973a. A new genus and species of Oecophoridae from tropical America. J. Lepid. Soc. 27(2):99–102 (ill.).
90. 1973b. Recent Smithsonian Lepidoptera Accessions. J. Lepid. Soc. 27(3):240–241.
91. 1973c. The genus *Eumarozia* Heinrich (Olethreutidae). J. Lepid. Soc. 27(4):268–274 (ill.).
92. 1974. Presidential address—1973. The National Collection of Lepidoptera. J. Lepid. Soc. 28(3):181–204 (ill.).
93. 1976. Microlepidoptera: Tortricoidea. Ins. Micronesia 9(1):1–144 (ill.).
94. 1978a. A new species of *Stathmopoda* from Colombia (Lepidoptera: Stathmopodidae). Entomol. News 89(1, 2):51–54 (ill.).
95. 1978b. Neotropical microlepidoptera, XXI: New genera and species of Oecophoridae from Chile. Smithsonian Contrib. Zool. 273:v + 1–80 (ill.).
96. [1979a] 1978. A lost and misplaced taxon (Lepidoptera: Tortricidae). J. Lepid. Soc. 32(4):251–255 (ill.). [publ. 28 February 1979].
97. 1979b. Notes on Chilean Oecophoridae. J. Lepid. Soc. 33(2):139–43 (ill.).
98. 1980a. Transfer of microlepidoptera types to the Smithsonian Instutition. Proc. Entomol. Soc. America 82(4):540.
99. 1980b. Two new species of *Proeulia* from the Desventuradas Islands (Tortricidae). J. Lepid. Soc. 34(2):182–186 (ill.).
100. 1982. A new genus and two new species of Oecophoridae from Colombia (Lepidoptera). J. Res. Lepid. 20(1):46–50 (ill.).
101. 1983a. A new species of *Eomichla* from Costa Rica (Oecophoridae). J. Lepid. Soc. 37(2):155–159 (ill.).
102. Brown, R. L., J. F. G. Clarke & D. H. Habeck. 1983b. New host records for Olethreutinae (Tortricidae). J. Lepid. Soc. 37(3):224–227.
103. 1984. Insects of Micronesia microlepidoptera: Gelechioidea. Ins. Micronesia 9(2): 145–155 (ill.).
104. 1986. Pyralidae and microlepidoptera of the Marquesas Archipelago. Smithsonian Contrib. Zool. 416:iii + 1–485 (ill.).
105. 1987a. The correct identity of *Acleris inana* Robinson (Lepidoptera: Tortricidae). Proc. Entomol. Soc. Washington 89(1):175–176 (ill.).
106. 1987c. Range extension of the genus *Asymphorodes* (Lepidoptera: Cosmopterigidae). Proc. Biol. Soc. Washington 100(3):596–599 (ill.).
107. 1987d. Two new species of *Cryptophlebia* Walsingham from Chile (Lepidoptera: Olethreutidae). Acta Entomologica Chileana 14:7–12 (ill.).
108. 1989. Spencer collection given to the Smithsonian. J. Lepid. Soc. 43(2):147–148.
109. [1991a] 1989. A new species of *Argyrotaenia* from Arizona (Lepidoptera: Tortricidae). J. Res. Lepid. 20(1–2):97–99 (ill.). [publ. January 1991].
110. [1991b] 1990. A new species of *Mompha* (Momphidae) from the Queen Charlotte Islands, British Columbia. J. Lepid. Soc. 44(4):252–256. [publ. 16 May 1991].
111. *In press*. Immidae. Ins. Micronesia.

NON-LEPIDOPTERA

1. 1963. Buxom Rebekah at the well. Antiques 87:91.
2. 1978a. Rebekah-at-the-well teapots (part one). Spinning Wheel 34(6):17–20 (ill.).
3. 1978b. Rebekah-at-the-well teapots (part two). Spinning Wheel 34(7):11–15 (ill.).
4. 1978c. Rebekah-at-the-well teapots (part three). Spinning Wheel 34(9):27–30 (ill.).
5. 1978d. Rebekah-at-the-well teapots (part four). Spinning Wheel 34(10):35–37 (ill.).

RONALD W. HODGES, *Systematic Entomology Laboratory, United States Department of Agriculture, Agricultural Research Service, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.*

Journal of the Lepidopterists' Society
45(1), 1991, 82–84

IN THE FIELD WITH DR. CLARKE

The following is an account of three days in 1987 on a mountain top on the Queen Charlotte Islands, British Columbia, Canada with Dr. J. F. Gates Clarke. It was written by his assistant Nancy McIntyre. She took this photograph of Dr. Clarke. When he saw it later, he said this was how he wished to be remembered by his colleagues.

J. F. Gates Clarke in the field: Queen Charlotte Islands, 1987. (Photograph by Nancy McIntyre.)

After a brief time of beautiful sunshine, in an area that reminded us of the opening scene of "Sound of Music," the weather was changing. Our helicopter had left us on the mountain less than three hours before. A blanket of white fog began to fill in the valley below. Lovely to watch as it inched its way up the elevations, but as it engulfed our location we realized our collecting might be greatly curtailed.

It was Dr. Clarke's third collecting trip to these islands, and much effort and expense had been put into this expedition to an elevation of 2575 feet on Graham Island. When glaciers covered a large portion of North America, these peaks were still exposed and he felt there could be some very interesting finds. He had found new species on previous trips to similar elevations where he had collected during the day by "beating the bushes". This time he intended to collect using a black light and sheet.

As the fog enclosed our mountain saddleback we set up our equipment for the evening. A huge outcropping of rock made a perfect backing for our sheet. Our borrowed car battery and 12 volt black light were soon ready. It was not yet dark, so we had our handful of trail mix for supper and put on our warm gear for the damp, chilly night ahead. We had set up our primitive camp about 25 yards from the sheet near two depressions left by last year's snows. These gullies would provide good protection from the winds that often blow on these western slopes.

Dr. Clarke said he did not think we would have very good collecting because of the cold. Another reason, he said, was because we were well above the tree line and only sparse grasses and thick heather covered the nearly bare rock base. There did not seem to be much that would support a moth population.

About 2245 h it was dark enough to turn on the light. We made our way over the uneven terrain in the thick fog. No sooner did we attach the light cords to the battery than we were bombarded by dozens of a single species of moth. Dr. Clarke was in his glory! After collecting until we became frustrated by not being able to talk because the moths kept getting in our mouths and behind our glasses, we disconnected the battery to eliminate the attracting light.

Before dark we had carefully marked our camp area. Now that we had all the specimens we wanted, we started back to camp. The fog was thicker than ever and we became disoriented. We were wandering around an area no larger than a football field. We must have been within ten yards of all our gear, but our flashlights simply could not penetrate the fog. We each tried every "rule of the woods" we knew from experience and Scouting, but nothing worked. There were no mossy trees—no trees at all. There was no wind off the Pacific, which was several miles away. There were no clues except for the fact that our area was relatively flat and as we wandered, if we began to go downhill we knew to turn back to flatter land. We dared not separate. This fog reminded Dr. Clarke of a time when he lived in London and the fog was so thick he had to feel his way along the edge of the pathway to reach his home. He remained cheerful, encouraged me with stories, and would not let me be afraid. I am sure he was exhausted. The temperature had dropped into the upper 40's and we both knew the rest of the night would be very long and cold without our sleeping bags. Finally, out of the mist we spotted his red backpack just ten feet away. Wearily, we crawled into our damp sleeping bags to try to get a few hours sleep. I was still trying to get settled and warm when I heard Dr. Clarke begin to snore. Dr. Clarke had had a successful night of collecting.

The next two days were foggy and wet. Lepidoptera collecting was very poor. We spent most of our time turning over slate slabs of rock to see what treasures they hid. Anything alive, we captured. He was particularly interested in a small centipede we found. It appeared to be an immature, but we later found out it was a "pigmy" species. Melted snow pools yielded great finds. We were never at a loss for something to collect.

After our handful of trail mix for lunch on our third day, the fog began to lift. We could see a bright line along the horizon. For two and a half days we had worried about the helicopter getting back in to pick us up. Now, at last, conditions were beginning to improve. Excited about the weather change, I dashed up a slight incline, missed my footing, turned an ankle and heard a snap. Dr. Clarke tried to help me up, but we were both pretty sure my right ankle was broken. Just what he needed—an assistant with a broken bone! He wrapped it tightly in an ace bandage and my mountaintop collecting was over. The weather closed in again and things looked very doubtful for the helicopter to pick us up at the appointed time five hours later. There was no way we could be found in this fog. Our only tracking equipment was a borrowed walkie-talkie with a range of one mile. I could tell Dr. Clarke was very concerned. My ankle was really swelling and had turned a strange shade of green. Because of the cold and wet there was not much pain, but another night under these conditions would be difficult for both of us. As the hours crawled on and the weather did not improve, we worried even more. I had taken very few pictures because of the rain, but now we felt we needed a record of the conditions—just in case. That is when I took the picture of Dr. Clarke.

About 1730 h we heard a chopper. It was well below our location, but coming our way. The sound grew louder and Dr. Clarke quickly began collecting our gear. Then the engine noise faded as did our hopes for a prompt pickup. For the first time, I cried. Shortly, we heard the rotors again and this time the sound was louder and moving our way. Our greatest fear was that our pilot would not make an earnest effort to reach us in the fog since he did not know our desperate situation. He might decide to try again tomorrow. So with Dr. Clarke using the compass and me a short range radio, we anxiously explained our situation and actually led the pilot to a point where he could see the target Dr. Clarke had set up using our collecting sheet and backpacks. The helicopter was nearly on top of us before we could see it.

The helicopter landed and quickly all our gear was put on board. We were airborne in less than eight minutes. I counted only 37 seconds before we dropped out of our cloud to a bright sunny day. On the way to the hospital, our hard earned specimens received gentle care and so did I. Dr. Clarke had had another successful trip in the field.

Little did I know this would be the man I would marry.

NANCY L. DUPRE CLARKE, *Department of Entomology, NHB 127, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.*

Journal of the Lepidopterists' Society
45(1), 1991, 85

FEATURE PHOTOGRAPH

A Moveable Feast: Black tree ants (*Polyrachis dive*: Formicidae: Formiciinae: Camponotini) attend a mature larva (about 2.2 cm long) of the hairstreak butterfly *Remelana jangala mudra* (Fruhstorfer) (Lycaenidae) in Pak Sai O, Sai Kung, Hong Kong. Above: Ants caress the larva with tarsae and antennae; note the slit-like honey dew gland on the posterior dorsal surface of the larva. Below: One ant feeds on the sugary honey dew released by the eversible gland of the stimulated larva. Photographed September 1990 with a Nikon F3, micro-Nikkor 50-mm lens (Mitsubishi colour film, flash: 1/60 sec f32).

James J. Young, *8/F Manning House, 48 Queen's Road Central, Hong Kong.*

Journal of the Lepidopterists' Society
45(1), 1991, 86–87

MANUSCRIPT REVIEWERS, 1990

The merit of a scientific journal depends on the quality of its reviewers as well as of its authors, but the former are usually unknown to readers. The *Journal* relied on the expertise of 85 reviewers last year to provide 110 evaluations of manuscripts. It is with much gratitude that the *Journal* acknowledges the services of the people listed below from whom manuscript reviews were received in 1990.

*P. R. Ackery, London, England
David Adamski, Washington, DC
*Paul H. Arnaud, San Francisco, CA
*Richard A. Arnold, Pleasant Hill, CA
*George T. Austin, Las Vegas, NV

*M. Deane Bowers, Boulder, CO
Lincoln P. Brower, Gainesville, FL
F. Martin Brown, Colorado Springs, CO
*John W. Brown, Los Angeles, CA
Keith S. Brown, Jr., Campinas, São Paulo, Brazil
John M. Burns, Washington, DC

*Frances S. Chew, Medford, MA
J. F. Gates Clarke, Washington, DC
*Charles V. Covell, Jr., Louisville, KY

Julian P. Donahue, Los Angeles, CA

Thomas D. Eichlin, Sacramento, CA
Thomas Eisner, Ithaca, NY
Scott L. Ellis, Fort Collins, CO
John F. Emmel, Hemet, CA
*Thomas C. Emmel, Gainesville, FL
Marc Epstein, Washington, DC

Clifford D. Ferris, Laramie, WY
David Flaim, Baltimore, MD
Ronald J. Flaspohler, Parchment, MI

*Lawrence F. Gall, New Haven, CT
George L. Godfrey, Champaign, IL
Glenn A. Gorelick, Glendora, CA
Gary G. Grant, Sault Ste. Marie, Ontario, Canada
C. S. Guppy, Victoria, British Columbia, Canada

Dale H. Habeck, Gainesville, FL
Donald J. Harvey, Washington, DC
Jane Leslie Hayes, Stoneville, MS
Wade N. Hazel, Greencastle, IN
John B. Heppner, Gainesville, FL
Ronald W. Hodges, Washington, DC
John Holoyda, Chicago, IL

Nancy L. Jacobson, Ithaca, NY
Daniel H. Janzen, Philadelphia, PA
Dale W. Jenkins, Sarasota, FL

Gerardo Lamas Mueller, Lima, Peru
Robert C. Lederhouse, East Lansing, MI

---

* Reviewed two or more manuscripts.

David V. McCorkle, Monmouth, OR
Michael L. MacManus, Hamden, CT
Sterling O. Mattoon, Chico, CA
*Jacqueline Y. Miller, Sarasota, FL
James S. Miller, New York, NY
*Lee D. Miller, Sarasota, FL
Scott E. Miller, Honolulu, HI
*William E. Miller, St. Paul, MN
*Marc C. Minno, Gainesville, FL

Clas M. Naumann, Bielefeld, Germany
Herbert H. Neunzig, Raleigh, NC
Stanley S. Nicolay, Virginia Beach, VA

*Paul A. Opler, Fort Collins, CO

Dorothy P. Pashley, Baton Rouge, LA
John W. Peacock, Marion, OH
Richard S. Peigler, Denver, CO
Steven C. Peterson, Catonsville, MD
Austin P. Platt, Catonsville, MD
Michael Pogue, Washington, DC
Jerry A. Powell, Berkeley, CA
Gordon F. Pratt, Newark, DE
Robert M. Pyle, Gray's River, WA

Stuart J. Ramos, Mayaguez, Puerto Rico
John E. Rawlins, Pittsburgh, PA
Thomas J. Riley, Baton Rouge, LA
*Robert K. Robbins, Washington, DC

Theodore D. Sargent, Amherest, MA
Dale F. Schweitzer, Port Norris, NJ
Arthur M. Shapiro, Davis, CA
Julian Shepherd, Binghamton, NY
Gary A. Simmons, East Lansing, MI
Frank Slansky, Jr., Gainesville, FL
John T. Sorensen, Sacramento, CA
Ray E. Stanford, Denver, CO
Frederick W. Stehr, East Lansing, MI
*Steve Stone, Lakewood, CO

*B. Adrienne B. Venables, College Park, MD

Gilbert P. Waldbauer, Urbana, IL
Susan J. Weller, Washington, DC
David A. West, Blacksburg, VA
*Christer Wiklund, Stockholm, Sweden
Carroll M. Williams, Cambridge, MA

*Allen M. Young, Milwaukee, WI

Benjamin J. Ziegler, Summit, NJ

NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of Lepidoptera study. Categories are Articles, Profiles, 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 111 in Volume 44(2). *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 submit manuscripts in *triplicate*, typewritten, *entirely double-spaced*, with wide margins, on one side only of white, letter-sized paper. Prepare manuscripts according to the following instructions, and submit them flat, not folded.

Abstract: An informative abstract should precede the text of Articles and Profiles.

Key Words: Up to five key words or terms not in the title should accompany Articles, Profiles, General Notes, and Technical Comments.

Text: Contributors should write with precision, clarity, and economy, and should use the active voice and first person whenever appropriate. Titles should be explicit, descriptive, and as short as possible. The first mention of a plant or animal in the text should include the *full scientific name* with *author*, and *family*. Measurements should be given in metric units; times in terms of the 24-hour clock (0930 h, not 9:30 AM). Underline only where *italics* are intended.

Literature Cited: References in the text of Articles and Profiles should be given as Sheppard (1959) or (Sheppard 1959, 1961a, 1961b) and listed alphabetically under the heading LITERATURE CITED, in the following format without underlining:

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

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

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

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.

Tables: Tables should be numbered consecutively in Arabic numerals. Headings for tables should not be capitalized. Tabular material must be typed *on separate sheets*, and placed following the main text, with the approximate desired position indicated in the text. Vertical lines as well as vertical writing should be avoided.

Voucher specimens: When appropriate, manuscripts must name a public repository where specimens documenting identity of organisms can be found. Kinds of reports that require vouchering include life histories, host associations, immature morphology, and experimental enquiries.

Proofs: The edited manuscript and galley proofs will be mailed to the author for correction of printer's errors. Excessive author's changes at this time will be charged to authors at the rate of $2 per line. A purchase order for reprints will accompany proofs.

Page charges: For authors affiliated with institutions, page charges are $20 per *Journal* page. For unaffiliated authors, page charges are $10 per *Journal* page with a $50 maximum. Authors of Book Reviews and Obituaries are exempt from page charges. Authors unable to pay page charges for reasons such as difficulties with foreign exchange should apply to the editor for free publication.

Correspondence: Address all matters relating to the *Journal* to the editor.

PRINTED BY THE ALLEN PRESS, INC., LAWRENCE, KANSAS 66044 U.S.A.

CONTENTS

GENERAL NOTES

BOOK REVIEWS

OBITUARY

FEATURE PHOTOGRAPH

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

e 45 1991 Number 2

ISSN 0024-0966

JOURNAL

of the

LEPIDOPTERISTS' SOCIETY

Published quarterly by THE LEPIDOPTERISTS' SOCIETY

Publié par LA SOCIÉTÉ DES LÉPIDOPTÉRISTES

Herausgegeben von DER GESELLSCHAFT DER LEPIDOPTEROLOGEN

Publicado por LA SOCIEDAD DE LOS LEPIDOPTERISTAS

24 October 1991

THE LEPIDOPTERISTS' SOCIETY

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.

Active members—annual dues $25.00
Student members—annual dues $15.00
Sustaining members—annual dues $35.00
Life members—single sum $500.00
Institutional subscriptions—annual $40.00

Send remittances, payable to *The Lepidopterists' Society,* to: Fay H. Karpuleon, Treasurer, 1521 Blanchard, Mishawaka, Indiana 46544, U.S.A.; and address changes to: Julian P. Donahue, Natural History Museum, 900 Exposition Blvd., Los Angeles, California 90007-4057 U.S.A. For information about the Society, contact: William D. Winter, Secretary, 257 Common St., Dedham, Massachusetts 02026-4020, U.S.A. (617-326-2634). To order back issues of the *Journal, News,* and *Memoirs,* write for availability and prices to the Publications Coordinator: Ronald Leuschner, 1900 John St., Manhattan Beach, California 90266-2608, U.S.A.

Journal of the Lepidopterists' Society (ISSN 0024-0966) is published quarterly for $40.00 (institutional subscription) and $25.00 (active member rate) by the Lepidopterists' Society, % Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, California 90007-4057. Second-class postage paid at Los Angeles, California and additional mailing offices. POSTMASTER: Send address changes to the Lepidopterists' Society, % Natural History Museum, 900 Exposition Blvd., Los Angeles, California 90007-4057.

Cover illustration: Thirty years after its discovery, a new species of *Lithariapteryx* Chambers (Heliodinidae) gets a name (see page 89). The type locality of *L. elegans* Powell, which inhabits ocean beach foredune communities in central California, recently received protection from the California State Park System. Original drawing by Celeste Greene.

JOURNAL OF
THE LEPIDOPTERISTS' SOCIETY

Volume 45 1991 Number 2

Journal of the Lepidopterists' Society
45(2), 1991, 89–104

A REVIEW OF *LITHARIAPTERYX* (HELIODINIDAE), WITH DESCRIPTION OF AN ELEGANT NEW SPECIES FROM COASTAL SAND DUNES IN CALIFORNIA

JERRY A. POWELL

Department of Entomological Sciences, University of California,
Berkeley, California 94720

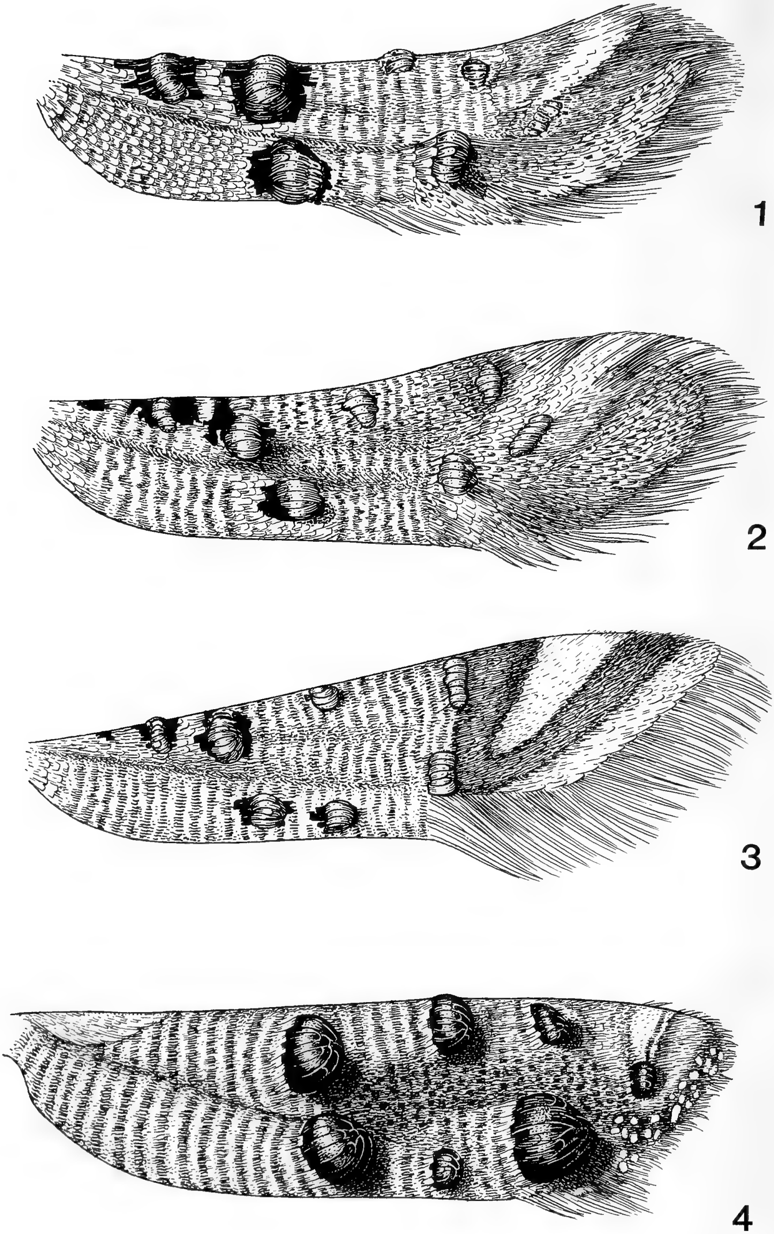
ABSTRACT. The genus *Lithariapteryx* Chambers comprises four species in the western U.S. and northwestern Mexico, although one, *L. mirabilinella* Comstock, is suspected to be a seasonal or geographical form of *L. abroniaeella* Chambers. *Lithariapteryx elegans* is a new species described from ocean beach foredunes in San Luis Obispo and Monterey counties, California. The adults are tiny, diurnal moths that have raised lead- or silver-colored spots on the forewings. The larvae are facultative leaf miners of *Abronia* and *Mirabilis* (Nyctaginaceae); each species is primarily or exclusively associated with either *Abronia* or *Mirabilis* but uses two or more species of the hostplant genus.

Additional key words: leaf miner, Nyctaginaceae, sand verbena, *Abronia*, *Mirabilis*.

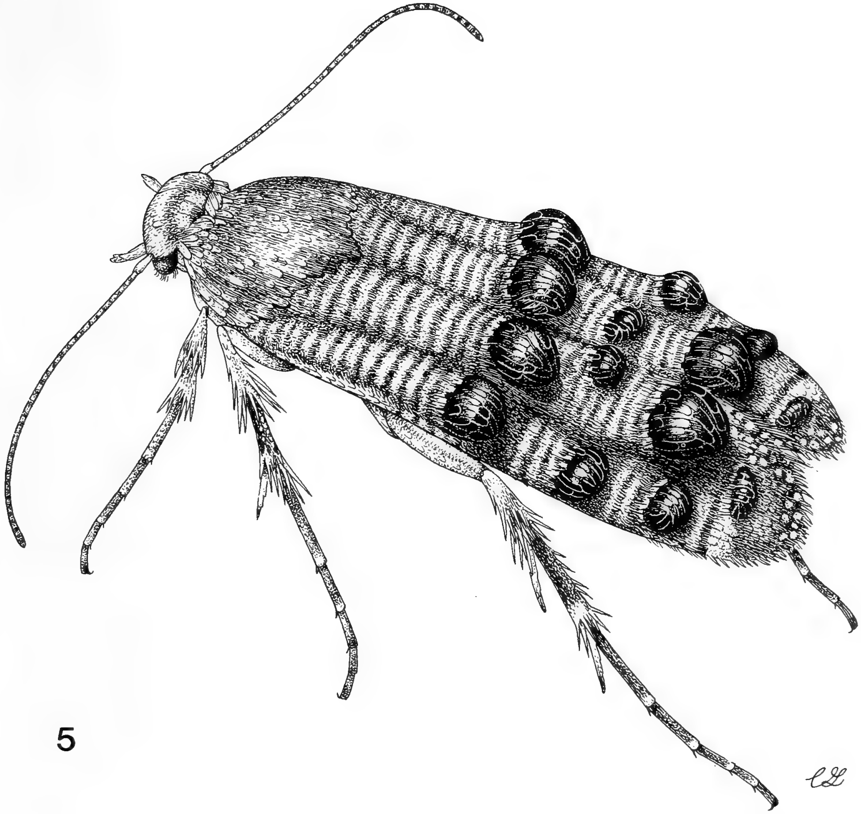
Members of the genus *Lithariapteryx* Chambers are tiny, diurnal moths that have the forewings adorned with upraised, gem-like, rounded tufts of shining lead- or silver-colored scales (Figs. 1–5). They occur primarily in sandy situations, in close association with the larval foodplants, *Abronia* (Sand Verbena) and *Mirabilis* (Four O'clock) (Nyctaginaceae). The genus is limited to the western United States and adjacent parts of Mexico.

Lithariapteryx was proposed by V. T. Chambers (1876) for *L. abroniaeella*, which he discovered at Edgerton, El Paso Co., Colorado. The concept of *Lithariapteryx* as a distinct genus has not been questioned, and there are no synonyms.

J. A. Comstock (1940) described two additional species without comparing them to *L. abroniaeella*. These are *L. jubarella* from the low Colorado Desert of southeastern California and from near Llano in the western Mojave Desert. At the Mojave locality he found adults of *L. jubarella* on *Mirabilis*, along with larvae, which, however, produced



FIGS. 1–4. Forewing of *Lithariapteryx*: **1,** *L. abroniaeella* Chambers, Pt. Reyes, Marin Co., California; **2,** *L. mirabilinella* Comstock, Tuttle Cr., Inyo Co., California; **3,** *L. jubarella* Comstock, The Gap, Coconino Co., Arizona; **4,** *L. elegans* Powell, Oso Flaco Lk., S.L.O. Co., California.



5

FIG. 5. Habitus of adult *Lithariapteryx elegans* Powell, Oso Flaco Lk., S.L.O. Co., California.

moths that are phenotypically different. These he named *L. mirabilinella*. Comstock suggested the possibility that the latter is a seasonal form of *jubarella*, but in reality *L. mirabilinella* morphologically is more similar to *L. abroniaeella*, from which it differs mainly in the reduced extent of orange on forewings. About 30 years ago we found a fourth species, on the coastal sand dunes of central California, that is abundantly distinct from the others; it is described here as *L. elegans*.

C. W. Baker, Boise State University, Boise, Idaho, has studied populations of moths phenotypically similar to *L. abroniaeella* and *L. mirabilinella* in Idaho, Oregon, and northern California. There are differences in size of individuals and in extent of orange on the forewings between first and second generation moths, which casts further doubt on the validity of *mirabilinella* as a taxon. Summer individuals are smaller than those of the spring generation in coastal dunes-inhabiting populations of *L. abroniaeella* and *L. elegans* in California, judging from field-collected adults. However, I do not see evidence of seasonal color change in these populations. This suggests that marked seasonal polyphenism is not the rule in *Lithariapteryx*, which would further contradict Comstock's suspicion that *L. jubarella* is a spring morph that gives rise to a later generation of the *mirabilinella* phenotype having different male genitalia.

I suspect that there are only three species because we have not documented sympatry of *L. abroniaeella* and *mirabilinella*, which would demonstrate that these two are not geographically or environmentally induced forms. It seems best to continue to regard all four as species pending further studies of the relationships.

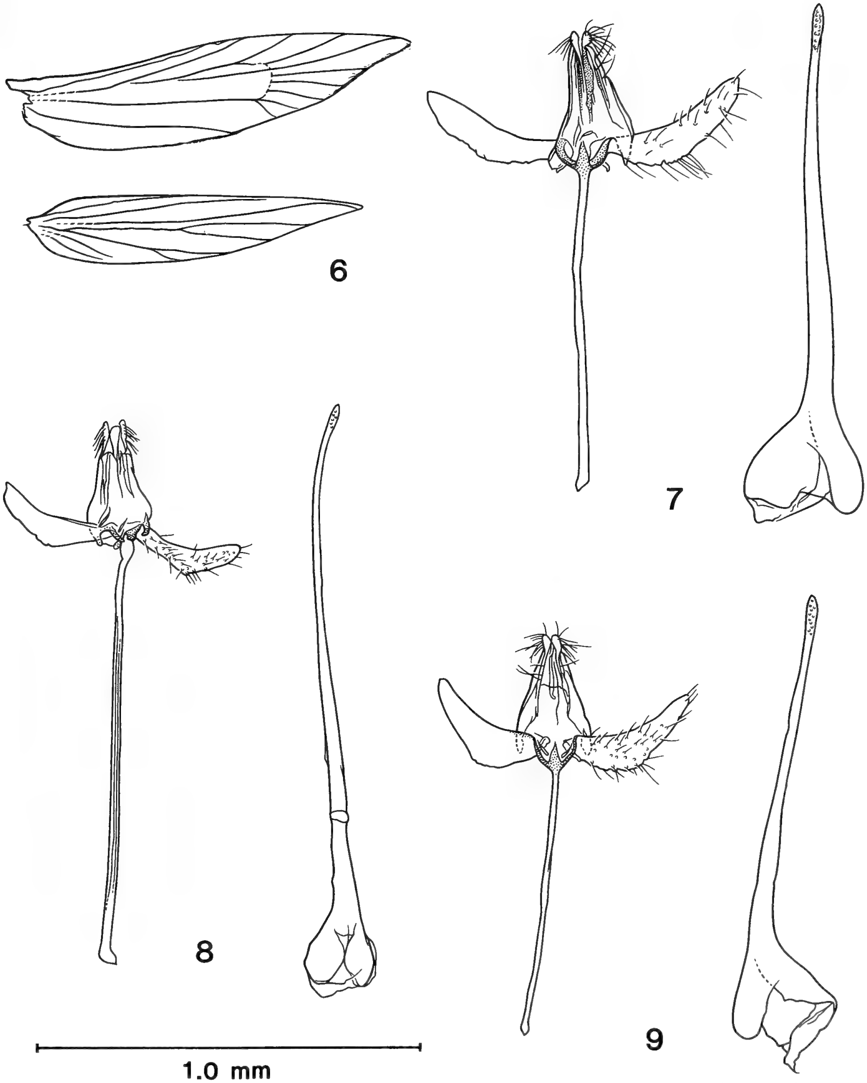
LITHARIAPTERYX CHAMBERS, 1876

Lithariapteryx Chambers, 1876, Canad. Entomol. 8:217.
Lithariopteryx Comstock, 1940, Bull. So. Calif. Acad. Sci. 38:175 (misspelling).

Type species. *Lithariapteryx abroniaeella* Chambers, 1876 (monotypy).

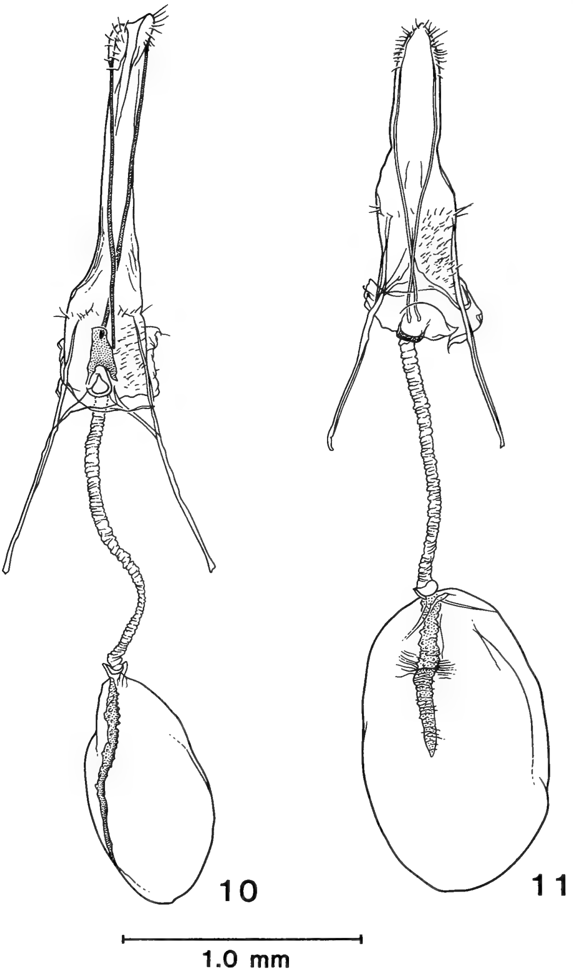
Diagnosis. Small, diurnal moths (FW length 2.8–6.5 mm). **Head:** smooth, clothed with tightly appressed, metallic colored scales; eye oval, small, index (length : height of front, measured from a horizontal line between antennal sockets to ventral margin of clypeus) = 0.75–0.83 in male, 0.67-0.70 in female; labial palpus smooth scaled, porrect, pointed, projecting to or ahead of plane of front; maxillary palpus reduced, not visible; tongue unscaled; antenna smooth-scaled, without projecting setulae in either sex, length about 0.67 FW length; ocellus prominent, situated below antennal socket, behind eye. **Forewing:** strongly attenuate distally; 10 veins all separate (Fig. 6), R stem partially to completely persistent through cell. A strong hair pencil from base of subcosta ventrally in both sexes. Scaling gray, uniformly strigulate transversely by rows of white tips; interrupted by prominent, bulging spots of elongate, metallic colored scales. **Hindwing:** lanceolate; 6 veins (+trace of 1st and 2nd A); Rs + M_1 separate, Cu_{1+2} forked near margin; fringe elongate, broader than membrane. Frenulum a single, strong bristle in both sexes. **Male genitalia:** (Figs. 7–9) with uncus undeveloped, socii relatively large, appressed to tegumen; saccus extremely elongate, slender (1.7–3.4 × tegumen length); aedeagus about 1.1 × longer than tegumen + saccus, with phallobase strongly swollen, abruptly narrowed, tapering to a lanceolate tip. **Female genitalia:** (Figs. 10, 11) apophyses moderately elongate, very slender; ostium surrounded by a thin, sclerotized ring; ductus bursae slender, elongate (more so after mating); corpus bursae oval, densely scobinate or foveolate over entire surface, sclerotization concentrated in a longitudinal band ventrally.

With the exception of color and the separate, rather than forked, $R_4 + R_5$ veins of the forewing, most of these characters apply equally well to species of *Heliodines* Stainton. Chambers (1876) compared his new genus to European *Glyphipteryx* Zeller, *Perittia* Stainton, and *Tinagma* Zeller, which at the time were placed together in Glyphipterygidae (Stainton 1859). Now they are considered to be Glyphipterigidae, Elachistidae, and Douglasiidae, respectively, members of three superfamilies. It is curious that Chambers did not mention his own genus *Aetole*, which he had described the previous year to accommodate *A.* (=*Heliodines*) *bella*, a new species from Texas (Chambers 1875). Presumably he believed his two genera were unrelated owing



FIGS. 6–9. **6,** Wing venation of *Lithariapteryx jubarella* Comstock, The Gap, Coconino Co., Arizona. FIGS. 7–9: Male genitalia of *Lithariapteryx*, ventral aspect, valvae spread, aedeagus removed: **7,** *L. abroniaeella* Chambers, The Gap, Coconino Co., Arizona; **8,** *L. jubarella* Comstock, Surprise Cyn., Inyo Co., California; **9,** *L. elegans* Powell, Oso Flaco Lk., S.L.O. Co., California. (Scale bar refers to Figs. 7–9, which are drawn at the same scale, including aedeagus.)

to differences in wing venation. Based on illustrations and examination of one male of the type species of *Heliodines*, *H. roesella* (L.), and study of several Nearctic species referable to this genus, I find few



FIGS. 10–11. Female genitalia of *Lithariapteryx*, ventral aspect: **10,** *L. abroniaeella* Chambers, The Dalles, Wasco Co., Oregon; **11,** *L. elegans* Powell, Oso Flaco Lk., S.L.O. Co., California.

consistent morphological differences between *Lithariapteryx* and *Heliodines*.

In *H. roesella*, *H. bella*, and *H. nyctaginella* Gibson (Spuler 1913, Forbes 1923) and *H. extraneella* (Walsingham) (JAP preps.), $R_4 + R_5$ are stalked about ½ their length, and $Rs + M_1$ are short-stalked in the hindwing. However, all veins are separate in *H. sexpunctella* (Walsingham), as is true of all four *Lithariapteryx* species. The forewing ground color in species of *Heliodines* is bright orange-red, with shining lead-gray markings, but these are not strongly raised like the metallic scale tufts of *Lithariapteryx* are. There is considerably greater variation in male genitalia in species assigned to *Heliodines* than is true in *Lithariapteryx*. In *H. roesella* the format is similar to *Lithariapteryx*, but with the socii sclerotized and widely separated (interpreted as "uncus paired" by Pierce & Metcalfe 1935), and there are thorn-like cornuti in the vesica; the saccus is slender and long (1.3–1.4 × tegumen length) but not as extremely so as in *Lithariapteryx*. In specimens identified as *H. bella* from Riverside, CA, the socii are greatly elongated and sclerotized, and the gnathos is membranous. *Heliodines extraneella* has the VIII tergite modified elaborately, extended middorsally into an uncus-like projection, laterally into attenuate projections, analogous to the development in some scythrids; the genitalia also differ markedly, with the tegumen reduced, the socii separated, gnathos lacking or membranous, and the valvae broadened. The answer as to whether the present separation of *Lithariapteryx* and *Heliodines* and assignment of some of the latter's species are valid will have to await a comprehensive reassessment of the Heliodinidae.

Biology of *Lithariapteryx*

Chambers (1876) discovered the larvae of *Lithariapteryx abroniaeella*, and the species was reared in California by H. H. Keifer and F. N. Pierce in the 1920's and 1930's (CAS, LACM specimens). Comstock (1940) obtained the original series of *L. mirabilinella* from field-collected larvae; R. Wielgus has reared *L. jubarella* in Arizona, and I have reared the four *Lithariapteryx* from about 25 larval collections, each species represented by samples from 2–8 localities. Recently, C. W. Baker has reared *L. abroniaeella* and *mirabilinella* in Idaho, Oregon, and northern California. Moreover, collections of adults from numerous additional populations have helped confirm the foodplant associations.

The larvae mine the subsucculent leaves of *Abronia* and *Mirabilis* (Nyctaginaceae). *Lithariapteryx abroniaeella* feeds on various species of *Abronia*, including *A. fragrans* in Colorado, *A. umbellata, maritima*, and *latifolia* on coastal sand dunes in California, *A. maritima* in Baja California, and *A. mellifera* on the Columbia River dunes near The Dalles, Oregon. I also found larvae on *Mirabilis froebelii* in northern Arizona, and Baker reared them from *M. macfarlanei* in Idaho. The newly described species, *L. elegans*, has been associated with *A. latifolia* and occasionally with *A. umbellata* growing in close proximity to *latifolia*. At its localities in the Santa Maria and Monterey Bay dune systems, *L. abroniaeella* is not closely sympatric, is rare, and we have found it only on *A. umbellata*, although *A. latifolia* is its primary host in San Francisco and northward.

By contrast, most records for *L. jubarella* and *L. mirabilinella* are from *Mirabilis*: the former from *M. laevis* in the Mojave Desert (Comstock 1940), at Riverside, and Santa Cruz Island, California. In addition, we found adults abundantly on *M. bigelovii* at several sites in Inyo Co., California, and Wielgus reared *jubarella* from that host in Arizona. We found larvae of *L. mirabilinella* on *M. bigelovii* at three localities in Inyo Co. and Baker discovered the same association in eastern Oregon. Baker also reared *mirabilinella* from *M. greenei* in Siskiyou Co., California, and from *Abronia fragrans* in southwestern Idaho.

The adults are diurnal and are encountered on sunny days perching and mating on the larval food plant. On windblown coastal dunes they often are found on the sand nearby. In appearance, they have been likened to small jumping spiders (Salticidae), which are common in dune habitats; when the moths are viewed from behind, the bulging metallic colored spots resemble the eyes of a salticid. I have not seen *Lithariapteryx* taking nectar from *Abronia* or *Mirabilis,* but *Heliodines* are found in the flowers of *Mirabilis,* so the larval hosts may serve as a nectar source. The moths often visit flowers of unrelated plants in the vicinity (see data in the species accounts): *L. abroniaeella* on *Senecio* and *Haplopappus* (Asteraceae) and *Croton* (Euphorbiaceae); *L. jubarella* on *Senecio* and *Hyptis* (Lamiaceae); *L. mirabilinella* on *Eriogonum* (Polygonaceae), *Senecio, Eriophyllum* (Asteraceae), and *Erysimum* (Brassicaceae); and numerous adults of *L. elegans* were observed nectaring on *Mesembryanthemum* (Aizoaceae), an African plant growing interspersed with *Abronia* on beach dunes at Monterey Bay.

There is considerable variation in mine form depending upon leaf thickness and other habitat factors. Typically larvae form a blotch-like mine basally in the leaf, from which digitate feeding tunnels project; often after mining out about half the leaf contents, the larva moves to another leaf. In thick-leafed plants such as *Abronia maritima* and *A. latifolia,* mines often are confined to the lower portion of the leaves and are not easily visible from above, and all of the late instar feeding may occur within one, or two overlapping leaves. In thin-leafed hosts (e.g. *A. umbellata, Mirabilis laevis*), several adjacent leaves are incorporated into a webbed shelter. Frass is ejected from a hole basally in the mine, where it lodges in silk webbing. In sand verbenas this usually is attached from the underside of the leaf, and the mine is evidenced by a glob of webbing caked with sand and frass. On *Mirabilis,* the webbing connects terminal leaves, and the larvae are found within the mine or in the webbing.

At maturity the larva leaves the last mine and affixes itself to a leaf or other surface (in the lab) for pupation, which occurs in a frail, nearly transparent cocoon. Possibly dormancy occurs in this stage, particularly in desert areas, but in my rearings, development occurred without a lengthy diapause, moths emerging in 13–14 days (*L. jubarella*), 20–24 days (*L. mirabilinella*), to as long as 25–30 days (*L. abroniaeella*) following pupation.

Coastal populations of *Lithariapteryx* evidently are multivoltine: at San Francisco Keifer reared *L. abroniaeella* in April, June, and August through October in 1926, and I found larvae in April, May, and July 50 years later; we have taken adults or larvae of *L. elegans* at the type locality in every month from March to November. Baker has observed two generations of *L. mirabilinella* in Idaho, but populations in some arid habitats may be normally univoltine, dictated by seasonal availability of food plants.

The larva of *Lithariapteryx abroniaeella* (given as *abromiella*) has been characterized and illustrated by Heppner (1987), and photographs of the pupa of *L. mirabilinella* were published by Comstock (1940).

KEY TO THE SPECIES OF *LITHARIAPTERYX*

1. FW costal area margined with orange at base, lacking silver spots in basal ⅓ .... *elegans* Powell, n. sp.
– FW costal area marked with silver & black on basal ⅓ 2
2. FW with 8–9 silver spots, including a well developed spot on dorsal margin between the black-rimmed one at mid-dorsum and tornal spot; HW fringe gray in anal area in both sexes. Saccus very long, 3.0–3.4 × tegumen length; ductus bursae elongate, >1.5 × posterior apophyses length .... *jubarella* Comstock
– FW with 6–7 silver spots, with at most a trace of silver before tornus beyond the black-rimmed spot at mid-dorsum; HW fringe in male and usually in female white, at least in anal area. Saccus shorter, 1.7–2.3 × tegumen length; ductus bursae shorter than posterior apophyses 3
3. FW ground color gray, usually with only a trace of orange in subterminal area .... *mirabilinella* Comstock
– FW with more extensive orange, forming a V-shaped spot surrounding subapical white triangle .... *abroniaeella* Chambers

Lithariapteryx abroniaeella Chambers
(Figs. 1, 7, 10, 12)

Lithariapteryx abroniaeella Chambers, 1876, Canad. Entomol. 8:217.
Lithariapteryx abromiella (misspelling) Heppner, 1987, Immature Insects: 411.

Diagnosis. FW length 2.8–5.0 mm. Head, tegulae, thorax dorsally shining lead-gray; labial palpus whitish; venter whitish blotched with gray. FW strigulate gray to tornus, followed by an orange V-shaped mark from costa, often incomplete; 3 conspicuous, raised, silvery spots margined with black on basal half: 2 along costa, 1 in dorsal area slightly displaced outwardly; 4 smaller silvery spots of lower relief, in distal half: 2 arising from white marks on costa at end of cell and above tornus, a larger one preceding and lining inner half of the orange V, one at apex of white marking inside V; additional white narrowly margining the V subterminally and at tornal margin. Fringe otherwise gray. HW fringe usually white blending to gray at apex, to entirely brownish gray in some females. Male genitalia as in Fig. 7 (drawn from JAP prep. 3697, The Gap, AZ; 4n); saccus 1.7–2.3 × longer than tegumen. Female genitalia as in Fig. 10 (drawn from JAP

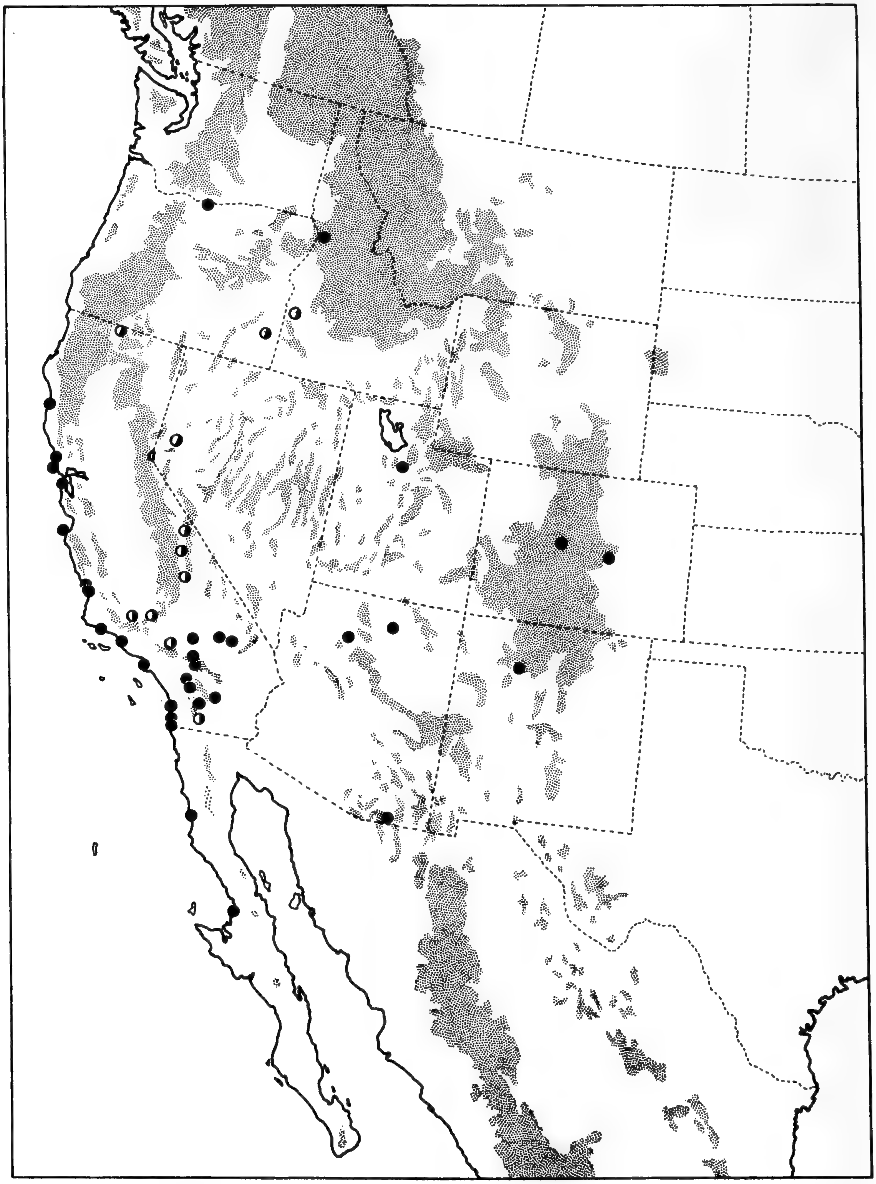


FIG. 12. Geographical distribution of *Lithariapteryx*: *L. abroniaeella* Chambers (closed circles); *L. mirabilinella* Comstock (half open circles).

prep. 6137, The Dalles, OR; 3n); ductus bursae ca. 0.75 (unmated) to 0.9 as long as posterior apophyses.

Lectotype male. By present designation: "Chambers Colo", "Lithariapteryx abroniaeella Cham Colo", "LECTOTYPE Lithariapteryx abroniaeella Chamb., by JAP '74", "Genitalia 3840 JAP '74", in MCZ. There are 9 syntypes with the same label data (2m, 5f, 1 no abd. MCZ; 1m USNM). Chambers (1876) cited the type locality as Edgerton, Colorado; Edgerton was a railroad stop on the Denver & Rio Grande line, about 15 airline km north of Colorado Springs, situated at about 1840 m elevation.

Geographical distribution. (Fig. 12) Populations assigned to this species are widespread in sandy, arid, riverine or seacoast dune habitats, from Colorado, Utah and Idaho, New Mexico, Arizona, deserts of California, and along the Pacific Coast from the Columbia River and beach dunes of northern California to Baja California Norte.

This species is closely sympatric with *L. jubarella* in northern Arizona and the Mojave Desert in California, but populations are spatially separated in regions of overlap with *L. mirabilinella* (Mojave Desert and Great Basin) and *L. elegans* (coastal California). We did not find *L. abroniaeella* occupying *Abronia latifolia* with *L. elegans* at any site. While the latter species often was abundant, *L. abroniaeella* was rare in those dune systems (1 specimen at Asilomar, Monterey Co. in 1959; a series in March to July on *A. umbellata* at Dune Lakes, which is inland, 3.5 km north of the type locality of *L. elegans*). However, in absence of *L. elegans*, *L. abroniaeella* was abundant on beach dunes at Morro Bay in 1961 and 1990 on *A. maritima*, and at several sites from San Francisco northward, on *A. latifolia*.

Data for plant associations. MEXICO: BAJA CALIF NORTE: Playa Sta. Maria, Bahia San Quintin, III-19-72, III-26-73, *ad*: assoc. *Abronia maritima* (JAP). ARIZONA: COCHISE CO.: Carr Cyn. Rd., 1680 m, Huachuca Mts., VII-20-72 *nect*: *Senecio douglasii* (JAP). COCONINO CO.: 16 km S The Gap, V-30-65, *lar*: r.f. *Mirabilis froebelii*, emgd. VI-VII-65 (JAP 65E5). CALIFORNIA: LOS ANGELES CO.: El Segundo, VIII-20-38, "larva on *Abronia maritima*" (W.D. Pierce), VII-17-75, *ad*: assoc. *A. umbellata* (JAP). MARIN CO.: Pt. Reyes, V-16-58, *ad*. assoc. *Abronia latifolia* (JAP), V-10-68, *lar*: r.f. *A. latifolia*, emgd. V-30-68 (JAP 68E21); No. Beach, Pt. Reyes Natl. Seashore, V-13-72, *ad*: assoc. *A. latifolia* (JAP), V-11-74, *lar*: r.f. *A. latifolia*, emgd. V-31 to VI-4-74 (JAP 74E27), V-1-76, VI-4-77, VI-3-78, *ad*: assoc. *A. latifolia* (JAP), VI-3-78, *lar*: r.f. *A. latifolia*, emgd. VII-2-78 (JAP 78F4), II-20-82, *lar*: r.f. *Abronia*, emgd. III-8/13-82 (D. L. Wagner, JAP 82B8). MENDOCINO CO.: Mackerricher Beach, V-7-76, V-1/2-77, *ad*: assoc. *A. latifolia* (JAP); Inglenook Fen, VII-24-75, *ad*: assoc. *A. latifolia* (JAP). RIVERSIDE CO.: Mecca, VIII-20-56, *ad*: on *Croton californicum* (M. Wasbauer). SAN BERNARDINO CO.: Afton Rd., 36 km SW Baker, IV-25-77, *ad*: assoc. *Abronia villosa* (Chemsak & JAP); Zzyzx Spr., 15 km S. Baker, IV-27-77, *ad*: assoc. and *lar*: r.f. *A. villosa*, emgd. V-26-77 (Buegler & JAP, 77D100). SAN DIEGO CO.: Border Field St. Beach, III-3-77, *ad*: assoc. *A. maritima* (JAP); Borrego, IV-2-53, *ad*: on *Larrea* (Zygophyllaceae) (P. D. Hurd); Solana Beach, VI-19-63, *ad*: assoc. *Abronia* (JAP). SAN FRANCISCO CO.: SAN FRANCISCO, many dates IV, VI, VIII, IX, X-1926, *lar*: r.f. *Abronia latifolia* (H. H. Keifer); Baker Beach, S.F., IV-13-77, *lar*: r.f. *A. latifolia*, emgd. V-9-77 (JAP 77D85), V-31-77, VIII-29-77, *ad*: assoc. *A. latifolia* (JAP); Laguna Puerca, S.F., V-6-61, *lar*: r.f. *A. latifolia*, emgd. V-22-61 (JAP 61E3); Sutro Hts., S.F., VII-25-76, *lar*: r.f. *A. latifolia*, emgd. VIII-21-76 (JAP 76G7), SAN LUIS OBISPO CO.: Dune Lakes, 5 km S. Oceano, VI-7-73, *ad*: assoc. *A. umbellata*, V-2-74, *lar*: r.f. *A. umbellata*, emgd. V-24-74 (JAP 74E2); Morro Bay, VIII-28-61, VIII-20-90, *ad*: assoc. *A. maritima*, *nect*: *Haplopappus squarrosus* (JAP). SANTA BARBARA CO.: U.C. Goleta, VII-17-65, *ad*: assoc. *A. maritima* (JAP); Coal Oil Pt., X-7-77, *ad*: assoc. *A. maritima* (JAP). SONOMA CO.: Dillon Beach, V-18-63, *ad*: assoc. *A. latifolia* (JAP). VENTURA CO.: Mouth Ventura River, IV-24-66, *ad*: assoc. *A. maritima* (JAP). IDAHO: IDAHO CO.: 14.5 mi N Riggins, U.S. 95, *lar*: ex *Mirabilis macfarlanei*, V-VI-1984 (C. W. Baker). ORE.: WASCO CO.: 13 km E The Dalles, VI-26-75, *ad*: assoc. and *lar*: r.f. *Abronia mellifera*, emgd. VII-24/29-75 (JAP 75F37).

Lithariapteryx mirabilinella J. A. Comstock
(Figs. 2, 12)

Lithariapteryx mirabilinella Comstock, 1940, Bull. So. Calif. Acad. Sci. 38:177.

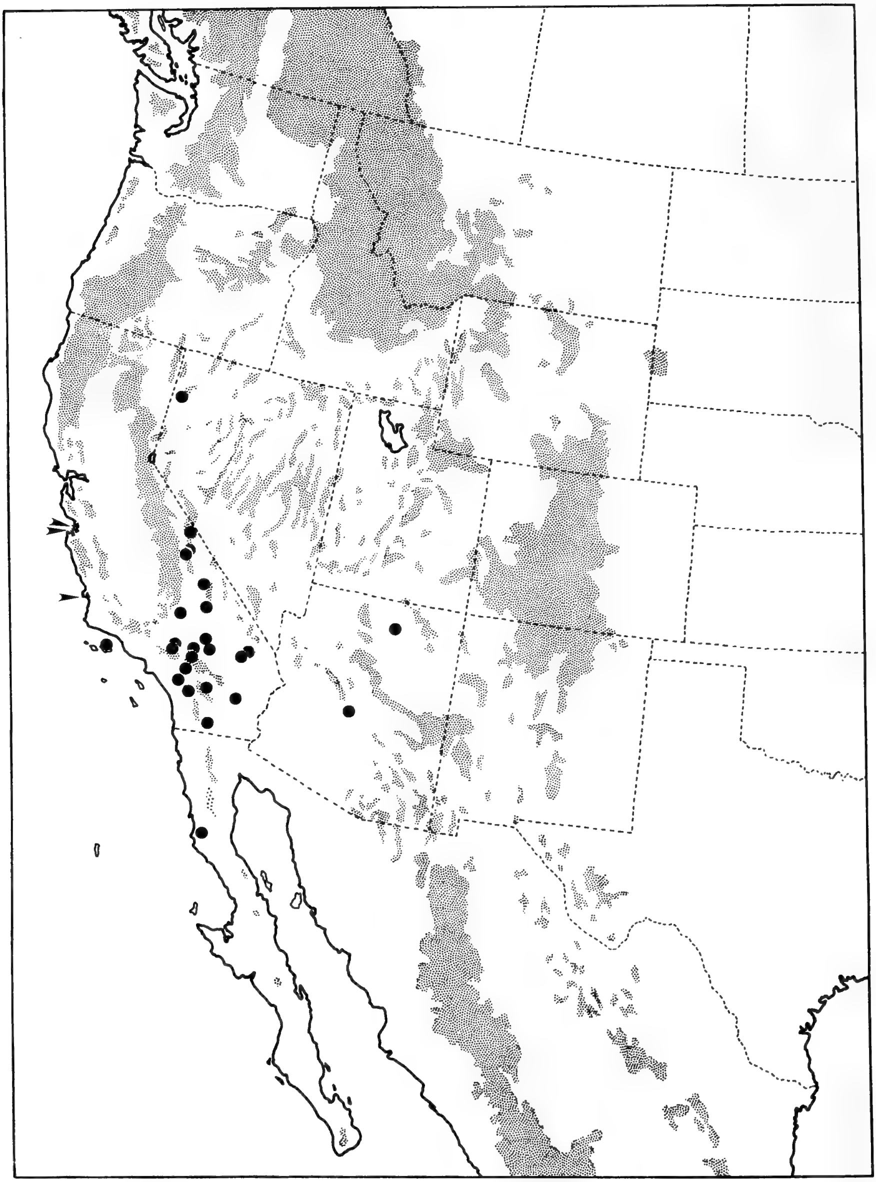


FIG. 13. Geographical distribution of *Lithariapteryx*: *L. jubarella* Comstock (closed circles); *L. elegans* Powell (beach foredunes at arrows).

Diagnosis. FW length 4.3–6.2 mm (3.6–4.0 mm, Ada Co., Idaho). As described for *L. abroniaeella* except FW paler, appearing pale gray to the unaided eye, with white scaling more extensive, the orange markings reduced to a trace or faint remnants of the V-shaped mark of *L. abroniaeella*. On one or both FW of some specimens there is a trace of an additional silvery spot midway between the large dorsal and tornal spots. HW fringe mostly white in both sexes. Genitalia indistinguishable from *L. abroniaeella* (n = 2m, 2f).

Holotype female. California: Lovejoy Buttes near Llano [10 airline km N Llano], Los Angeles Co., emgd. May 1939, larva on *Mirabilis laevis* (J. A. Comstock). The holotype as labelled is a female, the allotype a male, the reverse of that stated by Comstock (1940).

Geographical distribution. (Fig. 12): Foothills marginal to the Colorado and Mojave Deserts of California north in the Great Basin to southern Idaho and eastern Oregon. This appears to be a high desert race of *L. abroniaeella,* but if so the geographical relationships are complex and fragmentarily known, especially in the north.

Mojave populations are characterized by having larger adults than Arizona and California *L. abroniaeella.*

Data for plant associations. CALIFORNIA: INYO CO.: Carroll Cr., 14 km SW Lone Pine, V-10-69, *lar*: r.f. *Mirabilis bigelovii,* emgd. VI-4/9-69 (Opler & JAP 69E48); Mazourka Cyn., 13 km NE Independence, V-15-69, *lar*: r.f. *M. bigelovii,* emgd. VI-9-69 (Chemsak & JAP 69E85); Tuttle Cr., 3 km SW Lone Pine, V-9-69, *lar*: r.f. *M. bigelovii,* emgd. VI-4/9-69 (Opler & JAP 69E43). KERN CO.: N. Slope Mt. Pinos, 1680 m, 19 km NW Frazier Park, IX-12-64, *ad*: assoc. *Eriogonum latifolium* (JAP); Tehachapi Mt. Park, 1680–1830 m, VI-16-81, *ad*: assoc. *Erysimum capitatum* (JAP), VI-17-81, *ad*: *nect*: *Eriophyllum* and *Senecio* (De Benedictis & JAP). LOS ANGELES CO.: 3 km NW Valyrmo, V-1-68, pupa on *M. bigelovii,* emgd. V-2-68 (JAP 68E4). SISKIYOU CO.: 11 km E Hornbrook (Klamath Riv., 4.8 km E of Ager Rd. bridge), V-28-87, *lar*: r.f. *M. greenei,* emgd. VI-6/12-87 (C. W. Baker). IDAHO: ADA CO.: Bogus Basin, (T4N, R2E, SE ¼ SEC 14), *lar*: ex *Abronia fragrans* VI-VII-1986, III-29-87, emgd. IV-87 (C. W. Baker).

NEVADA: WASHOE CO.: 4.5 km W Wadsworth, VI-23-62, *ad*: assoc. *Tetradymia comosa* (G.I. Stage). OREGON: MALHEUR CO.: Owyhee River at Tunnel Cr., IV-12-87, *lar*: ex *M. bigelovii* (C. W. Baker).

Lithariapteryx jubarella J. A. Comstock
(Figs. 3, 6, 8, 13)

Lithariapteryx jubarella Comstock, 1940, Bull. So. Calif. Acad. Sci. 38:175.

Diagnosis. FW length 4.5–6.5 mm. Usually larger than sympatric or near sympatric *L. abroniaeella* and more brightly colored, with more extensive orange markings, often a transverse band preceding the subterminal V, white markings more extensive, including a spot at costa filling the inside of the orange V. Raised silvery spots distributed similarly but with a more well defined one at base of costa and an additional, clearly defined spot midway between the dorsal and tornal spots of *L. abroniaeella,* where there sometimes is a trace in *mirabilinella.* HW fringe entirely brownish gray in both sexes. Male genitalia as in Fig. 8 (drawn from JAP prep. 6128, Surprise Cyn., CA; 4n); saccus extremely long, 3.0–3.4 × tegumen length. Female genitalia similar to *L. abroniaeella,* ductus bursae more elongate, ca. 1.7 × length of posterior apophyses.

Holotype male. California: Mason Valley [16 airline km SE Julian], San Diego Co., 23 April 1939 (L. M. Martin) (LACM). Both the holotype and "allotype" as labelled are males. Comstock (1940) stated that the holotype is male, allotype female.

Geographical distribution. (Fig. 13) Arid areas in Baja California Norte, Mexico; Arizona, Nevada, and southern California, including Santa Cruz Island; in sandy habitats or in rocky places in association with *Mirabilis laevis.*

Larvae of this species have been observed only in February and March, and apparently they feed earlier than sympatric *Lithariapteryx* species. Comstock (1940) reported that he took a series of *L. jubarella* adults on *Mirabilis* at the Lovejoy Buttes in the Mojave Desert in April 1939, along with larvae of *L. mirabilinella*; I found the same situation at two sites in the foothills of the Owens Valley in May 1969. Similarly, in northern Arizona, adults of both *L. jubarella* and *L. abroniaeella* but only larvae of the latter were present on *M. froebelii* at the end of May.

Data for plant associations. MEXICO: BAJA CALIF. NORTE: 16 km SE El Rosario, III-31-76, *ad*: assoc. *Mirabilis* (J. T. Doyen). U.S.A.: ARIZONA: COCONINO CO.: 16 km S The Gap, V-30-65, *ad*: assoc. *Mirabilis froebelii* (JAP). MARICOPA CO.: 1.5 mi NE Desert Vista Pt., II-15-76, r.f. *Mirabilis bigelovii*, emgd. III-2/11-76 (R. Wielgus). CALIFORNIA: INYO CO.: Mazourka Cyn., 13 km NE Independence, V-11/15-69, *ad*: assoc. *Mirabilis bigelovii* (Chemsak, Doyen, Opler, Powell, Rude); Tuttle Cr., 3 km SW Lone Pine, V-10-69, *ad*: assoc. *M. bigelovii* (JAP). LOS ANGELES CO.: 3 km NW Valyrmo, V-1-68, *ad*: on *M. bigelovii* (JAP). RIVERSIDE CO.: Citrus Exp. Sta., Riverside, III-12-63, *lar*: r.f. *Mirabilis laevis*, emgd. IV-1/5-63 (JAP 63C6); Devil's Garden, *lar*: r.f. *M. laevis* emgd. II-25-39; 8 km S. Sage, IV-15/16-65, assoc. *M. laevis* (C. A. Toschi & JAP); Railroad Cyn., 6 km E Elsinore, IV-14/17-65, *ad*: assoc. *M. laevis* (D. F. Veirs & JAP). SAN DIEGO CO.: Cabezas, III-28-61, *ad*: assoc. *Hyptis emory* (Labiatae) (JAP). SAN BERNARDINO CO.: Ord Mtn. IV-19-60, *ad*: assoc. *Senecio douglasii* (JAP). New York Mts., *lar*: r.f. *Mirabilis*, emgd. V-20-39. SANTA BARBARA CO.: Prisoners' Harbor Creek, Santa Cruz Id., III-16-69, *lar*: r.f. *M. laevis*, emgd. IV-3-69 (JAP 69C53). NEVADA: WASHOE CO.: 20 km NW Gerlach, VI-11-70, *ad*: assoc. *M. bigelovii* (P. A. Opler).

Lithariapteryx elegans Powell, new species

(Figs. 4, 5, 9, 11, 13)

A distinctive species with snow white venter and peculiarly stubby forewings adorned with large, upraised scale tufts of shining steel-purplish. The costa is orange on basal half without metallic spots.

Male. FW length 3.25–5.0 mm (30n). **Head:** gray to whitish dorsally, becoming white at crown and ventrally including palpi. **Thorax:** gray dorsally, tinged with rust-orange anteriorly and on tegulae; white ventrally, legs banded with gray. **Forewing:** ground color dark gray, white transverse strigulae conspicuous as in *L. abroniaeella* to reduced. Costa narrowly rust-orange along basal half, sometimes a white patch at base; orange broader in terminal area between the markings but not extended into a V-shaped mark; 3 large, strongly upraised, rounded scale tufts of shining metallic steel color, reflecting purplish: 2 in middle of wing (one in cell and one slightly more distad in dorsal area), 3rd in tornal area; 3 or 4 small tufts of shining lead-colored scales about as prominent as in *L. abroniaeella*: just below costa before and beyond a transverse line drawn through the inner edge of the large tornal spot, 3rd in subapical area, connected to costa by a white band, 4th sometimes present or represented by a trace, in pretornal area midway between the large, purplish dorsal spots. Terminal area narrowly white before fringe, which is very short, gray sprinkled with white. **Hindwing:** gray, fringe scales white proximally becoming gray distally, around entire margin. **Abdomen:** steel gray with silvery white bands distally on A3-8, broader laterally and ventrally. Genital scaling dark gray. **Genitalia:** as in Fig. 9 (drawn from paratype, Oso Flaco Lk., CA, JAP prep. no. 3705; 5n); very similar to *L. abroniaeella*; saccus and aedeagus of *elegans* slightly more slender in relation to length.

Female. FW length 3.6–5.1 mm (40n). Generally as described for male, with raised spots of FW more well developed, colors usually more vivid. **Abdomen:** lacking the gray genital scaling of male, A7 terminated by a white band, A8 eversible, unscaled. **Genitalia:** as in Fig. 11 (drawn from paratype, Oso Flaco Lk., JAP prep. no. 6243; 6n); similar to *L. abroniaeella*, ductus bursae more elongate, ca. 1.5 × length of posterior apophyses.

Holotype male and allotype female. CALIFORNIA: Oso Flaco Lake, 5 mi [8 airline km] S. Oceano, San Luis Obispo Co., 7 June 1973, on *Abronia latifolia* (J. Powell); deposited in Essig Museum of Entomology (UCB).

Paratypes (135). CALIFORNIA: MONTEREY CO.: Ft. Ord, coastal dunes, 1 f V-18-77, *lar*: r.f. *Abronia umbellata*, emgd. VI-21-77 (JAP 77E118); Marina Beach, 2 m, 1 f, VII-15-76, r.f. *A. latifolia*, emgd. VIII-9/14-76 (JAP 76G2), 1 m VI-23-87 (R. L. Langston); Marina St. Beach, 8 km NE Seaside, 27 m, 21 f, VIII-26-81 (D. L. Wagner); Seaside, 1 m, IV-30-59 (J. A. Chemsak), 5 m, VII-4-59 (JAP), 1 f, IV-15-62 (Chemsak) 1 f, VIII-26-

TABLE 1. Size of individuals in *Lithariapteryx elegans*, comparing populations of Monterey and San Luis Obispo Co., CA, and spring vs. autumn adults in S.L.O. Co. (forewing length in mm).

	Males range/mean/SD	(n)	Females range/mean/SD	(n)
Monterey	3.4–4.3/3.90/±0.28	(13)	3.6–4.3/3.96/±0.23	(25)
S.L.O.	3.5–5.0/4.29/±0.42	(19)	3.6–5.1/4.28/±0.37	(16)
March–June	3.5–5.0/4.31/±0.45	(16)	3.9–5.1/4.35/±0.33	(12)
October	4.0–4.2/4.14/±0.09	(3)	3.6–4.5/4.06/±0.43	(4)

71 "Sand Verbena" (R. L. Langston); Salinas River mouth dunes, 7 m, 13 f, VII-15-76, assoc. *A. latifolia* and 5 f, r.f. *A. latifolia* emgd. VIII-12/14-76 (JAP 76G1), 1 f, VII-15-76, r.f. pupa in sand sift sample (P. A. Rude), 2 m, 10 f, V-18-77, assoc. *A. latifolia, nect. Mesembryanthemum* and *Eriophyllum*, 1 m, *lar*: r.f. *A. latifolia*, emgd. VI-1-77 (JAP 77E111), 1 f, *lar*: r.f. *A. umbellata*, emgd. VI-15-77 (JAP 77E114), 2 m, XI-9-77 (JAP & Rude); Zmudowski St. Beach, mouth Pajaro Riv., 5 m, 1 f, VII-2-76 (J. T. Doyen & Rude). SAN LUIS OBISPO CO.: Oso Flaco Lk, 8 air km S Oceano, 7 m, 4 f, VI-7-73, on *A. latifolia* (JAP), 5 m, 5 f, III-21-74, r.f. *A. latifolia*, emgd. IV-10/21-74 (JAP 74C12), 6 m, 5 f, IV-2-77, r.f. *A. latifolia*, emgd. IV-21/29-77 (JAP 77D4), 3 m, 4 f, X-7-77 (JAP).

Individuals tend to be smaller in the Monterey Bay population than those at the Santa Maria dunes (even though the proportion that was reared was larger in the latter population sample and possibly included artificially stunted individuals); also the few moths taken in October averaged smaller than those collected as late instar larvae in March and April, or as adults in June, in S.L.O. Co. (Table 1).

Lithariapteryx elegans is almost exclusively an insect associate of beach foredune communities. It depends upon *Abronia latifolia*, an active sand dune invader, but uses *A. umbellata* on stabilized sand where it grows near *A. latifolia*. The type locality consisted of chaparral-covered stabilized dunes in the 1960's, and *A. latifolia* in the vicinity presumably was limited to foredunes to the west that I did not visit. With increasing off-road vehicle (ORV) activity, extensive sand roads and active sand invaded the Oso Flaco Lake area by 1971; the active sand gradually increased its takeover of dune vegetation during 1971–77 (see photos, Powell 1981), when *A. latifolia* became prevalent and the collections of *L. elegans* were made. In 1980 the California State Park System gained control of the area, which had been operated as a county park, and beginning in 1982 excluded further ORV activity at the Oso Flaco Lake site. By 1987, when only fragments of natural vegetation survived in the active sand dunes where *L. elegans* lived in the 1970's, a revegetation project was initiated by planting two species of native grasses. The exclusion of vehicular traffic and the planting/irrigation project evidently provided sufficient stabilization that, despite four successive dry years, colonization by a variety of native plants has been successful, including *Abronia latifolia* and *A. umbellata*. Hence, we can expect survival of *L. elegans* at the type locality.

ACKNOWLEDGMENTS

The habitus drawings of *L. elegans* and forewings were made by Celeste Greene; genitalia figures were drawn by Tina Jordan. Y.-F. Hsu assisted with data compilation. Special thanks is given to Charles W. Baker, Boise State University, Boise, Idaho, who collected and reared most of the material representing northern populations of *Lithariapteryx*. His work was funded by the U.S. Fish and Wildlife Service, Endangered Species Program. Dr. Baker also reviewed a draft of the manuscript and provided helpful comments. In addition to the collectors cited in the text, I thank the following, whose cooperation enabled study of type specimens and other material in their care: C. W. Baker, Boise St. U., Boise, Idaho (BSU); J. M. Burns and D. Furth, Museum of Comparative Zoology, Harvard U., Cambridge, Massachusetts (MCZ); J. P. Donahue, Museum of Natural History of Los Angeles County, Los Angeles, California (LACM); D. K. Faulkner, San Diego Museum of Natural History, San Diego, California (SDNHM); R. W. Hodges, U.S. National Museum of Natural History, Washington, D.C. (USNM); R. L. Langston, Kensington, California (RL); N. D. Penny, California Academy of Sciences, San Francisco (CAS). Paratypes of the new species will be distributed to all these collections. This study was based on ca. 1100 specimens, of which 74% are in UCB, 12% in LACM, 5% in USNM, 4% CAS and BSU. Field work and laboratory surveillance of rearing lots during 1965–70 was funded by N.S.F. Grants GB-4014 and GB-6813X.

LITERATURE CITED

CHAMBERS, V. T. 1875. Tineina from Texas. Canad. Entomol. 7:73–75.

——— 1876. Tineina. Canad. Entomol. 8:217–220.

COMSTOCK, J. A. 1940. Four new California moths with notes on early stages. Bull. So. Calif. Acad. Sci. 38:172–182.

FORBES, W. T. M. 1923. The Lepidoptera of New York and neighboring states. Cornell U. Agric. Exp. Sta., Memoir 68, 729 pp.

HEPPNER, J. B. 1987. Heliodinidae (Yponomeutoidea), pp. 410–411. *In* Stehr, F. W. (ed.), Immature insects. Kendall-Hunt, Dubuque, Iowa. 754 pp.

PIERCE, F. N. & J. W. METCALFE. 1935. The genitalia of the Tineid familes of the Lepidoptera of the British Isles. Pierce, Oundle, Northants, U.K. 116 pp. + 68 pl.

POWELL, J. A. 1981 ("1978"). Endangered habitats for insects: California coastal sand dunes. Atala 6:41–55.

SPULER, A. 1913. Die sogenannten Kleinschmetterlinge Europas. Stuttgart: E. Schmeizer bart'sche Verlags. CXXVII + pp. 121–523, pl. 72–91.

STAINTON, H. T. 1859. A manual of British butterflies and moths. Vol. II. London, J. Van Voorst. xi + 480 pp.

Received for publication 18 October 1990; revised and accepted 4 April 1991.

Journal of the Lepidopterists' Society
45(2), 1991, 105–111

LARVAL FEEDING PREFERENCES OF *PLATYPREPIA GUTTATA* BOISDUVAL (ARCTIIDAE) FROM BEACH HABITAT AT POINT REYES NATIONAL SEASHORE, CALFORNIA

ROBERT S. BOYD

Department of Botany and Microbiology and Alabama Agricultural Experiment Station,
Auburn University, Alabama 36849-5407

ABSTRACT. Preferences of *Platyprepia guttata* caterpillars among foliage of 10 species of beach plants were determined in a laboratory experiment. *Cakile maritima, Lathyrus littoralis,* and *Mesembryanthemum chilense* (in that order) were preferred species; *Camissonia cheiranthifolia* ssp. *cheiranthifolia* and *Abronia latifolia* were secondary species; and *Elymus mollis, Ammophila arenaria, Ambrosia chamissonis, Atriplex leucophylla,* and *Calystegia soldanella* were non-preferred species. Sampling transects showed 51% of *Cakile* seedlings in the field were damaged by herbivores, implying that *Platyprepia* herbivory might have significant effects upon survival of *Cakile*.

Additional key words: plant population biology, *Cakile, Lathyrus, Mesembryanthemum,* Brassicaceae.

Herbivores may greatly influence the species composition of plant communities (Harper 1977). Insect herbivores often exhibit a temporal periodicity of abundance, during the peaks of which their influence is highly apparent. Causes of these 'outbreaks', and their effects on vegetation, have received increased attention in recent years (Barbosa & Schultz 1987).

The importance of herbivory in beach habitats rarely has been examined due to the obvious importance of physical factors such as salt spray (Barbour 1978, Barbour & DeJong 1977), wave disturbance (Payne & Maun 1984), etc. Yet a few studies indicate that insect herbivores may have a significant influence on the population biology of beach plants. Payne and Maun (1984) found a variety of insects attacked *Cakile edentula* (Bigel.) Hook. ssp. *edentula* var. *lacustris* Fernald (Brassicaceae) on a Lake Huron beach, and Keddy (1980) reported an outbreak of caterpillars which affected survival of East Coast *Cakile edentula* (Bigel.) Hook. ssp. *edentula* var. *edentula* plants.

Platyprepia guttata Boisduval (Arctiidae), the only species of the genus in North America, is found along the West Coast from northern California to Puget Sound, and thence inland to Colorado, Wyoming, and Montana (Holland 1915). During several years of field work on the biology of the beach plant *Cakile maritima* Scop. at Point Reyes National Seashore, I noted caterpillars of *Platyprepia* in some years but not others. In outbreak years, larvae apparently moved away from hinddune areas into beach (foredune and open beach) areas. In 1983, an outbreak of *Platyprepia* caterpillars was large enough that they could be found wandering on the open beach in the area washed by waves. During such outbreak years, *Platyprepia* may be abundant enough to have noticeable effects on plants in the beach habitat. Powell and Hogue (1979) mention *Platyprepia* is "common" at Point Reyes National Seashore and Pitts (1976) reported larvae as "abundant" on her Point Reyes study site.

Larval feeding preferences of *P. guttata* are virtually unknown. The reported larval food plant is bush lupine, *Lupinus arboreus* Sims (Tietz 1972), but larvae also have been reported to feed on *Amsinckia spectabilis* F. & M. (Boraginaceae) and *Cakile maritima* (Pitts 1976). Powell and Hogue (1979) stated larvae could be found "on bush lupine and probably other plants", but no preference study for plants from the beach habitat had yet been conducted. This study was designed to examine the feeding preferences of *Platyprepia* caterpillars to determine which beach species would be most affected by them during outbreak years.

METHODS

Point Reyes National Seashore is located on the California coast 50 km north of San Francisco. The northern beach of Point Reyes National Seashore forms one of the longest unbroken stretches of beach in northern California, extending 18 km. As with many northern West Coast beaches (Barbour et al. 1976), the foredune of the majority of this beach is dominated by the introduced grass *Ammophila arenaria* (L.) Link (Poaceae). One exception is a 1-km section of Kehoe Beach, where *Ammophila* patches are found interspersed with patches of the native grass, *Elymus mollis* Trin. ex Spreng. (Poaceae). The *Elymus* areas contain other beach plant taxa that are relatively scarce in the *Ammophila* areas. The 10 beach taxa selected for the preference experiment (see Table 1) were reported by Barbour et al. (1976) to be characteristic members of the beach community in California. Voucher specimens of these taxa were collected in an earlier study of plant–animal interactions in the beach habitat in this area of Point Reyes National Seashore (Pitts & Barbour 1979) and were deposited in the Carl W. Sharsmith Herbarium, San Jose State University.

Larvae were collected in late May on the foredune area of the beach near Abbott's Lagoon at Point Reyes National Seashore. Most of those collected were found on *Cakile* plants. Larvae were probably in their final instar, as many of them pupated before being released after the end of the experiment. Larvae were fed Romaine lettuce (*Lactuca sativa* L., Asteraceae) for 3 days, starved 1 day, and then placed in feeding containers. Feeding containers were an aluminum pie tin for the bottom with the top being a second inverted tin. A small piece of sponge was wired to the inside of the top and soaked with water to elevate humidity inside the feeding container to maintain plant freshness.

Plant samples were collected from the same area where larvae were obtained. A sample was the terminal portion of a forb stem, or an entire leafy shoot in the case of grasses. For forbs, one sample was taken from each clump encountered in the field. For grasses, one sample was taken every several meters of beachfront. Samples were sealed into plastic bags, taken to the laboratory, refrigerated, and used the following day. Forb shoots were trimmed to fit the feeding containers, yet have both young and old leaves present. One stem of each forb species was placed in each container. For grasses, 6-cm segments were cut from younger leaves and 4 placed together in a container to make up a sample. Plant samples were weighed and a larva placed into each of 44 containers. Nine additional containers, selected with a random numbers table, contained no larvae as controls. Samples were reweighed and examined for evidence of feeding damage daily for 3 days.

Moisture content of the plant samples was determined by gathering the control samples of each species into a paper bag and drying them at room temperature for several weeks. Initial weights for each species were totalled and compared to the collective dry weight to calculate initial percent moisture.

Transects to evaluate herbivore damage to *Cakile* in the field were established at Point Reyes National Seashore about 1 km south of Kehoe Creek in an area with abundant *Cakile*. I selected a location for the first transect and then established 14 subsequent ones spaced at 20-m intervals. Each 1-m-wide transect began at the seaward limit of the foredune and extended landward to the dune crest perpendicular to the shoreline. All *Cakile* seedlings found were examined for evidence of herbivory on 13 May 1983.

RESULTS AND DISCUSSION

Larvae showed a definite preference for the foliage of some beach taxa. Damage frequency curves indicate three levels of preference among the foliage offered (Fig. 1). *Cakile* and *Lathyrus* were highly preferred by the larvae on day 1, with at least two-thirds of the samples of both taxa showing some signs of herbivory. By day 2, about 50% of the samples of *Abronia* and *Mesembryanthemum* had been damaged, indicating they were secondary choices of the larvae. The remainder of the taxa offered were damaged in less than 33% of the trays by the third day, indicating that they were not preferred species.

Weight loss data verify some of these results, but show that in some cases damage was frequent but not severe or vice versa. Damaged

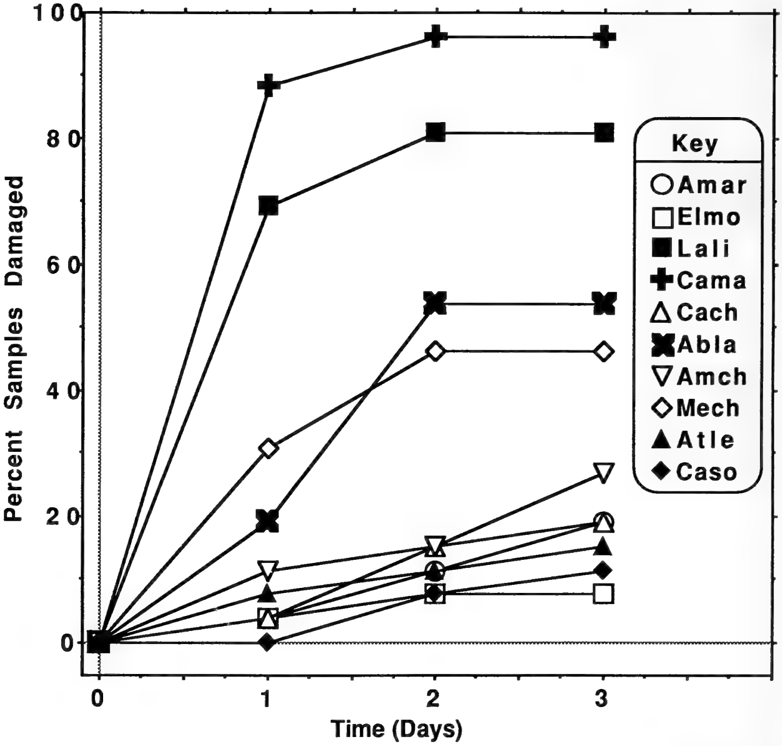


FIG. 1. Daily damage frequencies for the 10 plant species tested. Frequency data were compiled only from those feeding containers in which at least one plant sample was damaged by *Platyprepia guttata*. Species abbreviations are as listed in Table 1.

samples of *Cakile*, *Lathyrus*, and *Mesembryanthemum* all lost significantly more weight than undamaged samples (Table 1). Weight loss of damaged *Cakile* samples was greatest of all plant taxa (59%, versus 16% for undamaged samples), with some samples being almost completely consumed. *Lathyrus* and *Mesembryanthemum* were consumed less completely (Table 1). *Abronia*, which on the basis of damage frequency was a secondary choice of the larvae, was not consumed in detectable quantities. *Camissonia*, which was damaged quite infrequently, was consumed in quantity when damaged, resulting in statistically significant weight loss. Considering both damage frequency and the extent of damage to the samples, I conclude that the preference ranking was: *Cakile*, *Lathyrus*, *Mesembryanthemum* as preferred species (in that order); *Camissonia* and *Abronia* as secondary species; and the remainder as non-preferred species.

There was a general trend for preferred species to be those with higher moisture contents. Two of the three preferred species (*Cakile*

TABLE 1. Plant species tested for feeding preference by *Platyprepia guttata*. Moisture and weight loss data of damaged and undamaged leaves are also presented. Weight loss data are expressed as the percentage lost by the third day of the experiment (mean ± standard deviation, N in parentheses). Pairs of values for weight loss data marked with an asterisk (*) indicate a statistically significant difference between damaged and undamaged foliage (Mann-Whitney *U*-test, $P < 0.05$).

Species (family)	Abbreviation	% moisture	Weight loss (%) after 3 days	
			Damaged	Undamaged
Elymus mollis Trin. ex Spreng. (Poaceae)	Elmo	47.2	23 ± 3.7 (2)	22 ± 4.4 (51)
Ammophila arenaria (L.) Link. (Poaceae)	Amar	32.2	25 ± 9.8 (4)	29 ± 6.1 (49)
Cakile maritima Scop. (Brassicaceae)	Cama	88.4	59 ± 29 (25)*	16 ± 5.7 (28)*
Mesembryanthemum chilense Mol. (Aizoaceae)	Mech	91.0	8.3 ± 3.0 (12)*	4.5 ± 1.3 (41)*
Abronia latifolia Eschs. (Nyctaginaceae)	Abla	80.4	15 ± 3.5 (14)	14 ± 4.1 (39)
Ambrosia chamissonis (Less.) Greene (Asteraceae)	Amch	73.7	30 ± 5.3 (8)	26 ± 6.0 (44)
Atriplex leucophylla (Moq.) D. Dietr. (Chenopodiaceae)	Atle	68.2	26 ± 23 (4)	9.5 ± 6.6 (49)
Calystegia soldanella (L.) R. Br. (Convolvulaceae)	Caso	82.8	18 ± 4.5 (3)	19 ± 5.8 (49)
Lathyrus littoralis (Nutt. ex T. & G.) Endl. (Fabaceae)	Lali	61.9	36 ± 19 (21)*	20 ± 4.9 (32)*
Camissonia cheiranthifolia (Hornem. ex Spreng.) Raimann in Eng. & Prantl ssp. *cheiranthifolia* (Onagraceae)	Cach	72.9	36 ± 6.4 (5)*	25 ± 7.2 (48)*

and *Mesembryanthemum*) had the highest moisture contents (Table 1), whereas most of the non-preferred species had relatively low moisture contents. The major exception to this trend was *Lathyrus*, which had a low moisture content relative to other species yet was second only to *Cakile* in preference.

The preference of *Platyprepia* for *Cakile* and *Lathyrus* is interesting, as these two taxa belong to different plant families in which the foliage is chemically defended in different ways. *Cakile*, a member of the Brassicaceae, contains glucosinolates (Rodman 1974), whereas *Lathyrus*, a member of the Fabaceae, is protected by phytoalexins (Robeson & Harborne 1980) and alkaloids (Mears & Mabry 1971). Preference of *Platyprepia* for *Lathyrus* is not surprising. Its reported host plant, *Lupinus arboreus* (Tietz 1972), is another member of the Fabaceae in a genus also protected by alkaloids (Mears & Mabry 1971).

It is surprising that *Platyprepia* damaged some of the species tested. For example, Huiskes (1979) reported *Ammophila arenaria* to be relatively unpalatable to both vertebrate and invertebrate herbivores. In this experiment *Ammophila* was not preferred, but damage frequency was higher than for other non-preferred species (Fig. 1).

Besides *Lupinus arboreus, Platyprepia* larvae have been reported to feed on *Amsinckia spectabilis* F. & M. and *Cakile maritima* (Pitts 1976). Pitts (1976) reported that *Platyprepia* was "abundant" on her foredune study site at Point Reyes and consumed *Amsinckia* and *Cakile* blossoms. In my experiment, larvae avidly consumed leaves of *Cakile,* along with foliage of *Lathyrus* and *Mesembryanthemum. Lathyrus* was present on her study site but not reported as a host for *Platyprepia* (Pitts 1976).

More than half (51% of 175 individuals) of the first-year *Cakile* plants encountered in my foredune sampling transects had been damaged by herbivores. Damage varied greatly among individuals, but some small plants were almost leafless as a result of herbivore attack. I cannot be certain the damage was inflicted by *Platyprepia,* as other herbivores present in the area, e.g., the deer mouse, *Peromyscus maniculatus* (Wagner) (Muridae: Cricetinae), have been reported to consume *Cakile* foliage (Pitts & Barbour 1979).

Keddy (1980) studied the population biology of *C. edentula* ssp. *edentula* var. *edentula* on an East Coast beach gravel bar. He documented an outbreak of salt marsh caterpillars, *Estigmene acraea* (Drury), also in the Arctiidae, which killed at least 25% of the plants in the studied population. *Cakile maritima* is a facultative biennial in California, and is the only one of the species tested in this study which is not perennial. It germinates from October to May in California, so that some plants are very small when *Platyprepia* outbreaks occur (April–June). Young seedlings probably would be unable to recover from defoliation by *Platyprepia. Platyprepia*'s preference for *Cakile maritima* suggests it may play a role in *Cakile* population biology during outbreak years.

LITERATURE CITED

BARBOSA, P. & J. C. SCHULTZ (eds.). 1987. Insect outbreaks. Academic Press, San Diego. 578 pp.

BARBOUR, M. G. 1978. Salt spray as a microenvironmental factor in the distribution of beach plants at Point Reyes, California. Oecologia (Berlin) 32:213–224.

BARBOUR, M. G. & T. M. DEJONG. 1977. Response of West Coast beach taxa to salt spray, seawater inundation, and soil salinity. Bull. Torrey Bot. Club 104:29–34.

BARBOUR, M. G., T. M. DEJONG & A. F. JOHNSON. 1976. Synecology of beach vegetation along the Pacific Coast of the United States of America: A first approximation. J. of Biogeogr. 3:55–69.

HARPER, J. H. 1977. Population biology of plants. Academic Press, London. 892 pp.

HOLLAND, W. J. 1915. The moth book. Doubleday, Page and Company, Garden City, New York. 479 pp.

HUISKES, A. H. L. 1979. Biological flora of the British Isles. *Ammophila arenaria* (L.) Link. J. Ecol. 67:363–382.

KEDDY, P. A. 1980. Population ecology in an environmental mosaic: *Cakile edentula* on a gravel bar. Can. J. Bot. 58:1095–1100.

MEARS, J. A. & T. J. MABRY. 1971. Alkaloids in the Leguminosae, pp. 73–178. *In* Harborne, J. B., D. Boulter & B. L. Turner (eds.), Chemotaxonomy of the Leguminosae. Academic Press, New York. 612 pp.

PAYNE, A. M. & M. A. MAUN. 1984. Reproduction and survivorship of *Cakile edentula* var. *lacustris* along the Lake Huron shoreline. Amer. Midl. Nat. 111:86–95.

PITTS, W. D. 1976. Plant/animal interaction in the beach and dunes of Point Reyes. Ph.D. dissertation, University of California, Davis. 260 pp. University Microfilms Dissertation Abstracts Order Number 77-6355.

PITTS, W. D. & M. G. BARBOUR. 1979. The microdistribution and feeding preferences of *Peromyscus maniculatus* in the strand at Point Reyes National Seashore, California. Amer. Midl. Nat. 101:38–48.

POWELL, J. A. & C. L. HOGUE. 1979. California insects. Calfornia Natural History Guide 44. University of California Press, Berkeley. 388 pp.

ROBESON, D. & J. B. HARBORNE. 1980. A chemical dichotomy in phytoalexin induction within the Tribe Vicieae of the Leguminosae. Phytochemistry 19:2359–2366.

RODMAN, J. E. 1974. Systematics and evolution of the genus *Cakile* (Cruciferae). Contributions from the Gray Herbarium, Harvard University 4:3–146.

TIETZ, H. M. 1972. An index to the described life histories, early stages and hosts of the Macrolepidoptera of the continental United States and Canada. The Allyn Museum of Entomology, Sarasota, Florida. 1041 pp. (in 2 volumes).

Received for publication 13 December 1990; revised and accepted 10 June 1991.

Journal of the Lepidopterists' Society
45(2), 1991, 112–116

LAST STAGE LARVA AND PUPA OF *GLYPTOCERA CONSOBRINELLA* (ZELLER) (PYRALIDAE: PHYCITINAE)

H. H. NEUNZIG

Department of Entomology, North Carolina State University,
Raleigh, North Carolina 27695-7613

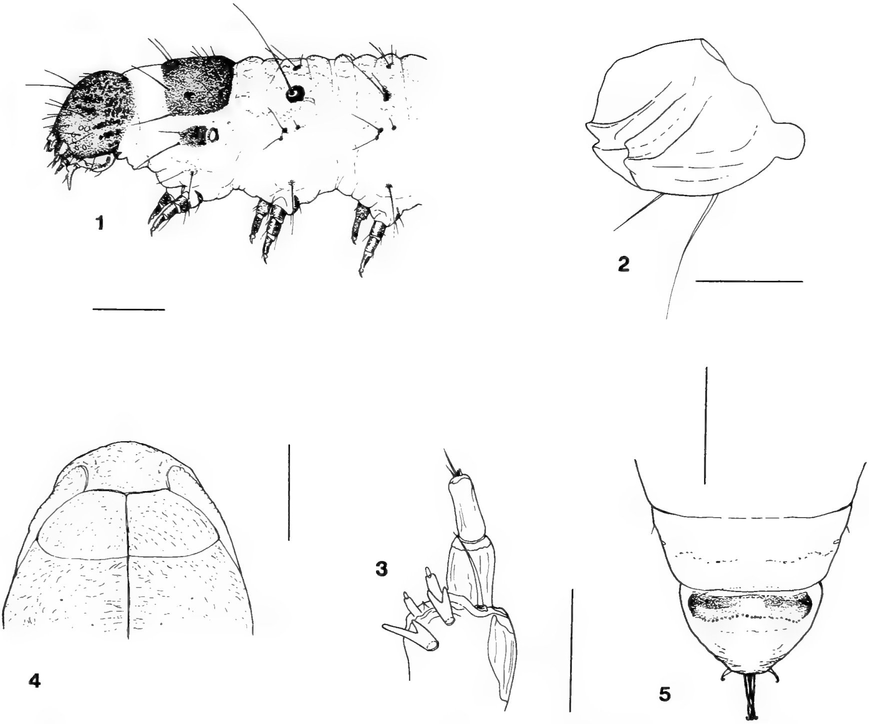
ABSTRACT. The last stage larva and pupa of *Glyptocera consobrinella* (Zeller) (Pyralidae) are described and illustrated, and the biology of this phycitine with reference to *Viburnum* (Caprifoliaceae), its larval food plant, is briefly outlined.

Additional key words: taxonomy, immature stages, biology, *Viburnum*, *Nephopterix*.

Glyptocera consobrinella (Zeller) is a relatively common phycitine (Pyralidae) widely distributed over the eastern United States and southeastern Canada. Since its description in 1872, as *Nephopteryx* [sic] *consobrinella*, little additional information on this species has appeared in the literature. Ragonot in 1889 transferred the species to *Glyptocera*, and in 1893 redescribed and illustrated the adult in his monumental monograph. Hulst (1890) and Forbes (1923) included the species in their publications but contributed no new information. *Viburnum lentago* L. (Caprifoliaceae) was reported as the larval food plant by Dyar in 1910, when he also very briefly (in six lines) described the larva. Heinrich (1956) provided a description of the adult and listed as the larval food plants *Viburnum* and maple (*Acer*) (Aceraceae). Ferguson (1975) gave *Viburnum* as the larval host. Recently, I collected larvae and reared associated pupae and adults of *G. consobrinella* from *Viburnum* in North Carolina. Here I describe in detail the larva and pupa, provide additional information on the biology of the immatures, and discuss affinities of this species with species of the genus *Nephopterix*. Setal chaetotaxy follows Stehr (1987), and the abbreviations for the body stripes are from Neunzig (1979).

Last Stage Larva
(Figs. 1–3)

Color. Head dark reddish brown with indistinct black tonofibrillary platelets. Prothoracic shield and prespiracular plate dark reddish brown to black. Remainder of prothorax mostly dark purple with grayish white to pale green ventrally. Mesothorax and metathorax grayish white dorsally to pale green ventrally with broad, dark purple, partly fused md, sd, sst and est stripes (md slightly darker than other stripes); st and hst stripes red to purple, fragmented; broad red to purple patches ventrally (representing sv and mv stripes); mesothoracic SD1 pinaculum rings dark reddish brown to black with greenish gray centers. Thoracic legs dark reddish brown to black. Abdomen similar to mesothorax and metathorax, but paler, particularly at and below spiracles (mostly pink and green); eighth abdominal SD1 pinaculum rings dark reddish brown to black with greenish gray center; anal shield brown with darker platelets and maculation. Peritreme of spiracles dark reddish



FIGS. 1–5. Last stage larva and pupa of *Glyptocera consobrinella*. **1,** Larval head and thorax, lateral view. **2,** Right larval mandible, mesial view. **3,** Right larval maxilla, dorsal view. **4,** Pupal head and thorax, dorsal view. **5,** Pupa, caudal segments, dorsal view. Scale bars: (1, 4, 5) 1.0 mm; (2, 3) 0.25 mm.

brown to black. Pinacula dark reddish brown to black. Tonofibrillary platelets of abdomen relatively distinct, dark gray.

Morphological features. Length of entire insect 15.0–20.0 mm, avg. 18.0 mm. **Head.** Width 1.48–1.60 mm, avg. 1.55 mm; surface slightly uneven; adfrontals reach ca. $^{5}/_{7}$ distance to epicranial notch; AF2 setae usually slightly above level of forking of epicranial suture; AF2 setae slightly below imaginary line between P1 setae; P1 setae farther apart than P2 setae; labrum deeply emarginate; inner surface of mandible with strongly developed transverse retinaculum; sensilla trichodea of maxilla forked.

Prothorax. Shield with distance between D1 setae less than distance between XD1 setae, on each side distance between SD1 and SD2 setae considerably greater than between SD1 and XD2 setae, distance between D1 and D2 greater than distance between D1 and XD1 setae, and XD2, SD1 and SD2 form an acute angle; L setae of each side in a nearly vertical configuration.

Mesothorax and metathorax. SD1 pinaculum rings of mesothorax well developed; SD1 setae of mesothorax ca. 2× as long as SD1 setae of mesothorax; on each side of mesothorax and metathorax D1 and D2 pinacula fused and SD1 and SD2 pinacula usually fused.

Abdomen. D2 setae of anterior segments ca. 0.75 mm long; D1 setae of anterior segments ca. 0.7 to 1.0× as long as D2 setae; distance between D2 setae on segments 1–7 slightly greater than distance between D1 setae; distance between D1 and D2 on each side of segments 3–6 slightly less than distance between D1 and SD1; SD1 setae of segments 1–7 without pinaculum rings; crochets in a biordinal to triordinal ellipse, number on prolegs of segments 3, 4, 5, 6 and anal segment, 62–68, 72–74, 67–70, 74–76 and 64–66, respectively; vertical diam. of spiracles on segment 8 ca. 1.5× larger than same diam. of spiracles on segment 7; horizontal diam. of spiracle on each side of segment 8 almost 2× as great as distance between L1 and L2; SD1 pinaculum rings of segment 8 relatively broad and complete; SD1 setae of segment 8 ca. 1.6× longer than SD1 setae on segment 7; 2 SV setae on each side of segment 8; distance between D1 and D2 on each side of segment 9 ca. 1.2× distance between D1 and SD1; 2 SV setae on each side of segment 9.

Pupa
(Figs. 4, 5)

Color. Yellowish brown to pale reddish brown; abdominal segment 10 reddish brown; gibba dark reddish brown.

Morphological features. Length of entire pupa (exclusive of cremastral setae) 9.0–10.5 mm, avg. 9.7 mm. **Head:** Surface slightly uneven; pilifers contiguous; length of maxillae 5.0–5.3, avg. 5.2 mm; setae very short.

Thorax. Prothorax slightly wrinkled; spiracles absent; mesothorax slightly wrinkled, without punctures; metathorax slightly wrinkled with ca. 30 punctures on each side of meson and extending about ⅘ distance from meson to lateral margin; setae very short.

Abdomen. Segments 1–4 with proximal ⅘ moderately punctate dorsally; punctures of segment 4 reaching and extending beyond spiracles; segments 5–7 with distinct punctures encircling proximal ⅝ to ⅘ of segments; spiracles subcircular, slightly raised; segment 4 with D1, SD1 and L2 setae; segments 5–7 with D1, SD1, L2 and sometimes SV2 setae; segment 8 usually with L2 setae; no setae on segment 9; gibba ca. 6× as wide as median length; caudal margin of gibba with small punctures; cremastral setae consisting of 4 centrally located, posteriorly directed, somewhat slender setae with strongly curved tips, and 2 outer posterolaterally directed, relatively robust, slightly to strongly hooked setae; outer setae ca. 0.3× length of inner setae.

Material examined. North Carolina, ca. 20 km N of Raleigh, 10 larvae, *Viburnum rafinesquianum* Schultes, 30-IX-84, H. H. Neunzig; 2 larvae, 2 pupae, *Viburnum rafinesquianum* Schultes, 14-X-85, H. H. Neunzig. Deposited in the North Carolina State University Insect Collection.

Biology

Along the coast of Maine, in August, Dyar (1910) collected larvae of *G. consobrinella* from the leaves of *Viburnum lentago*. He reported that larvae reached the last stage and formed cocoons for overwintering in September, and adults emerged the following spring. Based on label data of adults caught in light traps in eastern North America, and on the basis of my own rearing studies in North Carolina, the species also has a spring generation throughout its range. In north central North Carolina, adults from the overwintering generation fly about the middle of May, eggs are laid, and there is about a two-month development period with pupation about mid-July. Adults of this generation eclose and oviposit from the end of July to early August, and large larvae are present on the host from late September to mid-October.

Small larvae form loose tubes of frass and silk on leaves of the host. Feeding at this stage usually occurs along the edges of leaves that are curled with silk around the frass tube. The last pair of leaves of a shoot is frequently infested. Shelters of larger larvae consist of several, loosely

6

FIG. 6. Larval shelter and feeding injury of *Glyptocera consobrinella* on *Viburnum rafinesquianum*.

silked-together leaf fragments and considerable frass (Fig. 6). Large larvae cut off lower leaves, or parts of leaves, and carry these to their terminal shelters to eat or add to their place of concealment. Cocoons are formed in the soil, usually at the base of the host plants.

DISCUSSION

Heinrich (1956) suggested that the genus *Glyptocera* is closely related to the genus *Nephopterix* on the basis of similar character states in the adults. Morphological features of the larvae and pupae of *G. consobrinella*, and those of *Nephopterix* species as elaborated by Doerksen and Neunzig (1975) and Neunzig (1979), support this view. Shared character states include: in the last stage larvae: mandible with strong inner transverse retinaculum, the distance between SD1 and SD2 on each side of the prothorax almost always greater than the distance between SD1 and XD2, and the distance between D1 and D2 on each side of abdominal segments 3–6 less than the distance between D1 and SD1; and in the pupae: the absence of thoracic spiracles.

ACKNOWLEDGMENT

The larval shelter and feeding injury (Fig. 6) was photographed by K. M. Neunzig.

LITERATURE CITED

DOERKSEN, G. P. & H. H. NEUNZIG. 1975. Descriptions of some immature *Nephopterix* in the eastern United States (Lepidoptera: Pyralidae: Phycitinae). Ann. Entomol. Soc. Amer. 68:623–644.

DYAR, H. G. 1910. The larva and food-plant of *Glyptocera consobrinella* Zeller. [Lepidoptera, Pyralidae.]. Proc. Entomol. Soc. Wash. 12:52.

FERGUSON, D. C. 1975. Host records for lepidoptera reared in eastern North America. U.S. Dept. Agr. Tech. Bull. 1521. 49 pp.

FORBES, W. T. M. 1923. Lepidoptera of New York and neighboring states. Cornell Univ. Agr. Exp. Sta. Mem. 68. 729 pp.

HEINRICH, C. 1956. American moths of the subfamily Phycitinae. Bull. U.S. Natl. Mus. 207. 581 pp.

HULST, G. D. 1890. The Phycitidae of North America. Trans. Amer. Entomol. Soc. 17: 93–228.

NEUNZIG, H. H. 1979. Systematics of immature phycitines (Lepidoptera: Pyralidae) associated with leguminous plants in the southern United States. U.S. Dept. Agr. Tech. Bull. 1589. 119 pp.

RAGONOT, E. L. 1889. Phycitidae and Galleriidae of North America. Some new species and a general catalogue. Entomol. Amer. 5:113–117.

——— 1893. Monographie des Phycitinae and Galleriinae. *In* Romanoff, N. M. (ed.), Mem. Sur les Lépid., vol. 7. 658 pp.

STEHR, F. W. 1987. Immature insects. Kendall/Hunt, Dubuque, Iowa. 754 pp.

ZELLER, P. C. 1872. Beiträge zur Kenntnis der nordamerikanischen Nachtfalter, besonders der Mikrolepidopteren. Verh. Zool.-bot. Gesell. Wien 22:447–566.

Received for publication 7 October 1989; revised and accepted 25 April 1991.

Journal of the Lepidopterists' Society
45(2), 1991, 117–123

REVIEW OF THE GENUS *EPIMORIUS* ZELLER AND FIRST REPORT OF THE OCCURRENCE OF *E. TESTACEELLUS* RAGONOT IN THE UNITED STATES (PYRALIDAE: GALLERIINAE)

DOUGLAS C. FERGUSON

Systematic Entomology Laboratory, Agricultural Research Service, USDA,
% U.S. National Museum of Natural History, Washington, D.C. 20560

ABSTRACT. The neotropical galleriine genus *Epimorius* is redescribed to include the previously unknown male. *Epimorius* belongs to the tribe Tirathabini and is closely related to *Paralipsa* Butler and *Aphomia* Hübner, but is without the modified male forewing venation. Four species of *Epimorius* are recognized: *suffusus* (Zeller), *testaceellus* Ragonot, *prodigiosus* Whalley, and *caribellus*, **new species.** A fifth species, *Epimorius epipaschiella* Hampson, was misplaced and is now reassigned to the Macrothecini, genus *Macrotheca*. Specimens reared from *Tillandsia fasciculata* Swartz (Bromeliaceae) in Florida are identified as *E. testaceellus* by comparison with the female holotype from Jamaica. They are the first records of the genus for the United States, the first specimens of *testaceellus* known to have been collected since the original description in 1887, and include the first males known for any species of *Epimorius*.

Additional key words: Tirathabini, *Tillandsia*, geographical distribution, new species, Dominica.

Larvae collected and reared by J. B. Heppner in southern and south-central Florida yielded adults of a pyralid moth that is a new record for Florida and the United States. The larvae are associated with the flower pods of *Tillandsia fasciculata* Swartz (Bromeliaceae), a large species of air plant related to Spanish moss, and the early stages are to be further described in a separate paper by Heppner. This moth belongs to the Galleriinae; it has the venation (Fig. 6), genitalia (Figs. 7, 8), and general aspect characteristic of that subfamily, as well as the modified male labial palpi and flattened pouch full of specialized scales on the underside of the male forewing seen in some other genera. Within the present galleriine classification (Whalley 1964: 565, Munroe 1983: 80), it is easily assigned to the tribe Tirathabini, being excluded from the Galleriini by its simple, broad, and rounded rather than twin-pointed uncus; from the Megarthridini by its lack of ocelli; and from the Macrothecini by the presence of all three medial veins in the hindwing, the presence of a proboscis, and the absence on the male labial palpi of the curious scale tufts characteristic of Macrothecini.

Identification to genus and species was not so simple, but the wing shape, size, and reddish-brown coloring seemed to narrow the search to *Epimorius* Zeller, a small neotropical genus of three described species, of which only females were known. For the benefit of future investigators, I include here a review of what I learned about *Epimorius* and a description of one additional species.

Although similar, the Florida specimens did not agree with three females of the type species, *E. suffusus* (Zeller), which were the only identified specimens of any *Epimorius* species in the National Collection (USNM). The moths from Florida have a more definite forewing pattern of dark transverse bands and discal spot, and lack the smudgy brown basal patch of *E. suffusus*. Paul E. S. Whalley, to whom I showed specimens at the British Museum in 1976, thought that they would prove to be a new species of *Epimorius*. I hesitated to describe it because no material of the Jamaican *E. testaceellus* Ragonot could be found, and I wrongly supposed the unique female type to be lost. More recently, after finding the redescription and colored illustration of *testaceellus* in the rare 8th volume of the *Romanov Mémoires* (Ragonot 1901:430, pl. 45, fig. 22), I wrote Pierre Viette, Muséum National d'Histoire Naturelle, Paris (MNHNP), and he kindly responded by sending the holotype of *testaceellus*.

Although in poor condition, the holotype appears to have been a moth of similar structure, size, color, and wing pattern, and the genitalia (DCF Slide No. 1559) are so nearly identical to those of the Florida specimens that it would be difficult to argue that the latter are anything other than *E. testaceellus*. As the female type from Jamaica is the only other specimen known, no comparison of male genitalia could be made, and the description of the male in the present paper is the first for any species of *Epimorius*.

EPIMORIUS ZELLER, 1877

Epimorius Zeller (1877:76, pl. 2, fig. 28), Ragonot (1887:20; 1901:430, pl. 45, fig. 22), Hampson (1917:45 (in part)), Whalley (1964:581, 610; pl. 19, figs. 40, 42; pl. 41, fig. 101), Fletcher and Nye (1984:53).

Type species: *Melissoblaptes suffusus* Zeller (1877:76, pl. 2, fig. 28), monobasic. *Epimorius* was established as a subgenus of *Melissoblaptes* Zeller, 1839.

Diagnosis. A small neotropical group of reddish-brown moths with a simple, diffuse, darker brown forewing pattern, or hardly any pattern. Structurally typical of the tribe Tirathabini and not differing greatly from species of the genera *Paralipsa* Butler or *Aphomia* Hübner except in their unusual coloring, diffuse pattern, and unmodified forewing venation in both sexes of all included species. The cell of the male forewing in some species of those two genera is greatly enlarged, extending almost to the outer margin, but in *Epimorius* the venation is never thus modified. Forewing length 8.5–15.0 mm (expanse 18–35 mm), with possibility of rare exceptions; females often much larger than males. Scape not enlarged, hardly tufted; antenna of both sexes filiform, finely pubescent ventrally, scaled dorsally; labial palpus sexually dimorphic, that of male reduced, stiffly upcurved to about middle of front much as in related genera, largely concealed by long, conical, frontal scale tuft; female palpus long, about twice length of frontal tuft, porrect, with third segment distinct and normal; tongue well developed, coiled, but proximally stout, especially in male, not very long, heavily scaled; venation of forewing complete except for 1st anal, alike in male and female, without enlarged discal cell in male, cell closed; venation of hindwing with all veins present, cell open (Fig. 6). Male forewing with lustrous-white, somewhat flattened pouch containing dense, compact tuft of specialized scales on underside near costa, at about ⅓ of wing length from base (Fig. 4), this presumably a pheromone-dispensing organ involved in courtship. Similar structures occur in some species of *Paralipsa, Aphomia* (but not in *A. sociella* (Denis & Schiffermüller)), *Trachylepidia* Ragonot, and in the neotropical *Schistotheca gigantella* (Druce), and doubtless other genera. Genitalia hardly differing in either sex from those of *Paralipsa* or *Aphomia,* although ductus bursae may be abnormally short. Ductus bursae varies in length from less than length of corpus bursae (*testaceellus*) to more than twice its length (*prodigiosus*). Male genitalia differ only in minor details from those of about eight other recognized genera of Galleriinae. Posterior margin of eighth abdominal sternum roundly, shallowly emarginate, not deeply notched.

The included species are: **1)** *Epimorius suffusus* (Zeller) (1877:76, pl. 2, fig. 28), described from one female from Novo Friburgo, Brasil, in the Staudinger Collection, Zoological Museum, Berlin (see also Whalley 1964:581, fig. 42); **2)** *E. testaceellus* Ragonot (1887:20), described from one female from Jamaica in the MNHNP (see also Ragonot 1901: 430, pl. 45, fig. 22); and **3)** *E. prodigiosus* Whalley (1964:610, figs. 40, 101), described from five females from 9000′-10,000′ in Peru. Whalley expressed doubt as to whether this species belonged in *Epimorius.* I have not seen it. A previously included fourth species, *E. epipaschiella* Hampson, 1917, from Colombia, was investigated by M. A. Solis of this laboratory on a recent trip to the Natural History Museum, London, and is now considered not to belong to *Epimorius.* It differs in its less convex forewing outer margin, more discrete forewing pattern and gray-brown rather than reddish coloring, more elaborate valve and vesica in the male genitalia, and two instead of three medial veins in the hindwing. For the present it is referred to *Macrotheca* Ragonot in the galleriine tribe Macrothecini. Also, it appears to be a junior synonym of *Stenopaschia gallerialis* Hampson, 1916 (Ann. Mag. Nat. Hist. (8) 18:153), from Colombia (M. A. Solis and Michael Shaffer, pers. comm.).

The collection of the USNM contains one female of an unnamed species of *Epimorius* from Dominica that appears closely related to *E. testaceellus,* and I describe it as new, thereby restoring to four the number of recognized species. *Passelgis xanthothricalis* Dyar from Panama (male unknown) was at first mistaken by me for a species of *Epimorius,* but is has peculiar palpi that appear to lack the third segment. It may belong in the Chrysauginae where originally placed.

Epimorius testaceellus Ragonot
(Figs. 1–4, 6–8)

Epimorius testaceellus Ragonot (1887:20; 1901:430, pl. 45, fig. 22), Whalley (1964:581).

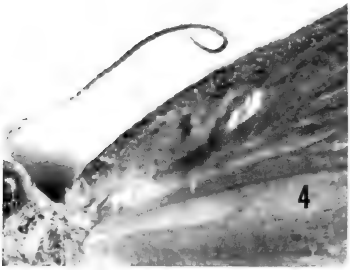
Type locality: Jamaica. Described from one female type in MNHNP.

Description. External structure as described for genus, and general wing form and pattern as illustrated (Figs. 1–3). Labial palpus about equal in length to foretibia and shorter than forefemur. Vestiture of head, thorax, and appendages pinkish or purplish tinged, of abdomen concolorous with hindwing. **Forewing:** reddish brown, variably suffused and marked with darker brown; curved, diffuse, antemedial and postmedial bands usually present and emphasized by areas of paler yellowish-brown coloring distad of


1


2


3


4


5

FIGS. 1–4. *Epimorius testaceellus*. **1,** ♂, Fisheating Creek, 2 mi E. of Palmdale, Glades Co., Florida, larva on *Tillandsia fasciculata*, emerged 29 May 1974, J. B. Heppner. **2,** ♀, same data but emerged 27 May 1975. **3,** ♀, same data but emerged 8 May 1975. **4,** ♂, part of left forewing, showing white scent pouch.

FIG. 5. *Epimorius caribellus*, ♀ holotype. All twice natural size except Fig. 4, which is about 10×.

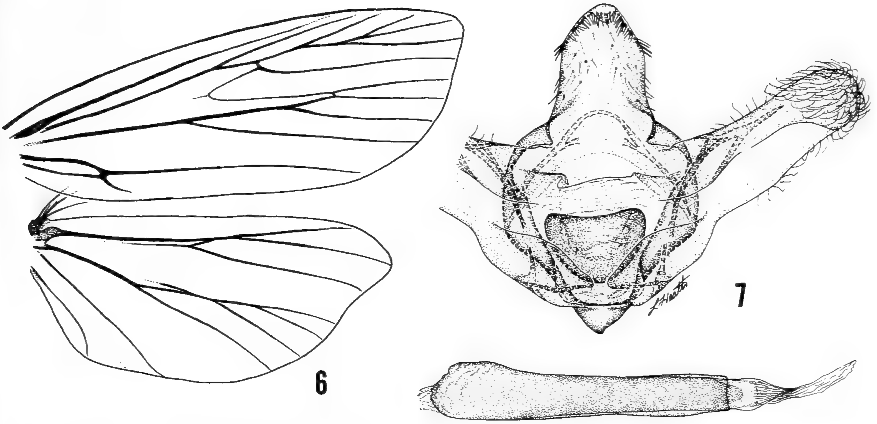
postmedial, and often also in median space or basad of antemedial; discal spot large, dark brown, very diffuse. **Hindwing:** pale brown basally (more so in females), darkening to pinkish or reddish brown distally, without markings. Fringes concolorous with adjoining wing surfaces. Underside almost unmarked, both wings with strong reddish tint, intensifying somewhat toward outer margins. Forewing length: males, 8.5–10.0 mm (n = 6); females, 10.0–12.0 mm (n = 10) (female holotype, 11.5 mm).

Male genitalia. As illustrated (Fig. 7). No other males known with which to compare them.

Female genitalia. As illustrated (Fig. 8). *Epimorius suffusus* has distinctively deeper, more funnel-like ostial cavity and less elongated ovipositor, and its bursa copulatrix extends cephalad to anterior margin of 7th segment, thus about same length as that of *testaceellus*. *Epimorius prodigiosus* also appears to have a deep ostial cavity, but differs from both of the foregoing species in the much greater length of the ductus bursae + bursa copulatrix, which apparently surpasses the 7th segment; this cannot be measured from the figure accompanying the original description of *prodigiosus* because the segment was dissected off and not shown. The new species from Dominica differs in having a smaller ostial cavity about twice as deep as that of *testaceellus*, but much extended bursa copulatrix that surpasses the cephalad margin of the 7th segment by about ⅓ its total length.

Distribution. JAMAICA (type only). FLORIDA: Matheson Hammock, 14.5 km (9 mi) SW of Miami, Dade Co.; Fisheating Creek, 3.2 km (2 mi) E of Palmdale, Glades Co.; 9.6 km (6 mi) SE of Lake Placid, Highlands Co. A total of about 6 males and 10 females reared from larvae found on *Tillandsia fasciculata* Swartz at these localities in Florida by J. B. Heppner; adults emerged 15 Jan. 1974 (Dade Co.), and 5–8 May 1974 and 1975 (other localities). Specimens deposited in collections of the USNM, Washington, D.C., and the Florida State Collection of Arthropods, Gainesville.

Remarks. Although evidently well established, this species seems not to have been collected in Florida prior to 1974–75 and has not been seen since. It apparently does not



FIGS. 6, 7. *Epimorius testaceellus*. **6,** wing venation (♀). **7,** ♂ genitalia (aedeagus removed).

come to light. I looked for larvae more recently at Fisheating Creek and elsewhere in Florida without success.

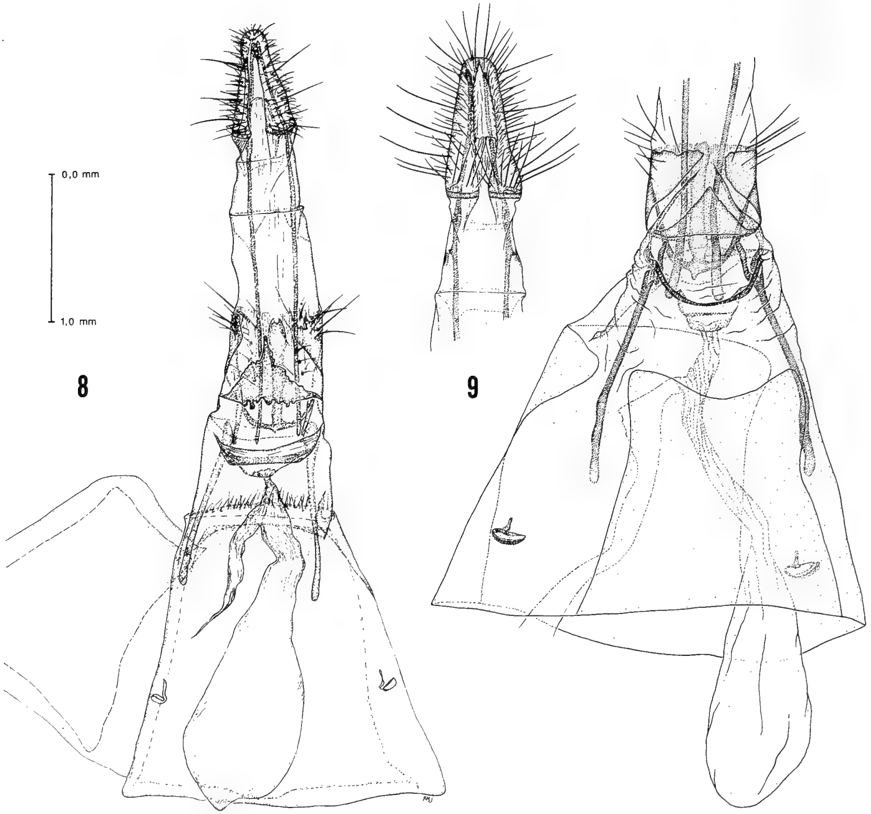
Epimorius caribellus Ferguson, new species
(Figs. 5, 9)

Description (female only, Fig. 5). Generally similar to *testaceellus* in color and external structure, except that forewing is slightly more produced toward apex, and labial palpus is much longer, being about equal in length to forefemur and half again as long as foretibia (that of *testaceellus* shorter than forefemur and about equal to foretibia). Legs also longer than those of *testaceellus*. Antenna filiform, slender, more densely pubescent ventrally than that of *testaceellus,* closely scaled above, pale brownish. Body, head, palpus, and legs pale brown, more or less tinged with pink. **Forewing:** light reddish brown, sparsely dusted with black scales, with antemedial and postmedial band darker reddish brown, wide, very diffuse, irregularly, coarsely dentate; discal spot small, dark brown. **Hindwing:** gray brown, much darker than that of *E. testaceellus* and almost without pinkish tints. Fringes concolorous with wings. Undersurfaces gray brown, forewing with pink costa and pink-tinged subterminal band. Forewing length: 15 mm; wing expanse: 32 mm.

Female genitalia (Fig. 9). About one and one-third times larger than those of *E. testaceellus* or *E. suffusus,* with relatively long ductus bursae, which, like that of *suffusus,* is about equal in length to corpus bursae. However, ductus and bursa together are much longer, so that corpus bursae protrudes for more than half its length beyond anterior margin of seventh segment. Ostial opening lies at bottom of rounded, bowl-shaped depression, smaller than that of *suffusus* and differing in that maximum width of bowl-shaped ostial cavity is less than distance between anterior apophyses at their bases. Ostial cavity, unlike that of other two species, has roundly concave posterior margin subtending a long, bowed, rodlike, transverse sclerite. *Epimorius prodigiosus* (Whalley 1964: fig. 101) differs by having still longer ductus bursae, twice as long as corpus bursae, and much larger, deeper ostial cavity, apparently somewhat like that of *suffusus.*

Type. Holotype, female (Fig. 5), 2 mi NW of Pont Casse, Dominica, 6 June 1965, D. R. Davis; USNM genitalia slide No. 57,305; in collection of USNM.

Remarks. The type is the only known specimen, and its wings are somewhat damaged. Relative to *E. testaceellus,* which also occurs in the West Indies, *caribellus* has a larger, longer winged, more uniformly reddish aspect, and dusky rather than pale pinkish-brown hindwings. The forewing discal spot is smaller and more sharply defined, and the trans-



FIGS. 8, 9. ♀ genitalia. **8,** *Epimorius testaceellus*. **9,** *E. caribellus*, holotype, ovipositor cut off and shown to left.

verse bands are wider and bright reddish brown rather than grayish brown as in *testaceellus*.

ACKNOWLEDGMENTS

For their advice and assistance in various forms I thank Paul E. S. Whalley, M. Alma Solis, and Vitor Osmar Becker. Pierre Viette, by sending me the type of *E. testaceellus* from Paris, made the final identification possible. John B. Heppner deserves special tribute for providing the first material of this species known to have been collected since it was described in 1887. The genitalia drawings are by SEL staff illustrator Linda Heath Lawrence and SEL summer intern Kathy Jones, and the wing venation drawing is by the author. For reviewing the manuscript, I thank J. B. Heppner, E. G. Munroe, M. A. Solis, J. P. Donahue, A. L. Norrbom, and an anonymous reviewer.

LITERATURE CITED

FLETCHER, D. S. & I. W. B. NYE. 1984. The generic names of moths of the world, vol. 5, Pyraloidea. British Museum (Nat. Hist.) Publ. No. 880. 185 pp.

HAMPSON, G. F. 1917. A classification of the Pyralidae, Subfamily Gallerianae [sic]. Nov. Zool. 24:17–58.

MUNROE, E. G. 1983. Pyraloidea. *In* Hodges, R. W., et al., Check list of the Lepidoptera of America north of Mexico. E. W. Classey Ltd. and The Wedge Entomological Research Foundation, London. xxiv + 284 pp.

RAGONOT, E. L. 1887. Diagnoses of North American Phycitidae and Galleriidae. Published by the author, Paris. 20 pp.

——— 1901. Monographie des Phycitinae et des Galleriinae. *In* N. M. Romanov, Mémoires sur les Lépidoptères, vol. 8. St. Petersburg. 602 pp., 34 pls.

WHALLEY, P. E. S. 1964. Catalogue of the Galleriinae (Lepidoptera, Pyralidae) with descriptions of new genera and species. Acta Zoologica Cracoviensia 9:561–618, pls. 14–44.

ZELLER, P. C. 1877. Exotische Microlepidoptera. Horae Societatis Entomologicae Rossicae 13:1–493, 6 pls.

Received for publication 28 January 1991; revised and accepted 7 June 1991.

Journal of the Lepidopterists' Society
45(2), 1991, 124–129

REDESCRIPTION AND REASSIGNMENT OF THE BRAZILIAN *ANERASTIA HEMIRHODELLA* HAMPSON TO *VOLATICA* HEINRICH (PYRALIDAE: PHYCITINAE)

JAY C. SHAFFER

Department of Biology, George Mason University, Fairfax, Virginia 22030

ABSTRACT. *Anerastia hemirhodella* Hampson from São Paulo, Brazil, is redescribed and illustrated on the basis of the female holotype and newly associated male and female specimens, and transferred from *Rhinaphe* Berg to *Volatica* Heinrich in the Phycitinae (Pyralidae).

Additional key words: Neotropics, Brazil, taxonomy, *Rhinaphe*.

Hampson (1901) described *Anerastia hemirhodella* in the Anerastiinae and later (Hampson 1918) transferred the species to *Rhinaphe* Berg in his new subfamily Hypsotropinae, a taxon encompassing largely the same genera as Anerastiinae, though excluding *Anerastia*. In my own revisionary work (1968, 1976) on the group I have used Hulst's (1890) older name Peoriinae and transferred *Anerastia* and additional genera and species to the Phycitinae. More recently (1984) I redescribed and transferred to the Phycitinae eight Neotropical species previously placed in either Anerastiinae or Hypsotropinae, and indicated three other Neotropical species, including *A. hemirhodella,* needed to be similarly dealt with when types could be examined.

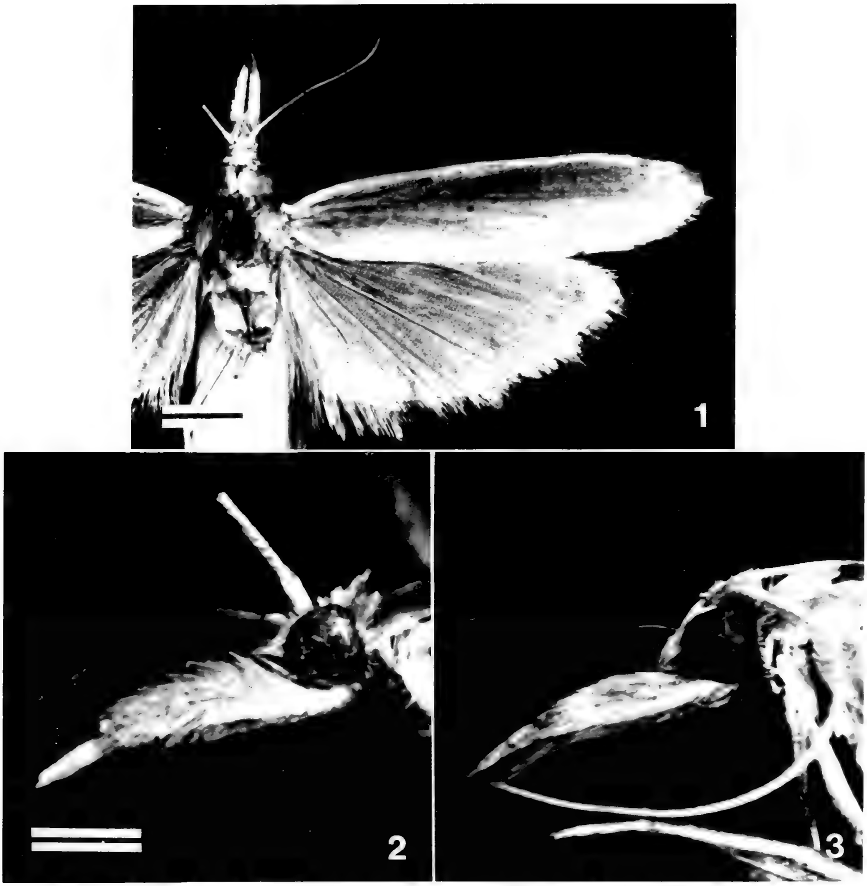
Through the kindness of Mr. Michael Shaffer of the Department of Entomology, Natural History Museum, London, I have recently examined the female holotype of *hemirhodella* and associated it with three male and two female specimens from Brazil. A detailed examination of these six specimens reveals relationship with neither *Anerastia* nor *Rhinaphe*, but rather with *Volatica* Heinrich (1956) in the Phycitinae.

The ISCC-NBS Color-Name Charts (Kelly 1965) were used so far as practical in the following descriptions, though for very small structures only general color designations could be given.

Volatica hemirhodella (Hampson), new combination
(Figs. 1–14)

Anerastia hemirhodella Hampson in Ragonot, 1901:402, plate 52, fig. 12 [in Anerastiinae].
Rhinaphe hemirhodella (Hampson), 1918:85 [in Hypsotropinae].

Description. Head: Frons conical; dark yellowish pink laterally, yellowish white medially. Labial palpus porrect in both sexes, 4.7 times as long as eye diameter; basal segment white to yellowish white; second white to yellowish white ventrolaterally near base and brownish pink laterally near eye, otherwise dark yellowish pink laterally with a few yellowish white scales near apex; third dark yellowish pink with a few scattered yellowish white scales. Maxillary palpus well developed, cylindrical, obliquely ascending along and dorsal to second segment of labial palpus; dark yellowish pink to brownish pink. Proboscis

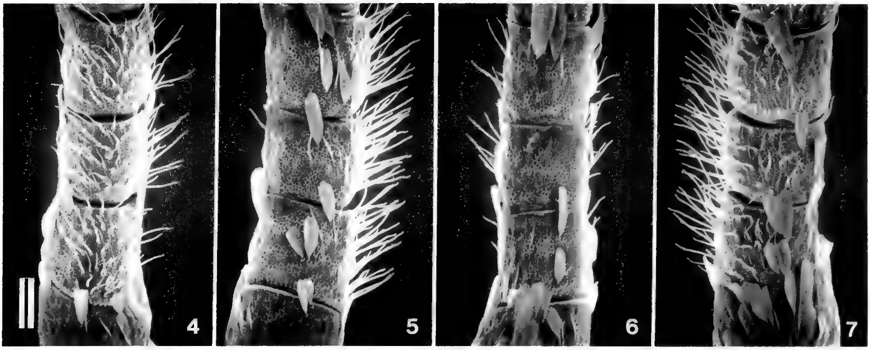


FIGS. 1–3. *Volatica hemirhodella.* **1**, holotype ♀; **2**, holotype, head, lateral view; **3**, male head, lateral view, Rio Negro (Becker). Scale bar = 2.0 mm (1), 1.0 mm (2, 3).

reduced, but not concealed between labial palpi; scales light brown. Antenna filiform in both sexes, basal two segments of flagellum fused in male, otherwise unmodified; cilia about ⅔ segment width in male (Figs. 4–7), finely ciliate in female; scape pink anteriorly, yellowish white elsewhere; shaft yellowish white. Eye diameter 0.7 mm. Ocellus much reduced, with a narrow dark circular ring bordering lens (holotype, see Discussion). Chaetosemata well developed. Vertex (partly denuded in holotype) yellowish white medially, dark yellowish pink laterally. Occiput dark yellowish pink laterally, yellowish white dorsally.

Thorax: Patagium mostly dark yellowish pink, pale yellow toward body midline, white along lateral margin. Tegula dark yellowish pink on inner ⅔, gradually becoming pale yellow on posterior third; lateral third bearing conspicuous and sharply demarcated light yellow band that continues onto wing as the costal band. Pectus light reddish brown. Foreleg moderate brown (reddish brown in some specimens) on outer side, yellowish white on inner side. Mesothorax light reddish brown ventrally. Mid- and hind legs light reddish brown on outer sides, yellowish white on inner sides.

Forewing: Median radius 11.5 mm (range: 10.5–13 mm). With 11 developed veins. R_1 from distal $^7/_{10}$ of cell; bases of R_2, R_{3+5}, and M_1 all well separated. R_{3+4} stalked with R_5 about ⅔ free length of latter. M_1 from upper outer angle of cell. M_2 stalked with M_3 about



FIGS. 4–7. *Volatica hemirhodella,* male antenna showing pedicel (in part) and first 3 shaft segments. **4**, anterior; **5**, lateral; **6**, posterior; and **7**, medial views. Scale bar = 50 μm.

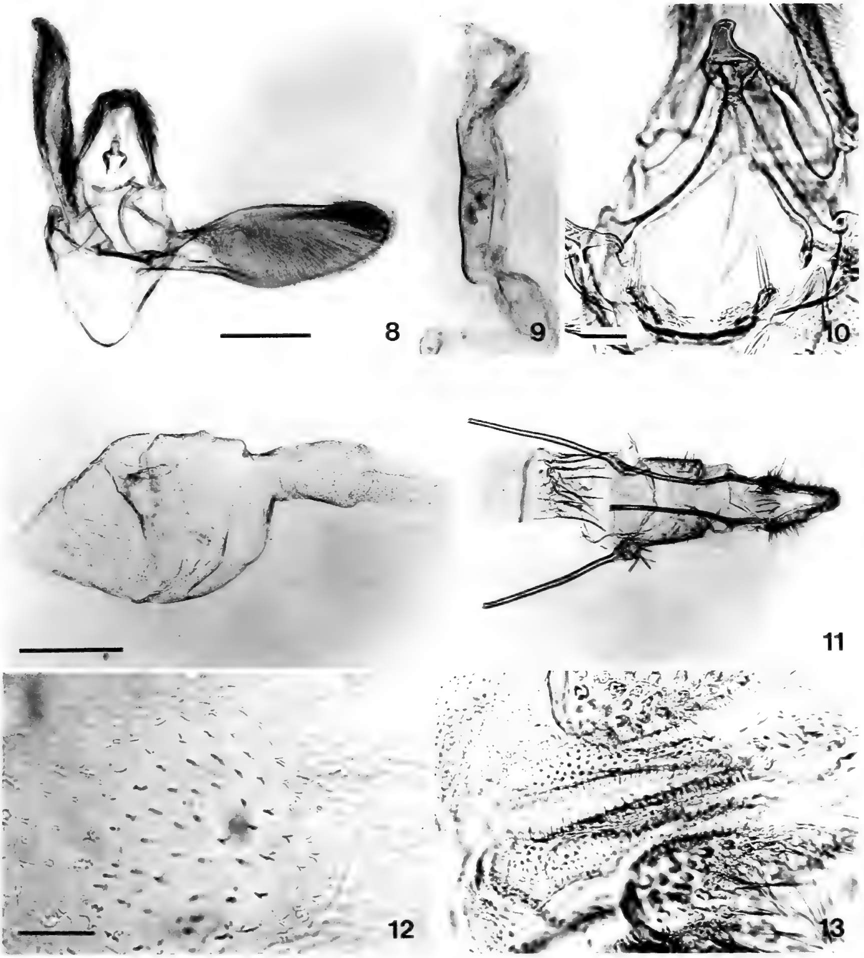
half its length or longer; from lower outer angle. Cu_1 from before the angle, well separated from M_3 and Cu_2. Costa narrowly marked with light reddish brown on basal ⅕; prominent yellowish white costal band uniformly wide on basal ¼, then tapering distally and extending to wing apex, there extremely narrow; costal band marked with only a very few dark yellowish pink scales (visible only with magnification). Broad band of dark yellowish pink extending throughout cell and distally to wing margin, its posterior margin somewhat indistinct, bounded approximately by 1st anal fold, but extending farther posteriorly on basal ¼ of wing. Ground on posterior ⅓ of wing nearly uniformly yellowish white. Undersurface in both sexes with base of subcosta bearing yellowish pink tuft of slender scales extending distad along subcosta approximately as far as retinaculum.

Hindwing: With 7 veins. M_{2+3} fused, stalked with Cu_1 about ⅕ length of free portion of Cu_1; from lower outer angle of cell. Cell very nearly ½ wing length as measured along Cu_2. Anal veins very nearly straight. Nearly uniformly white, brownish tinge along anterior margin.

Abdomen: All exposed abdominal segments light orange yellow on dorsal surfaces.

Male genitalia: (Figs. 8–13) With uncus hoodlike, laterally decurved, apex broadly rounded, dorsal and lateral surfaces rather densely setose. Gnathos with medial process hooked, lateral arms ligulate. Transtilla V-shaped, the arms long slender bars roughly parallel to gnathos arms, weakly joined just anterior to medial process of gnathos. Juxta broadly U-shaped, distal end of each arm with tuberacle bearing about 4 moderately long straight setae. Valve simple, rounded apically; costa strongly sclerotized, flared at base; inner surface of valve with longitudinal subrectangular depression medially at base; sacculus somewhat expanded basally, its base less strongly developed than that of costa. Tegumen broad. Vinculum broadly rounded anteriorly. Aedeagus subcylindrical, about 0.3 times as wide as long; vesica unarmed. Eighth abdominal segment simple.

Female genitalia: (Fig. 14) With ovipositor lobes long, triangular in lateral view with posteroventral margin elongate and diagonal, apex narrowly rounded. Posterior apophysis very nearly as long as anterior; outer margin concave on posterior half, convex on anterior half; small nodule in center of concavity—in midregion of 8–9 intersegmental membrane. Posterior apophyses nearly parallel, anterior divergent. Eighth segment membranous midventrally, lateroventral lobes of collar well separated; collar with moderate number of setae ventrally, laterally and dorsally on posterior half except near dorsal midline; dorsally nearly devoid of setae on posterior half and on and near midline. Ostial chamber short, ligulate, walls lightly sclerotized, with about a dozen longitudinal folds. Ductus bursae with posterior half moderately well sclerotized, flattened, somewhat wider than long; anterior half narrow, membranous. Ostium bursae consisting of narrow cylindrical posterior portion bearing on its posterior half numerous minute anteriorly directed acu-



FIGS. 8–13. *Volatica hemirhodella* genitalia. **8,** male genitalia (aedeagus omitted), J. Shaffer slide 2267; **9,** aedeagus; **10,** transtilla and gnathos region, USNM slide 58158; **11,** female genitalia, USNM slide 58156; **12,** bursa neck spines; **13,** ostium oviductus, holotype. Scale bar = 0.5 mm (8, 9, 11), 0.1 mm (10), 0.05 mm (12, 13).

minate cusps; remainder of bursa unarmed, signum absent. Ductus seminalis from midregion of corpus bursae, basally digitate and posteriorly directed, then tapering to very slender.

Holotype. ♀. Labelled: "Sao Paulo. 88.-169."; "Type"; "Pyralidae Brit. Mus. Slide No. 10912" [BMNH].

Other specimens examined. (3♂, 2♀): BRAZIL, Santa Catarina, Nova Teutonia (F. Plaumann), IX-1963 (2♀), one undissected; the other, USNM genitalia slide 58156, wing slide 58157; X-1963 (♂), USNM genitalia slide 58158 [USNM]; Paraná, Lapa (Becker), 17. XI. 1971 (♂), J. Shaffer genitalia slide 2358; Paraná, Rio Negro (Becker), 22. IX. 1970 (♂), J. Shaffer genitalia slide 2267 [VOB].

FIG. 14. *Volatica hemirhodella*, holotype, female genitalia. Scale bar = 0.5 mm.

DISCUSSION

The species resembles a peoriine in its reduced proboscis and its habitus, notably the pink coloration (though rarely this intense in peoriines), slender forewings with longitudinal pattern, long porrect palpi and light orange yellow scales on the dorsal surface of the abdomen; but genital and other characters place it within the phycitine genus *Volatica*. As compared with previously described species of *Volatica*, *hemirhodella* specimens are less robust and more slender winged with pinkish longitudinal wing markings rather than brownish transverse ones, and with proboscis much reduced.

Despite their superficial dissimilarity, *hemirhodella* corresponds closely with other *Volatica* species in wing venation, labial palpi (porrect), ocellus (reduced), male antenna shaft (unmodified), male 8th abdominal segment (absence of hair tufts and other modifications), and genitalia of both sexes. The male genitalia in particular are quite similar, differing mainly in the transtilla, this structure in *hemirhodella* consisting of very slender right and left sclerites that are weakly joined dorsally, whereas in other species of *Volatica* these sclerites are broad and well joined dorsally.

The degree of fusion of M_{2+3} varies from approximately half way in three of the six specimens examined, to ¾ in the fourth (IX-63) specimen, to completely fused on the holotype and in the Lapa specimen.

In each specimen the degree of fusion was similar in right and left wings.

Although all six specimens examined are very similar in coloration and structure, the holotype differs from the others in two respects: the ocellus is better developed and the bursa (Fig. 14) lacks the neck seen in slide 58156 (Fig. 11). Either of these distinctions could represent individual variation, difficult to evaluate in such a small series, and the latter could be an artifact of slide preparation. Nonetheless, the possibility of sibling species must be considered and it is hoped that one day a sufficient number of specimens will be available to permit resolution of this question.

ACKNOWLEDGMENTS

I thank Mr. Michael Shaffer, Department of Entomology, Natural History Museum, London [BMNH] for the loan of the holotype; Dr. Alma Solis, Systematic Entomology Laboratory, USDA, for arranging the loan of Smithsonian specimens [USNM]; Dr. Vitor Becker, Planaltina, Brazil for the loan of the male specimens from his personal collection [VOB]; and Ms. Linda Trimmer for assistance with SEM work. The Hitachi S-530 scanning electron microscope used in producing Figs. 4–7 was supported in part by NSF Grant No. BSR-8511148.

LITERATURE CITED

HAMPSON, G. F. 1901. See Ragonot, E. L. 1901.

——— 1918. A classification of the Pyralidae Subfamily Hypsotropinae. Proc. Zool. Soc. Lond. 1918:55–131.

HEINRICH, C. H. 1956. American moths of the Subfamily Phycitinae. U.S. Nat. Mus. Bull. 207:viii + 581 pp.

HULST, G. D. 1890. The Phycitidae of North America. Trans. Amer. Entomol. Soc. 17: 93–228.

KELLY, K. L. 1965. ISCC-NBS color-name charts illustrated with centroid colors. Supplement to Nat. Bur. Standards Circular 553. U.S. Government Printing Office, Washington, D.C.

RAGONOT, E. L. 1901. Monographie des Phycitinae et des Galleriinae. *In* N. M. Romanoff, Memoires sur les Lépidoptères, vol. 8:i–xli, 1–602. Paris. (Manuscript completed by G. F. Hampson.)

SHAFFER, J. C. 1968. A revision of the Peoriinae and Anerastiinae (Auctorum) of America north of Mexico (Lepidoptera: Pyralidae). U.S. Natl. Mus. Bull. 280:vi + 124 pp.

——— 1976. A revision of the Neotropical Peoriinae (Lepidoptera: Pyralidae). Syst. Entomol. 1:281–331.

——— 1984. Neotropical Pyralid Moths transferred from Anerastiinae (Auctorum) to Phycitinae. Proc. Entomol. Soc. Wash. 86:383–395.

Received for publication 22 January 1991; revised and accepted 28 May 1991.

Journal of the Lepidopterists' Society
45(2), 1991, 130–134

RHINAPHE ENDONEPHELE AND *R. IGNETINCTA* REDESCRIBED AND REASSIGNED TO *DIVITIACA* BARNES & MCDUNNOUGH (PYRALIDAE: PHYCITINAE)

JAY C. SHAFFER

Department of Biology, George Mason University, Fairfax, Virginia 22030

ABSTRACT. *Rhinaphe endonephele* and *R. ignetincta* described from Brazil and Argentina respectively by Hampson, 1918 in the Hypsotropinae are transferred to *Divitiaca* in the Phycitinae and redescribed with adult moths and genitalia illustrated. Lectotypes are designated.

Additional key words: Neotropical moths, Brazil, Argentina, taxonomy.

In his world revision of the Hypsotropinae, Hampson (1918) placed 37 species in *Rhinaphe* Berg, including his newly described *endonephele* and *ignetincta*. As so defined the genus consisted of numerous disparate elements most or all of which properly belong either to the Peoriinae (a taxon predating and largely overlapping Hampson's Hypsotropinae) or the Phycitinae. Seven of the 9 New World species that Hampson placed in *Rhinaphe* have already been dealt with (Shaffer 1968, 1976, 1984, 1991) and through the kindness of Mr. Michael Shaffer, Department of Entomology, the Natural History Museum, London [BMNH], I have recently examined the lectotypes (designated below) of *endonephele* and *ignetincta*.

Both the male lectotype of *endonephele* and the female lectotype of *ignetincta* key out in Heinrich (1956) to *Divitiaca* Barnes & McDunnough, 1913 and fit well within the confines of that genus. It should be noted that *Macrorrhinia* Ragonot, 1887 differs significantly from *Divitiaca* only in that forewing veins M_{2+3} are stalked in the former genus and fused into a single vein in the latter. Heinrich maintained the generic distinction based on the constancy of that venation character. Although the question of whether or not this distinction should be sustained needs to be reexamined, its resolution is beyond the scope of this paper and must await a thorough review of *Divitiaca, Macrorrhinia,* and related genera.

Color names used herein largely follow the ISCC-NBS Color-Name Charts (Kelly 1965), though for very small structures only more general designations have been given.

DIVITIACA BARNES & MCDUNNOUGH

Divitiaca Barnes & McDunnough, 1913:183; Heinrich, 1956:189–190; Whalley, 1970:43; Hodges et al., 1983:83. Type species: *Divitiaca ochrella* Barnes & McDunnough; Everglade, Florida, USA.

Divitiaca endonephele (Hampson), new combination
(Figs. 1, 3, 5–7)

Rhinaphe endonephele Hampson, 1918:87 [in Hypsotropinae].

Female. Unknown.

Male. Head: Frons conical (Fig. 3), pale orange yellow with a few grayish yellowish brown scales. Labial palpus porrect, 2.9 times as long as eye diameter, pale orange yellow with scattered grayish yellowish brown scales. Maxillary palpus not visible. Proboscis well developed. Antenna shaft filiform, cilia about as long as shaft width toward base; basal portion of shaft with shallow sinus partly enclosed by pair of parallel scale tufts. Eye diameter 0.8 mm. Ocellus well developed, black with clear lens, separated from eye by arc of whitish scales. Vertex pale orange yellow. Occiput pale orange yellow, behind eye mixed with grayish yellowish brown scales. **Thorax:** Patagium and tegula pale orange yellow with scattered grayish yellowish brown scales.

Forewing: (Fig. 1) Radius 10.0 mm, venation as described for the genus (see Heinrich p. 189). Ground pale orange yellow; scattered grayish yellowish brown scales, most abundantly on anterior half of wing. Markings of grayish yellowish brown as follows: on costa near wing base, large round spot centered on 2nd anal vein on basal third of wing, small diffuse spots at upper and lower outer angles of cell, poorly developed postmedial band extending diagonally inward from costa before apex to 2nd anal about half distance from cell to outer wing margin, terminal line of well developed spots in folds between veins along outer wing margin.

Male genitalia: (Figs. 5–6) With uncus triangular, apically acute, anteriorly broadly rounded and centrally truncate; dorsal and lateral surfaces with moderately densely set fine setae, setae absent from small semilunar anteromedial area. Gnathos with medial process very narrowly and unevenly triangular, apex hooked; lateral arm rather robust, curved, anterior half broadly flanged. Juxta (Fig. 6) shield shaped, anterior margin well sclerotized, posterior with lateral pair of setaceous tubercles. Transtilla (Fig. 6) with central element weakly sclerotized, short, broad, triangular; lateral elements each well sclerotized, small, saddle shaped. Valve broadly rounded, transverse ridge extending from near base of costa to basal region of valvula, its basal end projecting, setose. Vinculum broadly rounded, anterior margin with short medial protuberance. Aedeagus extremely slender, very gradually broadened toward basal end.

Lectotype. ♂, hereby designated. Labelled: "Lectotype" [round purple bordered label]; "Rio"; "Type" [round red bordered label]; "Rio Janeiro Saunders' Coll. 94-68."; "Rhinaphe endonephele type ♂. Hmpsn."; "Pyralidae Brit. Mus. Slide. No. 10910" [BMNH].

Paralectotype. ♂, labelled: "Paralectotype" [round blue bordered label]; "Rio"; "Rio Saunders' Coll. 94-68"; "Pyralidae Brit. Mus. Slide No. 14358 ♂"; "♂ genitalia on slide 889 J.C. Shaffer"; "Paralectotype Rhinaphe endonephele Hampson det. M. Shaffer, 1967" [BMNH].

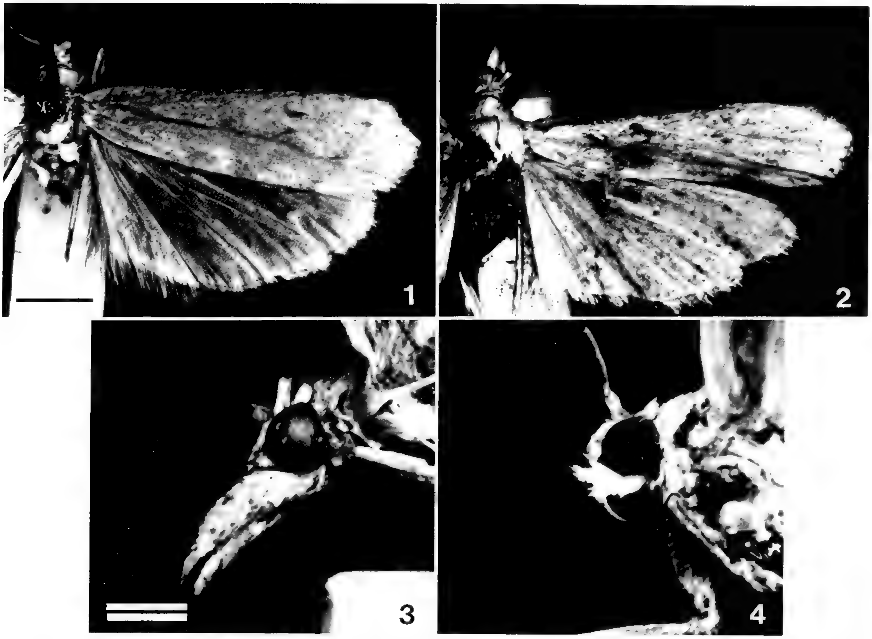
Discussion. The maxillary palpi are not visible in the type. They are probably minute and hidden by the labial palpi and as the latter are intact it is unlikely that the maxillary palpi have been lost from the specimen. The 8th abdominal segment (Fig. 7) bears a pair of slender hair tufts, apparently of the eversible type described by Heinrich for *Divitiaca*, but the pair of short hair tufts that he mentions are either absent, or more likely deciduous and not preserved in the dissection.

Divitiaca ignetincta (Hampson), new combination
(Figs. 2, 4, 8–11)

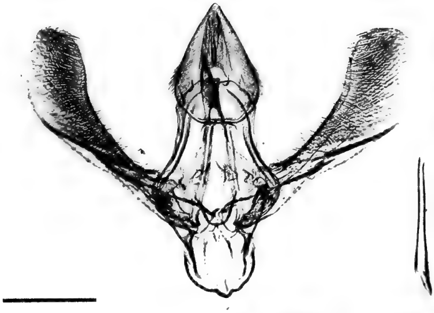
Rhinaphe ignetincta Hampson, 1918:87 [in Hypsotropinae].

Male. Unknown.

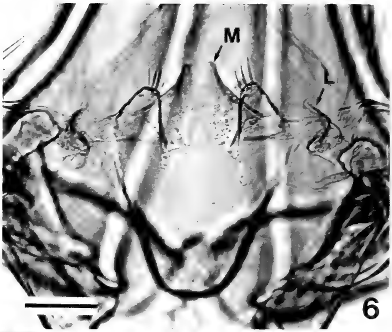
Female. Head: [Frons (Fig. 4) denuded in lectotype]. Labial palpus porrect. Maxillary palpus minute, filiform. Proboscis well developed. Antenna filiform, shaft very finely



FIGS. 1–4. Adult moths and head profiles. **1, 3,** *Divitiaca endonephele,* male lectotype. **2, 4,** *D. ignetincta,* female lectotype. Scale bar = 2.0 mm (1, 2), 1.0 mm (3, 4).

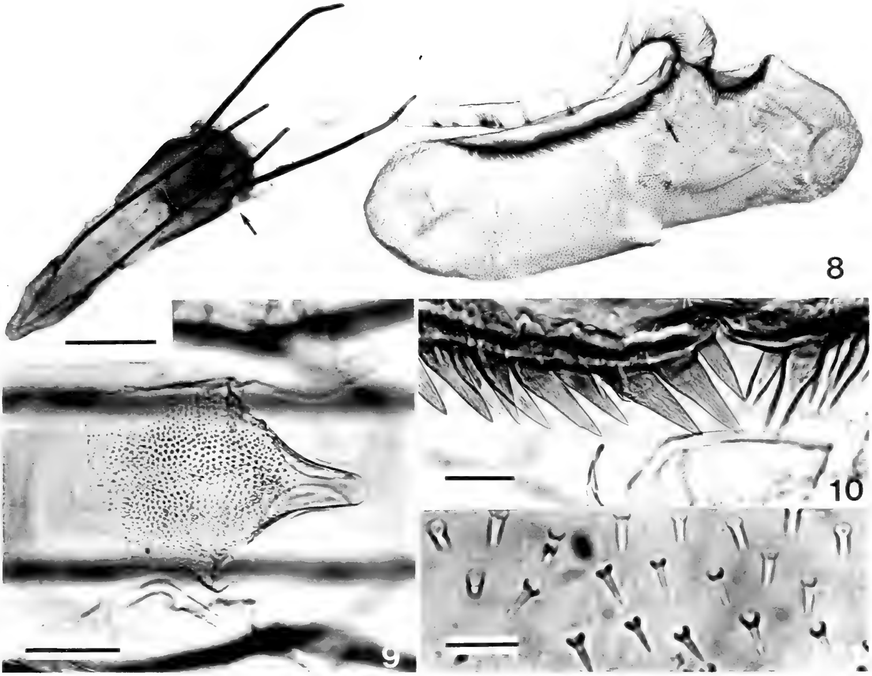


5



6

7



FIGS. 8–11. *Divitiaca ignetincta,* female lectotype. **8,** genitalia (left arrow at level of out of focus ostium, right arrow indicating area enlarged in 10). **9,** ostium. **10,** large bursa spines. **11,** minute bursa spines (seen as granulation in 8). Scale bar = 0.5 mm (8), 0.1 mm (9), 50 µm (10), 20 µm (11).

ciliate. Eye diameter 0.75 mm. Ocellus well developed, black with clear lens; separated from eye by arc of whitish scales. **Thorax:** Patagium and tegula dark orange yellow.

Forewing: (Fig. 2) Radius 10 mm; ground light yellow brown anterior to cell, dark orange yellow posterior to cell, cell intermediate in coloration. Medial line straight, sharply delimited, but of very low contrast and indistinct, extending through cell and diagonally outward from anterior to posterior wing margins. Postmedial line similar, somewhat more prominent, straight, extending diagonally inward from before apex on anterior wing margin to posterior wing margin.

Female genitalia: (Figs. 8–11) With ovipositor tapering dorsocaudally, apex bluntly rounded. Posterior apophysis slightly curved, about 1.3 times as long as anterior. Anterior apophysis angled mediad on anterior ⅙. Eighth segment with row of long setae dorsally and laterally along posterior margin, scattered very short setae laterally and laterodorsally throughout; posterior ⅓ very weakly sclerotized. Ostium (Fig. 9) small, midventrally with small patch of densely set minute (about 6–8 µm long) acuminate spines (resolvable in dissecting microscope at 50× as a granular patch); small, ⅘ as long as wide, well sclerotized triangular plate at anterior of patch joins ductus bursae. Ductus bursae very slender on posterior ⅓, then abruptly wider on anterior ⅔ and hooked toward junction with corpus

---

←

FIGS. 5–7. *Divitiaca endonephele,* male lectotype. **5,** male genitalia, aedeagus separated. **6,** transtilla (M = medial element, L = lateral element) and juxta. **7,** eighth abdominal segment. Scale bar = 0.5 mm (5, 7), 0.1 mm (6).

bursae; widened portion internally with scattered bladelike spines, these most numerous near corpus bursae and continuing onto inner surface of the latter (Fig. 10); joining corpus bursae at its anterior ⅓. Corpus bursae elongate, its inner surface of granular appearance resolvable as numerous minute acuminate spines (Fig. 11) each about 10 μm long, these absent on extreme posterior end and on inner (toward ductus bursae) half of posterior half. Ductus seminalis from anterior ⅓ of slender posterior portion of ductus bursae.

Lectotype. ♀, hereby designated. Labelled: "Argentina. Santa Fe. Ocampo. Aug 1902. S. R. Wagner. 1903.-180."; "Rhinaphe ignetincta type ♀. Hmpsn."; "Type"; "Pyralidae Brit. Mus. Slide No. 10915" [BMNH].

Paralectotypes. 2♀, labelled: "Paralectotype" [round blue bordered label]; "Argentina, Santa Fe, Ocampo. Aug. 1902, S. R. Wagner, 1903-180"; "Paralectotype Rhinaphe ignetincta Hampson det. M. Shaffer, 1990" [BMNH].

"Paralectotype" [round blue bordered label]; "Argentina, Buenos Ayres. H. Wilkinson. 1907-239"; "Paralectotype Rhinaphe ignetincta Hampson det. M. Shaffer, 1990" [BMNH].

Discussion. The lectotype is worn, the discoidal and terminal line spots mentioned by Hampson are difficult to discern, the frons nearly bare and the labial palpi mostly lost, only the basal segment of the right palpus and the basal and part of the second segment of the left palpus remain. My notes from 1967 state the labial palpi to be porrect. Both paralectotypes have the abdomen present.

ACKNOWLEDGMENTS

I thank Michael Shaffer, Department of Entomology, the Natural History Museum, London [BMNH] for the loan of specimens herein designated as lectotypes, and for examining and quoting label data for the paralectotypes.

LITERATURE CITED

BARNES, W. & J. H. MCDUNNOUGH. 1913. Some apparently new Lepidoptera from Southern Florida. Contributions to the natural history of the Lepidoptera of North America 2(4):165–195.

HAMPSON, G. F. 1918. A classification of the Pyralidae Subfamily Hypsotropinae. Proc. Zool. Soc. Lond. 1918:55–131.

HEINRICH, CARL. 1956. American moths of the Subfamily Phycitinae. U.S. Nat. Mus. Bull. 207:viii + 581 pp.

HODGES, RONALD W., ET AL. (eds.). 1983. Check list of the Lepidoptera of America north of Mexico. E. W. Classey Ltd. and The Wedge Entomological Research Foundation, London. xxiv + 284 pp.

KELLY, K. L. 1965. ISCC-NBS color-name charts illustrated with centroid colors. Supplement to Nat. Bur. Standards Circular 553. U.S. Government Printing Office, Washington, D.C.

SHAFFER, J. C. 1968. A revision of the Peoriinae and Anerastiinae (Auctorum) of America north of Mexico (Lepidoptera: Pyralidae) U.S. Nat. Mus. Bull. 280: vi + 124 pp.

——— 1976. A revision of the Neotropical Peoriinae (Lepidoptera: Pyralidae). Syst. Entomol. 1:281–331.

——— 1984. Neotropical Pyralid moths transferred from Anerastiinae (Auctorum) to Phycitinae. Proc. Entomol. Soc. Wash. 86(2):383–395.

——— 1991. Redescription and reassignment of the Brazilian *Anerastia hemirhodella* Hampson to *Volatica* Heinrich (Pyralidae: Phycitinae). J. Lepid. Soc. 45:124–129.

WHALLEY, P. E. S. 1970. A synonymic catalogue of the genera of Phycitinae (Lepidoptera: Pyralidae) of the world. Bull. Brit. Mus. (Nat. Hist.) Entomol. 25(2):33–72.

Received for publication 22 January 1991; revised and accepted 28 May 1991.

Journal of the Lepidopterists' Society
45(2), 1991, 135–141

A REVIEW OF *APODEMIA HEPBURNI* (LYCAENIDAE: RIODININAE) WITH A DESCRIPTION OF A NEW SUBSPECIES

GEORGE T. AUSTIN

Nevada State Museum and Historical Society,
700 Twin Lakes Drive, Las Vegas, Nevada 89107

ABSTRACT. *Apodemia hepburni* Godman and Salvin (Lycaenidae: Riodininae) is reviewed. A new subspecies, *Apodemia hepburni remota* Austin, is described from southern Baja California, Mexico, based on 112 specimens. Both taxa of the species exhibit biphenism.

Additional key words: Baja California Sur, Sonora, Mexico, *A. palmerii, A. murphyi.*

Apodemia hepburni is a small metalmark (Lycaenidae: Riodininae) described from Chihuahua, Mexico (Godman & Salvin 1886). In conjunction with a study of the phenotypically similar *Apodemia palmerii* (W. H. Edwards) (Austin 1987), I had the opportunity to examine series of *A. hepburni* in several major museums in the United States and those in a number of private collections. The degree of seasonal and geographical variation I noted prompted this review.

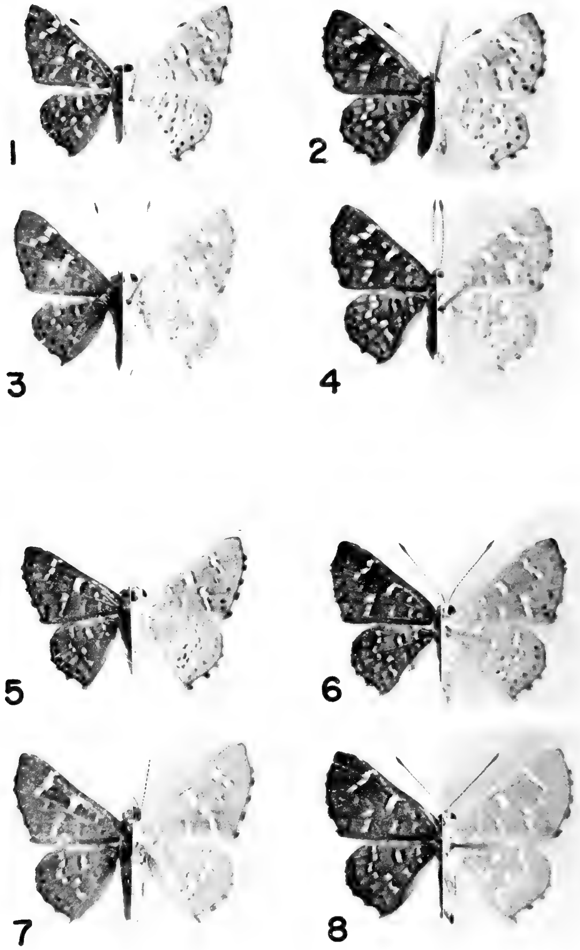
Throughout, butterfly size (mean and range in mm) is the length of the forewing from base to apex. Specimens indicated by "M" and "F" are male and female, respectively. Capitalized color names are after Smithe (1975, 1981).

Apodemia hepburni hepburni Godman and Salvin (Figs. 1–4)

Apodemia hepburni Godman and Salvin 1886:468 (type locality: Pinos Altos, Chihuahua, Mexico); holotype male at The Natural History Museum, London (Miller & Brown 1981).

The species was figured and very briefly described from a single male by Godman and Salvin (1886). I examined photographs of the type, a somewhat worn male without antennae and with a phenotype of the first brood. This specimen has six labels: a white hand-lettered label "HOLOTYPE/Apodemia/hepburni/Godman & Salvin/det. P. Ackery, 1989"; printed white labels with "B.C.A.Lep.Rhop./Apodemia/hepburni,/G. & S./Godman-Salvin/Coll. 1914.-5.", "Pinos Altos,/Chihuahua,/Mexico/Buchan-Hepburn.", "Type./Sp. figured.", and a small label with a male symbol; and a round white label with a red border printed with "Type/H.T.".

Male. July–October, size = 10.9 (10.4–11.1, N = 13). Dorsum blackish-brown (Sepia, color 119); marginal row of black dots often with faint white points proximally especially towards forewing apex; forewing with four quadrate subapical white spots, continued submarginally as irregular row of small and poorly defined white spots; large quadrate white bar at end of discal cell with smaller, less distinct bar below it in cell CuA_2; postbasal white bar in discal cell and similar one below it in cell CuA_2; subapical, submarginal and cell-end white marks indistinctly outlined distally and proximally with black; similarly, postbasal bar outlined distally and bar below cell-end bar outlined proximally. Hindwing with markings as forewing except entire submarginal row of approximately equal-sized



FIGS. 1–8. *Apodemia hepburni* subspecies (dorsal surface on left, ventral surface on right of each figure). **1–4,** *A. h. hepburni* (all MEXICO: Sonora)—(1) male, Rt. 16, 8.5 mi W Rio Yaqui, 26 Aug. 1984, *leg.* D. Mullins, (2) female, 36 mi W Moctezuma, 3 Aug. 1984, *leg.* D. Mullins, (3) male, Hwy. 16, 17 mi E Tecoripa, 15 March 1984, *leg.* J. P. Brock, (4) female, same data as fig. 3; **5–8,** *A. h. remota* (all MEXICO: Baja California Sur)—(5) holotype, data in text, (6) allotype, data in text, (7) male, Mulege, ½ mi E, 23 March 1974, *leg.* G. S. Forbes, (8) female, 3 mi S Loreto, *leg.* Faulkner, Brown.

spots; slight reddish-brown area at middle of costal margin, sometimes extending medially into discal cell; fringes of both wings white, lightly checked with black at vein tips.

Ventral surface dull reddish-brown; forewing near Pratt's Rufous proximally grading to Robin Rufous distally; hindwing Pratt's Rufous throughout; hindwing and base of forewing overscaled with white (often heavily); white marks as on dorsum but larger, especially submarginally; submarginal row of hindwing forming continuous, irregular band; white spots outlined with black as on dorsum but more prominent against paler ground color; marginal black dots with indistinct white smudges proximally; hindwing anal margin whitish.

March, size = 11.7 (10.9–12.4, N = 7). Dorsum paler (near Hair Brown), forewing subapical and cell-end white marks prominent; posterior spots faint to nearly obsolete, position indicated by their black outlines; hindwing white marks similarly faint, most persistent in submarginal series; marginal black spots small, nearly disappearing anteriorly on forewing; hindwing flush of reddish-brown tending more prominent. Ventral surface paler (near Salmon Color, color 106) proximally, grayer distally; black markings obsolete; white marks less contrasting.

Female. August–October, size = 11.1 (10.3–11.8, N = 14). Wings more rounded than male; ground color as male; white marks as male; forewing with indistinct Pratt's Rufous margin; marginal black spots with proximal indistinct points of white apically; hindwing with anterior ⅓ and margin Pratt's Rufous.

Ventral surface similar to male but slightly paler; ground color near Cinnamon Rufous throughout, less overscaled with white except between marginal black dots and submarginal white spots giving appearance of whitish band.

March, size = 12.2 (11.9–12.4, N = 2). As male, anterior ⅓ of hindwing with reddish-brown flush, forewing with more restricted marginal reddish-brown than later in year.

Distribution and phenology. The distribution of this taxon apparently is incompletely known. Nearly all records that I know of are from Sonora, Mexico (Fig. 9) where it may be locally common. It was described from western Chihuahua, Mexico; there are old records from southern Arizona (various museums), additional, more recent, Arizona records from northeast of Douglas, Cochise County (*fide* R. Bailowitz) and at Sycamore Canyon, Santa Cruz County (Langston 1991), and it was taken in the Chisos Mountains, Brewster County, Texas (Carnegie Museum). The flight period in Sonora is from late February to late March and late July to late October reflecting at least two broods. Arizona records are for May and June (one in August) and the Texas record is for July.

Discussion. This taxon is at least bivoltine in spring and again in autumn and strongly biphenic. The spring brood is pale with reduced markings; the fall phenotype is smaller, darker and the ventral surface is relatively heavily overscaled with white and appears mottled.

Apodemia hepburni remota, new subspecies
(Figs. 5–8)

Male. August–November, size = 11.6 (10.2–12.6, N = 25). Dorsum dark brown (Sepia, color 219); submarginal row of black spots on both wings as on *A. h. hepburni* but without associated white points; white marks and black outlines as on *A. h. hepburni* but narrower; hindwing usually with medial flush of reddish-brown anteriorly, extending into discal cell.

Ventral surface nearly uniform Pratt's Rufous with little white overscaling; white spots as on dorsum, their black outlines thin; black marginal dots small, often obsolete anteriorly on forewing, and with associated white very vague or absent.

February–April, size = 12.3 (11.9–13.4, N = 7). Dorsal ground color paler (Hair Brown), posterior white marks on forewing and basal marks on hindwing faint to obsolete; marginal black spots very small (may be absent on forewing); reddish-brown on hindwing present or absent.

Ventral ground color pale (near Orange-Rufous); very little whitish overscaling basally, white marks very thin with black outlines faint to obsolete; marginal black spots reduced to points or entirely absent.

Female. August–November, size = 12.4 (11.0–14.1, N = 30). Wings more rounded than male; hindwing with relatively heavy flush of reddish-brown anteriorly; margins with smudges of similar color in each cell; white markings thin as on male.

Ventral surface paler than male (near Orange-Rufous); markings as on male.

April, size = 12.6 (12.3–12.9, N = 2). Dorsum similar to later in year but tending towards more reddish-brown on hindwing. Ventral surface very pale (near Flesh Ocher), markings as on male.

Types. Holotype M—MEXICO: Baja California Sur; Arroyo San Bartolo, 28 Aug. 1982, *leg.* [J. W.] Brown and [D. K.] Faulkner. Allotype F—same data as holotype. Paratypes (60M, 50F, all MEXICO: Baja California Sur)—same data as holotype (1M, 10F); same location as holotype, 28 Nov. 1980, *leg.* J. Brown (1F); San Bartolo, 3 Oct. 1981, *leg.* F. Andrews & D. Faulkner (2F); 30 Nov.–1 Dec. 1979, *leg.* Brown & Faulkner (2M, 3F); A. San Bartolo, 2 Nov. 1961, *leg.* Cary-Carnegie Expedition [=CCE] (1F); 3 Nov. 1961, *leg.* CCE (3M, 2F); 12 Nov. 1961, *leg.* CCE (1F); San Bartolo microwave tower, 28 Nov. 1980, *leg.* J. Brown (1M); 3 mi SE San Bartolo, 15 March 1974, *leg.* G. S. Forbes (1M); 2 mi SW Caduano, 26 Aug. 1982, *leg.* Faulkner & Brown (7M, 1F); 7 km S Caduano, 26 Aug. 1982, *leg.* Faulkner and Brown (1M, 1F); Caduano, 25 Nov. 1961, *leg.* CCE (1M); Ro. Palmarito 4 Nov. 1961, *leg.* CCE (2F); 5 Nov. 1961, *leg.* CCE (1M), 30 Nov. 1961, *leg.* CCE (1F); 31 Nov. 1961, *leg.* CCE (1M, 1F); Rancho San Bernardo de Sierra Laguna, 14 Nov. 1961, *leg.* CCE (1M, 1F); 17 Nov. 1961, *leg.* CCE (1M); Bahia de Palmas, 20 Nov. 1961, *leg.* CCE (1M, 2F); 33 mi N Todos Santos, 4 Oct. 1981, *leg.* D. Faulkner & F. Andrews (1M); 28 km N Todos Santos, 29 Nov. 1980, *leg.* Brown & Brown (1F); 31 km N Todos Santos, 29 Nov. 1980, *leg.* J. Brown (1F); 4 mi E La Barrera (nr. Todos Santos), 21 March 1974, *leg.* R. Holland (1M); 8 mi W La Paz, 30 Oct. 1946, *leg.* E. Y. Dawson (1M); Ramel de Naranjas, 6 mi W Hwy. 1 nr. Santa Anita, 11 Oct. 1983, *leg.* Andrews & Faulkner (2M); San Antonio microwave, 13 Oct. 1983, *leg.* D. Faulkner & F. Andrews (3F); Boca de la Sierra, 13 Nov. 1961, *leg.* CCE (4M); 17 Nov. 1961, *leg.* CCE (4M, 1F); 22 Nov. 1961, *leg.* CCE (1M, 1F); 24 Nov. 1961, *leg.* CCE (2M, 2F); 28 Nov. 1961, *leg.* CCE (3M, 2F); Puerto Chileno, 22 Nov. 1961, *leg.* CCE (2M, 1F); Guaycura Hotel, La Paz, 29 Nov. 1961, *leg.* CCE (1M); 15 mi S La Paz, 1 Nov. 1946, *leg.* E. Y. Dawson (16M, 2F); 2 mi S Buena Vista, 30 Nov. 1979, *leg.* Brown & Faulkner (1F); 5 km S R Buenavista, 25 Oct. 1961, *leg.* CCE (2F); Santiago, 6 Nov. 1946, *leg.* E. Y. Dawson (2F); 3 mi S Santiago, 25 Oct., *leg.* ? (1F); San Jose del Cabo, 23 Nov. 1961, *leg.* CCE (1F).

Deposition of types. The holotype, allotype, and 58 paratypes are deposited at the Natural History Museum, San Diego, California; 49 paratypes are at the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; one paratype is in the private collection of G. S. Forbes, Las Cruces, New Mexico, and two paratypes are retained by the author.

Type locality. MEXICO: Baja California Sur; Arroyo San Bartolo. San Bartolo is on Mexico Highway 1 between La Paz and San Jose del Cabo.

Distribution and phenology. *Apodemia h. remota* occurs only in Baja California Sur from Mulege south to the southern tip (Fig. 9). Specimens have been taken from mid February to mid April and from late August to early December, about 70% (of 117 examined) in November.

Etymology. This subspecies is named after its isolated distribution at the tip of the Baja California peninsula.

Diagnosis and discussion. *Apodemia h. remota* is seasonally biphenic in size, color, and pattern; this is similar in form but somewhat less pronounced than for nominotypical *A. hepburni*. *Apodemia h. remota* differs in several respects from *A. h. hepburni*. It is a larger insect (averaging 0.5 mm larger in the first brood and 1 mm in the second), both the ventral and dorsal ground colors are paler, the white markings and their black outlines are thinner (especially on the ventral surface where they are about twice as broad on *A. h. hepburni*), the black marginal spots are smaller, and there is considerably less whitish overscaling on the ventral surface (see Figs. 1–8). Overall, the ventral surface of *A. h. remota* appears uniformly colored; that of *A. h. hepburni* has a mottled appearance, especially on late season specimens. *Apodemia h. remota* tends to have more red-brown medially on the dorsal hindwing (this sometimes extends distally to the outer margin on females) and along the margins on both wings than *A. h. hepburni* and rarely has white associated with the black marginal spots.

It is curious that most references do not mention the occurrence of *A. hepburni* in Baja California Sur. Hoffmann (1976) acknowledged the occurrence of the species only on the mainland. He, Rindge (1948), and Holland (1972) reported only *A. palmerii* (=*Apodemia*

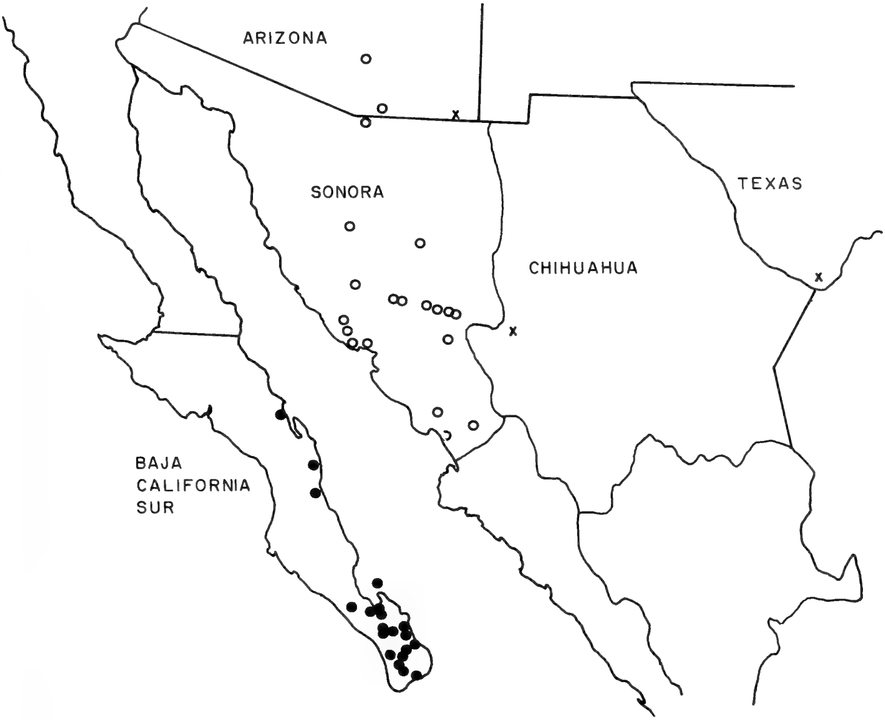


FIG. 9. Known distribution of *Apodemia hepburni*. Open circles = *A. h. hepburni*, closed circles = *A. h. remota*, "×" = specimens not seen.

murphyi Austin) of this group in Baja California. Of other general references, Howe (1975) reported its occurrence in Baja California but Scott (1986) did not.

DISCUSSION

Both taxa of *A. hepburni* are relatively rare in collections although the species appears to be common locally. The dates of collection seem to reflect two well defined and disjunct flight periods in both Sonora and Baja California Sur, Mexico. It is unknown how much of the known phenology reflects collector phenology. In Baja California, however, there are records for *A. murphyi* from every month, suggesting that the absence of *A. hepburni* records in some months is real. The few records for Arizona and Texas bridge the phenological gap in Mexico, perhaps reflecting a single brood at the northern extreme of the distribution. I have found no information on the early stages or larval food plant of *A. hepburni*.

Seasonal variation of both *A. hepburni* taxa is parallel. Individuals from early in the year (spring) are large and pale with small white markings; those from later in the year (late summer-fall) are of a smaller,

TABLE 1. Characteristics of species of the *Apodemia palmerii* complex.

Character	*A. palmerii*	*A. murphyi*	*A. hepburni*
FW shape	not produced	produced	produced
FW apex	rounded	subfalcate	subfalcate
Dorsal margin	prominent series of white spots	prominent series of white spots	no or inconspicuous white spots
Dorsal maculation	prominent	prominent	vague, esp. posteriorly on forewing
VHW postmedian band	medium width	very broad	narrow to medium width
Distribution	SW US to central Mexico	southern Baja California, Mexico	southern Baja California and western Mexico

darker phenotype with more extensive white spots. Seasonal biphenism was noted in size and color of *A. p. palmerii* and in color for *A. murphyi* although none was detected for two other *A. palmerii* taxa (Austin 1987).

Apodemia hepburni occurs sympatrically and synchronically with *A. palmerii* or *A. murphyi*; the two have been taken together at several locations in Sonora and Baja California. The known distribution and flight period of *A. palmerii* and *A. hepburni* are practically identical in Sonora. In Baja California, *A. hepburni* has a shorter flight period and does not extend as far north as *A. murphyi*.

Apodemia hepburni is sometimes confused (in collections) with *A. palmerii*. *Apodemia palmerii* always has a prominent row of white spots just proximal to the marginal black dots on both wings; these are absent or represented at most by inconspicuous white points on *A. hepburni*. The white marks of the submarginal series on the ventral surface are usually conspicuously outlined with black on both sides on late season *A. hepburni*; this black outline is usually absent distally on spring *A. hepburni* and all *A. palmerii* (some *A. palmerii* may have a darker shade here but never a well-defined line of black). Additionally, the forewings of both sexes of *A. hepburni* are more produced apically than those of *A. palmerii*. *Apodemia h. remota* likewise resembles *A. murphyi*. The wing shape of the two is similarly produced. *Apodemia hepburni*, however, has smaller dorsal spots, no reddish-brown basally on the forewing (occasional female *A. hepburni* have a hint of this but it is never prominent as on some *A. murphyi*), lacks the marginal white spots, and has a very narrow white postmedian band on the ventral hindwing (very broad and prominent on *A. murphyi*). These characters are summarized in Table 1.

The male genitalia of the two subspecies of *A. hepburni* are identical; they are also very similar to those of *A. palmerii*. The processes of the valvae diverge at a greater angle on A. *hepburni* than on A. *palmerii* and the lower process is slightly shorter and twisted outward. The vinculum of A. *hepburni* appears more upright compared to the sloping aspect of A. *palmerii*. The male genitalia of A. *murphyi* are more robust than those of either A. *hepburni* or A. *palmerii*.

ACKNOWLEDGMENTS

I thank various curators and others for loans of specimens: L. D. and J. Y. Miller (Allyn Museum of Entomology), F. H. Rindge (American Museum of Natural History), D. K. Faulkner (Natural History Museum, San Diego), J. P. Donahue (Natural History Museum of Los Angeles County), R. K. Robbins (National Museum of Natural History), J. E. Rawlins (Carnegie Museum of Natural History), J. A. Powell (California Insect Survey), and T. W. Davies (California Academy of Sciences). I am grateful for specimen loans and data from the private collections of J. Brock, G. S. Forbes, R. W. Holland, R. O. Kendall, D. Mullins, and M. J. Smith. I also thank P. R. Ackery of the Natural History Museum, London, for sending photographs of the type of A. *hepburni*. I thank Scott Klette of the Nevada State Museum for the photographs in the text.

LITERATURE CITED

AUSTIN, G. T. 1987. *Apodemia palmerii* (Lycaenidae: Riodininae): Misapplication of names, two new subspecies and a new allied species. J. Res. Lepid. 26:125–140.

GODMAN, F. D. & O. SALVIN. 1879–1901 [1886]. Biologia Centrali-Americana. Lepidoptera: Rhopalocera. Vol. 1. London. xlv + 487 pp.

HOFFMANN, C. C. 1976. Catálogo sistemático y zoogeográfico de los lepidópteros mexicanos. Soc. Mex. Lepid., publ. esp. 1. 214 pp.

HOLLAND, R. 1972. Butterflies of middle and southern Baja California. J. Res. Lepid. 11:147–160.

HOWE, W. H. 1975. The butterflies of North America. Doubleday, Garden City, New York. xiii + 633 pp.

LANGSTON, R. L. (coordinator). 1991. 1990 season summary. Southwest: Arizona, California, Nevada. News Lepid. Soc. 1991:16–19.

MILLER, L. D. & F. M. BROWN. 1981. A catalogue/checklist of the butterflies of America north of Mexico. Lepid. Soc. Mem., No. 2. vii + 280 pp.

RINDGE, F. H. 1948. Contributions toward a knowledge of the insect fauna of Lower California. No. 8, Lepidoptera: Rhopalocera. Proc. Calif. Acad. Sci. 24:289–312.

SCOTT, J. A. 1986. The butterflies of North America: A natural history and field guide. Stanford Univ. Press, Stanford, California. xiii + 583 pp.

SMITHE, F. B. 1975. Naturalist's color guide. Amer. Mus. Nat. Hist., New York, New York. 4 pp. + 8 color charts.

——— 1981. Naturalist's color guide part III. Amer. Mus. Nat. Hist., New York, New York. 37 pp. + 9 color charts.

Received for publication 8 March 1990; revised and accepted 13 June 1991.

Journal of the Lepidopterists' Society
45(2), 1991, 142–157

TYPES OF NEOTROPICAL THECLINAE (LYCAENIDAE) IN THE MUSÉUM NATIONAL D'HISTOIRE NATURELLE, PARIS

KURT JOHNSON

Department of Entomology, American Museum of Natural History,
Central Park West at 79th Street, New York, New York 10024

ABSTRACT. Specimens marked as types are examined critically for the first time. Sixty primary types of Lathy, four of Draudt, and two of Blanchard are documented. Lectotypes are designated for Lathy binomials *Thecla draudti, inconspicua, lilacina, tagyroides*, and *Trichonis immaculata*; and Lathy trinomials *Thecla ambrax septentrionalis, cyllarus reducta, linus paraguayensis, l. separata, phoster parvipuncta, rocena major, strephon occidentalis, Eumaeus minijas obsoleta, m. peruviana*, and *Theclopsis eryx occidentalis*. Lathy junior primary homonyms described in *Thecla—inornata, mirabilis, violacea*, and *viridis*—are replaced, respectively, with *lathyi, rhaptissima, magnapurpurata*, and *familiaris*. The name *pentas* Nicolay (*Symbiopsis*) is recognized as replacing Lathy junior primary homonym *Thecla peruviana*. Five Lathy specimens are invalidated as types. Types of three Lathy taxa were not found. Four primary types of Draudt are documented. Lectotypes are designated for *Thecla catharina, crispisulcans*, and *quassa*. Five primary types of Godart—*Polyommatus bazochii, falacer, irus, megarus*, and *strophius*—are discussed, along with a possible type of *P. damastus*. Five specimens marked as types of Druce, Hewitson, or Staudinger are invalidated. Types of recent authors at MNHN are cite-referenced and a guide to specimen locations at MNHN provided. Eighteen types not previously illustrated are figured along with fifteen other selected types and one specimen of questionable status.

Additional key words: Eumaeini, systematics, taxonomy.

Types of neotropical Theclinae at the Muséum National d'Histoire Naturelle (MNHN) have been poorly known. Many were described without illustration and the uncertain status of others has complicated both early and recent taxonomic work (Draudt 1917–24 [1921], Comstock & Huntington 1958–64, Miller & Brown 1981, Nicolay 1982, Robbins 1986, Bridges 1988). At the MNHN in 1981, 1985, 1987, and 1989 I was able to survey type material of neotropical Theclinae and prepare a definitive list, allowing not only enumeration and illustration of types but specification of appropriate lectotypes, replacement names, and instances of invalid usage or incorrect marking of specimens.

Recently, C. A. Bridges (1988) cited certain information from a 1987 draft of this paper. Where such citations differ from the present work, the latter should be considered authoritative.

MNHN PRIMARY TYPE SPECIMENS

Collections. Butterfly holdings at the MNHN are separated into three primary collections: the **Fournier Collection**, the **General Collection** (term from G. Bernardi, pers. comm.), and the **Supplemental Collection** (my term).

The **Fournier Collection**, housed in locked cabinets in a special room (the "Fournier room"), includes 96 Cornell size drawers of neotropical Theclinae. No diagram is available for layout of the collection; neotropical Theclinae are located on the upper south face of the central row of tall cabinets and on the upper west face of the west wall cabinets.

The **General Collection** is housed in numerous rooms at the MNHN. Neotropical Theclinae of the General Collection are found in 106 glass-topped boxes stored on shelves facing the upper west wall of the room immediately west of the Fournier room. These specimens are unsorted and the individual boxes are moved around frequently.

In recent years new accessions have been placed aside the General Collection in the same room(s) as the General Collection, but not fully incorporated. Hereafter, these non-integrated collections are referred to as the **Supplemental Collection**. Concerning neotropical Theclinae, the largest of these collections are labelled as donations of Doubles, Herbulot, Stempffer, and Zerkowitz. The Stempffer Collection contains substantial numbers of neotropical Theclinae, most of which are unidentified. Neotropical Theclinae in the Supplemental Collection generally are located on shelves on the east wall of the room directly west of the Fournier room.

Type specimens. The largest number of MNHN type specimens, and those most obviously marked, are of Percy I. Lathy in the Fournier Collection. These types bear a characteristic label written by Lathy in dark ink on rectangular white labels attached to the specimen pins. These labels read either "Specimen Typicum [and name]" or "Spec. Typicum [and name]", depending on the length of the associated binomen. In addition, Lathy placed a separately pinned label, typeset in upper case, reading "TYPE" adjacent to most of these type specimens. Lathy also placed such "voucher" labels next to specimens he considered to be types of other authors. Of these, certain specimens marked as types of Max Draudt appear valid, considering their label data and what is known of purchase sources for Fournier material (G. Lamas, pers. comm.). Other specimens marked as types are questionable. Of these, certain specimens purported to be types of H. H. Druce, W. C. Hewitson, and O. Staudinger appear to be invalid (see below).

Type specimens in the General Collection usually bear, in addition to original labels, a round green label affixed by MNHN staff. On this label is inscribed, in black india ink, the particular type designation. These specimens are not segregated except in cases where a special drawer has been created by MNHN staff or by a visiting specialist. Segregated types (now in the care of Jacques Pierre, Curator) include types of J. B. Godart and C. E. Blanchard. Types of recent authors are found in drawers within the General Collection, which I have marked as noted below.

ANNOTATED LIST OF MNHN TYPES

Format. Types are reviewed by collection and author with lists under each author in alphabetical order of the terminal names. Label data on types are recorded verbatim, as read by me. Unclear label data, as deciphered, is noted by a subsequent parenthetical "(?)". Where a knowledgeable reviewer has suggested a probable translative meaning for unclear label data, this opinion is placed in adjoining brackets with the source credited. Undecipherable labels are noted as such. Brackets are also used for incidental notes by me (e.g., [sic], etc.). Differences in various authors' label formats are summarized in introductory comments concerning each author. Original descriptions are cited in standard abbreviated format. Annotations (following the heading "Note:") treat (i) discrepancies between original descriptions ("OD" 's) and extant label data concerning the type locality ("TL") and/or (ii) specific taxonomic comments. Lectotype designations and new replacement names are in bold face. All lectotypes designated bear a label "Lectotype by Kurt Johnson, *J. Lepid. Soc.*, 1991". An evaluation of status has been made for each MNHN specimen labelled as a type. However, because it is possible that a first reviser may discover additional information, no labels have been removed and lists are provided below of specimens judged not to be valid types. Illustrations are provided as explained in the "Format Notes" under each author. Forewing lengths (FWL) measured from base to apex are provided for type specimens not measured in OD's and for specimens illustrated here.

Fournier Collection

Author: Percy I. Lathy

Format notes. The list is divided by status of types into three categories: (1) valid names, (2) homonyms and replacement names, and (3) specimens invalidated as types. The standard Lathy type label, "Specimen Typicum, [name]" is abbreviated below as "s.t., etc." and Fournier drawer numbers noted as "FD #". Lathy did not illustrate all types. Some species described in 1926 were illustrated in 1930 (Plate IX) but it is not certain that the individuals figured then were types (see Note under *Thecla tristis*). Thus, I illustrate with few exceptions (noted as "photograph not available") type specimens not illustrated in OD's, along with certain lectotypes and types of replacement names. Lathy sometimes listed all the specimens he viewed for a particular taxonomic description (see Lathy 1926). Thus, according to the Code of the International Commission on Zoological Nomenclature (ICZN Code) all of these specimens could be construed as syntypes. However, though not always indicated in publication, Lathy also labeled one specimen (or two—when both sexes were available) as primary type(s). For consistency, I have always chosen one of these as lectotype and, conforming to MNHN procedures, considered the remaining primary type as a paralectotype.

CATEGORY 1. Valid Names:

***albolineata*:** holotype male, *Thecla albolineata* Lathy 1936:230 (pl. 8, fig. 5), label data: "s.t., etc., ex. coll. Brabant, type male, Rio Aquatal (?) [Rio Aguacatal, Valle del Cauca, Colombia: G. Lamas, pers. comm.], Nov. 08". FD 409.

***bouvieri*:** holotype male, *Thecla bouvieri* Lathy 1936:231 (pl. 8, fig. 13), label data: "s.t., etc., "Ecdr [probably = "Ecuador" of OD], ex Grose Smith, 1910". FD 401.

***cinerea*:** holotype male, *Thecla cinerea* Lathy 1936:231 (pl. 8, fig. 11), label data: "s.t., etc., Rio Grande". Note: locality of OD is "Rio Grande do Sul" [Brazil]. FD 388.

***cuprea*:** holotype male, *Thecla cuprea* Lathy 1930:134 (pl. 9, fig. 6), label data: "s.t., etc., Macas-Ecuador, 1905–6". FD 354.

***decorata*:** holotype male, *Lamprospilus decorata* Lathy 1926:47, label data: "s.t., etc., Oxapampa, Peru". FD 423. Fig. 1 (FWL = 18 mm).

***decyanea*:** holotype female, *Lamprospilus azaria* ab. *decyanea* Lathy 1932:182, label data: "s.t., etc., Petropolis [Brazil: OD], 5/2/73, ex. Coll. Monteiro". FD 423. Fig. 2 (16 mm).

***demilineata*:** holotype male, *Thecla demilineata* Lathy 1936:231 (pl. 8, fig. 16), label data: "s.t., etc., Arojo (?) [probably Arroyo], Paraguay, 6/11/1926, ex. C. S. Larsen coll." Note: specimen data of OD is only "Paraguay". FD 388.

***dicaeoides*:** holotype female, *Thecla dicaeoides* Lathy 1936:229 (pl. 8, fig. 1), label data: "s.t., etc., Uboveva (?) [probably "Mbovevo": G. Lamas, pers. comm.], Paraguay, 2/11/1926, ex. C. S. Larsen coll." Note: specimen data of OD is only "Paraguay". FD 416.

draudti (a): holotype male, *Lamprospilus draudti* Lathy 1932:181, label data: "s.t., etc., Nov. '08, Rio Aquatal (?) [Rio Aguacatal, Valle del Cauca, Colombia: G. Lamas, pers. comm.]". Note: OD adds "1800 m.". FD 423. Fig. 3 (FWL = 14 mm).

draudti (b): **lectotype** male, paralectotype female, *Thecla draudti* Lathy 1926:40, label data: male—"s.t., etc., "Bogota, Colombie", female—"s.t., etc., Colombie". Note: OD says TL "Colombia and Central America". FD 351. Fig. 29 (FWL = 21 mm, lectotype).

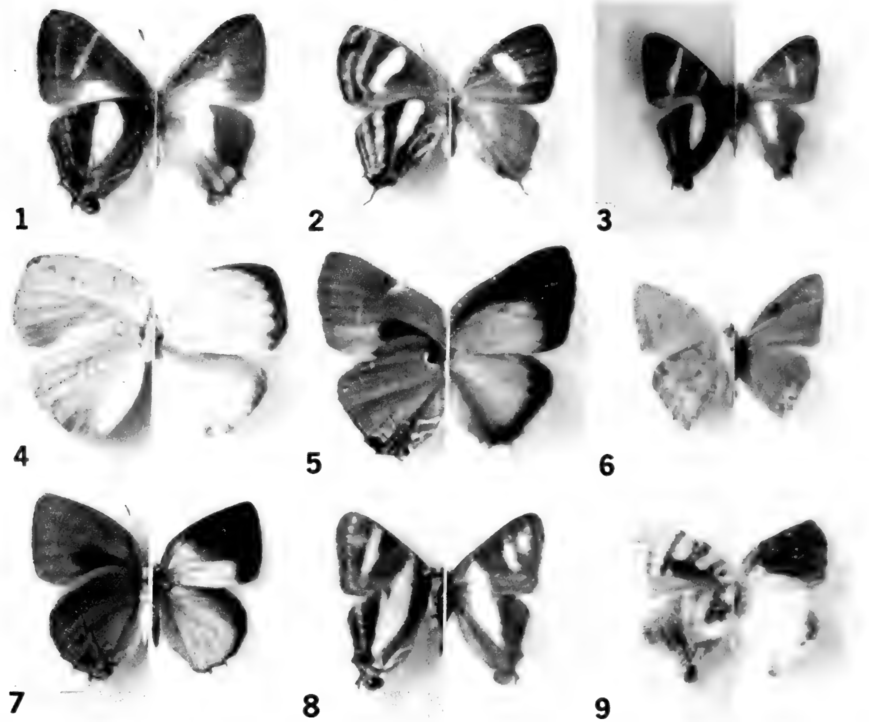
***drucei*:** holotype male, *Thecla drucei* Lathy 1926:41, label data: "s.t., etc., Brésil-etat de Ste. Catherine [sic]". FD 364. Fig. 26 (FWL = 23 mm).

***dubiosa*:** holotype female, *Thecla dubiosa* Lathy 1936:232 (pl. 8, fig. 20), label data: "s.t., etc.", no other data. Note: OD notation of TL as "Patria ignota" could be construed literally from Latin as "origin unknown" (Marchant & Charles 1956); however, it should also be noted that in cross-references of the physical feature "hills" in U.S.B.G.N. (1961–68 [1961c, 1964, 1968]) names beginning with "Patri-", and possibly originating from that Latin root [meaning "source" (Marchant & Charles 1956)?], are listed for Mexico, Colombia and Argentina. FD 418.

***elegans*:** holotype male, *Thecla elegans* Lathy 1936:230 (pl. 8, fig. 4), label data: "s.t., etc., F. Soiade (?) [probably Schade, a collector: G. Lamas, pers. comm.], Paraguay, Arojoquasi (?) [Arroyo Guazú: G. Lamas, pers. comm.], 16/11/1926". Note: specimen data of OD is only "Paraguay". FD 416.

***gloriosa*:** holotype male, *Thecla gloriosa* Lathy 1930:134 (pl. 9, fig. 5), label data: "s.t., etc.", no other data. Note: locality of OD is "Chocó, Rio Micai-Joly [sic], Colombia". OD adds specimen date "23V-18VI, 1924, collector Werner Hopp". FD 354.

***immaculata*:** lectotype male, *Trichonis immaculata* Lathy 1930:133, label data: "s.t., etc., ex. Coll. Monteiro". Note: Robbins (1986:144) presumed this specimen and a reputed Natural History Museum, London (NHM), syntype as extant. Searches of the NHM by me, P. Ackery (NHM) (pers. comm.), L. D.and J. Y. Miller (Allyn Museum of Entomology, University of Florida) (AME) (J. Miller, pers. comm.), and J.N. Eliot and P. Ackery using correspondence from Robbins (P. Ackery, J. N.Eliot, pers. comm.) have failed to locate



FIGS. 1–9. Wing upper surface (ups), right, and under surface (uns), left, of selected MNHN types. **1,** *Lamprospilus decorata* Lathy, holotype. **2,** *L. azaria* ab. *decyanea* Lathy, holotype. **3,** *L. draudti* Lathy, holotype. **4,** *Trichonis immaculata* Lathy, lectotype. **5,** *Thecla rocena major* Lathy, lectotype. **6,** *T. eurytulus nigra* Lathy, holotype. **7,** *Theclopsis eryx occidentalis* Lathy, lectotype. **8,** *Lamprospilus nicetus ochracea* Lathy, holotype. **9,** *Thecla dolylas pallida* Lathy, holotype.

a NHM syntype. Thus, I designate the MNHN specimen as the lectotype. It differs from Robbins' characterization of the species by being unicolorous on the hindwing under surface. However, there is also evidence this surface has been repaired. OD gives no TL. FD 343. Fig. 4 (FWL = 17 mm, lectotype).

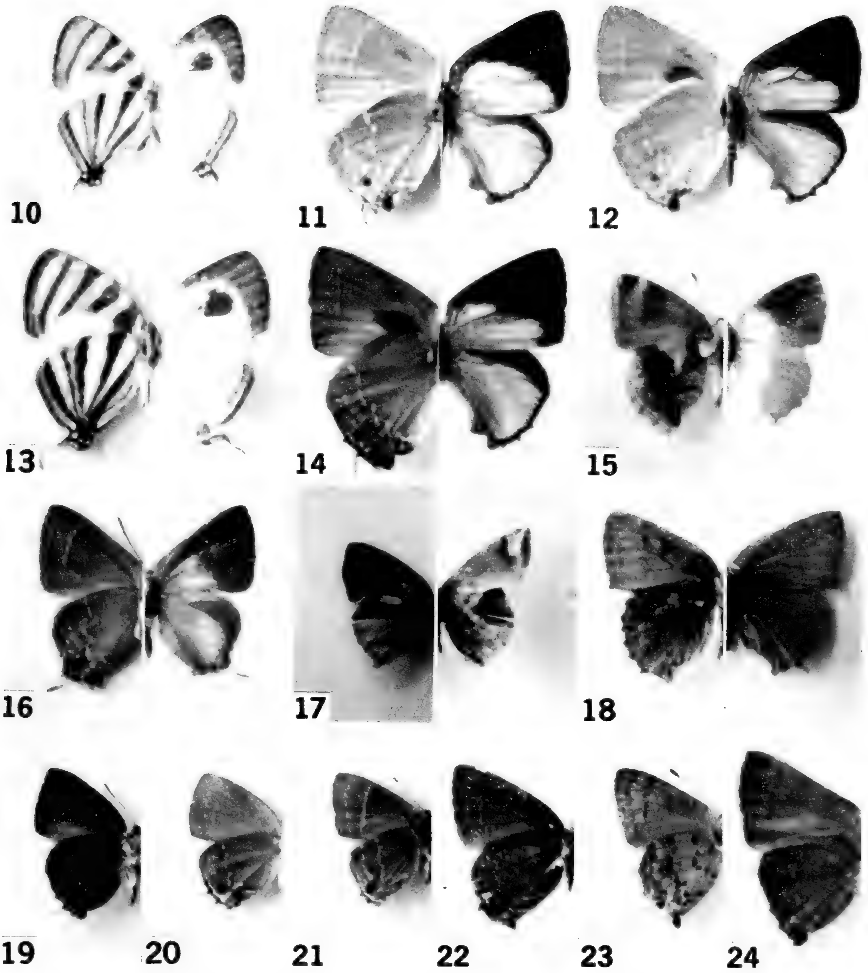
***inconspicua*: lectotype** male, *Thecla inconspicua* Lathy 1930:136 (pl. 9, fig. 15), label data: "s.t., etc., Petropolis [Brazil], 94:169, 28-8-73".

***larseni*:** holotype male, *Thecla larseni* Lathy 1936:230 (p. 8, fig. 7), label data: "s.t., etc., Mendoza 28/12 1906, Argentina, Coll. C. S. Larsen, Faaborg". Note: OD states holotype is female; dissection indicates it is male (Johnson 1990a, in treatment of generic placement of this species, noted that dull wing coloration complicates superficial sex recognition). Fig. 24 (FWL = 13 mm). FD 420.

***lilacina*: lectotype** male, paralectotype male [marked "female" by Lathy], *Thecla lilacina* Lathy 1930:136 (pl. 9, Fig. 13), label data (both): "s.t., etc., Petropolis [Brazil], 27-2-74". FD 401.

***lineata*:** holotype male, *Thecla lineata* Lathy 1936:231 (pl. 8, fig. 14), label data: "s.t., etc., Balzapamba, Ecuador, C. S. Larsen coll.". Note: OD states holotype is female; dissection indicates it is male. FD 407.

***maculata*:** holotype male, allotype female, *Thecla maculata* Lathy 1936:230 (pl. 8, fig. 8), label data: male—"s.t. etc., Huancabamba, Peru, Carl Zacher [collector]", female—



FIGS. 10–24. Selected MNHN types and other specimens continued (10–18, format as in Figs. 1–9, H = homonym, R = replacement). **10,** *Thecla linus paraguayensis* Lathy, lectotype. **11,** *T. phoster parvipuncta* Lathy, lectotype. **12,** *T. cyllarus reducta,* lectotype. **13,** *T. linus separata* Lathy, lectotype. **14,** *T. cyllarus* ab. *xanthica* Lathy, holotype. **15,** *Thecla commodus viridis* Lathy (H, R = *familiaris* Johnson), holotype. **16,** *T. catharina* Draudt, lectotype. **17,** *Polyommatus bazochii* Godart, holotype. **18,** *P. irus* Godart, holotype. **(19–24),** under surfaces of taxa with generally concolorous upper surfaces. **19,** *Thecla ortaloides* Lathy, holotype. **20,** *Thecla peruviana* Lathy (H, R = *pentas* Nicolay), holotype. **21,** *Thecla tristis* Lathy, holotype. **22,** *Polyommatus falacer* Godart, holotype. **23,** *P. megarus* Godart, holotype. **24,** *P. strophius* Godart, holotype.

"s.t., etc., Sao P. d'Olivenca, 22 March". FD 381. Note: in OD Lathy departed from his earlier practice and specifically noted respective holotype and allotype.

***major*: lectotype** male, paralectotype male [marked "female" by Lathy], *Thecla rocena major* Lathy 1926:42, label data (both): "s.t., etc., Muzo, Colombia". FD 382. Fig. 5 (FWL = 18 mm, lectotype).

nigra**:** holotype male, *Thecla eurytulus nigra* Lathy 1926:46, label data: "s.t., etc., Tucuman, 9-6-22". Note: locality of OD is "Tucuman, Argentina"; the status of *nigra* was recently revised by Johnson et al. 1990. FD 417. Fig. 6 (FWL = 12 mm).

obliterata**:** holotype female, *Thecla obliterata* Lathy 1936:230, label data: "s.t., etc., Pampas, 3000 m., Peru". Note: taxon omitted by Comstock and Huntington (1958–64) [1961, 1962] by editorial error omitting all citations before "ocr . . .". FD 371. Photograph not available.

obsoleta**: lectotype** male, paralectotype male [marked "female" by Lathy], *Eumaeus minyas* [=*minijas*] *obsoleta* Lathy 1926:39, label data (both): "s.t., etc., Bolivia, Prov. de Sara, C. Bolivia". Note: taxon omitted by Comstock and Huntington (1958–64) [1961, 1962] by editorial error omitting all citations before "ocr . . .". FD 338. Fig. 30 (FWL = 28 mm, lectotype).

occidentalis (a): **lectotype** male, paralectotype female, *Thecla strephon occidentalis* Lathy 1926:44, label data (both): "s.t., etc., Rio Tono, Peru, 1,200 ft., Watkins". Note: taxon omitted by Comstock and Huntington (1958–64) [1961, 1962] by editorial error omitting all citations before "ocr . . .". FD 396. Fig. 32 (FWL = 20 mm, lectotype).

occidentalis (b): **lectotype** male, paralectotype female, *Theclopsis eryx occidentalis* Lathy 1926:47, label data (both): "s.t., etc., Rio Tono, Peru, 1,200 ft., Watkins". Note: taxon omitted by Comstock and Huntington (1958–64) [1961, 1962] by editorial error omitting all citations before "ocr . . .". FD 423. Fig. 7 (FWL = 16 mm, lectotype).

ochracea**:** holotype male, *Lamprospilus nicetus ochracea* Lathy 1932:182, label data: "s.t., etc., 32.21 ex Dognin 1921, Loja, Equiteur (?) [Equateur = Ecuador] 1886" plus three undecipherable notation labels. Note: taxon omitted by Comstock and Huntington (1958–64) [1961, 1962] by editorial error omitting all citations before "ocr . . .". FD 423. Fig. 8 (FWL = 15 mm).

ortaloides**:** holotype male, *Thecla ortaloides* Lathy 1930:135 (pl. 9, fig. 12), label data: "s.t., etc., Petropolis [Brazil], 10-2 '76". Note: refigured because OD fig. shows under surface medial band continuous. FD 389. Fig. 19 (FWL = 12 mm).

pallida**:** holotype male, *Thecla dolylas pallida* Lathy 1930:135, label data: "s.t., etc., Hab? [sic]", no other data. Note: OD has no TL. FD 377. Fig. 9 (FWL = 13 mm).

paraguayensis**: lectotype** male, *Thecla linus paraguayensis* Lathy 1926:42, label data: "s.t., etc., Patino, Paraguay, C. S. Barnes". Note: aside lectotype male (with specimen type label reading "paraguayana") Lathy pinned his standard label "TYPE"; additional 11 male syntypes of OD were not specifically marked. FD 373. Fig. 10 (FWL = 13 mm).

parvipuncta**: lectotype** male, paralectotype female, *Thecla phoster parvipuncta* Lathy 1926:44, label data (both): "s.t., etc., Rio Tono, C. Peru, 1,200 ft., Watkins". FD 397. Fig. 11 (FWL = 19 mm).

peculiaris**:** holotype male, *Thecla peculiaris* Lathy 1930:136 (pl. 9, fig. 14), label data: "s.t., etc., Petropolis, Brazil, 11-x-1875". FD 401.

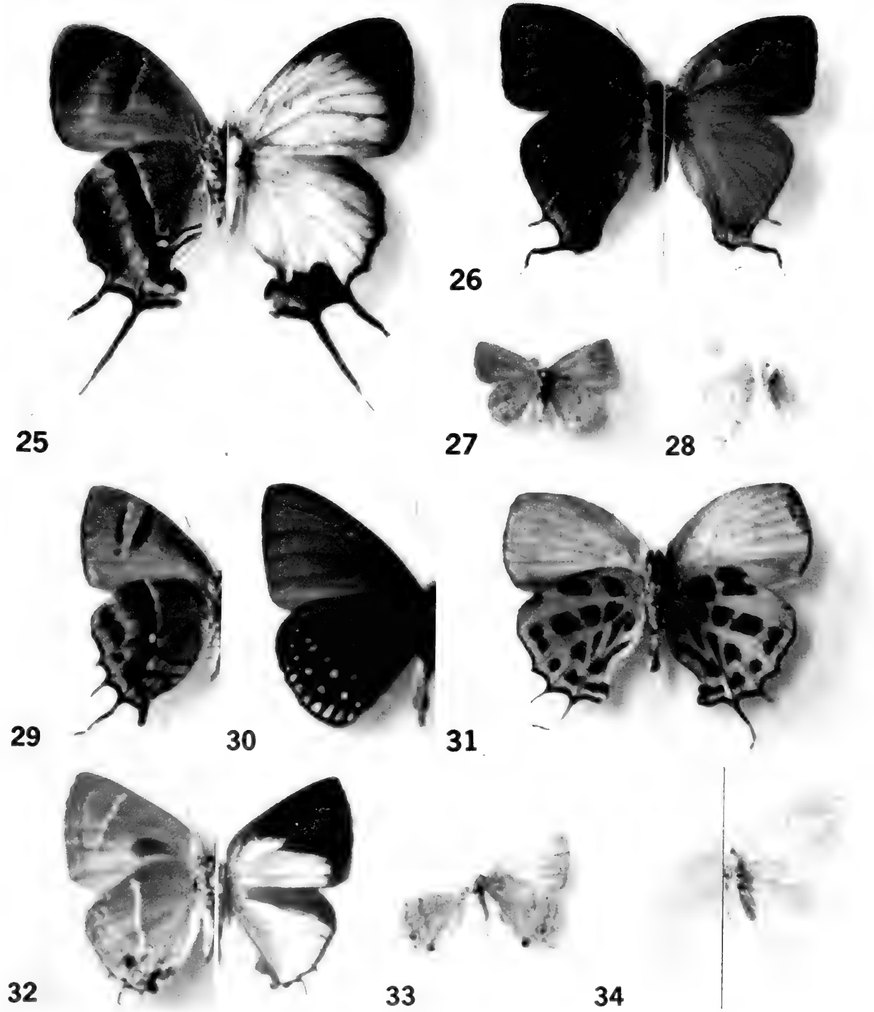
peruviana**: lectotype** female, *Eumaeus minyas* [=*minijas*] *peruviana* Lathy 1926:39, label data, "s.t., etc., Chanchamayo, C. Peru". Note: for *Thecla peruviana* Lathy 1936 see invalid names (Category 3). Concerning *E. m. peruviana,* aside lectotype female Lathy pinned his standard label "TYPE"; additional 20 female and 32 male syntypes of OD were not specifically marked. Photograph not available. FD 355.

reducta**: lectotype** male, *Thecla cyllarus reducta* Lathy 1926:44, label data: "s.t., etc., Rio Tono, C. Peru, 1,200 ft., Watkins". Note: aside lectotype male Lathy pinned his standard label "TYPE"; additional 6 male syntypes of OD were not specifically marked. FD 397. Fig. 12 (FWL = 20 mm).

restricta**:** holotype male, *Thecla restricta* Lathy 1936:230 (pl. 8, fig. 9), label data: "s.t. etc., Salta, N. Argentina, iv–vi 1921". Note: a companion female with identical data is also marked as a type but OD is from a holotype male. FD 371.

separata**: lectotype** male, paralectotype female, *Thecla linus separata* Lathy 1926:42, label data: "s.t., etc.", no other data. Note: locality of OD includes "Rio Tono" and "Chanchamayo" (both noted as in "Peru") and "Matto Grosso" [Brazil]. FD 373. Fig. 13 (FWL = 17 mm, lectotype).

septentrionalis**: lectotype** male, *Thecla ambrax septentrionalis* Lathy 1926:44, label data: "s.t., etc., Muzo, Colombie". Note: second syntype male (label data "Chontales,



FIGS. 25–33. Selected MNHN types and other specimens continued. **25,** ups right, uns left, *Thecla coronata watkinsi* Lathy, holotype. **26,** format as above, *T. drucei* Lathy, holotype. **27,** uns, both wings, *T. crispisulcans* Draudt, lectotype. **28,** uns, both wings, *Thecla americensis* Blanchard, lectotype. **29,** uns, *Thecla draudti* Lathy, lectotype. **30,** uns, *Eumaeus minyas* [sic] *obsoleta* Lathy, lectotype. **31,** uns, both wings, *Thecla mirabilis* Lathy (H, R = *rhaptissima* Johnson), holotype. **32,** ups right, uns left, *T. strephon occidentalis* Lathy, lectotype. **33,** uns, both wings, *Polyommatus damastus* Godart, possible holotype. **34,** ups right, uns left, *Thecla larseni* Lathy, holotype.

Nicaragua") is at NHM (personal examination and Bridges 1988); OD does not explicitly state TL; contrary to usual Lathy practice (see Discussion), TL does not specify deposition of types. Considering the OD and label data, I and G. Lamas (pers. comm.) consider the above specimens as original syntypes. FD 398. Photograph not available.

***tagyroides*: lectotype** male, paralectotype female, *Thecla tagyroides* Lathy 1930:134 (pl. 9, fig. 7), label data: "s.t., etc., Bas Maroni, Guyane Francaise". FD 354.

***talboti*:** holotype male, *Thecla talboti* Lathy 1936:232 (pl. 8, fig. 18) label data: "s.t., etc., S. Blas [sic], Paraguay, 12-1926, ex. C. S. Larsen coll.". FD 389.

***trinitatis*:** holotype female, *Thecla trinitatis* Lathy 1936:232 (pl. 8, fig. 19), label data: "s.t., etc., "Caparo, W. Cent. Trinidad, F. Birch". Note: OD states holotype is male; dissection indicates it is female. TL of OD cited "Trinité". FD 418.

***tristis*:** holotype male, *Thecla tristis* Lathy 1926:45, label data: "s.t., etc., Nivac, Matto Grosso, Brazil". Note: variance between this specimen and 1930 figure (Plate IX, 16) led me to doubt that the four individuals of this plate with 1926 OD's necessarily represented the types. All are refigured (see *L. decorata, T. draudti, T. drucei*). FD 407. Fig. 21 (FWL = 14 mm).

***variegata*:** holotype male, *Thecla variegata* Lathy 1936:231 (pl. 8, fig. 12), label data: "s.t., etc., Santa Fe de Bogota". Note: locality of OD is "Bogota, Colombie". FD 388.

***watkinsi*:** holotype female, *Thecla coronata watkinsi* Lathy 1926:39, label data: "s.t., etc., Pichis Rd., Peru, 1800 ft., xi–xii '19, C. Watkins". FD 349. Fig. 25 (FWL = 48 mm).

***xanthica*:** holotype male, *Thecla cyllarus* ab. *xanthica* Lathy 1926:44, label data: "s.t., etc., Bas [="Lower" of OD] Maroni [French Guiana]". FD 397. Fig. 14 (FWL = 20 mm).

***xoremoides*:** holotype male, *Thecla xorema xoremoides* Lathy 1936:231 (pl. 8, fig. 15), label data: "s.t., etc. Villarrica, Paraguay, 11-1924, ex. C. S. Larsen coll.". Note: Specimen data of OD is only "Paraguay". Hyphenated "*xorema-xoremoides*" combination of OD has confused status of each name under ICZN Code (C. Bridges, pers. comm.); G. Lamas (pers. comm.) suggests best construing intention of Lathy as latter name being subspecies of former. I find this view consistent with wing and morphological fascies of each taxon (*Thecla xorema* Schaus, TL Castro, Parana, Brazil, holotype National Museum of Natural History, Smithsonian Institution). FD 389.

CATEGORY 2. Junior Primary Homonyms and Replacement Names:

Five Lathy names constitute junior primary homonyms and require replacement names according to sections 59 and 60 of the ICZN Code.

inornata*:** holotype female, *Thecla inornata* Lathy 1936:229 (pl. 8, fig. 3), label data: "s.t., etc., R. Grande". Note: invalid homonym of *Thecla inornata* Verity (1911). A replacement name is needed (Bridges 1988) for which I propose ***lathyi, referring to OD cited above and designating OD's holotype female as holotype of the new name. OD states holotype is male; dissection indicates it is female. Etymology refers to Lathy's original description of the taxon. TL of OD is "Rio Grande do Sul, Brazil". FD 416.

mirabilis*:** holotype male, *Thecla mirabilis* Lathy 1930:135 (pl. 9, fig. 8), label data: "s.t., etc., Rio Pastazza [sic], Ecuador". Note: invalid homonym of *Thecla mirabilis* Erschoff (1874). A replacement name is needed (Bridges 1988) for which I propose ***rhaptissima, referring to OD cited above and designating OD's holotype male (Fig. 31, 23 mm) as holotype of the new name. Etymology means "greatly speckled" and refers to the under surface wing pattern. OD adds "Eastern" to Ecuador TL. FD 351.

***peruviana*:** holotype female, *Thecla minyas* [=*minijas*] *peruviana* Lathy 1936:229 (pl. 8, fig. 2), label data: "s.t., etc., Chanchamayo, C. Peru". Note: invalid homonym of *Thecla peruviana* Erschoff (1876). A replacement name is not needed since Nicolay (1971) described *Symbiopsis pentas* and study of its types (Carnegie Museum of Natural History) indicates it and *peruviana* Lathy (Fig. 20) are the same species. Based on this synonymy, *pentas* Nicolay replaces *peruviana* Lathy 1936 [not *peruviana* Lathy 1926, which was described in *Eumaeus* (see Category 1, above)]. FD 416.

violacea*:** holotype male, *Thecla violacea* Lathy 1936:230 (pl. 8, fig. 6), label data: "s.t., etc., Abuna, Amazons, Oct. 15, 1929". Note: invalid homonym of *Thecla quercus* var. *violacea* Niepelt (1914). A replacement name is needed (Bridges 1988) for which I propose ***magnapurpurata, referring to the OD cited above and designating OD's holotype male as holotype of the new name. Etymology refers to the purplish coloration noted originally by Lathy. OD specimen data is only "Amazon." FD 405.

viridis*:** holotype male, *Thecla commodus viridis* Lathy 1930:135, label data: "s.t., etc. [but as "Thecla viridis"], Ex. Coll. Monteiro". Note: invalid homonym of *Thecla viridis* Edwards (1862). Dissection of *viridis* holotype indicates it is a species distinct from *commodus* (syntypes, NHM); I propose the replacement name ***familiaris for the Lathy taxon, referring to the OD cited above and designating OD's holotype male (Fig. 15, 15 mm) as holotype of the new name. Etymology denotes the common occurrence of this generally Andean butterfly. OD suggests "Bolivia" as TL. FD 375.

CATEGORY 3. Specimens Invalidated as Types:

FD's 355–356 contain a number of specimens of the genus *Eumaeus* labelled as types but for which there are no known descriptions. The species names attached to these specimens are invalid and noted here only as "x". This list is provided because the species names used by Lathy duplicate others he applied validly in other genera. None of these specimens is a type:

(1) a male, label data: "s.t. Eumaeus "x" Lathy, Iquito [sic], Amazon, iii–iv '30", FD 355;
(2) a male, label data: "s.t. Eumaeus "x" Lathy, S. Andaeas [sic], Ecuador", FD 355;
(3) a male and female, label data: "s.t. Eumaeus "x" Lathy [male] Huigra, W. Ecuador, 3000 ft., 15 Febr." [female] Huigra, W. Ecuador, 3000 ft., 16 Febr. 1913, A. Hall";
(4) a female, label data "s.t. Eumaeus "x" Lathy, R. Grande";
(5) a male, label data: "s.t. Eumaeus "x" Lathy, Rio Chili, Colombia, xii-'20".

Author: Max Draudt

Format notes. Numerous Draudt types have been of uncertain location since World War II and generally considered destroyed (Kiriakoff 1948). Bridges (1988) suggested the Naturhistorisches Museum, Basel, Switzerland as a possible depository but such specimens have not been found (G. Lamas, pers. comm.). Gerardo Lamas recently located Draudt types in Europe and will report soon on this important discovery. Following from this, and knowledge of historical purchases of material by Fournier, Lamas (pers. comm.) construes the following MNHN specimens labelled as types of Draudt to be authentic. Since label format on Draudt types varies, entries below are formatted according to the various labels with remarks immediately following.

CATEGORY 1. Valid Names:

***catharina*:** **lectotype** male, paralectotype male, *Thecla catharina* Draudt 1917–24 [1920]:(Vol. 5) 788 (pl. 156, fig. k), label data: lectotype—handwritten red label "type", Lathy voucher label and "Timbo, Blumenau, St. Catharina [sic], Modt. 11/8/27, af H. Kotzsch, Dresden-Blasewitz, ex. C. S. Larsen coll."; paralectotype—same, but no specific mention of "Timbo, Blumenau". Note: G. Bernardi (pers. comm.) indicates that on Larsen Collection labels, data following "Modt." (located on a second label line following collection data, if provided) includes data concerning purchase. Consistent with this observation, G. Lamas (pers. comm.) reports these specimens, and the types of subsequent entries, "were sold to Larsen by H. Kotzsch, from Dresden". The OD mentions only two syntype males; accordingly, Lamas (pers. comm.) notes that, based on label data above, report of a third syntype in Dresden and a fourth in São Paulo, Brazil (Lamas 1973:183) is probably incorrect. Because of the previously unclear status of Draudt types since World War II, recent revisionary work including *catharina* noted purported MNHN syntypes but did not designate a lectotype (Johnson 1990a). FD 407. Fig. 16 (FWL = 15 mm).

***crispisulcans*: lectotype** female, *Thecla crispisulcans* Draudt 1917–24 [1920]:(Vol. 5) 799 (pl. 158, fig. g), label data: red label "type", Lathy voucher label and "Timbo Blumenau, St. Catharina [sic]". FD 414. Fig. 27 (FWL = 10 mm).

***quassa*: lectotype** male, *Thecla quassa* Draudt 1917–24 [1920]:(Vol. 5) 784 (pl. 156, fig. a), label data: red label "type", Lathy voucher label and "Timbo Blumenau, St. Catharina [sic]". FD 401. Photograph not available (FWL = 11 mm).

Other Authors

Certain Fournier Collection drawers contain specimens marked as types attributed to various authors but determined here as invalid. None of these specimens is a type:

(1) a female, FD 401, marked "TYPE" of *Thecla vesper* Druce (1909), label data: "Rio Tono, 1,200 ft., Watkins". Note: valid type (OD TL Chanchamayo, Peru) is at the NHM (personal examination and Bridges 1988);

(2) a male, FD 423, marked "s.t., etc. *Lamprospilis azaria*" [*Thecla azaria* Hewitson (1863–78 [1867]], label data: "Itatiaya [Brazil], ix'24, 1000 m., coll E. May". Note: MNHN labels misattribute authorship to Lathy. Valid syntypes are at the NHM and lack locality labels [personal examination]; OD did not include TL (OD, Comstock & Huntington 1959, Bridges 1988);

(3) a male, FD 360, marked "s.t., etc. *Thecla orsina*" [Hewitson 1863–78 [1877]], label data: "Rio Tono, C. Peru, 1,200 ft., Watkins". Note: MNHN labels misattribute authorship to Lathy. Valid type (OD TL Bolivia) is at the NHM;

(4) a male and female, FD 389, each marked "TYPE" of *Micandra sapho* Staudinger 1884–88:[(Vol. 1) 289 (Vol. 2, pl. 97)], label data: male—"Rio Micai"; female—"Kolumb., Chocó, Rio Micai [sic], Joly [sic] 23.5–18.6 1924, Werner Hopp". Note: valid type (OD TL Rio San Juan, Panama) is in Staudinger collection at Zoologisches Museum der Humbolt Universität zu Berlin (H. J. Hannemann, pers. comm.).

General Collection

Author: Jean Baptiste Godart

Format notes. The list is divided by status of types into two categories: (1) extant type specimens and valid names and (2) reputed MNHN type specimens not located or of uncertain identity. Label data are appropriately noted as "handwritten" and/or "typeset". Photographs are as described above. G. Lamas and R. Robbins (pers. comm.) note additional Godart types may be at the MNHN. The list below includes all that could be located in consultation with P. Viette, G. Bernardi and J. Pierre (MNHN) and all presently included in the MNHN drawer segregated for Godart types under the care of J. Pierre.

CATEGORY 1. Extant Type Specimens and Valid Names:

***bazochii*:** holotype male, *Polyommatus bazochii* Godart 1819–24 [1824]:681, label data: handwritten: "T. Basochii [sic], God. [sic], thius, Hübn/ basochii Godt. type, Brésil, Delalande"; typeset: "Museum Paris, Brésil, Delalande". Note: this specimen had been judged a type by MNHN curators P. Viette and G. Bernardi (pers. comm.). Fig. 17 (FWL = 13 mm).

***falacer*:** holotype male, *Polyommatus falacer* Godart 1819–24 [1824]:633, label data: handwritten: "Falacer God. [sic], type de Godart probable, (Strymon falacer)". Note: this specimen has been suggested as a probable type by MNHN curators P. Viette and G. Bernardi (pers. comm.). Fig. 21 (FWL = 18 mm).

***irus*:** holotype male, *Polyommatus irus* Godart 1819–24 [1824]:674, label data: handwritten: "P. Irus God. [sic] arsace Boisd. [sic]", "Incisalia irus Holotype det. by R. R. Gatrielle 1975, Allyn Museum Photo No. 0900975-A 13-14-15"; typeset: "Museum Paris, Polyommatus irus Godart, Encycl. méthod. p 674, no 177". Note: this specimen had been judged a type by MNHN curators P. Viette and G. Bernardi (pers. comm.). Fig. 18 (FWL = 16 mm).

***megarus*:** holotype male, *Polyommatus megarus* Godart 1819–24 [1824]:638, label data: handwritten: "P. Megarus, God. [sic], echion, Linn., basalides [sic], Hübn., megarus, Godt. type"; typeset: "TYPE, Museum Paris". Note: this specimen had been judged a type by MNHN curators P. Viette and G. Bernardi (pers. comm.). The name *megarus* was previously considered a subjective synonym of *Tmolus basilides* (Geyer 1832–37 [1837]) (Bridges 1988); a new status and combination are documented for *P. megarus* in Johnson et al. (1990). Fig. 23 (FWL = mm).

***strophius*:** holotype male, *Polyommatus strophius* Godart 1819–24 [1824]:632, label data: handwritten: "Strophius Godt. type, T. cerus, Boisd., Strepon, Fabr., Strophius God." [sic]; typeset: "Museum Paris, Brésil, Delalande, TYPE". Note: this specimen had been judged a type by MNHN curators P. Viette and G. Bernardi (pers. comm.). Fig. 24 (FWL = 20 mm).

CATEGORY 2. Reputed MNHN Type Specimens Not Located or of Uncertain Identity:

damastus and ***hugon*:** both described in *Polyommatus* by Godart (1819–24 [1824], p. 640 and with holotypes listed by Bridges (1988) and Miller and Brown (1981) as MNHN. Bridges (pers. comm.) followed Miller and Brown; Miller (pers. comm.) relied on correspondence from Viette and also borrowed one of the types (*P. irus*). The identifications of types listed by Viette for Miller were made by Viette (Miller, pers. comm.) and Bernardi communicated the same to R. K. Robbins (pers. comm.). According to the examination made by me and by Bernardi and Pierre in 1989, the type of *hugon* is not among Godart types segregated at MNHN. However, there is a specimen among the types (Fig. 33, FWL = 13 mm) that bears only the handwritten label "type de Godart probable". For the following reasons, this specimen may be the type listed by Viette as "*P. damastus*" in his correspondence with Miller. Although the specimen represents *Hesperia cecrops* Fabricius (1792–99 [1793]) (now placed in genus *Calycopis* Scudder [Field 1967, Bridges 1988]), because *P. damastus* was originally proposed as a replacement name for *Papilio damon* Stoll 1780–90 [1782], *P. damastus* (since Morris 1860) has been consistently considered a subjective synonym of *Lycus gryneus* Hübner 1816–26 [1819] (now placed in *Mitoura* Scudder [Bridges 1988]). Both *cecrops* and *gryneus* have orange under surface bands and colorful limbal areas; crude description or renderings of the two taxa could be easily confused. Thus, if the poorly labelled MNHN specimen is indeed the type of *P. damastus*, it is possible the identity of *P. damastus* has been hitherto misconstrued. It would constitute a synonym of *H. cecrops*, not *L. gryneus*. However, although this information is important to record, I see no objective way to decide the identity of this poorly labelled specimen.

Author: Charles Emile Blanchard

CATEGORY 1. Valid Names:

***americensis*:** lectotype male, paralectotype male *Thecla americensis* Blanchard (in Gay 1852: Vol. 7:38, pl. 3, fig. 10), label data (both): green type label, "T. americensis, Bl., 15/43 [referring to entry no., in Gay's personal journal, dated 1843 and noting the Coquimbo, Chile TL], Museum Paris, Chili [sic], Gay 1843". Note: syntype referenced above was first located by G. Bernardi (pers. comm. dated 25 January 1983) but its location subsequently unknown until 1989 when it was found with the Godart types. Since it lacked an abdomen, the lectotype (Fig. 28, FWL = 12 mm) was designated from another syntype located by me in 1985 with abdomen still intact (Johnson et al. 1990). Both original syntypes are now segregated with the Godart material under the care of J. Pierre as above noted.

Recent Authors

MNHN is depository for an increasing number of primary types of this author. These are listed in Johnson et al. (1988, 1990) and Johnson (1989a, 1989b; 1990a, 1990b, 1991) and are located in two drawers of the cabinets facing the west wall in the room directly west of the Fournier room. These drawers have an external label "Neotropical Type Specimens of Dr. Kurt Johnson".

Supplemental Collection

No Neotropical Thecline types are apparent in the supplemental collections in the two rooms consecutively west of the Fournier room (the rooms most likely for incorporation of Neotropical butterflies on an "as is" basis). This includes the collections attributed to Doubles, Herbulot, Stempffer, and Zerkowitz. I have examined the contents of these collections on three separate occasions.

DISCUSSION

Of MNHN types, those of P. I. Lathy are most straightforward and easiest to evaluate. Regarding Neotropical Theclinae, Lathy (1926, 1930, 1936) (with the exception of *Thecla ambrax septentrionalis*) indicated species were described from the Fournier Collection. Types from Lathy (1904) have been documented at the NHM (personal examination and Bridges 1988). Confusion can arise concerning Lathy names in cases where he proposed the same specific name in various genera (Bridges 1988) but did not specify more than a specific name on the type label. Unfortunately, such labels were placed on some specimens for which names were never published. Because some of this undescribed material represents significant species additions to various groups of Eumaeini, I plan to describe the taxa that can be assigned to genera recently revised.

It appears that types of three Lathy taxa described from the Fournier Collection still have not been located: *Thecla obsoleta* Lathy 1926, *T. janthina venezuelae* Lathy 1930, and *T. angusta* Lathy 1936. As several Lathy types were located in the farflung Fournier holdings as late as 1989, it is probable that these types are extant and eventually will be found.

In the four instances of MNHN types attributed to Draudt, authenticity initially appeared questionable because of published reports that most of these types had been destroyed in World War II (Kiriakoff 1948, Bridges 1988). However, in 1991 G. Lamas (pers. comm.) located many of the "missing" Draudt types and, from their data and consideration of known purchase sources of Fournier material, concluded that MNHN types attributed to Draudt are apparently genuine.

Other MNHN specimens marked as types of various authors appear to be invalid. Those attributed to Druce, Hewitson, or Staudinger were readily assessed as inauthentic because data did not match OD's and because types of these taxa were already well-documented from other institutions. G. Lamas (pers. comm., 1991) suggests that some Theclinae types of Embrik Strand and Wilhelm Niepelt also may be at the MNHN. In my examinations of the respective Fournier and General collections, I did not find any purported types of these authors marked either with MNHN green type labels or Lathy "voucher" type labels. However, it is possible such specimens may be in either collection but not specifically marked as types.

ACKNOWLEDGMENTS

G. Bernardi and Jacques Pierre (MNHN) provided invaluable assistance and hospitality while I was in Paris. Dr. Bernardi reviewed an initial draft of this paper and, later, worked with me on the specific questions and comments posed by other reviewers. These latter included Charles A. Bridges (University of Illinois, Urbana, who kindly reviewed my initial draft in relation to his computer data base on Neotropical Eumaeini) and William E. Miller (former *Journal* editor), Robert K. Robbins (National Museum of Natural History) and J. N. Eliot (Taunton, United Kingdom) who made particularly helpful review comments. Also, Frederick H. Rindge and Eric L. Quinter (American Museum of Natural History) reviewed preliminary drafts. Jacqueline Y. Miller (Allyn Museum of the Florida Museum of Natural History, Sarasota (AME)), Philip Ackery (NHM), and Eliot answered particular questions concerning types at the NHM. An extremely helpful review of a final draft was made by Gerardo Lamas (Museo de Historia Natural, Lima, Peru); any errors in incorporation of his comments are mine. At Paris, Jacques Pierre and Madame Pierre patiently helped match keys to cabinets during successive searches of stored Fournier material. Lorraine Hitz provided the specimen photographs. J. R. Pigott translated some comments and questions of reviewers into French for use at MNHN. Lee D. Miller (AME), Bridges, and Rindge responded to questions concerning the final draft.

LITERATURE CITED

BLANCHARD, C. E. 1852. Lepidoptera, pp. 1–468. *In* Gay, C., Historia fisica y politica de Chile. Vol. 7. Privately printed, Paris & Santiago. 468 pp.

BRIDGES, C. A. 1988. Catalogue of Lycaenidae & Riodinidae (Lepidoptera: Rhopalocera). Privately printed, Urbana, Illinois. 811 pp.

COMSTOCK, W. P. & E. I. HUNTINGTON. 1958–64. An annotated list of the Lycaenidae (Lepidoptera—Rhopalocera) of the western hemisphere. J. N.Y. Entomol. Soc. [1958] 66:103–118; [1959] 67:59–95, 163–212; [1960] 68:49–62, 105–122, 176–186, 232–240; [1961] 69:4–58, 105–118, 157–176, 191–200; [1962] 70:39–46, 100–118, 177–179; [1963] 71:45–57, 115–119, 189–197, 262–264; [1964] 72:62–64, 120–130.

COWAN, C. F. 1967. Enc. meth. 9. J. Soc. Bibliog. Nat. Hist. 4:307.

DRAUDT, M. 1917–24 [1920, 1921]. *Thecla,* pp. 794–811 [1920] and Addended Notes, p. 825 [1921]. *In* Seitz, A., Macrolepidoptera of the world. Alfred Kernen Verlag, Stuttgart. [1920–1921] Vol. 5, pp. 593–1139, [1920] Vol. 5 (plates), 194 pls.

DRUCE, H. H. 1909. On some new and little-known Neotropical Lycaenidae. Trans. Entomol. Soc. Lond. 57:431–438.

EDWARDS, W. H. 1862. Descriptions of certain species of diurnal Lepidoptera found within the limits of the United States and British America—No. 3. Proc. Acad. Nat. Sci. Philad. 14:221–226.

ERSCHOFF, N. G. 1874. Lepidoptera, pp. 1–127. *In* Fedchenko, Aleksyei Pavlovich, Reise in Turestan [sic] (1874–1899). Mem. Soc. Amis Sci. nat. Moscou 11(2):[vi]–134.

——— 1876. [title in Russian] @ "Descriptions of new species of exotic butterflies". Trudy russ. ent. Obshsch. 10:57–66.

FABRICIUS, J. C. 1792–99 [1793]. Entomologia systematica emendata et aucta, secundum classes, ordines, genera, species, adjectis synonymis, locis, observationibus, descriptionibus. Gottl. Proft, Copenhagen. p. 270 of Vol. 3(1) [1793], 488 pp.

FIELD, W. D. 1967. Preliminary revision of butterflies of the genus *Calycopis* Scudder (Lycaenidae: Theclinae). Proc. U.S. Nat. Mus. 119 (3552): 48 pp.

GODART, J. B. 1819–24 [1824]. [1824] pp. 632, 633, 638, 640, 674, 681. *In* Latreille, P. A. & J. B. Godart. Encyclopédie méthodique, Histoire naturelle des insectes. Vol. 9 and supplement. Privately printed, Paris. [1824] Godart prepared text pages 329–end (p. 828) [Cowan 1967].

GEYER, C. M. 1832–37 [1837]. Vol. 5, p. 42. *In* Hübner 1808–1837 [1837]. Zuträge zur Sammlung Exotischer Schmettlinge. Privately printed, Augsburg. [Vol. 5 attributed to Geyer (see Bridges 1988)]. 52 pp.

HEWITSON, W. C. 1863–78 [1867]. Illustrations of diurnal Lepidoptera, Lycaenidae. Supplement. John van Voorst, London. p. 87 [1867] Suppl., pp. 77–114; pl. 34 [1867] pls. 31–46.

——— 1863–78 [1877]. Illustrations of diurnal Lepidoptera, Lycaenidae. John van Voorst, London. p. 200 [1877], Vol. I, 229 pp.; pl. 79, Vol. II (plates), 92 pls.

HÜBNER, J. 1816–26 [1819]. Verzeichniss bekannter Schmettlinge. Privately printed, Augsburg. p. 74, entry 732 of [1819] (see Bridges 1988), pp. 17–176.

JOHNSON, K. 1989a. Revision of *Chlorostrymon* Clench and description of two new austral Neotropical species (Lycaenidae). J. Lepid. Soc. 43:120–146.

——— 1989b. A revision of the South American hairstreak butterfly genera *Tergissima* and *Femniterga* (Lycaenidae: Theclinae). Insecta Mundi 3:195–215.

——— 1990a. The new hairstreak butterfly genus *Orcya,* a revision of the Neotropical "*Thecla*" *orcynia* assemblage. J. N.Y. Entomol. Soc. 98:50–87.

——— 1990b. *Penaincisalia,* a new genus of "elfin"-like butterflies from the high Andes (Lepidoptera: Lycaenidae). Pan-Pacific Entomol. 66:97–125.

——— 1991. Neotropical hairstreak butterflies: Genera of the "*Calycopis/Calystryma* grade" of Eumaeini (Lepidoptera, Lycaenidae, Theclinae) and their diagnostics. Reports Mus. Nat. Hist., Univ. Wisc. (Stevens Point) 21:1–127.

JOHNSON, K., R. C. EISELE & B. MACPHERSON. 1988. The "hairstreak butterflies" (Lycaenidae, Theclinae) of northwestern Argentina. I. Introduction, *Calycopis, Calystryma, Tergissima* & *Femniterga.* Bull. Allyn Mus. 123:1–49.

——— 1990. *Ibid. op. cit.,* II. *Strymon* sensu stricto. Bull. Allyn Mus. 130:1–77.

KIRIAKOFF, S. G. 1948. A report on the war damage to Lepidopterology in Europe. Lepid. News 2(5):49.

LAMAS, G. 1973. The type-material of Lepidotera Rhopalocera contained in the collections of the Museu de Zoologia da Universidade de São Paulo. Papéis avulsos Dept. Zool., São Paulo 26(13):179–185.

LATHY, P. I. 1904. A contribution towards the knowledge of the Lepidoptera-Rhopalocera of the Dominica, B.W.I. Proc. Zool. Soc. London 1904(2):450–454.

——— 1926. Notes on the American Theclinae (Lepidoptera). Ann. Mag. Nat. Hist. 17(9):35–47.

——— 1930. Notes on South American Lycaenidae with descriptions of new species. Trans. Entomol. Soc. London 78(1):133–137.

——— 1932. The genus *Lamprospilus* (Lepidoptera). Ann. Mag. Nat. Hist. 10(9):180–182.

——— 1936. *Thecla* nouveaux d'Amérique de Sud (Lepidopt. Lycaenidae), pp. 229–232. *In* M. Eugene-Louis Bouvier, Livre jubilaire de M. Eugene-Louis Bouvier. Firmin-Didot, Paris. 379 pp.

MARCHANT, J. R. V. & J. F. CHARLES. 1956. Cassell's Latin Dictionary. Funk & Wagnalls, New York. 927 pp.

MILLER, L. D. & F. M. BROWN. 1981. A catalogue/checklist of the butterflies of America north of Mexico. Mem. Lepid. Soc. 2. 280 pp.

MORRIS, J. G. 1860. Catalogue of the described Lepidoptera of North America. Smithson. Misc. Publ., Washington. 68 pp.

NICOLAY, S. S. 1971. A new genus of hairstreak from Central and South America (Lycaenidae, Theclinae). J. Lepid. Soc. 25 (suppl. 1):1–39.

——— 1982. Studies in the genera of America Hairstreaks. 6. A review of the Hübnerian genus *Olynthus* (Lycaenidae: Eumaeini). Bull. Allyn Mus. 74:30 pp.

NIEPELT, W. 1914. Neue formen palaearktischer Rhopalocera. Int. ent. Z. 8(26):144–145.

ROBBINS, R. K. 1986. Evolution and identification of the New World Hairstreak Butterflies (Lycaenidae: Eumaeini): Eliot's *Trichonis* Section and *Trichonis* Hewitson. J. Lepid. Soc. 40:138–157.

STAUDINGER, O. 1884–88. Exotische Tagfalter, Theil I. *In* Staudinger, O. & E. Schatz (eds.), Exotische Schmetterlinge. G. Löwensohn, Fürth (Bayern). [Band 1, Beschreibungen], 333 pp. [Band 2, Abbildungen], 100 pls.

STOLL, C. 1780–90 [1782]. p. 208, pl. 390 [Vol. 4]. *In* Cramer, P. De uitlandische Kapellen, voorkomende in de drie Waereld-Deelen Asia, Africa en America. Amsterdam, Baalde & Utrecht, Wild. [Vol. 4 onwards completed by Stoll; pages not sequentially numbered (Bridges 1988)]. [Vol. 4], 136 pp.

U.S.B.G.N. [UNITED STATES BOARD ON GEOGRAPHIC NAMES]. 1961–68 [1961a, 1961b, 1961c; 1964, 1968]. Gazetteer. U.S. Government Printing Office, Washington, D.C. [1961a] Venezuela, 245 pp.; [1961b] Peru, 609 pp.; [1961c] Mexico, 749 pp.; [1964] Colombia, 396 pp.; [1968] Argentina, 699 pp.

VERITY, R. 1911. Alcuni Lepidoptteri inediti o non ancora figurati. Boll. Soc. Entomol. Ital. 42:266–281.

Received for publication 18 November 1987; revised 10 August 1989 and 23 June 1990; revised and accepted 3 June 1991.

Journal of the Lepidopterists' Society
45(2), 1991, 158–168

BODY SIZE IN NORTH AMERICAN LEPIDOPTERA AS RELATED TO GEOGRAPHY

William E. Miller

Department of Entomology, University of Minnesota, St. Paul, Minnesota 55108

ABSTRACT. Body-size patterns among eight main regions and subregions of North America are established with species-level entities in 37 genera and 18 families of Lepidoptera. Patterns are compared with expectations arising from certain underlying causes of body size variability. Main regions are East, West, North, South; subregions are Northeast, Northwest, Southeast, and Southwest; all are defined by latitude 40°N and longitude 100°W. Published wing measure, either forewing or span length, serves as an index of body size. Heat-transfer principles determining thoracic temperatures necessary for flight suggest that diurnal genera should converge on medium body size at high latitudes and high elevations. The large-bodied *Papilio* (Papilionidae) actually do so in the North and West, and perhaps *Hesperia* (Hesperiidae) also, the West having higher elevations than the East. Three other diurnal genera of medium body size vary little in size geographically as might also be expected from heat-transfer principles. Among 32 nocturnal genera surveyed, no distinct latitudinal pattern in body size is evident, nor does prior knowledge predict one. Prior positive relations between altitude of capture site and body size in Tortricidae suggest that nocturnal moths generally might prove larger-bodied in the West because of higher elevations. Nearly all the nocturnal genera do show distinct longitudinal body-size variation, 30 of 32 genera being larger in the West by a mean 16% in wing measure. This longitudinal regularity suggests a new ecogeographic size rule. No unequivocal explanation for the underlying altitudinal increase in body size of nocturnal lepidopterans has yet emerged, but higher food-plant quality at higher elevations is a likely factor.

Additional key words: biogeography, wing measure, latitude, longitude, altitude.

The idea that body size in North American Lepidoptera is related to geography arose more than a century ago. Packard (1876) claimed that Colorado and Pacific Coast specimens of some two dozen species of Geometridae were larger bodied than Atlantic Coast specimens. Later he reported similar variation in several species of Notodontidae (Packard 1895).

Longitude was the geographic dimension involved in these early observations. Since Packard's time, knowledge of insect body size as related to longitude has progressed but little. Modern observations of longitudinal effects on lepidopteran body size are scant and refer to a mere handful of species. A few authors have noted statistical correlations between longitude and body measurements such as forewing length, or have incidentally noted longitudinal changes in forewing length, or included data that show such changes. The magnitude of longitudinal change in wing length in these reports ranges from 10 to 18%; the species involved are *Pontia protodice* (Boisduval & Leconte) (Pieridae) (Abbott et al. 1960), *Dichomeris gleba* Hodges (Gelechiidae) (Hodges 1986), *Autochton cellus* (Boisduval & Leconte) (Hesperiidae) (Burns 1984), *Euxoa c. churchilliensis* (McDunnough) (Noctuidae) (Lafontaine

1987), and *Hyalophora columbia* (Smith) (Saturniidae) (Collins 1973), data for the last-named also having a latitudinal component. In all these observations, as in Packard's, body size is larger in the West than in the East.

In Lepidoptera, measures such as forewing length and span can be taken as reliable indexes of body size up to family level (Miller 1977b, Wasserman & Mitter 1978, and others). Throughout this paper, I use wing measure and body size as interchangeable concepts.

As for latitudinal effects, Packard reported none, although he was aware of the latitudinal size gradients in homeotherms now known as Bergmann's and Allen's rules. These ecogeographical rules state, respectively, that overall body size increases from south to north whereas body extremities like ears and tails diminish (Allee & Schmidt 1951). The concept of latitude as a possible factor in insect body size arose later than longitude and apart from it. Field and laboratory observations show some nonlepidopterous insects superficially conforming to Bergmann's rule, and some not (Ray 1960). In Lepidoptera, sweeping statements have been made about latitudinal body-size effects: "The generally recognized north-south trend for increase in size in Great Lakes butterflies seems to be associated mainly with non-migratory species. Members of such butterfly genera as *Papilio, Pieris, Cercyonis, Euptychia, Lethe, Boloria, Speyeria, Erynnis, Hesperia,* and *Poanes,* for example, tend to show southward size increases. Similar observations may be made in certain moths, such as the saturniids *Eacles, Antheraea,* and *Hyalophora*" (Wagner & Hansen 1980). Some of these trends may be expected for lepidopterans, as discussed below, but few have been actually demonstrated.

Bergmann's and Allen's rules for homeotherms are now explained as heat-conserving surface/mass adjustments to latitudinal temperature gradients (Mayr 1976, Vernberg 1962). Similarly, studies of butterfly body heat capacity and thoracic temperatures necessary for flight lead to the conclusion that butterflies should converge on an optimum size at arctic latitudes (Douglas 1986). This convergence may proceed in opposite directions depending on characteristic body size: from large to medium as in *Parnassius phoebus* (Fabricius) (Papilionidae) (Guppy 1986) and *Papilio glaucus* Linnaeus (Papilionidae) (Scriber 1982); or from small to medium, as in *Pieris napi* (Linnaeus) (Pieridae) (Wagner & Hansen 1980). If body size is already optimal for northern latitudes, it may not change at all latitudinally, as in *Pontia protodice* (Abbott et al. 1960). Critical limits cannot be stated for the three butterfly body-size classes because factors other than size are also involved.

Butterflies also show a body-size response to altitude. The explanation seems much the same as that for the latitudinal response described above, namely body heat capacity (Douglas 1986). As expected for characteristically large-bodied butterflies, negative correlations between altitude and body size are reported for *Occidryas chalcedona* (Doubleday) (Nymphalidae) (Hovanitz 1942), *Parnassius phoebus* (Fabricius) (Guppy 1986), and *Polites draco* (Edwards) (Hesperiidae) (Brown 1962), the last without display of supporting data. On the other hand, in Tortricidae, which are nocturnal or crepuscular, a positive correlation exists between altitude of capture site and body size, an empirical finding thus far without unequivocal explanation (Miller 1991).

There has never been an attempt to put body size and geography into perspective for any large insect group like an order. I present here an order-wide survey of body size in North American Lepidoptera, and compare results with expectations derived from prior knowledge of body size variability. The survey examines body size indexes among four main regions and four subregions defined by longitude and latitude. My approach differs from those of the past for insects because species in multiregional genera provide most of the size data rather than populations in multiregional species. If populations within species exhibit geographic differences in body size, the factors responsible for such differences should produce them at the next two higher taxonomic levels in exactly the same way. Thus similar geographic differences in body size can be expected among subspecies in polytypic species, and among species in genera. This approach has been productive with vertebrates (Allee & Schmidt 1951, Ray 1960). Because properly defined genera are monophyletic, the species of a genus constitute an analogue of the populations within a species. Use of this analogue here yields ready-made body-size data because forewing length or span has been published for most species of North American Lepidoptera.

The literature reviewed above suggests that certain patterns should emerge from a geographic body-size survey of North American Lepidoptera. With respect to latitude, diurnal forms should increase, decrease, or remain the same in body size depending on their characteristic size. For nocturnal forms, there is no prior knowledge on which to base a latitudinal expectation. With respect to longitude, body-size patterns should reflect the differing elevations between East and West. Thus diurnal forms should show body-size patterns similar to those expected latitudinally, and nocturnal forms should show the increased body size associated with higher elevations in the West.

METHODS

This study surveys transcontinental, species-rich genera in which forewing lengths or spans are available for constituent species-group entities (species, subspecies, populations). Summary forewing lengths or spans are computed and compared within genera by the following eight main regions and subregions of North America excluding Mexico: East, West, North, South, Northeast, Northwest, Southeast, Southwest. These regions and subregions are defined by latitude 40°N and longitude 100°W, map-lines which divide temperate North America into subequal halves and quadrants.

Genera were included in the survey if five or more constituent entities fell in each of the West and East main regions. The search for suitable genera was exhaustive, and no genus meeting the foregoing criterion was excluded. If more than one source of data for a genus was available, the most recent one was used, except that original reports were chosen in preference to later reviews or books based on them, and earlier treatments were chosen if later ones contained less precise wing measurements. Treatments published before 1940 were compared with the most recent Lepidoptera check list (Hodges et al. 1983) for current reliability; all included in the study had 95% or more of their entities still recognized taxonomically.

Entities were assigned to main regions and subregions in which their known ranges fell entirely or predominantly. Entities not falling predominantly in one subregion were not assigned to one, but were assigned to a main region if possible; entities not falling predominantly in either a subregion or main region were excluded from the study.

Northwest, Northeast, Southwest, and Southeast subregions are nested within North, South, East, and West main regions. Thus wing measurements for entities occurring in, say, the Northwest were included not only in the body-size computation for that subregion, but also in body-size computations for the North and West main regions.

Means of forewing length or span were computed for each genus in every main region and subregion encompassing five or more entities. The data entering these computations were entity means when available, but most commonly were midpoints of reported ranges, which approximate entity means. Separate ranges published for males and females were combined into a single entity range for midpoint determination.

Mean elevations were computed as described below from the *National Atlas* relief map, sheet No. 56, published by the Geological Survey, U.S. Dept. of Interior. Each main-regional and subregional mean is based on 50 or more altitudes obtained with transparent dot-grid overlays. Dots on overlays were evenly spaced, and spacing was chosen so that each subregion encompassed at least 50 dots.

Classification and nomenclature follow Hodges et al. (1983).

RESULTS AND DISCUSSION

Body-size means were computed in two or more main regions for 37 genera (Table 1). These data enable 37 East-West comparisons, 18

TABLE 1. Summary forewing lengths (L) or spans (S) (mm) by eight main regions and subregions of North America for 37 genera of Lepidoptera. Each value is a mean for five or more species-group entities computed chiefly from midpoints of published ranges. Boldface denotes a mean significantly larger than its East-West counterpart; italics, a mean significantly larger than its North-South counterpart (Student *t*-test, P < 0.05). Dashes denote fewer than five entities in a geographic partition or its counterparts.

Genus	Source	Measure	Geographic partition							
			W	E	N	S	NW	SW	NE	SE
Nepticulidae										
Stigmella	Wilkinson & Scoble 1979	L	**5.6**	4.3	—	—	—	—	—	—
Tischeriidae										
Tischeria	Braun 1972	S	**7.8**	7.0	—	—	—	**7.8**	—	6.8
Tineidae										
Acrolophus	Hasbrouck 1964	S	22.7	21.2	—	—	—	**22.9**	—	19.0
Lyonetiidae										
Bucculatrix	Braun 1963	S	7.9	8.0	7.7	7.9	8.2	7.8	7.4	8.2
Gracillariidae										
Phyllonorycter	Braun 1908	S	**8.2**	7.1	7.4	7.4	7.8	**8.4**	7.0	7.1
Oecophoridae										
Agonopterix	Hodges 1974	L	9.1	8.5	9.1	8.2	—	—	—	—
Ethmia	Powell 1973	L	9.4	9.4	—	—	—	9.0	—	9.2
Antaeotricha	Duckworth 1964	S	**23.9**	19.0	—	—	—	—	—	—
Elachistidae										
Elachista	Braun 1948	S	**10.4**	8.8	9.9	9.0	10.4	—	*9.5*	7.8
Coleophoridae										
Batrachedra	Hodges 1966	S	**14.4**	9.0	—	—	—	—	—	—
Gelechiidae										
Dichomeris	Hodges 1986	L	7.0	6.5	6.8	6.4	—	6.9	6.2	5.9
Argyresthiidae										
Agryresthia	Busck 1907	S	**11.1**	9.2	10.6	9.9	—	10.6	—	9.4
Sesiidae										
Synanthedon	Eichlin & Duckworth 1988	L	9.6	9.1	9.3	9.3	—	—	—	—
Carmenta	Eichlin & Duckworth 1988	L	7.9	8.3	—	—	—	7.8	—	8.1
Tortricidae										
Olethreutes	Heinrich 1926	S	**17.4**	14.5	—	—	—	—	—	—
Rhyacionia	Powell & Miller 1978	L	**8.0**	6.3	—	—	—	—	—	—
Phaneta	Heinrich 1923	S	17.0	15.5	17.5	16.8	17.6	16.8	16.6	—
Eucosma	Heinrich 1923	S	**22.0**	18.5	22.2	21.4	**22.9**	**22.8**	17.3	19.5
Epiblema	Brown 1973	S	16.9	15.8	17.0	15.4	—	—	17.5	14.9
Epinotia	Brown 1980	L	8.0	7.2	—	—	**8.0**	—	7.2	—
Grapholita	Heinrich 1926	S	12.6	10.7	—	—	—	—	—	—
Cydia	Heinrich 1926	S	15.3	13.5	13.7	15.6	14.6	17.0	—	—
Acleris	Razowski 1966	L	9.4	8.8	—	—	9.7	—	8.8	—
Argyrotaenia	Freeman 1958	S	18.2	17.4	17.5	16.5	—	—	—	—

TABLE 1. Continued.

Genus	Source	Mea-sure	Geographic partition							
			W	E	N	S	NW	SW	NE	SE
Hesperiidae										
Erynnis	Burns 1964	L	17.3	17.6	—	—	—	—	—	—
Hesperia	Lindsey 1942	S	30.5	31.5	30.2	32.0	—	—	—	—
Papilionidae										
Papilio	Tyler 1975	S	76.3	**89.2**	70.5	79.4	—	73.7	—	86.1
Pyralidae										
Pyrausta	Munroe 1976	L	**9.4**	7.9	*10.4*	8.8	—	**9.0**	—	7.5
Nephopteryx	Heinrich 1956	S	24.7	20.6	—	—	—	—	—	—
Pterophoridae										
Oidaematophorus	Barnes & Lindsey 1921	S	24.4	20.1	24.7	24.0	—	—	—	—
Geometridae										
Itame	McGuffin 1972	S	25.2	23.4	—	—	—	—	—	—
Semiothisa	McGuffin 1972	S	24.9	23.2	—	—	—	—	—	—
Anacamptodes	Rindge 1966	L	**16.8**	14.9	—	—	—	16.5	—	14.8
Nemoria	Ferguson 1969	L	**14.0**	11.6	—	—	—	**13.8**	—	11.3
Eupithecia	Bolte 1990	S	20.4	19.0	—	—	—	—	—	—
Noctuidae										
Euxoa	Hardwick 1970	S	35.0	32.7	34.8	36.0	33.8	35.8	—	—
Schinia	Hardwick 1958	S	**21.1**	17.0	19.7	20.1	—	—	—	—

North-South comparisons, and 6 to 12 comparisons each between Northeast and Northwest, Southeast and Southwest, Northeast and Southeast, and Northwest and Southwest. The surveyed genera are in 18 families and 12 superfamilies. The represented families contain 82 percent of North American Lepidoptera species (Hodges et al. 1983).

Latitudinal Comparisons

Of the 18 genera in North-South comparisons, 10 had means larger in the North, 1 significantly larger; 6 had means larger in the South; and 2 had tied means (Table 1). The frequency distribution of larger means departs little from the equal numbers expected in each main region by chance alone ($P > 0.20$, sign test). This outcome indicates no order-wide directional trend. The lack of trend is repeated in the Northeast-Southeast and Northwest-Southwest comparisons. Of the 12 genera in these subregional comparisons, 6 had means larger in the North, 1 significantly larger; and 6 had means larger in the South (Table 1).

The butterfly genera *Papilio* and *Hesperia* show trends of smaller North body sizes as expected for large-bodied forms, the first one statistically significant (Table 1). The diurnal moth genus *Synanthedon* shows a null trend (Table 1), an outcome that might be expected for medium sized forms if heat-transfer principles from butterfly investigations apply to other diurnal Lepidoptera. Critical size limits for trend direction in the *Synanthedon* body type are unknown, however.

The two genera with significantly different North and South means, *Elachista* and *Pyrausta*, have the larger mean in the North (Table 1). It is tempting to think that these genera represent northward convergence from small to medium, as expected for small-bodied diurnal forms. Neither genus is diurnal, however. Different and unknown factors probably account for body-size trends among nocturnal genera.

Longitudinal Comparisons

Of the 37 genera in East-West comparisons, 31 had means larger in the West, 15 of them significantly larger; 5 had larger means in the East, 1 of them significantly larger; and 1 had tied means (Table 1). The frequency distribution of larger means in each main region departs sharply from the equal numbers expected by chance ($P < 0.01$, sign test). This outcome suggests an order-wide phenomenon, and matches the published longitudinal trends for species cited in the Introduction. Larger western means are repeated in the Northeast-Northwest and Southeast-Southwest comparisons: of the 20 genera in these subregional comparisons, 16 had means larger in the West, 7 significantly larger; and 4 had indexes larger in the East (Table 1).

If the five surveyed diurnal genera, namely *Synanthedon, Carmenta, Erynnis, Hesperia,* and *Papilio,* are removed from consideration, then an astonishing 30 out of 32 nocturnal genera show larger West means (Table 1). The mean increase in forewing length or span in these genera, computed algebraically, is 16%.

Papilio stands out with its significantly smaller West mean, and *Carmenta, Erynnis,* and *Hesperia*—all the remaining diurnal general except *Synanthedon*—show similar but weaker trends (Table 1).

North and South main-regional elevations are subequal at ca. 1000 m; the West regional elevation at ca. 1600 m exceeds the East one by more than 1000 m; and the four subregions follow suit (Table 2). *Papilio* sharply decreases in body size toward the altitudinally higher West (Table 1). Altitudinal decrease also occurs in two strictly western species: *Parnassius phoebus* (Guppy 1986) and *Polites draco* (Brown 1962). Smaller-bodied diurnal genera might remain the same at higher elevations or converge from small to medium. Both trends are evident but weakly expressed among the diurnal genera surveyed. Also, both trends have been previously recorded in individual species: larger body size in *Colias philodice* Godart (Pieridae) (Kingsolver 1983), and no change

TABLE 2. Summary elevations in North America by main regions and subregions. Each value is a mean computed from 50 or more observations chosen systematically with dot-grids from a topographic map.

Main region or subregion	Mean altitude (m)
North	1161
South	939
East	481
West	1619
Northeast	675
Southeast	286
Northwest	1648
Southwest	1591

in *Pontia protodice* (Abbott et al. 1960). Again, critical size limits for trend direction in the body types represented are unknown.

Ultimate reasons for increased body size of nocturnal genera in the West might include one or more of the physical factors varying with altitude, namely atmospheric pressure, evaporation, oxygen pressure, temperature, and solar radiation (Allee & Schmidt 1951). Evaporation also increases with increasing aridity, and there are many desert regions in the West. The influence of physical factors might be direct or indirect. As examples of direct effects, slightly lowered temperature during development sometimes produces larger body size (Miller 1977a, and others), and increased evaporation may select for large body size which favors water retention by decreasing surface/volume ratio (Remmert 1981, and others). Indirect effects might involve food-plant quality, and recent findings make food-plant quality a highly likely explanatory factor. With increasing altitude, plants usually contain more nitrogen per unit of leaf area, sometimes greater concentration of nitrogen, which is associated with greater photosynthetic rate (Körner 1989). Insect body size is known to be directly correlated with amount of dietary nitrogen (Mattson & Scriber 1987). Moreover, body size in a folivorous sawfly has been reported to vary directly with elevation, with nitrogen concentration of the leaves of its food plant varying similarly and simultaneously (Niemelä et al. 1987).

CONCLUSION

Dividing surveyed genera into diurnal and nocturnal helps to order the North American geographic body-size patterns observed. The diurnal genera reveal patterns reasonably consistent with convergence toward medium body size both at higher latitudes and at higher elevations associated with increasing longitudes. The characteristically large-bodied *Papilio* converges toward medium size, perhaps *Hesperia* also, and the medium-bodied genera either do not converge or converge too little to be detected in this study. No distinctively small-bodied diurnal genera were available in the survey to confirm their convergence toward medium size. Also, the lack of critical size limits for trend direction allows only broad comparisons between actual and expected results.

Among the 32 nocturnal genera surveyed, only *Elachista* and *Pyrausta* show a clear latitudinal body-size trend, both having larger North body sizes. An explanation is doubtless peculiar to these genera. On the other hand, nearly all nocturnal genera increase in body size with increasing longitude, as expected from prior knowledge of Tortricidae increasing in body size with increasing altitude. The regularity of this longitudinal trend suggests a new ecogeographic size rule, but whether it applies beyond moths remains to be investigated.

ACKNOWLEDGMENTS

I thank M. G. Pogue for helping gather data, and W. H. Wagner Jr., R. J. Blahnik, A. M. Fallon, J. M. Burns, and D. E. Gaskin for manuscript reviews.

LITERATURE CITED

ABBOTT, W., L. S. DILLON & R. R. SHRODE. 1960. Geographic variation in *Pieris protodice* Boisduval and Leconte (Lepidoptera: Pieridae). Wasmann J. Biol. 18:103–127.

ALLEE, W. C. & K. P. SCHMIDT. 1951. Ecological animal geography. 2nd ed. Wiley, New York. 715 pp.

BARNES, W. & A. W. LINDSEY. 1921. The Pterophoridae of America, north of Mexico. Contr. Nat. Hist. Lepid. N. Amer. 4:281–483.

BOLTE, K. B. 1990. Guide to the Geometridae of Canada (Lepidoptera) VI. Subfamily Larentiinae 1. Revision of the genus *Eupithecia*. Mem. Entomol. Soc. Can. 151, 253 pp.

BRAUN, A. F. 1908. Revision of the North American species of the genus *Lithocolletis* Hübner. Amer. Entomol. Soc. Trans. 34:269–357.

——— 1948. Elachistidae of North America (Microlepidoptera). Amer. Entomol. Soc. Mem. 13, 110 pp.

——— 1963. The genus *Bucculatrix* in America north of Mexico (Microlepidoptera). Amer. Entomol. Soc. Mem. 18, 208 pp.

——— 1972. Tischeriidae of America north of Mexico (Microlepidoptera). Amer. Entomol. Soc. Mem. 28, 148 pp.

BROWN, F. M. 1962. The variation of *Polites draco* (Hesperiidae) with altitude. J. Lepid. Soc. 16:239–242.

BROWN, R. L. 1973. Phylogenetic systematics: Its application to the genus *Epiblema* (Lepidoptera). M.S. Thesis, University of Arkansas, Fayetteville. 179 pp.

——— 1980. A revision of the genus *Epinotia* (Hübner) (Tortricidae: Eucosmini), part 1: The North American species of the *stroemiana* lineage. Ph.D. Dissertation, Cornell University, Ithaca, N.Y. 470 pp. (Diss. Abst. Int. 41/9 (B):3302. Microfilm No. 8102899).

BURNS, J. M. 1964. Evolution in skipper butterflies of the genus *Erynnis*. Univ. Calif. Publ. Entomol. 37, 214 pp.

——— 1984. Evolutionary differentiation: Differentiating gold-banded skippers—*Autochton cellus* and more (Lepidoptera: Hesperiidae: Pyrginae). Smiths. Contr. Zool. 405, 38 pp.

BUSCK, A. 1907. Revision of the American moths of the genus *Argyresthia*. U.S. Natl. Mus. Proc. 32:5–24.

COLLINS, M. M. 1973. Notes on the taxonomic status of *Hyalophora columbia* (Saturniidae). J. Lepid. Soc. 27:225–235.

DOUGLAS, M. M. 1986. The lives of butterflies. Univ. of Michigan Press, Ann Arbor. 241 pp.

DUCKWORTH, W. D. 1964. North American Stenomidae (Lepidoptera: Gelechioidea). U.S. Natl. Mus. Proc. 116:23–71.

EICHLIN, T. D. & W. D. DUCKWORTH. 1988. Sesioidea: Sesiidae. *In* Dominick, R. B. et al. (eds.), The moths of America north of Mexico, including Greenland. Fasc. 5.1. 176 pp.

FERGUSON, D. C. 1969. A revision of the moths of the subfamily Geometrinae of America north of Mexico (Insecta, Lepidoptera). Yale Univ. Peabody Mus. Natur. Hist. Bull. 29, 251 pp.

FREEMAN, T. N. 1958. The Archipinae of North America (Lepidoptera: Tortricidae). Can. Entomol. Suppl. 7 (vol. 90), 89 pp.

GUPPY, C. S. 1986. Geographic variation in wing melanism of the butterfly *Parnassius phoebus* F. (Lepidoptera: Papilionidae). Can. J. Zool. 64:956–962.

HARDWICK, D. F. 1958. Taxonomy, life history, and habits of the elliptoid-eyed species of *Schinia* (Lepidoptera: Noctuidae), with notes on the Heliothidinae. Can. Entomol. Suppl. 6 (vol. 90), 116 pp.

——— 1970. The genus *Euxoa* (Lepidoptera; Noctuidae) in North America. I. Subgenera *Orosagrotis, Longivesica, Chorizagrotis, Pleonectopoda,* and *Crassivesica.* Entomol. Soc. Can. Mem. 67, 177 pp.

HASBROUCK, F. F. 1964. Moths of the family Acrolophidae in America north of Mexico (Microlepidoptera). U.S. Natl. Mus. Proc. 114:487–706.

HEINRICH, C. 1923. Revision of the North American moths of the subfamily Eucosminae of the family Olethreutidae. U.S. Natl. Mus. Bull. 123, 298 pp.

——— 1926. Revision of the North American moths of the subfamilies Laspeyresiinae and Olethreutinae. U.S. Natl. Mus. Bull. 132, 216 pp.

——— 1956. American moths of the subfamily Phycitinae. U.S. Natl. Mus. Bull. 207, 581 pp.

HODGES, R. W. 1966. Review of the New World species of *Batrachedra,* with descriptions of three new genera (Lepidoptera: Gelechioidea). Trans. Amer. Entomol. Soc. 92:585–651, pls. 29–53.

——— 1974. Gelechioidea, Oecophoridae. *In* Dominick, R. B. et al. (eds.), The moths of America north of Mexico, including Greenland. Fasc. 6.2, 142 pp.

——— 1986. Gelechioidea: Gelechiidae (in part). *In* Dominick, R. B. et al. (eds.), The moths of America north of Mexico, including Greenland. Fasc. 7.1, 195 pp.

HODGES, R. W., T. DOMINICK, D. R. DAVIS, D. C. FERGUSON, J. G. FRANCLEMONT, E. G. MUNROE & J. A. POWELL (eds.). 1983. Check list of the Lepidoptera of America north of Mexico, including Greenland. E. W. Classey & The Wedge Entomological Research Foundation, London. 284 pp.

HOVANITZ, W. 1942. Genetic and ecologic analyses of wild populations in Lepidoptera. I. Pupal size and weight variation in some California populations of *Melitaea chalcedona*. Ecology 23:175–188.

KINGSOLVER, J. G. 1983. Thermoregulation and flight in *Colias* butterflies: Elevational patterns and mechanistic limitations. Ecology 64:534–545.

KÖRNER, C. 1989. The nutritional status of plants from high altitudes: A worldwide comparison. Oecologia 81:379–391.

LAFONTAINE, J. D. 1987. Noctuoidea: Noctuidae (part) Noctuinae (part—*Euxoa*). *In* Dominick, R. B. et al. (eds.), The moths of America north of Mexico, including Greenland. Fasc. 27.2, 237 pp.

LINDSEY, A. W. 1942. A preliminary revision of *Hesperia*. Denison Univ. Bull., J. Sci. Lab. 37:1–50.

MATTSON, W. J. & J. M. SCRIBER. 1987. Nutritional ecology of insect folivores of woody plants: Nitrogen, water, fiber, and mineral considerations, pp. 105–146. *In* Slansky, F. & J. G. Rodriguez (eds.), Nutritional ecology of insects, mites, and spiders. Wiley, New York. 1016 pp.

MAYR, E. 1976. Evolution and the diversity of life: Selected essays. Belknap Press of Harvard Univ. Press, Cambridge, Massachusetts. 721 pp.

MCGUFFIN, W. C. 1972. Guide to the Geometridae of Canada (Lepidoptera) II. Mem. Entomol. Soc. Can. 86, 159 pp.

MILLER, W. E. 1977a. Weights of *Polia grandis* pupae reared at two constant temperatures (Lepidoptera: Noctuidae). Great Lakes Entomol. 10:47–49.

——— 1977b. Wing measure as a size index in Lepidoptera: The family Olethreutidae. Ann. Entomol. Soc. Amer. 70:253–256.

——— 1991. Positive relation between body size and altitude of capture site in tortricid moths (Tortricidae). J. Lepid. Soc. 45:66–67.

MUNROE, E. G. 1976. Pyraloidea, Pyralidae, comprising the subfamily Pyraustinae, Tribe Pyraustini (conclusion). *In* Dominick, R. B. et al. (eds.), The moths of America north of Mexico, including Greenland. Fasc. 13.2b, 150 pp.

NIEMELÄ, P., M. ROUSI & H. SAARENMAA. 1987. Topographical delimitation of Neodiprion sertifer (Hym., Diprionidae) outbreaks on Scots pine in relation to needle quality. J. Appl. Entomol. 103:84–91.

PACKARD, A. S. 1876. A monograph of the geometrid moths or Phalaenidae of the United States. Rep. U.S. Geol. Surv. Territories 10, 607 pp.

——— 1895. Monograph of the bombycine moths of America north of Mexico. Part I, Family 1—Notodontidae. Mem. Natl. Acad. Sci. 7, 291 pp.

POWELL, J. A. 1973. A systematic monograph of the New World ethmiid moths (Lepidoptera: Gelechioidea). Smiths. Contr. Zool. 120, 302 pp.

POWELL, J. A. & W. E. MILLER. 1978. Nearctic pine tip moths of the genus *Rhyacionia*: Biosystematic review (Lepidoptera: Tortricidae, Olethreutinae). U.S. Dept. Agr., Agr. Handb. 514, 51 pp.

RAY, C. 1960. The application of Bergmann's and Allen's rules to the poikilotherms. J. Morph. 106:85–108.

RAZOWSKI, J. 1966. World fauna of the Tortricini (Lepidoptera, Tortricidae). Panstw. Wydawn. Nauk. (Poland), 576 pp.

REMMERT, H. 1981. Body size of terrestrial arthropods and biomass of their populations in relation to the abiotic parameters of their milieu. Oecologia (Berlin) 50:12–13.

RINDGE, F. H. 1966. A revision of the moth genus *Anacamptodes* (Lepidoptera, Geometridae). Bull. Amer. Mus. Natur. Hist. 132:175–244.

SCRIBER, J. M. 1982. Food plants and speciation in the *Papilio glaucus* group, pp. 307–314. *In* Visser, J. H. & A. K. Minks (eds.), Insect-plant relationships. Proc. Intern. Symp. Ins.-Plant Relationships 5, 464 pp. Wageningen, Netherlands.

TYLER, H. 1975. The swallowtail butterflies of North America. Naturegraph, Healdsburg, California. 192 pp.

VERNBERG, F. J. 1962. Comparative physiology: Latitudinal effects on physiological properties of animal populations. Ann. Rev. Physiol. 24:517–546.

WAGNER, W. H. & M. K. HANSEN. 1980. Size reduction southward in Michigan's mustard white butterfly, *Pieris napi* (Lepidoptera: Pieridae). Great Lakes Entomol. 13:77–80.

WASSERMAN, S. S. & C. MITTER. 1978. The relationship of body size to breadth of diet in some Lepidoptera. Ecol. Entomol. 3:155–160.

WILKINSON, C. & M. J. SCOBLE. 1979. The Nepticulidae (Lepidoptera) of Canada. Mem. Entomol. Soc. Can. 107, 129 pp.

Received for publication 17 January 1991; revised and accepted 10 June 1991.

GENERAL NOTES

Journal of the Lepidopterists' Society
45(2), 1991, 169–171

TWO PALEARCTIC SPECIES OF *DICHRORAMPHA* DISCOVERED IN MAINE (TORTRICIDAE)

Additional key words: *D. petiverella, D. gueneeana,* Olethreutinae, introduced species, Asteraceae.

In 1987 I began to inventory the moths of Steuben, Washington Co., Maine, a northeastern coastal community.

Among material in the genus *Dichrorampha* Guenée (Tortricidae: Olethreutinae) assembled in this context I identified two Old World species—*petiverella* (L.) and *gueneeana* Obraztsov—hitherto not reported from North America.

Both species were collected from the same small and isolated estuarine saltmarsh. A single male of *Dichrorampha gueneeana* was taken on 13 July 1988 at 1500 h EST, without further details regarding its capture. *Dichrorampha petiverella* was collected in short series (16 specimens in all) on 24 and 27 July 1989, on a narrow rock outcrop at the water's edge. Subsequent investigation of this site revealed a variety of *Achillea millefolium* L. (Asteraceae), a primary foodplant for both species in Europe (Bradley, J. D., W. G. Tremewan & A. Smith, 1979, British tortricoid moths. Tortricidae: Olethreutinae, The Ray Society, London, 336 pp., 21 pls.), growing sparsely among the grasses and sedges. On the 24th, a warm, still day, the moths flew sporadically from at least 1400 h on; on the equally fair, but brisk, afternoon of 27 July, only occasional specimens were flushed before 1700 h, when, as if on cue, an extended spontaneous flight began.

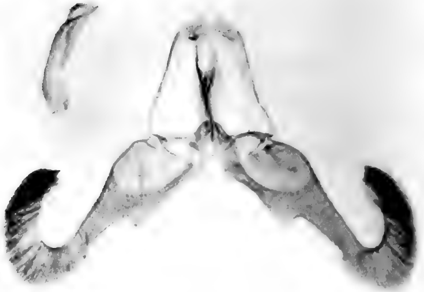
A pair of *D. petiverella* has been deposited in the collection of the American Museum of Natural History (New York); the balance of the material (14 *D. petiverella* and 1 *D. gueneeana*) remains in the author's collection.

The appearance of two Old World species in so isolated a location seems to call for some attempt at explanation. The collecting site, a narrow, half-hectare stretch of marshland bordering the mouth of Whitten Stream and the extreme head of Joy Cove, an inlet of Gouldsboro Bay, on their north side, is both too confined and too remote from natural ports of entry to provide a plausible beachhead for these species. On the other hand, neither moth to date has been encountered further inland in the area, despite intensive collecting and although their foodplant is widespread and abundant.

In light of these facts, perhaps the readiest explanation is that the moths were originally introduced to Mount Desert Island, 23 km to the southwest, where a strong tradition of ornamental gardening has seen the importation of much exotic horticultural material over the course of the present century (R. G. Dearborn pers. comm.). Thus larvae of *Dichrorampha,* which overwinter in plant roots (Bradley et al. *op. cit.*), might easily have entered the area with some of the showier cultivars of *Achillea*. On this assumption, it must be supposed that both *D. petiverella* and *D. gueneeana* are locally established on Mount Desert Island and the populations reported here are the result of dispersal by wind. To date there has been no opportunity to attempt to verify the existence of such primary colonies.

The actual period of introduction can only be a matter of speculation. Had the species been established in the initial phase of estate gardening in the Bar Harbor region, roughly from 1890 to 1930 (P. Chassé, Jr. pers. comm.), it might be expected that they would have been discovered in the course of the Procter survey (Procter, W., 1938, Biological Survey of the Mount Desert region. Pt. VI. The insect fauna, Wistar Inst. of Anat. & Biol., Philadelphia, 496 pp.; 1946, Biological Survey of the Mount Desert region. Pt. VII. The insect fauna, being a revision of Pts. I and VI with the addition of 1100 species, Wistar Inst. of Anat. & Biol., Philadelphia, 566 pp.), more particularly because in the immediate aftermath of this period, from 1931 to 1938, Dr. A. E. Brower maintained


1


2


3


4

FIGS. 1, 2. *Dichrorampha petiverella*. Steuben, Washington Co., Maine. 27 July 1989. M. Roberts *leg*. **1**, wings (FWL = 6 mm); **2**, male genitalia, ventral view (Slide No. G345M, MAR, 27 Oct 89).

FIGS. 3, 4. *Dichrorampha gueneeana*. Steuben, Washington Co., Maine. 13 July 1988. M. Roberts *leg*. **3**, wings (FWL = 5.75 mm); **4**, male genitalia, ventral view (Slide No. G381M, MAR, 13 Nov 89).

the Maine Forest Service's Insect Field Laboratory in Bar Harbor and contributed the results of his extensive collecting to Procter's work.

The possibility of an introduction between the mid-1930's and the late 1970's is more problematic. During these years estate gardening fell into desuetude as a result of the Depression, the Second World War, and the severe droughts and fires of the 1940's, though it was never of course wholly extinguished (P. Chassé, Jr. pers. comm.). Had *D. petiverella* and *D. gueneeana* established themselves in this period, however, they should by now have successfully colonized more of the surrounding inland coastline than appears to be the case. On balance, therefore, it seems most likely that the moths have been introduced only in the past decade, when, coincidentally, ornamental gardening on Mount Desert Island has seen its most active revival since the 1920's (P. Chassé, Jr. pers. comm.).

Nonetheless, the possibility cannot be entirely discounted that both species arrived along the Eastern seaboard much earlier, either incidentally with ship ballast before the turn of the century or directly with *A. millefolium* or the closely-related alternative host, *Tanacetum vulgare* L. (Asteraceae) (Bradley et al. *op. cit.*), both of which were familiar medicinals in Colonial times and staples of Early American gardens (Leighton, A., 1976, American gardens in the Eighteenth Century, Houghton Mifflin Co., Boston, 514 pp.). In this event, it must be assumed that the moths have been overlooked in collections through confusion with the superficially similar indigenous species *D. simulana* (Clem.) and *D. bittana* (Bsk.), from which, however, they are genitalically clearly distinct.

Fortunately this is a possibility that can be readily checked by those with material in their care, and the accompanying illustrations of wings and male genitalia of *D. petiverella* (Figs. 1–2) and *D. gueneeana* (Figs. 3–4) should facilitate their discrimination from native populations of *Dichrorampha*. For comparison, wings and line drawings of genitalic features of *D. simulana* and *D. bittana* are provided by W. E. Miller (1987, Guide to the olethreutine moths of midland North America (Tortricidae), U.S.D.A. For. Serv., Agric. Handbook 660, 104 pp.) and complete figures of male and female genitalia by C. Heinrich (1926, Revision of the North American moths of the subfamilies Laspeyresiinae and Olethreutinae, U.S. Natl. Mus. Bull. 132, 216 pp., 76 pls.). Additional illustrations of *D. petiverella* and *D. gueneeana*, including female genitalia, can be found in G. Bentinck and A. Diakonoff (1968, De Nederlandse bladrollers (Tortricidae), Mon. Ned. Entomol. Ver. No. 3, Amsterdam, 200 pp., 99 pls.). Bradley et al. (*op. cit.*) provide color figures of both moths. Systematics of the Palearctic species of *Dichrorampha* have been treated by N. Obraztsov (1953, Mitt. Münchner Entomol. Ges. 43:10–101; 1958, Tijdschr. v. Entomol. 101:229–261).

I am grateful to R. G. Dearborn of the Maine Insect and Disease Laboratory and L. P. Grey, of Enfield, for counsel and encouragement. W. E. Miller kindly reviewed an earlier draft of the manuscript; two anonymous reviewers also contributed suggestions. S. R. Hill of Clemson University provided botanical advice, and P. Chassé, Jr. of Harvard University and A. Crichton-Harris responded to horticultural questions. W. Buyers-Basso and S. K. Katona, of the College of the Atlantic, made the illustrations possible.

MICHAEL A. ROBERTS, *R.F.D. 1, Box 71A, Steuben, Maine 04680.*

Received for publication 7 April 1990; revised and accepted 1 June 1991.

Note added in proof. Both *Dichrorampha* species recently have been discovered at a new locality: Steuben, at Chair Pond Point, on the eastern shore of the Petit Manan National Wildlife Refuge. Thirty-one specimens of *D. gueneeana* and 14 specimens of *D. petiverella* were collected at the new locality on 26 and 28 July 1991, and many more were observed on the latter date after 1600 h EST, when the moths flew freely on a narrow gravel beach overgrown with *Lathyrus japonicus* Willd. (Fabaceae), and *Achillea millefolium*. This site lies on a wooded and largely rock-bound peninsula 11 km SE of the original study area; its remote situation is consistent with the hypothesis of an introduction over water from a presumptive primary colony in the Bar Harbor region, ca. 25 km to the west. A pair of *Dichrorampha gueneeana* from this latest series has been deposited in the American Museum of Natural History (New York). I am grateful to T. A. Goettel of the U.S. Fish and Wildlife Service for permission to sample moths in the refuge.

Journal of the Lepidopterists' Society
45(2), 1991, 172–173

CAPTURE OF *CHORISTONEURA PINUS MARITIMA* IN TRAPS BAITED WITH *C. PINUS PINUS* PHEROMONE COMPONENTS (TORTRICIDAE)

Additional key words: mating behavior, budworm, attractant, Massachusetts.

Species relations among conifer-feeding *Choristoneura* (Tortricidae) have received increased attention because many *Choristoneura* species are economic pests. The polymorphic nature and extensive overlap of morphological characters among species has made species identification within the genus difficult.

Choristoneura pinus maritima Freeman is rarely collected but has been recorded in northeastern North America from Nova Scotia south to Kentucky (Freeman, T. N. 1967, Can. Entomol. 99:449–455; Powell, J. A. 1980, Nomenclature of nearctic conifer-feeding *Choristoneura* (Lepidoptera: Tortricidae): Historical review and present status. U.S.D.A. For. Ser. Pac. NW For. Range Exp. Sta., Gen. Tech. Rep. PNW-100, 18 pp.; Harvey, G. T. 1985, pp. 16–48 *in* Sanders, C. J., R. W. Stark, E. J. Mullins & J. Murphy (eds.), Recent advances in spruce budworms research: Proceedings, CANUSA Spruce Budworms Research Symposium. Bangor, Maine, 527 pp.). It is differentiated from *C. pinus pinus* by morphological features and by its association with *Pinus rigida* Mill (*C. pinus pinus* feeds primarily on *P. banksiana* Lamb).

Sex-pheromone components have been documented for several *Choristoneura* species (Silk, P. J. & L. P. S. Kuenen. 1988, Ann. Rev. Entomol. 33:83–101). This information is useful for understanding species relations within the genus because reproductive isolation between sympatric species is mediated by sex-pheromone specificity. P. J. Silk, L. P. S. Kuenen, S. H. Tan, W. L. Roelofs, C. J. Sanders and A. R. Alford (1985, J. Chem. Ecol. 11:159–167) identified a mixture of (85:15) (*E*:*Z*)-11-tetradecenyl acetates (90%) and (85:15) (*E*:*Z*)-11-tetradecenyl alcohols (10%) from virgin female *C. pinus pinus*. This mixture was as attractive as virgin female *C. pinus pinus* in field tests. We conducted this study to determine if *C. pinus maritima* populations are attracted to traps baited with *C. pinus pinus* pheromone components.

All field tests were done in a mature stand of *Pinus rigida* at Bourne, Cape Cod, Massachusetts. Three component mixtures were compared: a 1:1 ratio of (85:15) (*E*:*Z*)-11-tetradecenyl acetates: (85:15) (*E*:*Z*)-11-tetradecenyl alcohols (0.3% by weight); a 1:1 ratio (0.003% by weight); and a 9:1 mixture (0.03% by weight). Mixtures were incorporated and dispensed from a polyvinyl chloride rod (Fitzgerald, T. D., A. D. St. Clair, G. E. Daterman & R. G. Smith 1973, Environ. Entomol. 2:607–610) placed in a Pherocon 1CP trap (Zoecon Corp., Palo Alto, California). Each mixture was replicated 12 times; control (unbaited) traps were replicated 10 times. Traps were deployed randomly in a grid (40 m between each trap point) on July 3, 1986; all trapped *Choristoneura* were counted August 10. A subset of 12 trapped males was degreased, curated, and identified as *C. pinus maritima*. All four treatments were compared using six pairwise Wilcoxon two-sample tests. The experiment-wide error rate was controlled by using a smaller pairwise alpha level (0.0085) calculated from Sidak's inequality (Sokal, R. P. & F. J. Rohlf 1981, Biometry. 2nd ed. Freeman and Company, San Francisco, California, 859 pp.).

The 1:1 AC:OH (0.3%) pheromone mixture and the 9:1 AC:OH (0.03%) mixture captured significantly more males than both the controls and the 1:1 AC:OH (0.003%) mixture (Table 1). However, there was no significant difference in trap captures between the 1:1 AC:OH (0.3%) and the 9:1 AC:OH mixtures.

These results indicate that male *C. pinus maritima* are attracted to the primary sex-pheromone components of *C. pinus pinus*. This finding indicates a behavioral similarity between *C. pinus maritima* and *C. pinus pinus*. However, potential hybridization between these subspecies can only be determined from cross-attraction experiments. Unfortunately, *C. pinus maritima* apparently exists at very low densities; thus collection of adequate experimental material for these tests may be impossible. Nevertheless, the attraction of *C. pinus maritima* to *C. pinus pinus* pheromone components should be useful in future studies of the geographic range of *C. pinus* populations and analyses of morphological variation among these populations.

TABLE 1. Numbers of *C. pinus maritima* captured in traps baited with *C. pinus pinus* sex pheromone components.

Ratio of (85:15) (E:Z)-11-14:Ac to (85:15) (E:Z)-11-14:OH	% concentration by weight	Mean number of males per trap[1]
1:1	0.3	3.75 a
9:1	0.03	4.08 a
1:1	0.003	0.50 b
control		0.00 b

[1] Means followed by different letters are significantly different ($P < 0.0085$), Wilcoxon two-sample test.

We thank J. A. Powell, University of California, Berkeley, California, for identifying trapped specimens, and R. Hansen, D. Jennings, and D. Seegrist for reviewing this manuscript.

ANDREW M. LIEBHOLD, *USDA Forest Service, Northeastern Forest Experiment Station, Morgantown, West Virginia 26505.*

PETER J. SILK, *Pheromone Research Group, Research and Productivity Council, Fredericton, New Brunswick E3B 5H1, Canada.*

Received for publication 3 March 1990; revised and accepted 10 June 1991.

Journal of the Lepidopterists' Society
45(2), 1991, 173–175

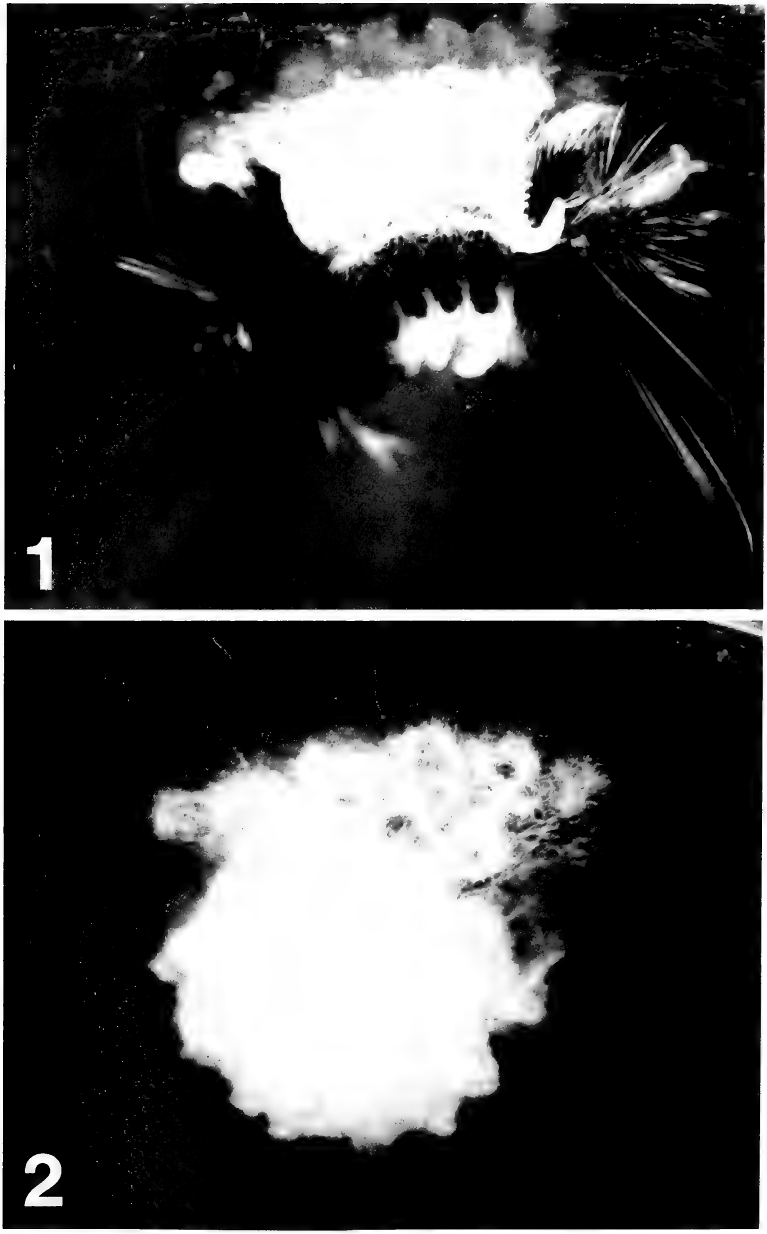
PARASITOID AND LARVAL FOOD PLANT RECORDS FOR THREE PERUVIAN MOTHS (ARCTIIDAE, SATURNIIDAE)

Additional key words: *Dysschema, Carales, Automeris,* Braconidae, Tachinidae.

The following are parasitoid and larval food plant records for three moths: two species of Arctiidae and one species of Saturniidae, reared from larvae found in the field. The larvae were collected during August and September of 1987, 31 km NE of Villa Rica in the Pasco Department of Peru. Identifications of moths were based on adults reared from larvae presumed to be the same as those parasitized.

Dysschema sacrifica (Hubner) (Arctiidae: Pericopinae) larvae and adults were very common. Larvae were reared on *Bidens* sp. (Asteraceae). Two *D. sacrifica* larvae (J87-34(1) and J87-34(2)) were hosts to *Cotesia* (Hymenoptera: Braconidae), probably representing two species. The braconid larvae in both cases emerged from the larvae and spun cocoons on the cuticle of their live hosts (35 cocoons were spun on J87-34(2)). The adult *Cotesia* eclosed from the cocoons over a period of several days, during which time the larvae walked rapidly around the rearing containers. *Cotesia* is a large, ubiquitous genus (over 1500 species) that parasitizes macrolepidoptera. Arctiids have been known to serve as hosts in North America (Mason, W. R. M. 1981, Mem. Entomol. Soc. Canada, 115:1–147).

A larva (J87-79) of *Carales astur* (Cramer) (Arctiidae: Arctiinae: Phaegopterini), feeding on *Citrus* sp. (Rutaceae), also hosted a braconid parasite, *Parapanteles* sp. Species of *Parapanteles* previously have been recorded as using Notodontidae and Noctuidae as hosts (Mason 1981, *op. cit.*), so this record broadens the known host range. The *Parapanteles* larvae emerged from the body of their host (Fig. 1), then left it and spun their



FIGS. 1, 2. Larvae of *Parapanteles* sp. exiting their host, a larva of *Carales astur* (Arctiidae) (Fig. 1), then spinning their cocoons on the side of the rearing container (Fig. 2).

cocoons together, in this case on the side of the plastic rearing container (Fig. 2). Sixteen *Parapanteles* adults were preserved.

Automeris liberia (Cramer) (Saturniidae: Hemileucinae) reared on *Bidens* sp. (Asteraceae), hosted parasitic flies of *Leptostylum* sp. (Diptera: Tachinidae). Thirty-three puparia resulted from the parasitization of a single caterpillar. No previous host records have been given for *Leptostylum* spp. (Arnaud, P. H. 1978, U.S. Dept. Agric., Misc. Pub. 1319:1–860; Guimaraes, J. H. 1977, Arq. Zool., S. Paulo 28(3):1–131), but species are known to occur in Mexico, Panama, and Brazil (Guimaraes, J. H. 1971, Mus. Zool., S. Paulo 104:1–333).

Representatives of the parasitoids reared have been deposited in the National Museum of Natural History in Washington, D.C., and duplicates in the Cornell University Insect Collection (CUIC) in Ithaca, New York. The parasitized larvae of *D. sacrifica* (J87-34(2)) and *C. astur* (J87-79) were preserved in KAAD, then EtOH, and have been deposited in the CUIC, along with a larva of *A. liberia* (J87-62(3)). The adult moths upon which the identifications were based have also been deposited in the CUIC. All vouchers in the CUIC are under lot number 1202.

I thank P. M. Marsh (U.S. Dept. of Agriculture) for identifying the braconid wasps, N. D. Woodley (U.S. Dept. of Agriculture) for identifying the tachinid flies, and R. W. Scott and T. J. Ayers (Northern Arizona University) for identifying the *Bidens* and the *Citrus*, respectively. I also thank J. G. Franclemont (Cornell University) for his help in identifying the moths. Many thanks go to Gerardo Lamas, Antonio Brack, Pedro Lozada, and the wonderful people of the Proyecto Pichis-Palcazu. Fieldwork in Peru was funded by National Science Foundation grant number BSR87-00892.

NANCY L. JACOBSON, *Department of Entomology, Cornell University, Ithaca, New York 14853.*

Received for publication 29 June 1990; revised and accepted 4 May 1991.

Journal of the Lepidopterists' Society
45(2), 1991, 176–178

BOOK REVIEWS

LEPIDOPTERORUM CATALOGUS (NEW SERIES), FASCICLE 118: NOCTUIDAE, by Robert W. Poole. 1989. E. J. Brill/Flora & Fauna Publications, Leiden, The Netherlands. Distributed by E. J. Brill (USA) Inc., 24 Hudson Street, Kinderhook, New York 12106 U.S.A., and Flora & Fauna Books, P.O. Box 15718, Gainesville, Florida 32604 U.S.A. Three volumes. Hard cover, Smythe sewn, 22 × 28 cm. Vol. 1: pages xii and 1–500, Vol. 2: pages 501–1014, Vol. 3: pages 1015–1341. ISBN 0-916846-45-8, $237.50 U.S.

These three volumes by Poole revive a series of publications that was interrupted in part by World War II. Except for two subfamilies, the Agaristinae and Nolinae, the Noctuidae were not included in the original series. As a catalogue of world-wide coverage, this work is overdue and greatly needed, if for no other reason than that the Noctuidae is the largest family of Lepidoptera and contains many economic species. As stated by John B. Heppner, the Series Editor, "The Noctuidae catalog provides for almost 40% completion of the *Lepidopterorum Catalogus* series, due merely to the size of the family." It is nice to see a continuation of this series, and because I study the Noctuidae, Poole's catalog is especially welcome.

Poole's three volumes on the Noctuidae are nicely bound in cloth with gold foil lettering. The bindings are Smythe sewn, which allows the books to open flat for ease of use. Poole's catalog includes approximately 38,000 species' names, including subspecies and synonyms. He conducted an exhaustive literature search and traveled world wide to visit museums and other repositories while executing the research for this publication, which encompasses all names published through 1985.

Lists of Lepidoptera are popular, and, if properly written, worthwhile. By including details such as distributional data, abundance, and flight periods, authors make their published lists more useful. Likewise, literature that provides a bibliographic handle on faunal lists is also helpful. As such, the *Lepidopterorum Catalogus* series is an important part of my library because it provides these lists from around the world. Poole has done an outstanding job of including abundant information in a useful format.

Poole's presentation is different from the format found in the original series, mostly in matters of style, but substantively in the welcome inclusion of references to the biology, larval foodplants, and published illustrations of noctuids. It is arranged into five major sections. The introductory sections (Volume 1, pages i–xii) explain the arrangement of the work, tell how to use the catalog and provide sample entries.

The main body of the work is the species list (Volumes 1 and 2, pages 1–1014) arranged alphabetically by genus and species. Synonyms of genera are provided in alphabetical order. Synonyms of species are listed under the genus. Poole's genus-species combination for each taxon, as well as the genus-species combination in the original description, can be found in the Index to Species. Although the subfamily for each genus is provided, there are no other indications of evolutionary relationships among genera nor species.

Volume 1 begins the list of species with *Ablemma bilineata* on page 3 and ends with *Heraclia pampata* on page 500. Volume 2 continues the list of species with *Heraclia pardalina* on page 501 and concludes the species list with *Zutragum likianga* on page 1013.

Each species account includes the literature citation of the original description, which is cross referenced to the Bibliography. The taxonomic status and systematic status of each name is presented. For example, *Claterna submemorans* is said to be a synonym of *C. cydonia*, whereas *Cleonymia marocana* is introduced not only as a new combination, but also as a name considered to represent a full species. Other relevant information is included. For example: the date for *Claterna cydonia* is affixed as 1776 because the combination occurs only in the index of the 1776 publication, the type locality (including errors) and the location of the types are provided, and references to larval descriptions and to foodplants are given. I especially like the references to illustrations of adults, genitalia, and other useful information.

Since Poole does not subscribe to the subspecies concept, subspecies are listed as synonyms in the alphabetical species list. For example, *Anomis fimbriago* is listed as a synonym of *A. flava* rather than as a subspecies of *A. flava*. Poole gives no indication that other authors consider *A. fimbriago* to be a subspecies of *A. flava*. Because this situation can be confusing, Poole should have clarified his divergence from other lists. He could have done this by noting that other authoritative lists (e.g., Hodges, Ronald, W. et al. 1983. *Check List of the Lepidoptera of America North of Mexico*. E. W. Classey Limited, London, 284 pp.) consider some of Poole's synonyms to be subspecies. Such annotations would have been helpful in clarifying discrepancies between published lists.

Poole reported that he did not settle all taxonomic and systematic problems. He resolved these predicaments by grouping species as best as he could and giving appropriate explanations. For example, he lumped all the species of several Herminiinae genera into the genus *Polypogon*, justifying this action by noting that the dividing lines between the included genera are not well understood, and that further research is needed. In another situation, he used the generic name *Polia* of authors (in contrast to *Polia* Ochsenheimer, 1816) to group several unplaced species pending further research. Poole's explanations are straightforward.

The Bibliography (Volume 3, pages 1015–1102) provides complete literature references to all the citations for species and generic descriptions. This type of bibliography is useful for verifying spellings, dates, and other details.

Immediately following the Bibliography is the alphabetical Index to Species (Volume 3, pages 1103–1313). Each species listing includes the author, the original generic assignment, and the combination used in this work. Information pertinent to the taxon's status as a subspecies, variety, or race at the time of the original description is also provided. The dates of the original descriptions are given in cases involving homonyms.

The Index to Species should have included the year of the original description. Many authors described several species by the same name in different genera. The year of description can be a useful tool to narrow the search for an entry, especially if the original generic assignment or the combination used by Poole is unknown. For example, Hampson described five different species as *disticta*. To locate *disticta* Hampson, 1926, I was forced to look up five separate entries. If the year had been included in the Index to Species, I could have quickly determined that only one entry, instead of five potential entries, was the target.

The work concludes (Volume 3, page 1314) with a list of 96 New Objective Replacement Names for species and one New Objective Replacement Name for a genus. These names are provided to straighten out taxonomic problems.

The greatest shortcoming of this work is the omission of many form, variety, and aberration names, which Poole refers to as "the hemorrhoids of systematics." Although his assessment may be correct, I do not always recognize each and every form, varietal, and aberrational name as such. Additionally, form, varietal, and aberrational names are important to collectors of some groups, such as *Catocala*. Poole could have used this opportunity to educate me and others. In some descriptions, the full context of the text is a useful tool to determine if the name is available or represents a form, variety, or aberration. A researcher may be required to interpret an author's intention in proposing a new name. By not including form, varietal, or aberrational names, Poole makes it impossible to determine whether such names fall under his definition of hemorrhoids or are errors of omission. I would have preferred that such names be included with appropriate explanation so that I could fully understand why a name is available or is not available.

I personally experienced the usefulness of this catalog during preparation of a monograph on the Owlet Moths (Noctuidae) of Ohio. The laborious task of researching correct generic assignments, spellings, and dates of original descriptions would have been nearly impossible without Poole's catalog, which served as an indispensable reference that allowed me to accomplish this objective. I cross checked the spellings of many taxa from the *Check List of the Lepidoptera of America North of Mexico* (Hodges et al. 1983, *op. cit.*) with Poole's catalog. When a discrepancy was found, I was able to use Poole's catalog to locate the original description and verify the correct spelling.

This work is not without error. Expectations of perfection for a monumental work such as this would be folly. I did find a couple of minor errors while conducting my research. For example, Poole states that the primary type of *Paectes delineata* is in the BMNH, London, whereas Mr. Martin R. Honey (in litt., 1989) states that the type is not at the Natural History Museum. In another situation, Poole omits the fact that *Agrotis texanus* is a synonym of *Agrotis segetum.*

Poole's *Noctuidae* should be an important part of any serious lepidopterist's resources, not only as a check list, but also as a bibliography and as an example of how such a work should be prepared. Although the high price may limit individual purchases, library copies should be available. Poole should be thanked by the entire Lepidoptera community for successfully completing this monumental work.

ERIC H. METZLER, *Ohio Department of Natural Resources, 1952 Belcher Drive, Columbus, Ohio 43224.*

Journal of the Lepidopterists' Society
45(2), 1991, 178–179

CATALOGUE OF FAMILY-GROUP AND GENUS-GROUP NAMES (LEPIDOPTERA: RHOPALOCERA), by Charles A. Bridges. 1988 (2nd ed.). Published and distributed by the author, 502 W. Main Street, Apt. 308, Urbana, Illinois 61801, USA. 390 pp.: *vi*; *ii* + 8 (I); *ii* + 3 (II); *ii* + 4 (III); *ii* + 141 (IV); *ii* + 33 (V); *ii* + 68 (VI); *ii* + 18 (VII); *ii* + 61 (VIII); *ii* + 20 (IX); *ii* + 8 (X). Hard cover, 22 × 28.5 cm, no ISBN, $60.00 in North America, $62.50 elsewhere (postpaid).

CATALOGUE OF PAPILIONIDAE & PIERIDAE (LEPIDOPTERA: RHOPALOCERA), by Charles A. Bridges. 1988. Published and distributed by the author, 502 W. Main Street, Apt. 308, Urbana, Illinois 61801, USA. 737 pp.: *vii*; *ii* + 324 (I); *ii* + 93 (II); *ii* + 131 (III); *ii* + 98 (IV); *ii* + 37 (V); *ii* + 12 (VI); *ii* + 1 (A1); *ii* + 4 (A2); plus 14 pp. of appended annotations. Hard cover, 22 × 28 cm, no ISBN, $85.00 in North America, $87.50 elsewhere (postpaid).

Charles Bridges has embarked on a monumental task: that of assembling all published names of butterflies and skippers, evaluating their status, and publishing them with supporting documentation in a series of cross-referenced catalogs. To date, five volumes have been published: three treat species-group names, one treats family and generic names, and the fifth is a bibliography. All five volumes are sturdily bound in hard cover and are printed on 8½ × 11 inch paper.

The two volumes reviewed here treat, respectively, names used in the higher classification of butterflies and skippers, and the names of species, subspecies, varieties, and forms in two families of butterflies: Papilionidae and Pieridae. Previously reviewed in the *Journal of the Lepidopterists' Society* are *Lepidoptera: Hesperiidae. Notes on Species-Group Names* (1983; reviewed by Lee D. Miller in *JLS* 39:51, 1985) and *Catalogue of Lycaenidae & Riodinidae (Lepidoptera: Rhopalocera)* (1988; reviewed by Donald J. Harvey in *JLS* 43:250–251, 1989). The Hesperiidae volume has been revised and the second edition was published in 1988 as *Catalogue of Hesperiidae (Lepidoptera: Rhopalocera),* a 6-part compendium of 461 pages that treats 9327 species-group names (it is available in hard cover from the author for $70.00 in North America and $72.50 elsewhere, postpaid). That leaves the nymphalids as the only group not yet covered. Bridges is working on a catalog of the huge superfamily Nymphaloidea, but its completion is years away.

The fifth published volume in this series is the *Bibliography* (576 pages; $75.00 in North America and $77.50 elsewhere, postpaid), which lists 19,407 publications and is the most comprehensive compilation of butterfly literature published in this century. Even so, Bridges is the first to admit its shortcomings—it is not exhaustive (it was compiled by listing every paper Bridges encountered during his work on the other four volumes, and thus it leaves out much of the literature on the Nymphaloidea and is heavily biased toward taxonomic papers) and it has never been rigorously edited (resulting in quite a few errors and duplications).

The four volumes treating names all carry the caveat: "The arrangement of the names is based entirely on bibliographic references. No specimens have been examined, and no new names are introduced." Clearly, these volumes are meant to be references to aid the taxonomist and are not intended to be revisionary works themselves. One might say that their purpose is to Bridge the gap between taxonomists and the butterfly literature. However, they contain much more than simple listings of names and references. Using the *International Code of Zoological Nomenclature* as his guide, Bridges has coded all names as to their nomenclatural status (available or unavailable, objectively valid or invalid) and has assembled synonymic lists of taxa. In the *Catalogue of Family-Group and Genus-Group Names,* Bridges even designates type species for three genera: *Idmais* Lucas, 1836; *Odontasama* Aurivillius, 1929; and *Thymele* [Iliger], 1837. It is the care that Bridges has taken in organizing this vast array of complex information that makes these volumes so accessible and useful.

Each volume has a brief introductory section that describes its contents, methodology, and data base, and which includes a fascinating table that lists the number of names published in each five-year period since 1758 (the date of publication of the 10th edition of Linnaeus' *Systema Naturae,* recognized as the starting point of zoological nomenclature). These chronological numerical summaries are broken down by status (availability, validity, etc.), providing insight into the dynamics and complexity of taxonomic activity over the past two centuries.

The *Catalogue of Family-Group and Genus-Group Names* has ten parts, paginated separately, that are grouped into three major sections: family-group names (Parts I–III), genus-group names (Parts IV–VII), and bibliography (Parts VIII–X). Each Part has its own brief introduction and a list of abbreviations used. Part I is an alphabetic list of the type genera of the family-group names; different fonts are used to indicate valid, invalid, and unavailable names. Part II is a synonymic list of 362 family-group names, including superfamily, family, subfamily, tribe, and subtribe designations. Part III is an index to the authors and literature of family-group names. In the Genus Group section, Part IV lists 4190 genus names alphabetically and gives the reference of the original description, the type methodology, the type species, taxonomic status (1540 names are invalid or unavailable), and higher classification. Part V is a synonymic list, Part VI is an index to authors and bibliography, and Part VII is an index to type-species. The Bibliography section contains a list of 2270 references arranged alphabetically by author (Part VII), an index to Journals and Serials (Part IX), and an index to year of publication (Part X).

The *Catalogue of Papilionidae & Pieridae* is formatted like the catalogs treating Hesperiidae and Lycaenidae & Riodinidae. Following the Introduction, there are six Parts, paginated separately. Part I is an alphabetic list of 14,117 names, with data on authorship, year and place of original publication, current usage, location of type specimens, type locality, references, and occasional brief notes. Part II is a synonymic list of names. Part III is a list of the names arranged by author and publication, and serves as an index to the bibliography. Part IV is the bibliography, listing 4330 publications. Part V is an index to the bibliography, arranged by journal title. Part VI is an index to the bibliography, arranged by year of publication. There are two appendices, giving synonymic lists of family group names (Appendix I) and genus-group names (Appendix II) of the Papilionidae and Pieridae. Annotations are issued irregularly to allow additions and corrections to the *Catalogue*; the first four of these (all dated 1988) are bound in my copy at the end of the volume.

In summary, the five published volumes in this series comprise a comprehensive, although incomplete, world catalog of butterflies and skippers (Bridges favors the largely ignored but still useful term Rhopalocera to separate butterflies and skippers from the tens of thousands of other Lepidoptera we lump under the name "moths"). The extraordinary usefulness of these volumes makes them indispensable tools for all taxonomists and systematists who work on butterflies. This project represents an astonishing amount of work (especially for one person!) and the world's lepidopterists owe Mr. Bridges a great deal of thanks for his herculean efforts, and for publishing his work in such a useful and affordable format.

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

Journal of the Lepidopterists' Society
45(2), 1991, 180

FEATURE PHOTOGRAPH

Life across the border: A colony of *Lycaena* (=*Epidemia*) *dorcas claytoni* Brower was discovered by the author in 1989 near Woodstock, Carleton County, New Brunswick, Canada. Subspecies *claytoni*, which has a very restricted distribution and may be endangered (Opler, P. A. & G. O. Krizek, 1984, *Butterflies East of the Great Plains,* Johns Hopkins University Press, Baltimore, 294 pp.), was known previously only from central Maine. The new locality is across the Canadian border, about 95 km NNE of the type locality, Springfield, Maine. **A:** adult resting on leaves of *Pentaphylloides floribunda* (Pursh) A. Löve (=*Potentilla fruticosa*). **B:** male nectaring at flowers of *P. floribunda,* which is also the larval food plant. Photographs taken 22 July 1990 near Woodstock, New Brunswick, with a Nikon FE2 camera with a 200 mm micro-Nikkor lens and extension tubes (Kodachrome 200, Nikon SB15 electronic flash, f16, TTL exposure, speed not recorded).

Anthony W. Thomas, *P.O. Box 4000, Fredericton, New Brunswick E3B 5P7, Canada.*

Date of Issue (Vol. 45, No. 2): 24 October 1991

NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of Lepidoptera study. Categories are Articles, Profiles, 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 111 in Volume 44(2). *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 submit manuscripts in *triplicate*, typewritten, *entirely double-spaced*, with wide margins, on one side only of white, letter-sized paper. Prepare manuscripts according to the following instructions, and submit them flat, not folded.

Abstract: An informative abstract should precede the text of Articles and Profiles.

Key Words: Up to five key words or terms not in the title should accompany Articles, Profiles, General Notes, and Technical Comments.

Text: Contributors should write with precision, clarity, and economy, and should use the active voice and first person whenever appropriate. Titles should be explicit, descriptive, and as short as possible. The first mention of a plant or animal in the text should include the *full scientific name* with *author*, and *family*. Measurements should be given in metric units; times in terms of the 24-hour clock (0930 h, not 9:30 AM). Underline only where *italics* are intended.

Literature Cited: References in the text of Articles and Profiles should be given as Sheppard (1959) or (Sheppard 1959, 1961a, 1961b) and listed alphabetically under the heading LITERATURE CITED, in the following format without underlining:

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

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

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

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.

Tables: Tables should be numbered consecutively in Arabic numerals. Headings for tables should not be capitalized. Tabular material must be typed *on separate sheets*, and placed following the main text, with the approximate desired position indicated in the text. Vertical lines as well as vertical writing should be avoided.

Voucher specimens: When appropriate, manuscripts must name a public repository where specimens documenting identity of organisms can be found. Kinds of reports that require vouchering include life histories, host associations, immature morphology, and experimental enquiries.

Proofs: The edited manuscript and galley proofs will be mailed to the author for correction of printer's errors. Excessive author's changes at this time will be charged to authors at the rate of $2 per line. A purchase order for reprints will accompany proofs.

Page charges: For authors affiliated with institutions, page charges are $20 per *Journal* page. For unaffiliated authors, page charges are $10 per *Journal* page with a $50 maximum. Authors of Book Reviews and Obituaries are exempt from page charges. Authors unable to pay page charges for reasons such as difficulties with foreign exchange should apply to the editor for free publication.

Correspondence: Address all matters relating to the *Journal* to the editor.

PRINTED BY THE ALLEN PRESS, INC., LAWRENCE, KANSAS 66044 U.S.A.

CONTENTS

GENERAL NOTES

BOOK REVIEWS

FEATURE PHOTOGRAPH

e 45 1991 Number 3

ISSN 0024-0966

JOURNAL
of the
LEPIDOPTERISTS' SOCIETY

Published quarterly by THE LEPIDOPTERISTS' SOCIETY
Publié par LA SOCIÉTÉ DES LÉPIDOPTÉRISTES
Herausgegeben von DER GESELLSCHAFT DER LEPIDOPTEROLOGEN
Publicado por LA SOCIEDAD DE LOS LEPIDOPTERISTAS

5 December 1991

THE LEPIDOPTERISTS' SOCIETY

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.

Active members—annual dues $25.00
Student members—annual dues $15.00
Sustaining members—annual dues $35.00
Life members—single sum $500.00
Institutional subscriptions—annual $40.00

Send remittances, payable to *The Lepidopterists' Society*, to: Fay H. Karpuleon, Treasurer, 1521 Blanchard, Mishawaka, Indiana 46544, U.S.A.; and address changes to: Julian P. Donahue, Natural History Museum, 900 Exposition Blvd., Los Angeles, California 90007-4057 U.S.A. For information about the Society, contact: William D. Winter, Secretary, 257 Common St., Dedham, Massachusetts 02026-4020, U.S.A. (617-326-2634). To order back issues of the *Journal, News*, and *Memoirs*, write for availability and prices to the Publications Coordinator: Ronald Leuschner, 1900 John St., Manhattan Beach, California 90266-2608, U.S.A.

Journal of the Lepidopterists' Society (ISSN 0024-0966) is published quarterly for $40.00 (institutional subscription) and $25.00 (active member rate) by the Lepidopterists' Society, % Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, California 90007-4057. Second-class postage paid at Los Angeles, California and additional mailing offices. POSTMASTER: Send address changes to the Lepidopterists' Society, % Natural History Museum, 900 Exposition Blvd., Los Angeles, California 90007-4057.

Cover illustration: *Agraulis vanillae* (L.) (Nymphalidae: Heliconiinae) emerging from its chrysalis on its larval food plant, *Passiflora pfordtii* (Passifloraceae). Original drawing by J. D. Dietrich Larsen, 4201 N. 20th St., Suite 216, Phoenix, Arizona 85016.

JOURNAL OF

THE LEPIDOPTERISTS' SOCIETY

Volume 45 1991 Number 3

Journal of the Lepidopterists' Society
45(3), 1991, 181–187

ADELPHA IXIA LEUCAS: IMMATURE STAGES AND POSITION WITHIN *ADELPHA* (NYMPHALIDAE)

ANNETTE AIELLO

Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa,
Ancon, Republic of Panamá

ABSTRACT. The larva and pupa of the nymphalid butterfly *Adelpha ixia leucas* are described, and it is concluded that the species belongs to the same species-group as *A. delphicola*, *A. isis*, *A. melanthe*, *A. mesentina*, and *A. phylaca pseudaethalia*. *Luehea seemannii* (Tiliaceae) is reported as a larval food plant.

Additional key words: life history, larval food plant, Panama, Tiliaceae.

Although close to 100 species have been assigned to the nymphalid genus *Adelpha* Hübner, 1819, the immature stages are known for only 21 species, including 11 Panamanian ones (Müller 1886, Swainson 1901, Jorgensen 1921, Moss 1933, Comstock & Vázquez 1960, Young 1974, Aiello 1984). This scarcity of life history information is unfortunate because it appears that larval and pupal characters hold the best clues to species relationships within this large and complex genus, whereas wing pattern, traditionally used, may be quite misleading (Aiello 1984). Based on characters of the larvae and pupae, and the larval food plant relationships (Aiello 1984), the 21 species can be sorted into 7 species-groups. Because they are based on limited knowledge of a few *Adelpha* species only, these groups must be treated as provisional.

In this paper I describe the larva and pupa of a twelfth Panamanian species, *Adelpha ixia leucas* Fruhstorfer (Fig. 1), report its larval food plant, and assign the species to an *Adelpha* species-group.

MATERIALS AND METHODS

Two penultimate stadium *Adelpha* larvae were found on leaves of *Luehea seemannii* Triana & Planchon (Tiliaceae), on Pipeline Road near Gamboa, Republic of Panama, on 22 November 1989. The larvae and several leaves of their food plant were placed in small cages made from window screening and petri dish covers. The cages were kept

FIGS. 1–4. Adult: (1) *Adelpha ixia leucas*, dorsal (left), ventral (right) (reared lot 89-22 no. 2). Final instar larvae: (2) *Adelpha ixia leucas* on *Luehea seemannii* (Tiliaceae) (reared lot 89-22 no. 2); (3) *Adelpha phylaca pseudaethalia* on *Cecropia obtusifolia* (Cecropiaceae) (reared lot 83-78); (4) *Adelpha melanthe* on *Trema micrantha* (Ulmaceae) (reared lot 83-8 no. 3). [Scale bars = 0.5 cm.]

inside Ziploc plastic bags together with a piece of folded, dampened paper towel. The two larvae were designated as Rearing Lot 89-22, and were labelled as individuals 1 and 2. A record of molting and other behaviors was kept on a rearing sheet for that lot.

The adult butterfly, pointed larval head capsules, and pupal skin (Lot 89-22 no. 2) are in the author's collection, together with the fungus-killed final instar larva (dried, mounted, and pinned) and its larval head capsule (Lot 89-22 no. 1).

My field identification of the larval food plant was verified by consulting Robyns (1964) and D'Arcy (1987). A voucher specimen (*Aiello 1437*) of the plant is in the collection of the author.

Plant classification follows Dahlgren (1980).

Larva and Food Plant

Except for a paler dorsal area, both larvae were rusty brown, a darker shade of the underside color of their food plant leaves. Each larva ate the apex of its leaf except for the midvein, which it exposed and then extended, using fecula held in place with silk. The resulting slender supports were used by larvae to rest upon when not feeding and also during molting. The larvae attached large pieces of leaf and clumps of fecula to the base of their supports. These assemblages gave the impression of fallen debris caught on the apex of a broken leaf, and the larvae were well camouflaged whether feeding or resting.

On 26 November, larva no. 1 rested on its support, facing away from the leaf. The prothorax became quite swollen as the new head capsule formed inside. By the next morning the larva had molted to the final stadium (Figs. 2 and 5), and was beige except for the sides of the thorax through abdominal segment 2, which were chestnut in color. The scoli were long, slender, and straight, including those of abdominal segment 2, which in many species of *Adelpha* bears scoli different from those of other segments. Such "two-toned" larvae, with slender scoli on abdominal segment 2, are typical of *Adelpha* Group-II (see Aiello 1984).

Larva no. 2 molted to the final stadium, identical in form, pattern, and color to larva no. 1, on 29 November.

On 6 December, larva no. 1 died. Presumably, it succumbed to an entomogenous fungus because several days later, white filaments began to emerge from it, and by 11 December it was clothed in long white fungal fruiting bodies that emitted clouds of white spores with the slightest air current.

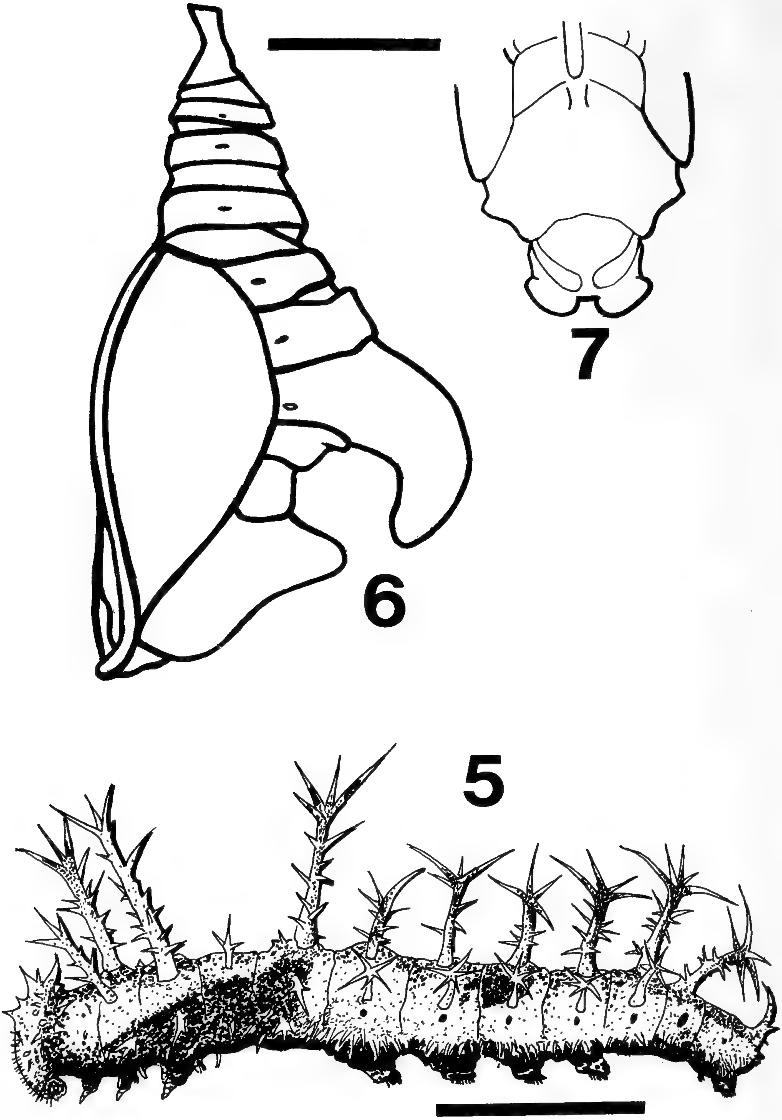
Pupa

Larva no. 2 was found hanging for pupation from the cage cover on 11 December. By the next morning it had molted to the pupa (Fig. 6): straw-colored, with abdominal segment 2 expanded to form a huge dorsal hook. "Huge-hook" pupae also are typical of *Adelpha* Group-II (Aiello 1984). The head horns (Fig. 7) were very small as in *A. melanthe* Bates, but unlike the rounded, asymmetrical horns of *A. melanthe*, these were more symmetrical and somewhat squared off.

Based on pupation times reported for *A. melanthe* and *A. phylaca pseudaethalia* Hall, I estimated that the adult would eclose on or about 22 December, after ten days as a pupa. Eclose it did, but we'll never know just when, because from 20 through 26 December we were confined to our homes due to the U.S. invasion of Panamá. When, on 27 December, we were able to visit our offices briefly, I found the adult dead on the cage floor. Its wings were undamaged, evidence that it had not fluttered against the cage walls.

Position within *Adelpha*

In all cases for which both the larva and pupa are known, *Adelpha* species that have "two-toned" larvae also have "huge-hook" pupae, and vice versa. Six *Adelpha* species, *A. delphicola* Fruhstorfer, *A. isis* Drury, *A. ixia leucas*, *A. melanthe* (Fig. 4), *A. mesentina* Cramer, and *A. phylaca pseudaethalia* (Fig. 3), have such larvae and pupae, and in my opinion are more clearly related to one another than to other *Adelpha* species for which information on the immatures is available.



FIGS. 5–7. Immature stages of *Adelpha ixia leucas*: (5) Final instar larva; (6) Lateral view of entire pupa; (7) Dorsal view of pupa head and thorax. [Scale bars = 0.5 cm.]

Larvae of two of the three Group-II species reared by me, *A. ixia leucas* and *A. phylaca pseudaethalia*, are nearly identical. The only difference between them seemed to be that the ground color of *A. ixia leucas* was beige, whereas that of *A. phylaca pseudaethalia* was bone white. How consistent those colors are within and between species remains to be seen. The larva of the third species, A. *melanthe*, differs from them in the abundant white speckles and the grayish body spines that obscure its cream to brown ground color, and in the black-tipped scolus spines. These three conditions give the larva a distinctive frosted appearance.

Based on descriptions of immatures of A. *abyla* Hewitson (Swainson 1901) and A. *calliphiclea* Butler (Jorgensen 1921), those two species may belong to Group-II (Aiello 1984), but I have seen neither specimens nor illustrations of the immature stages.

Of the seven *Adelpha* species-groups outlined by Aiello (1984), Groups-I and -II are the most clearly defined. Group-I, with its distinctive genitalia, may prove to be more closely allied to *Limenitis* Fabricius, 1807, than to *Adelpha*. But Group-II, although its characteristic "two-toned" larvae and "huge-hook" pupae seem to set it apart, has genitalia similar to those of the remaining *Adelpha* groups, and with them it appears to form a natural assemblage.

Larval Food Plants of *Adelpha* Group-II

Luehea seemannii, the larval food plant of A. *ixia leucas,* has been recorded for one other species of *Adelpha* (*boetia* (Felder & Felder), from Parque Corcovado, Costa Rica), by J. Mallet (in DeVries 1986). Because I have not seen the larva or pupa of A. *boetia* I can draw no conclusions concerning its relationship to other *Adelpha* species. The only other record of *Adelpha* on the Tiliaceae is for A. nr. *celerio* (Bates) (*Adelpha* Group-I) on *Heliocarpus popayanensis* (Aiello 1984).

Although the Cecropiaceae (Urticales) appears to be the dominant larval food plant family for species of *Adelpha* Group-II, a total of seven larval food plant genera (*Bombax, Cecropia, Coussapoa, Luehea, Pourouma, Trema, and Urera*) have been reported for the six species that clearly belong to this *Adelpha* species group (references cited in Aiello 1984). These seven plant genera represent five plant families in two orders, Urticales and Malvales (Table 1). Dahlgen (1980) assigns the two orders to the same superorder (Malviflorae), based on certain chemical similarities as well as morphological characteristics. That close alliance is also supported by the fact that two species of *Adelpha* (A. *delphicola*, Group-II and A. *celerio*, Group-I) have been reported on plants from both orders. The relationship is not without controversy however; Cronquist (1981) maintains the Urticales and Malvales in separate subclasses, Hamamelidae and Dilleniidae, respectively.

The larval food plant (*Ilex paraguariensis*) reported by Jorgensen (1921) for A. *calliphiclea*, a possible member of Group-II, represents a significant departure from the other larval food plants recorded for that

TABLE 1. Larval food plant genera reported for the six *Adelpha* species comprising species-group II. The affiliation of a seventh species, *A. calliphiclea,* is unconfirmed.

Larval food plant genus	*Adelpha* species
Superorder Malviflorae	
Order Urticales	
ULMACEAE	
Trema	*A. melanthe*
CECROPIACEAE	
Cecropia	*A. delphicola, isis, melanthe, phylaca*
Coussapoa	*A. isis*
Pourouma	*A. delphicola, isis, mesentina*
URTICACEAE	
Urera	*A. melanthe*
Order Malvales	
TILIACEAE	
Luehea	*A. ixia*
BOMBACACEAE	
Bombax	*A. delphicola*
Superorder Corniflorae	
Order Cornales	
AQUIFOLIACEAE	
Ilex	*A. calliphiclea*

group and for *Adelpha* as a whole, although it has been reported also for *A. serpa hyas* Boisduval, Group-I, by d'Araújo e Silva et al. (1967–68).

ACKNOWLEDGMENTS

I thank Marianne Akers and Henry Stockwell who accompanied me in the field and subsequently provided additional larval food plant leaves; Philip Ackery, Malcolm Scoble, and Donald Windsor who commented on the manuscript; Jaime Rodriguez who made the ink drawings; and Carl Hansen who photographed the adult. Philip Ackery also verified the identification of the butterfly. Without the facilities and support of the Smithsonian Tropical Research Institute, and the staff of the STRI Library, this work would not have been possible.

LITERATURE CITED

AIELLO, A. 1984. *Adelpha* (Nymphalidae): Deception on the wing. Psyche 91:1–45.

D'ARAÚJO E SILVA, A. G., C. R. GONCALVES, D. MONTEIRO GALVAO, A. J. LOBO GONCALVES, J. GOMES, M. DO NASCIMENTO SILVA & L. DE SIMONI. 1967–68. Quarto Catálogo dos insetos que vivem nas plantas do Brasil, sues parasitos e predadores. Parte I (2 vol., 906 pp.) and parte II (2 vol., 887 pp.). Ministerio da Agricultura. Rio de Janeiro, GB, Brasil.

COMSTOCK, J. A. & L. VÁZQUEZ G. 1960 (1961). Estudios de los ciclos biológicos en Lepidópteros Mexicanos. Anales del Instituto de biología (Mexico) 31:349–488.

CRONQUIST, A. 1981. An integrated system of classification of flowering plants. Columbia University Press, New York. xviii + 1262.

DAHLGREN, R. M. T. 1980. A revised system of classification of the angiosperms. Bot. J. Linn. Soc. 80:91–124.

D'ARCY, W. G. 1987. Flora of Panama: Checklist and index. Monogr. Syst. Bot., Missouri Bot. Garden 17:185.

DEVRIES, P. J. 1986. Host plant records and natural history notes on Costa Rican butterflies (Papilionidae, Pieridae, & Nymphalidae). J. Res. Lepid. 24:290–333.

JORGENSEN, P. 1921. Sobre algunos nuevos enemigos de la yerba-mate, *Ilex paraguariensis*. Revista de la Sociedad cientifica del Paraguay 1:27–30.

MOSS, A. M. 1933. Some generalizations on *Adelpha*, a neotropical genus of nymphalid butterflies of the group Limenitidi. Novitates Zoologicae 39:12–20 + pls. 1 and 2.

MÜLLER, W. 1886. Südamerikanische Nymphalidenraupen, versuch eines natürlichen Systems der Nymphaliden. Zoologische Jahrbücher, Zeitschrift für Systematik Geographie und Biologie der Thiere 1:417–678 + pl. 12–15.

ROBYNS, A. 1964. Tiliaceae. *In* R. E. Woodson Jr. & R. W. Schery (eds.), Flora of Panama, Part VI. Ann. Missouri Bot. Garden 51:1–35.

SWAINSON, E. M. 1901. Notes on lepidopterous larvae from Jamaica, B.W.I. J. N.Y. Entomol. Soc. 9:77–82.

YOUNG, A. M. 1974. Notes on the natural history of a rare *Adelpha* butterfly (Lepidoptera: Nymphalidae) in Costa Rica high country. J. N.Y. Entomol. Soc. 82:235–244.

Received for publication 26 June 1990; revised and accepted 30 July 1991.

Journal of the Lepidopterists' Society
45(3), 1991, 188–196

ACCEPTANCE OF *LOTUS SCOPARIUS* (FABACEAE) BY LARVAE OF LYCAENIDAE

GORDON F. PRATT
Entomology and Applied Ecology Department, University of Delaware,
Newark, Delaware 19716

AND

GREGORY R. BALLMER
Entomology Department, University of California,
Riverside, California 92521

ABSTRACT. Larvae of 49 species of Lycaenidae were fed *Lotus scoparius* (Nutt. in T. & G.) Ottley (Fabaceae). Twentyseven species grew normally and pupated; six others fed but exhibited retarded development. Sixteen species refused to feed, or fed but exhibited no growth. Fourteen of the species reared to adults on *L. scoparius* are not known to use food plants in the Fabaceae in nature.

Additional key words: coevolution, food plant, host shift.

The larvae of most butterfly genera feed specifically on either a single genus or family of plants (Ehrlich & Raven 1964, Ackery 1988). The host range of some genera of Lycaenidae is comparatively broad. For example, members of the genus *Callophrys* Billberg feed on a wide range of plants in the families Convolvulaceae, Crassulaceae, Cupressaceae, Ericaceae, Fabaceae, Agavaceae, Pinaceae, Polygonaceae, Rhamnaceae, Rosaceae, and Viscaceae (Powell 1968, Emmel & Emmel 1973, Scott 1986, Ballmer & Pratt 1989b). Some lycaenid species, such as *Strymon melinus* Hübner, are also extremely polyphagous, whereas others are monophagous or oligophagous.

One of us (GFP) observed that *Callophrys mcfarlandi* (Ehrlich & Clench) which, in nature, is monophagous on *Nolina texana* var *compacta* (Trel.) (Agavaceae), could be reared in the laboratory on *Lotus scoparius* with little or no retardation in development. This plasticity in larval feeding capacity could indicate a broader ancestral host range and might support the theory that ancestral butterflies fed on Fabaceae (Scott 1984). We tested 48 other Lycaenidae to determine if they would accept *Lotus scoparius* as a larval host.

MATERIALS AND METHODS

Larvae were reared in the laboratory under incandescent lights in screened vials (with two circular screens 2 cm in diameter, one on the side and one on the top) on fresh *Lotus scoparius* kept in water and changed every 3 days, at ca. 25°C as described by Ballmer and Pratt (1989a). *Lotus scoparius* plants were collected in the field at Riverside,

Riverside Co., California. Both leaves and flowers were presented to all larvae tested. Larvae were field collected or reared from ova obtained from captive females. For butterfly species with no feeding or in which feeding was retarded on *L. scoparius*, often we had a subsample of larvae from that population being reared on its natural host.

The origins of tested organisms are as follows (numbers of larvae tested in parentheses): *Apodemia mormo* (C. and R. Felder) *ex* ova *Eriogonum inflatum* Torr. & Frem. (Polygonaceae) (6), Sheephole Pass, San Bernardino Co., California, April 1988; *Lycaena cupreus* (W. H. Edwards) *ex* female (2), Tioga Pass, Inyo Co., California, July 1987; *L. gorgon* (Boisduval) *ex* female (2), Butterbread Peak, Kern Co., California, June 1986; *L. hermes* (W. H. Edwards) *ex* female (2), Guatay, San Diego Co., California; *L. heteronea* (Boisduval) *ex* female (2), Mt Bidwell, Modoc Co., California, July 1986; *L. nivalis* (Boisduval) *ex* female (2), Sonora Pass, Mono Co., California, July 1987; *L. phlaeas* (Linnaeus) *ex* female (3), White Mt, Inyo Co., California, July 1987; *L. xanthoides* (Boisduval) *ex* larvae on *Rumex crispus* L. (Polygonaceae) (2), Mojave River Forks, San Bernardino Co., California, April 1987; *Atlides halesus* (Cramer) *ex* ova on *Phoradendron tomentosum* (Englm. ex Gray) (Viscaceae) (2), Riverside, Riverside Co., California, May 1988; *Callophrys augustus* (W. Kirby) *ex* larvae on *Ceanothus* (Rhamnaceae) (2), San Bernardino Mts, San Bernardino Co., California, May 1988; *C. eryphon* (Boisduval) *ex* female (3), San Bernardino Mts, San Bernardino Co., California, June 1988; *C. fotis* (Strecker) *ex* larvae on *Cowania mexicana* D. Don (Rosaceae) (3), Providence Mts, San Bernardino Co., California, May 1988; *C. mossii* (Hy. Edwards) *ex* larvae on *Sedum spathulifolium* Hook. (Crassulaceae) (10), San Bernardino Mts, San Bernardino Co., California, May 1988; *C. perplexa* Barnes and Benjamin *ex* female (3), San Bernardino Mts, San Bernardino Co., California, May 1988; *C. polios* (Cook & Watson) *ex* female (20), Del Norte Co., California, April 1990; *C. siva* (W. H. Edwards) *ex* female (6), Barnwell, San Bernardino Co., California, May 1988; *C. spinetorum* (Hewitson) *ex* ova on *Arceuthobium campylopodum* Engelm. in Gray (Viscaceae) (2), Laguna Mts, San Diego Co., California, June 1988; *C. mcfarlandi ex* larvae on *Nolina texana* var *compacta* (Trel.) (Agavaceae) (6), San Augustin Pass, New Mexico, April, 1987; *Erora guaderna ex* female (6), Santa Rita Mts, Arizona, March 1987; *Chlorostrymon simaethis* (Drury) *ex* larvae (10), 6 mi W. Santa Rita, B. C. S., Mex, April 1991; *Habrodais grunus* (Boisduval) *ex* larvae on *Quercus chrysolepis* Liebm. (Fagaceae) (2), San Bernardino Mts, California, May 1988; *Ministrymon leda* (W. H. Edwards) *ex* female (3), Julian, California, April 1988; *Satyrium auretorum* (Boisduval) ova *ex* female (3), Guatay, California, June 1986; Frazier Park, California, May 1987; *Satyrium behrii* (W. H. Edwards) *ex* larvae on *Purshia glandulosa* Curran (Rosaceae) (3), Isabella Lake, California, May 1987; *Satyrium saepium* (Boisduval) ova *ex* female (2), Guatay, San Diego Co., California, June 1987; *Satyrium tetra* (W. H. Edwards) *ex* larvae on *Cercocarpus betuloides* Nutt. *ex* T. & G. (Rosaceae) (3), San Bernardino Mts, San Bernardino Co., California, May 1988; *Strymon columella* (Fabricius) *ex* female (2), 6 mi. S. San Agustin, B. C., Mex, April 1991; *S. melinus* (Hubner) *ex* female (2), Riverside, Riverside Co., California, May 1988; *Brephidium exilis* (Boisduval) *ex* ova on *Sesuvium verrucosum* Raf. (Aizoaceae) (3), Cronese Dry Lake, San Bernardino Co., California, April 1987; *Brephidium pseudofea* (Morrison) *ex* larvae on *Salicornia* L. (Chenopodiaceae) (2), Florida, July 1987; *Celastrina argiolus* (Linnaeus) *ex* female (6), Santa Rita Mts, Cochise Co., Arizona, March 1987; *Celastrina neglectamajor ex* ova on *Cemicifuga* (Ranunculaceae), State Game Lands #157, Bucks Co., PA, May 1988; *Euphilotes battoides* (Behr) *ex* female (3), Coxey Meadow, San Bernardino Co., California, May 1988; *Euphilotes mojave* (Watson and W. P. Comstock) *ex* ova on *Eriogonum pusillum* T. & G. (Polygonaceae) (3), Mojave River Forks, San Bernardino Co., California, April 1987; *Everes comyntas* (Godart) *ex* female (6), Bakersfield, Kern Co., California, *May 1987; Everes amyntula* (Boisduval) *ex* larvae on *Astragalus lentiginosus* Dougl. (Fabaceae), Coyote Ridge, Inyo Co., California, July 1987; *Glaucopsyche lygdamus* (Doublday) *ex* larvae on *Lotus Scoparius* (Fabaceae) (3), Mojave River Forks, San Bernardino Co., California, April 1985; *Glaucopsyche piasus* (Boisduval) *ex* ova on *Lupinus excubitus* Jones (Fabaceae) (>50), Nine Mile Canyon, Inyo Co., California, May 1988; *Icaricia acmon texana* (Goodpasture) *ex* female (20), San Augustin Pass, New Mexico, April 1987; *Icaricia icarioides* (Boisduval) *ex* ova on *Lupinus* (Fabaceae) (post-diapause larvae tested) (3), Crooked Creek Road, White Mts, Inyo Co., California, August 1987; *Icaricia lupini* (Boisduval) *ex* female (3), Pinyon Mt, Kern Co., California, April 1987; *Icaricia neurona* (Skinner) *ex* female (3), Pinyon Mt, Kern Co., California, April 1987; *Leptotes marina* (Reakirt) *ex* ova on *Amorpha fruticosa* L. (Fabaceae) (2), San Bernardino Mts, San Bernardino Co., California, June 1988; *Lycaeides idas* (Linnaeus) *ex* female (3), Warner Mts, Modoc Co., California, July 1986; *Lycaeides melissa* (W. H. Edwards) *ex* female (3), Mojave River Forks, San Bernardino Co., California, May 1987; *Philotes sonorensis* (C. and R. Felder) *ex* larvae on *Dudleya lanceolata* (Nutt.) Britt. & Rose (Crasulaceae) (3), San Bernardino Mts, San Bernardino Co., California, April 1988; *Philotiella speciosa* (Hy. Edwards) *ex* larvae on *Eriogonum reniforme* Torr. & Frem. (Polygonaceae) (1), In Ko Pah Gorge, Imperial Co., California, April 1988; *Plebejus saepiolus* (Boisduval) *ex* female (3), San Bernardino Mts, San Bernardino Co., California, July 1987; *Plebulina emigdionis* (F. Grinnell) *ex* larvae on *Atriplex canescens* (Pursh) Nutt. (Chenopodaceae) (4), Mojave River, San Bernardino Co., California, May 1987.

RESULTS

Although none of the 49 species of Lycaenidae tested (Table 1) are monophagous on *Lotus scoparius*, species (*Callophrys perplexa, Glaucopsyche lygdamus, Icaricia acmon, Leptotes marina,* and *Strymon melinus*) use it as a larval food plant (Ballmer & Pratt 1989b). Of the 14 tested species whose natural hosts include various Fabaceae, nine feed on Fabaceae exclusively (Table 2). Two of the latter, *Icaricia icarioides* and *Glaucopsyche piasus,* failed to develop on *L. scoparius;* both are specific to *Lupinus* (Table 2). None of the other lycaenids tested are specific to *Lupinus.*

Ten species tested feed on *Eriogonum* in nature; two of these also feed on Fabaceae. Of the eight *Eriogonum* feeding species that do not feed on Fabaceae, six (*A. mormo, E. battoides, E. mojave, I. lupini, I. neurona,* and *P. speciosa*) showed some development on *L. scoparius.* The two that did not feed on *Lotus* were *L. gorgon* (Boisduval) and *L. heteronea* (Boisduval). No species of the subfamily Lycaeninae is known to feed on species of Fabaceae.

Larvae of 16 species failed to develop on *L. scoparius* (Table 1). All of these are host-specific to a single species or genus of plants (Table 2). All seven Lycaeninae species tested refused to feed on *Lotus.* Although most Lycaeninae feed on Polygonaceae, one species tested, *L. hermes,* feeds on *Rhamnus crocea* Nutt. in T. & G. (Rhamnaceae) (Comstock & Dammers 1935, Ballmer & Pratt 1989b).

There was variation in the rate of feeding and survival among the butterfly species that fed on *Lotus scoparius.* Although both *Euphilotes* species and *P. speciosa* pupated, none formed an adult, and all three species took at least twice as long to develop as they did on their natural host. Of the two *S. saepium* larvae, one died, the other pupated. Only

TABLE 1. Feeding responses of larvae of different Lycaenidae to *Lotus scoparius*.

Species	Feeding response*	Species	Feeding response
Apodemia mormo	+ (A)	*S. tetra*	−
Lycaena cupreus	−	*Strymon columella*	+ (A)
L. gorgon	−	*S. melinus*	+ (A)
L. hermes	−	*Brephidium exilis*	+ (A)
L. heteronea	−	*B. pseudofea*	−
L. nivalis	−	*Celastrina neglectamajor*	+ (A)
L. phlaeas	−	*C. argiolus cinerea*	+ (A)
L. xanthoides	−	*Euphilotes battoides*	+, − (P)
Atlides halesus	−	*E. mojave*	+, − (P)
Callophrys augustus	+ (A)	*Everes comyntas*	+ (A)
C. eryphon	+ (A)	*E. amyntula*	+ (A)
C. fotis	+ (A)	*Glaucopsyche lygdamus*	+ (A)
C. mossii	+, − (P)	*G. piasus*	−
C. perplexa	+ (A)	*Icaricia acmon texana*	+ (A)
C. polios	+ (A)	*I. icariodes*	−
C. siva	−	*I. lupini*	+ (A)
C. spinetorum	+ (A)	*I. neurona*	+ (A)
C. mcfarlandi	+ (A)	*Leptotes marina*	+ (A)
Chlorostrymon simaethis	+ (A)	*Lycaeides idas*	+ (A)
Erora guaderna	+ (A)	*L. melissa*	+ (A)
Habrodais grunus	−	*Philotes sonorensis*	−
Ministrymon leda	+ (A)	*Philotiella speciosa*	+, − (P)
Satyrium auretorum	+ (A)	*Plebejus saepiolus*	+ (A)
S. behrii	+, − (3rd)	*Plebulina emigdionis*	−
S. saepium	+, − (A)		

* Feeding response: + = fed, development was normal, and pupated (P) (these species diapause as pupae) or later formed an adult (A); +, − = development was retarded compared to controls on natal food plant either formed a small adult (A), pupated (P), or developed to the third instar (3rd); − = refused to feed and died.

one of ten *C. mossii* larvae pupated and it grew slowly. All three *S. behrii* larvae fed on *Lotus scoparius* flowers, but did not grow. Fifty percent of the 20 *C. polios* survived to pupation, yet only one pupa formed an adult. The remaining species exhibited larval development times and percent survival on *L. scoparius* similar to those of larvae reared on their natural host.

The Lycaenidae tested can be divided into four classes depending on the plant parts on which the larvae feed: flowers; flowers and fruits; flowers, fruits, and leaves; and leaves (Table 2). Only two species feed exclusively on flowers in nature: *C. fotis* and *S. behrii*. Six species feed on flowers and fruits: *C. augustus*, *C. mcfarlandi*, *E. battoides*, *E. mojave*, *G. piasus*, and *E. amyntula*. Of these eight flower and flower/fruit feeding species only *S. behrii* and *G. piasus* did not feed or develop on *L. scoparius*. Of the sixteen species that feed exclusively on leaves in nature, only two developed on *L. scoparius*: *C. eryphon* and *C. spinetorum*. Of the remaining 25 species, which feed either on all parts

TABLE 2. Feeding behaviors of 49 Lycaenidae natural larval food plants.

			Feeding observations		
	Food plant families	Food plant genera	Fl	Fr	Le
Apodemia mormo	Po	Er, Ox	++	++	++
Lycaena					
cupreus	Po	Ru	–	–	++
gorgon	Po	Er	–	–	++
hermes	Rh	Rh	–	–	++
heteronea	Po	Er	–	–	++
nivalis	po	Po	–	–	++
phlaeas	Po	Ru, Oy	–	–	++
xanthoides	Po	Ru	+	–	++
Atlides halesus	Vi	Ph	–	–	++
Callophrys					
augustus	Rh, Ro, Er	2	++	++	–
eryphon	Pi	Pi	–	–	++
fotis	Ro	Co	++	–	–
mossi	Cr	Se	++	++	++
perplexa	Po, Fa	Er, Lo	++	++	++
polios	Er	Ao	++	–	++
siva	Cu	Ju	–	–	++
spinetorum	Vi	Ar	–	–	++
mcfarlandi	Ag	No	++	++	–
Chlorostrymon simaethis	Sa	Ca	++	++	++
Erora quaderna	Rh, Fg	Ce, Qu	++	++	++
Habrodais grunus	Fg	Qu	–	–	++
Ministrymon leda	Fa	Pr	++	–	+
Satyrium					
auretorum	Fg	Qu	++	–	++
behrii	Ro	Pu	++	–	–
saepium	Rh	Ce	–	–	++
tetra	Ro	Cr	–	–	++
Strymon					
columella	Ma	2	++	++	++
melinus	1	2	++	++	++
Brephidium					
exilis	Az, Ch	Ss, At, Ch	++	–	++
pseudofea	Ch	Sa	–	–	++
Celastrina					
argiolus	Ro, Rh, Fa	2	++	++	++
*neglectamajor**	Rn	Cm	++	++	+
Euphilotes					
battoides	Po	Er	++	++	–
mojave	Po	Er	++	++	–
Everes					
comyntas	Fa	Lo	++	+	++
amyntula	Fa	As	++	++	–

TABLE 2. Continued.

	Food plant families	Food plant genera	Feeding observations		
			Fl	Fr	Le
Glaucopsyche					
lygdamus	Fa	Lo, As	++	++	++
piasus	Fa	Lu	++	++	–
Icaricia					
acmon	Po, Fa	Lo, Er	++	++	++
icarioides	Fa	Lu	–	–	++
lupini	Po	Er	++	–	++
neurona	Po	Er	++	–	++
Leptotes marina	Fa, Pl	Lo, Am, Me, Pl	++	++	++
Lycaeides					
idas	Fa	Lo, Lu	+	–	++
melissa	Fa	Lo, Lu	+	–	++
Philotes sonorensis	Cr	Du	++	++	++
Philotiella speciosa	Po	Er, Ox	++	++	++
Plebejus saepiolus	Fa	Tr	++	+	++
Plebulina emigdionis	Ch	At	–	–	++

Plant families are as follows: 1 = many different plant families, Ag = Agavaceae, Az = Aizoaceae, Ch = Chenopodiaceae, Cr = Crassulaceae, Cu = Cupressaceae, Er = Ericaceae, Fa = Fabaceae, Fg = Fagaceae, Ma = Malvaceae, Pi = Pinaceae, Pl = Plumbaginaceae, Po = Polygonaceae, Rh = Rhamnaceae, Ro = Rosaceae, Rn = Ranunculaceae, Sa = Sapindaceae, Vi = Viscaceae.

Plant genera are as follows: 2 = many different plant genera, Am = *Amorpha*, Ao = *Arctostaphylos*, Ar = *Arceuthobium*, As = *Astragalus*, At = *Atriplex*, Ca = *Cardiospermum*, Ce = *Ceanothus*, Ch = *Chenopodium*, Cm = *Cimicifuga*, Co = *Cowania*, Cr = *Cercocarpus*, Du = *Dudleya*, Er = *Eriogonum*, Ju = *Juniperus*, Lo = *Lotus*, Lu = *Lupinus*, Me = *Medicago*, No = *Nolina*, Ox = *Oxytheca*, Oy = *Oxyria*, Ph = *Phoradendron*, Pi = *Pinus*, Pl = *Plumbago*, Po = *Polygonum*, Pu = *Purshia*, Qu = *Quercus*, Rh = *Rhamnus*, Ru = *Rumex*, Sa = *Salicornia*, Se = *Sedum*, Ss = *Sesuvium*, Tr = *Trifolium*.

Feeding observations are as follows: Fl = flowers, Se = seeds, Le = leaves or stems; – = no feeding has been observed; + = some feeding has been observed in either the laboratory or the field, but rarely; ++ = much feeding has been observed.

* The food plant for this species was reported by David M. Wright (pers. comm.).

of the plants or on both flowers and leaves, only two species did not develop on *Lotus: L. xanthoides* and *P. sonorensis*. Only once have we observed *Lycaena xanthoides* feeding on flowers of *Rumex crispus*.

DISCUSSION

Larvae were reared on cuttings of *Lotus scoparius* that were in advanced stages of blooming. At this stage in the plant's development new leaves are not being produced. Lycaenid larvae that feed on leaves generally are adapted to young leaves and shoots (Pratt & Ballmer, unpublished). Larvae of *Glaucopsyche lygdamus* and *Callophrys perplexa* will feed on young leaves of *Lotus scoparius*, both in the laboratory and the field. The adaptation to feeding on young shoots may be due to seasonal changes in the nutritional quality of leaves, as the amount of available nitrogen generally decreases with age (Strong et al. 1984). Therefore it was not surprising that most of the lycaenid larvae tested would not feed on the older vegetation (leaves) of *Lotus scoparius*. The only exception was *Apodemia mormo* larvae, which often have been observed feeding on the older vegetation of their food plant, *Eriogonum inflatum*.

Leaves and seeds often contain toxic compounds, such as cyanogenic glycosides in *Lotus corniculatus* L. (Scriber 1978). Pollen (a major nutritive resource in flowers) of plant species that have mutualistic associations with bees may not have these compounds. The reason for this possible absence of toxic compounds is that pollen is the indirect source of food for the larval development of bees (Weaver & Kuiken 1954). There is a remarkable similarity in the amino acid contents of pollen from diverse species of plants and royal jelly (Weaver & Kuiken 1954). Yet plants differ in their nutritive value and attractiveness to *Apis mellifera* L. (Hymenoptera). In a test of six bee pollinated plant species in six different families, Campana & Moeller (1977) reported sweet clover *Melilotus* sp. (Fabaceae) to be highest in preference and in contribution to brood production.

Of the 31 species observed to feed on flowers at some stage during their larval development, only 4 (12%) did not mature to the pupal stage when reared on the flowers of *L. scoparius*; these were *Satyrium behrii*, *Glaucopsyche piasus*, *Philotes sonorensis*, and *Lycaena xanthoides*. It is surprising that neither *S. behrii* nor *G. piasus* developed on the flowers of *Lotus*, as both species feed specifically on pollen of their food plants. The food plant of *Satyrium behrii*, *Purshia glandulosa*, is closely related to *Cowania mexicana*, the food plant for *Callophrys fotis*. Yet *C. fotis* did quite well on *Lotus* flowers. *Glaucopsyche piasus* is adapted to flowers of another genus of Fabaceae, yet did not develop on *Lotus*.

If the pollens of different species of plants are very similar in nutrition and composition, perhaps the adaptation to feeding on flowers at some stage in the larval development would make larvae capable of feeding on flowers of a large variety of plants. Because first instar larvae are limited in their ability to disperse in search of food, ovipositional mistakes (on flowers) by females of monophagous flower-feeding species may be less costly than those by monophagous leaf-feeding species. This could be extremely important in the historical evolution of host shifts in the Lycaenidae.

Sixteen of the 49 species in this study do not feed on flowers in nature. Of those 16 species, only two, *Callophrys eryphon* and *Callophrys spinetorum*, developed normally on the flowers of *Lotus scoparius*. Since many *Callophrys* species feed on flowers at some stage during their larval development, perhaps these two species have retained the ancestral ability to feed on flowers. In general, larvae of *Callophrys* species are adapted to a wide variety of plants, even though many of them are monophagous or oligophagous. Perhaps this group evolved from a somewhat polyphagous flower- or leaf-feeding species. Only one *Callophrys* species (*C. siva*) did not develop on *Lotus scoparius* flowers.

Of the 16 species that did not complete larval development on *Lotus* flowers, all are specific either to a single host genus or species. For instance, *Lycaena gorgon* and *Lycaena heteronea*, both of which feed on *Eriogonum* (Polygonaceae), do not develop on *Rumex crispus*, another member of Polygonaceae, and feed on it only for short periods; by contrast *L. xanthoides*, which feeds on *Rumex* species, will not even feed on *Eriogonum* (Pratt unpubl. data).

The results presented here do not support Fabaceae as the primitive larval host for the Lycaenidae. Instead, our results indicate that the ability of lycaenids to feed on *L. scoparius* may be correlated more with flower- and fruit-feeding habits than with natural utilization of other members of Fabaceae. Perhaps part of the reason that legumes are fed on by a wide variety of Lycaenidae is that legumes are often high in nitrogenous compounds due to their association with nitrifying bacteria (Pierce 1985).

ACKNOWLEDGMENTS

We Thank Glen Gorelick, John Emmel, and David M. Wright for their suggestions and comments on the manuscript. Also, Marc Minno provided ova of *B. pseudofea*, David M. Wright provided ova of *C. neglectamajor*, and Sterling Matoon provided larvae of *C. polios*.

LITERATURE CITED

ACKERY, P. R. 1988. Hostplants and classification: A review of nymphalid butterflies. Biol. J. Linn. Soc. 33:95–203.

BALLMER, G. R. & G. F. PRATT. 1989a. Instar number and larval development in *Lycaena phlaeas hypophlaeas* (Boisduval) (Lycaenidae). J. Lepid. Soc. 43:59–65.

———. 1989b. A survey of the last instar larvae of the Lycaenidae (Lepidoptera) of California. J. Res. Lepid. 27:1–80.

CAMPANA, B. J. & E. E. MOELLER. 1977. Honey bees: Preference for and nutritive value of pollen from five plant sources J. Econ. Entomol. 70:39–41.

COMSTOCK, J. A. & C. M. DAMMERS. 1935. Notes on the early stages of three butterflies and six moths from California. Bull. So. Calif. Acad. Sci. 34:120–142.

EHRLICH, P. R. & P. H. RAVEN. 1964. Butterflies and plants: A study in coevolution. Evolution 18:586–608.

EMMEL, T. C. & J. F. EMMEL. 1973. The butterflies of southern California. Nat. Hist. Mus. of Los Angeles County, Science Series 26:1–148.

PIERCE, N. 1985. Lycaenid butterflies and ants: Selection for nitrogen fixing and other protein rich food plants. Amer. Nat. 125:888–895.

POWELL, J. A. 1968. Foodplants of *Callophrys* (*Incisalia*) *iroides*. J. Lepid. Soc. 22:225–226.

SCOTT, J. A. 1984. The phylogeny of butterflies (Papilionoidea and Hesperidea). J. Res. Lepid. 23:241–181.

———. 1986. The butterflies of North America: A natural history and field guide. Stanford University Press, Stanford, California. 583 pp.

SCRIBER, J. M. 1978. Cyanogenic glycosides in *Lotus corniculatus*: Their effect upon growth, energy budget, and nitrogen utilization of the southern armyworm, *Spodoptera eridania*. Oecologia (Berl.) 34:143–155.

STRONG, D. R., J. H. LAWTON & S. R. SOUTHWOOD. 1984. Insects on plants. Harvard University Press, Cambridge, Massachusetts. 313 pp.

WEAVER, N. & K. A. KUIKEN. 1954. Quantitative analysis of the essential amino acids of royal jelly and some pollens. J. Econ. Entomol. 44:635–638.

Received for publication 22 November 1989; revised 22 June 1991; revised and accepted 8 July 1991.

Journal of the Lepidopterists' Society
45(3), 1991, 197–203

BIOLOGY OF *MORRISONIA CONFUSA* (NOCTUIDAE)

PETER S. WOOD
1403 Mt. Vernon Avenue, Alexandria, Virginia 22301

AND

LINDA BUTLER
Division of Plant and Soil Sciences, P.O. Box 6108, West Virginia University,
Morgantown, West Virginia 26506-6108

ABSTRACT. Studies on *Morrisonia confusa* were conducted in 1984 and 1985 in the laboratory and at Cooper's Rock State Forest in northern West Virginia. Adult flight period was from 2 May to 8 June, and larvae were collected from 6 June to 20 September. Nineteen host plants and 15 species of parasites are recorded for *M. confusa* larvae. The egg and seven larval instars are described. Larval duration averaged 71.4 days at 24°C.

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

Morrisonia confusa (Hübner) (Noctuidae: Hadeninae) is common throughout eastern North America with adults flying in April and May (Forbes 1954). Within this wide geographical area the larvae are defoliators of broad-leafed trees and shrubs and may be found from late June to mid-August in Canada (Prentice 1962).

The earliest larval description for *M. confusa* was given by Dyar (1891) who described coloration of the head and body. Brief descriptions of larvae were given by Crumb (1956) and Forbes (1954). A more detailed larval description was given by Godfrey (1972) who also figured the head, hypopharyngeal complex, and mandible. Crumb (1956) described *M. confusa* as a leaf folder, and Prentice (1962) indicated it to be a solitary webmaker.

During 1984 and 1985 as a part of a larger study, we studied *M. confusa* at Cooper's Rock State Forest in northern West Virginia, just west of the gypsy moth, *Lymantria dispar* (L.) (Lymantriidae), infestation as it was moving into the state. The objective of our larger study was to obtain baseline data for native macrolepidopterous defoliators and their parasites before the build-up of gypsy moth to enable evaluation of later native defoliator populations in face of projected gypsy moth population increases. During the part of the study reported here *Morrisonia confusa* was taken frequently in samples, but appeared to be producing insignificant defoliation. Since little information is available on the biology of *M. confusa*, we recorded its duration of larval development, larval food, and parasites. 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 forests 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 *M. confusa* was determined by blacklight trapping once each week from 7 March to 28 October 1984 and from 28 March to 6 November 1985. In 1985, 21 adult *M. confusa* were live-trapped at a blacklight trap and caged in the laboratory with foliage of red maple, black cherry, black birch, and red oak on which to oviposit; moths were provided with water and black cherry blossoms as a nectar source.

Larvae were reared in 150 × 25 ml plastic petri dishes; they were transferred onto fresh foliage in clean petri dishes every other day. Larvae were fed red maple since larval numbers taken from foliage in 1984 indicated a slight preference for red maple. Larvae were observed daily, and at each instar some were killed in KAAD (Peterson 1962) and preserved in 80% ethanol for head measurements. Pupation was in a 5 cm deep layer of moist vermiculite in quart canning jars provided with filter paper lids. 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) and Hinton (1946). Egg and larval head capsule measurements were made with an ocular micrometer.

To evaluate general biology, field sampling of *M. confusa* larvae was conducted by pole pruning foliage samples once each week from 16 May to 11 October 1984 and from 2 May to 30 October 1985. Foliage sampled was primarily *Acer rubrum*, *A. saccharum* Marsh., *A. saccharinum* L., *A. nigrum* Michx., *Prunus serotina*, *Betula lenta*, *Quercus alba*, *Q. rubra*, *Q. prinus* L., and *Q. velutina* Lam. Three 25-branch-tip samples per species group (mixed oaks, mixed maples, black birch, black cherry) were taken for a total of 300 branch tips per week. A branch tip represented about one square foot of foliage. Some additional host plants were observed during field sampling. All field collected larvae were laboratory reared on the appropriate host plant for isolation of parasites.

A cage of field-collected *M. confusa* larvae was set up in the laboratory for observation of feeding habits and webmaking activity. The cage contained six small red maple seedlings in six-inch pots embedded in moist vermiculite covered with leaf litter.

RESULTS

Phenology, Life History, and Food Plants

Flight period of *M. confusa* during 1984 was from 12 May to 8 June; 79 specimens wee trapped. In 1985, 119 specimens were collected between 2 May–16 May. Peak trap numbers were on 25 May 1984 (27 specimens) and 10 May 1985 (101 specimens).

In 1984, 228 larvae were collected on foliage in the field from 21 June to 20 September, and in 1985, 31 larvae were collected from 6 June to 8 August. During 1984, the percentage of larvae taken from each of the four regularly sampled tree species was as follows: 21% on black birch; 28% on mixed maples, 27% on black cherry, and 24% on mixed oaks.

During this study, larvae of *M. confusa* were found on the following plants: *Acer nigrum, A. rubrum, A. saccharinum, A. saccharum* (Aceraceae); *Betula lenta* (Betulaceae); *Castanea mollissima* Blume, *Quercus alba, Q. prinus, Q. rubra, Q. velutina* (Fagaceae); *Prunus serotina, Malus sylvestris* Mill., *Rosa* spp. (Rosaceae); *Cornus florida* L. (Cornaceae); and *Carya* spp. (Juglandaceae). Additional food plants given by other authors include: *Salix* spp. (Salicaceae) (Dyar 1891); *Vaccinium* spp. (Ericaceae) (Forbes 1954); *Tila americana* L. (Tiliaceae), *Betula papyrifera* Marsh. (Betulaceae), *Populus balsamifera* L. (Salicaceae), *Carpinus caroliniana* Walt. (Corylaceae), *Aesculus hippocastanum* L. (Hippocastanaceae), *Ulmus americana* L. (Ulmaceae) (Prentice 1962), and *Pinus* spp. (Pinaceae) (Covell 1984). We suspect that *Pinus* is not an acceptable food plant for *M. confusa* but has appeared in the literature because of an error in page arrangements in Tietz (1972).

Larval instar durations for the seven instars of *M. confusa* as determined from laboratory rearing from eggs are summarized in Table 1. During the 1984–85 study all laboratory reared larvae died during the 7th instar. The data given for that instar in Table 1 are from larvae field collected as instars 3–6 in 1989 during a similar study at Fernow Experimental Forest, Parsons, West Virginia. The rearing times noted here for *M. confusa* larvae are considerably longer than would be expected. We suspect that the prolonged development time resulted from the frequent disturbance of this web-constructing species as fresh foliage was added. No larva pupated at instar six. We believe that within the *M. confusa* population with which we worked, seven instars are normal.

TABLE 1. Larval period of *Morissonia confusa* reared on leaves of red maple (*Acer rubrum*) at 24°C.[1]

Instar	N	Mean time ± SD (days)
1	20	6.4 ± 1.8
2	19	4.2 ± 1.3
3	18	5.2 ± 1.2
4	17	7.9 ± 2.6
5	18	14.4 ± 3.0
6	13	19.3 ± 2.9
7	7	14.0 ± 0.6
Total		71.4

[1] Data for the 7th instar are from larvae field collected and reared in 1989. All 7th instar larvae in the 1984–85 laboratory study died prior to pupation.

Parasites reared from field collected *M. confusa* larvae during the 1984–85 study were as follows: *Hyphantrophaga virilis* (Aldrich and Webber) (Diptera: Tachinidae); *Euplectrus maculiventris* Westwood, *E. bicolor* (Swederus), and *Pediobius crassicornis* (Thomsom) (Hymenoptera: Eulophidae); *Perilampus* sp. (Hymenoptera: Perilampidae); *Cotesia* sp., *Microplitus hyphantriae* Ashmead, *Micropolitis* spp. (2 other species) (Hymenoptera: Braconidae), *Hyposoter annulipes* (Cr.), *Dusona wyomingensis* (Vier.), *Enicospilus merdarius* (Grav.), *Itoplectis conquisitor* (Say), *Isodromas lycaenae* How., and *Mesochorus vittator* Zett. (Hymenoptera: Ichneumonidae). *Euplectrus bicolor* was the most frequently reared parasite followed by *Hyposoter annulipes* and *Microplitis* spp.

Description of Eggs and Larvae

Eggs. In the laboratory, a total of 7 egg clusters was oviposited in single-layered masses ranging in size from 48 to 316 eggs (mean = 182). No ovipositional preference was noted as egg clusters were laid on walls of the cage as well as on all four plant species. The eggs were spherical in shape, 0.62 mm in diameter (n = 50). One egg observed by scanning electron microscopy was sculptured with 37 longitudinal ridges and paralleled by transverse striae forming rectangles on the egg surface. Nine rosette cells were observed in the micropylar area. Salkeld (1984) in a detailed study of noctuid eggs noted that *M. confusa* eggs had a width of 0.60 mm, 34–35 longitudinal ridges, and 11–13 rosette cells.

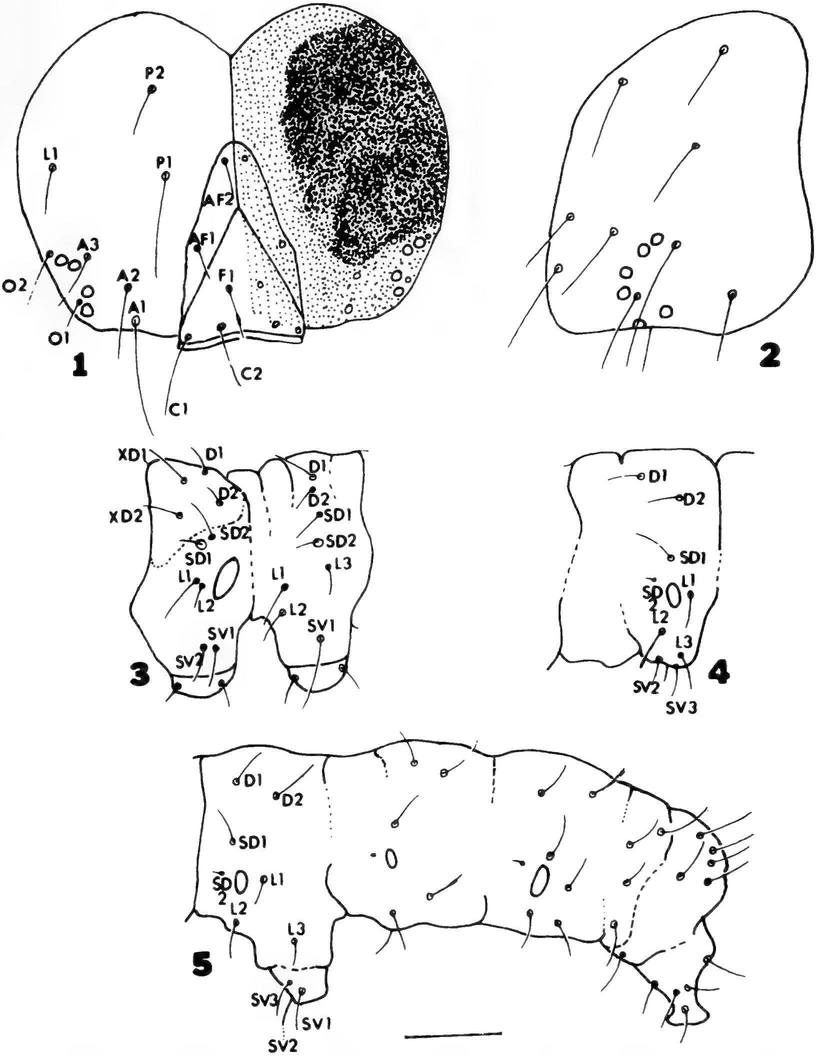
Larvae. Instar 1 (n = 20): Head capsule x̄ = 0.33 mm (range 0.32–0.36), orange brown. Pinacula dark brown; cervical shield tan; thoracic legs medium brown. Body transparent with green gut contents visible; proleg sclerites dark brown.

Instar 2 (n = 19): Head capsule x̄ = 0.56 mm (range 0.50–0.60), orange brown. Pinacula maroon; large maroon spot surrounds SD1 setae on abdominal segments 1–8 and is expanded to include SD2 on thorax; body uniformly pale green with white D, SD, and L lines.

Instar 3 (n = 20): Head capsule x̄ = 0.94 mm (range 0.90–1.05). Coloration similar to that of instar 2.

Instar 4 (n = 20): Head capsule x̄ = 1.51 mm (range 1.43–1.57), orange brown. Pinacula dark maroon; maroon patch remains around all SD1 setae and thoracic SD2 setae, but smaller than in previous instars; D, SD, and L lines white, prominent.

Instar 5 (n = 15): Head capsule x̄ = 2.0 mm (range 1.86–2.15). Coloration similar to that of instar 4.



FIGS. 1–5. *Morrisonia confusa* larva, instar 7: **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. Setal designations follow Hinton (1946). Scale bar = 1 mm.

Instar 6 (n = 10): Head capsule $\bar{x}$ = 3.06 mm (range 2.72–3.43), orange brown with faint darker brown reticulations. The maroon patches around SD2 setae begin fading away with those on abdominal segments 4, 5, and 6 disappearing first; white D and SD lines faint. Body becomes a mottled whitish-green as the D, SD, and L lines fade and scattered white dots appear.

Instar 7 (n = 8): Head capsule $\bar{x}$ = 3.84 mm (range 3.54–4.16), dark brown with the exception of the tan frons, adfrons and clypeus, giving the appearance of large ocular spots. Cervical shield and remainder of body an off-white to pale green; no maroon color remains; D and SD lines indistinct. Head capsule measurements given here for instar seven are within the range of those that we collected as mature larvae from the field and for that range given by Godfrey (1972). Body 22–33 mm long and 4 mm wide; prolegs present on abdominal segments 3–6, size increasing caudad; crochets uniordinal, 21–24 per third abdominal proleg, 23–28 per fourth, 26–29 per fifth, 28–30 per sixth. All setae simple. Chaetotaxy illustrated in Fig. 1–5.

Behavior: Larvae caged in the laboratory and observed in the field constructed a nest by webbing a single leaf or two adjacent leaves. When disturbed, larvae curl the body with the anal prolegs near the head.

Diagnosis: The only other *Morrisonia* species common within the Cooper's Rock study area is *M. evicta* (Grote). Godfrey's (1972) description of *M. evicta* states that it possesses a yellow-brown head with indistinct to dark brown reticulation and coronal stripes. At no larval instar does the *M. confusa* head have this appearance; it is orange brown and virtually unmarked until instar 7 when it is all dark brown except for the tan adfrons, frons, and clypeus. The grayish body color given for *M. evicta* differs from that of *M. confusa*. Also, *M. evicta* is described as having a shiny dark brown cervical shield, which *M. confusa* lacks in all instars. *Morrisonia mucens* (Hbn.) has not been collected at Cooper's Rock. The most diagnostic feature of *M. confusa* larvae from instars 2–6 is the presence of the large maroon spot around SD1 on all segments. This feature easily separates larvae of this species from all others in the study area.

During this two-year baseline study, *M. confusa* was one of the most frequently collected noctuids, along with *Polia latex* (Wood & Butler 1989). The Cooper's Rock study area shows a diverse community of Macrolepidoptera as indicated by blacklight trapping of 400 species of adults and the recording of 101 species of larvae from the four groups of sampled foliage (Butler, unpubl. data).

ACKNOWLEDGMENTS

We thank the U.S. Forest Service for partial support of this research; also Vicki Kondo, Lisa Bean, Ralph Iannone, Janice Jenkins, Robert Progar, Delray Shaffer, Judy Shaffer, and Laura Tate for field and laboratory assistance; James W. Amrine Jr., John E. Hall, and Joseph E. Weaver for review of the manuscript, and R. W. Carlson, E. E. Grissell, P. M. Marsh, M. E. Schauff, and N. E. Woodley of the U.S. Dept. Agr., Systematic Entomology Laboratory, for parasite identifications.

Published with the approval of the Director of the West Virginia Agricultural and Forestry Experiment Station as Scientific Article No. 2177. This research was supported with funds appropriated under the Hatch Act and by a grant from the U.S. Forest Service.

LITERATURE CITED

CARVELL, K. L. 1983. A summary of 1973–1982 weather data from the West Virginia University Forest. WVU Forestry Notes 10:13–16.

COVELL, C. V. JR. 1984. A field guide to the moths of eastern North America. The Peterson Field Guide Series, No. 30. Houghton Mifflin, Boston. 496 pp.

CRUMB, S. E. 1956. The larvae of the Phalaenidae. U.S. Dept. Agr. Tech. Bull. 1135: 356 pp.

DYAR, H. G. 1891. Description of certain lepidopterous larvae. Insect Life 3:519. USDA, Washington, D.C.

FORBES, W. T. M. 1954. Lepidoptera of New York and neighboring states. Part III. Memoir 329. Cornell Univ. Agr. Sta. 433 pp.

GODFREY, G. L. 1972. A review and reclassification of larvae of the subfamily Hadeninae

(Lepidoptera, Noctuidae) of America north of Mexico. U.S. Dept. Agr. Tech. Bull. 1450:265 pp.

HINTON, H. E. 1946. On the homology and nomenclature of the setae of lepidopterous larvae, with some notes on the phylogeny of the Lepidoptera. Trans. Roy. Entomol. Soc. 97:1–37.

PETERSON, A. 1962. Larvae of insects, part I: Lepidoptera and plant infesting Hymenoptera. Edward Bros., Inc., Ann Arbor, Michigan. 315 pp.

PRENTICE, R. M. 1962. Forest Lepidoptera of Canada, Vol. 2. Dept. of Forestry Bull. 128:77–281.

SALKELD, E. H. 1984. A catalogue of the eggs of some Canadian Noctuidae (Lepidoptera). Mem. Entomol. Soc. Can. 127:167 pp.

TIETZ, H. M. 1972. An index to the described life histories, early stages and hosts of the Macrolepidoptera of the continental United States and Canada, Vol. 1. The Allyn Museum of Entomology, Sarasota, Florida. 536 pp.

WOOD, P.S. & L. BUTLER. 1989. Biology and immature stages of *Polia latex* (Gueńee) (Noctuidae). J. Lepid. Soc. 43:299–304.

Received for publication 7 September 1989; revised and accepted 30 July 1991.

Journal of the Lepidopterists' Society
45(3), 1991, 204–208

THE LARVA OF *OMMATOSTOLA LINTNERI* (NOCTUIDAE: AMPHIPYRINAE)

KENNETH A. NEIL
Agriculture Canada, Research Station, Kentville, Nova Scotia
B4N 1J5, Canada

ABSTRACT. The last instar of *Ommatostola lintneri* Grote is described and illustrated.

Additional key words: larval morphology, host plant, hypopharyngeal complex, mouthpart structures, chaetotaxy.

Ommatostola lintneri Grote (Noctuidae: Amphipyrinae) is characteristically a species of coastal sand barrens. Although *O. lintneri* can be common in such habitats, its distribution is limited to an area from Nova Scotia, including Sable Island (Ferguson 1954), south to Long Island, New York, and New Jersey (Forbes 1954).

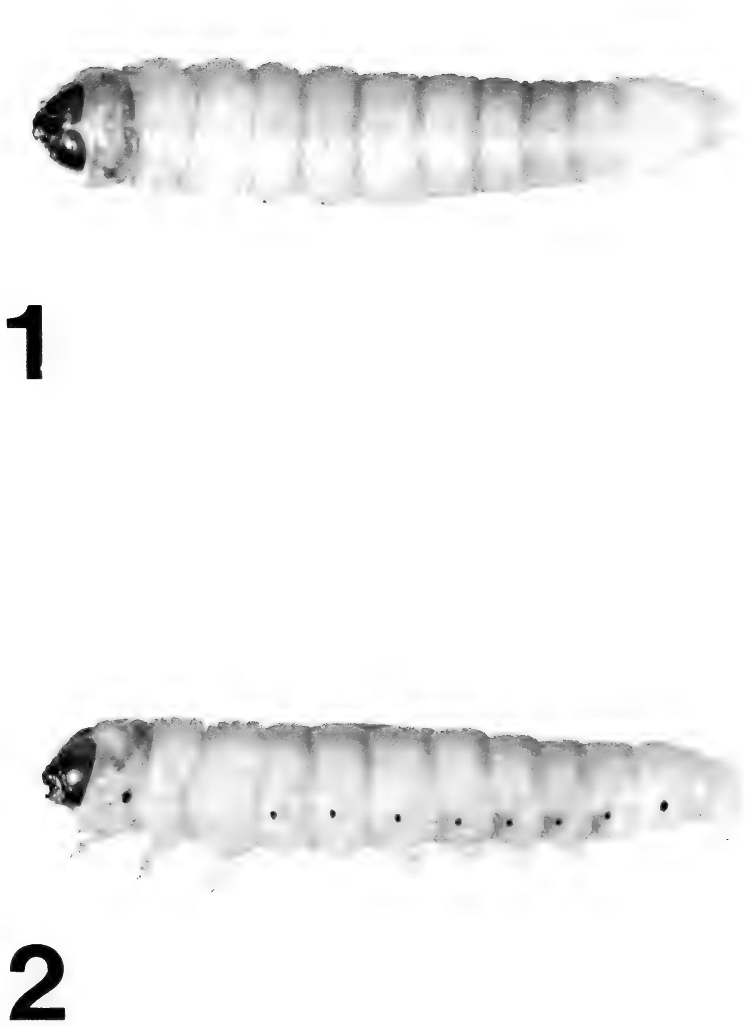
Little is known about the larval stages of *O. lintneri*. Forbes (1954) provided a very brief description of a larva he presumed to be *O. lintneri*, but indicated no adult association. Tietz (1972) listed *Arenaria* sp. (Caryophyllaceae) as a food plant, but gave no references.

To aid recent ecological investigations on Sable Island, I was asked to rear and identify several species of noctuid larvae from this locality. The most common species collected was a large, light sand colored larva which fed on the roots and stems of *Arenaria* sp., several centimeters below the surface of the sand. Delays in shipping the material from Sable Island to mainland Nova Scotia resulted in most of the larvae dying. A single specimen collected 1–6 July 1986 was reared on *Arenaria* sp. and an adult *O. lintneri* emerged 29 August 1986.

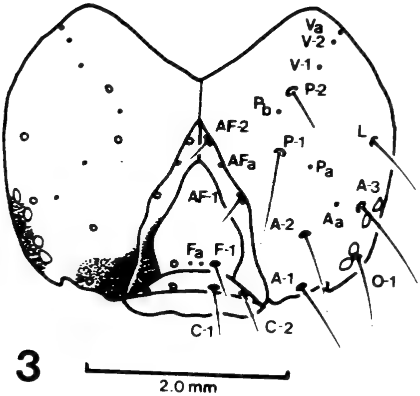
The following is a description of the last instar larva of *O. lintneri* based on the specimens collected on Sable Island, Nova Scotia. All illustrations were drawn to scale with the aid of a Wild stereomicroscope and ocular grid system. The terminology and abbreviations used follow those proposed by Godfrey (1972).

Ommatostola lintneri Grote

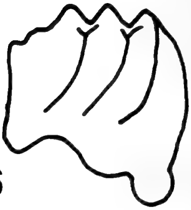
Morphological description (Figs. 1 and 2). Head width 2.9–4.3 mm (N = 4). Total body length 32.0–32.75 mm (N = 3). Body widest anteriorly, tapering posteriorly. Head semi-prognathous. Head and body smooth. Prolegs present on abdominal segments, (Ab) 3 to 6 poorly developed, all equal in size. Crochets uniordinal,8–12 per third abdominal proleg, 10–11 per fourth, 9–12 per fifth, 10–11 per sixth. All setae simple. **Coloration of living material:** Head (Fig. 3) reddish brown with black ocellar band; base of antennal socket black. Body (Figs. 1 and 2) light sand brown, dorsal area slightly darker, no lines or markings present. Cervical shield shining yellow brown, posterior margin slightly darker. Anal shield much lighter, also shining yellow brown. Pinacula light brown, dorsal pinacula slightly larger than lateral and ventral pinacula. Head yellowish brown, markings



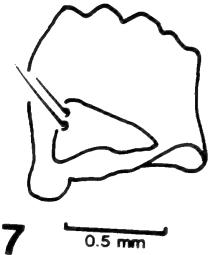
FIGS. 1 and 2. *Ommatostola lintneri* Grote larva (×5) **1,** lateral view. **2,** dorsal view.



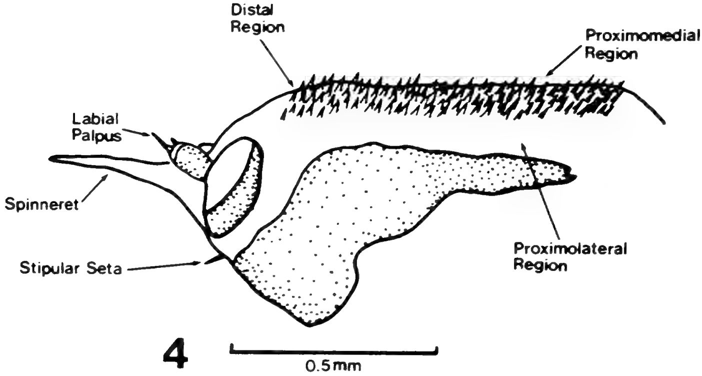
3



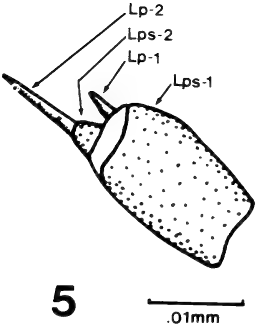
6



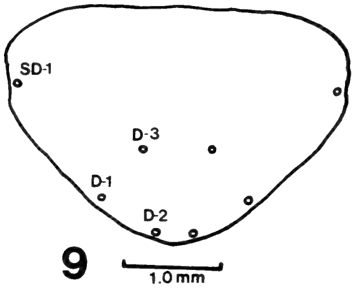
7



4

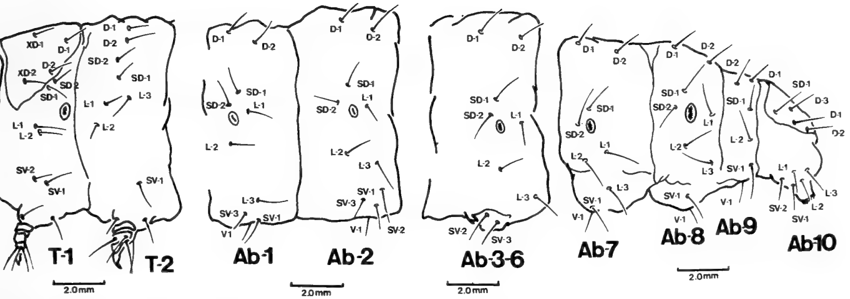


5



9

FIGS. 3–7, 9. *Ommatostola lintneri* Grote larval structures: **3**, head, frontal view. **4**, hypopharyngeal complex, left lateral view. **5**, labial palpus, lateral view. **6**, left mandible, oral surface. **7**, left mandible, outer surface. **9**, anal shield, dorsal view.



8

FIG. 8. *Ommatostola lintneri* Grote: dorsal and lateral chaetotaxy of prothoracic (T1), mesothoracic (T2), and abdominal segments (Ab1–3, Ab6–10).

as in living material. Body light creamy brown. Cervical shield pale yellowish brown. Spiracles dark yellow brown, peritremes black. **Head** (Fig. 3): Cervical indentation deep; adfrontal sutures terminating at epicranial suture: epicranial suture length about ⅔ height of frons; frons higher than width at base. Adfrontal setae (AF) 2 and posterior head setae (P) 1 above apex of frons; anterior head puncture (Aa) below a straight line projected through posterior head puncture (Pa) and anterior head setae (A) 3. P-1 below straight line through P-2 and AF-1; Aa equidistant from A-3 to A-2, A-1 to A-3 forming obtuse angle at A-2. Lateral head setae (L) above or below juncture of adfrontal sutures. Distance between ocelli (Oc)-3 to Oc-4 about half that between Oc-1 to Oc-2 or Oc-2 to Oc-3. Ends of postgenae well separated. **Mouth parts:** Hypopharyngeal complex (Fig. 4). Spinneret long, thin, and tapering anteriorly, about twice the length of Lps-1 and Lps-2 and Lp-2. Labial palpus (Fig. 5) with Lps-1 about 6 times the length of Lp-1, about 7 times the length of Lps-2 and twice the length of Lp-2; Lps-2 slightly longer than Lp-1. Stipular setae less than ½ the length of Lps-1, about twice the length of Lp-1 and over twice the length of Lps-2. Distal and proximal regions continuous, distal region above spinneret bare, remainder covered by long coarse spines, spines becoming shorter and thinner proximally. Mandible (Figs. 6 and 7): Outer setae approximate; inner surface with 3 distinct ridges, outer surface with 5 distinct teeth, 1st to 3rd well developed and angular, 4th to 5th blunt. **Thorax:** Prothoracic segment (T-1) (Fig. 8). Shield smooth and weakly sclerotized, subdorsal body setae (SD)-1 and SD-2 on separate setae; seta SD-1 and lateral body seta (L)-2 fine, hairlike, with a thickened annulus at base; major axis of prothoracic spiracle passing anterior to SD-1 and SD-2 and posterior of body setae (SV)-1 and SV-2; spiracle oval, height more than twice its width. T-2 to T-3 (Fig. 8). SD-1 fine, hairlike, a thickened sclerotized annulus at base. Tarsal claws with basal angles acute. Metathoracic coxae well separated. **Abdomen:** Dorsal and lateral chaetotaxy as in Fig. 8. Ab-1 with 2 SV setae; Ab-2 to Ab-6 with 3 SV setae; SV-1 to SV-2 setal insertions well separated. Ab-7 to Ab-8 with 1 SV seta; Ab-9. SD-1 fine and hairlike, with a thickened annulus at base. Ab-10: anal shield as in Fig. 9, dorsal margin flat, posterior margin entire; subanal setae well separated.

Material examined: Fifteen specimens: Sable Island, Nova Scotia. All larvae collected 1-6 July 1986 by Ms. Zoe Lucas, reared on *Arenaria* sp., and determined by K. A. Neil. One adult male emerged 29 August 1986. All specimens have been deposited in the Nova Scotia Museum, Halifax, Nova Scotia, Canada.

DISCUSSION

Subterranean feeding is a character shared by other Amphipyrine genera, such as *Apamea* (some species) and *Crymodes*. The larva of *Ommatostola lintneri* can be distinguished from these taxa by the light sandy brown coloration and external morphology, especially by the

SD-2 seta, which is separated from the cervical shield. According to Crumb (1956), this character is shared only with *Archanara oblonga* (Grt.), which is easily separated from *Ommatostola lintneri* by its coloration.

ACKNOWLEDGEMENTS

I thank Zoe Lucas for supplying me with the larvae of *O. lintneri* described here and Arthur Lightfoot of Agriculture Canada, Kentville, for photographing the plates.

LITERATURE CITED

CRUMB, S. E. 1956. The larvae of the Phalaenidae. U.S. Dept. Agr. Tech. Bull. 1135: 356 pp.

FERGUSON, D. C. 1954. The Lepidoptera of Nova Scotia (Macrolepidoptera). N.S. Mus. Sci. Bull. 33:214 pp.

FORBES, W. T. M. 1954. Lepidoptera of New York and neighboring states. Cornell Univ. Agr. Expt. Sta. Mem. 329. 433 pp.

GODFREY, G. L. 1972. A review and reclassification of larvae of the subfamily Hadeninae (Lepidoptera, Noctuidae) of America north of Mexico. U.S. Dept. Agr. Tech. Bull. 1450:265 pp.

TIETZ, H. W. 1972. An index to the described life histories, early stages, and hosts of the Macrolepidoptera of the continental United States and Canada. 2 vols. A. C. Allyn, Allyn Museum of Entomology, Sarasota, Florida. 1041 pp.

Received for publication 23 January 1990; revised and accepted 6 July 1991.

Journal of the Lepidopterists' Society
45(3), 1991, 209–214

FIRST RECORD OF THE GENUS *ACRAPEX* FROM THE NEW WORLD, WITH DESCRIPTION OF A NEW SPECIES FROM THE CAROLINAS AND VIRGINIA (NOCTUIDAE: AMPHIPYRINAE)

DOUGLAS C. FERGUSON

Systematic Entomology Laboratory, Agricultural Research Service, USDA,
% U.S. National Museum of Natural History, Washington, D.C. 20560

ABSTRACT. A new species, *Acrapex relicta*, is described from three localities on the southeastern coastal plain of the United States. About 85 species of *Acrapex* are known from the Old World tropics, but *A. relicta* is the first to be reported from the Americas. Because of its restricted habitat, it is believed to be native, not introduced. The morphology, especially of the ovipositor, indicates that *A. relicta* is a grass feeder.

Additional key words: moths, taxonomy, geographical distribution, genitalia.

This paper reports the occurrence of a species of the Old World genus *Acrapex* (Noctuidae: Amphipyrinae) in North America. The type species of *Acrapex* Hampson (1894) is *Leucania prisca* Walker (1866), by original designation. It was described from Ceylon (now Sri Lanka) but is present also in southern India. At least 85 species have been assigned to *Acrapex*, of which 71 are African; others occur on the Indian subcontinent, in Australia, New Guinea, New Caledonia, the Philippines, Taiwan, Japan, and Hawaii. Until now, however, they were thought to be absent from the Americas. For purposes of the present paper I considered it unnecessary to see and dissect the type species (illustrated by Hampson 1910: p. 319, fig. 139), although I examined many others placed in *Acrapex*. These included *A. hamulifera* (Hampson), another species described from Sri Lanka. It is uncertain whether all members of this widely distributed, diverse assemblage should be regarded as congeneric; but *Acrapex* is the only genus available to accommodate them.

Species of *Acrapex* are relatively small, predominantly light-brown (dead-grass colored) moths, with narrow wings and longitudinal markings, except for the characteristic pale discal spot that may have a dark center. They have moderately long, somewhat upturned palpi, of which the tips are about on a level with the middle of the front; a fairly well-developed proboscis; fully developed, hemispherical eyes; antennae that are simple or nearly so in both sexes; long, shaggy vestiture on the legs; and no special scale tufts on the thorax or abdomen. The new American species is typical of *Acrapex* in size, color, shape, and general habitus. The male genitalia are variable in the genus, and it is difficult to identify common features. Species that I examined show a tendency to have angulate points (variously situated) on the margins of the valves, and the American species has these. The female genitalia of *A. relicta* are typical of the group, with rigid, sharp, acutely conical ovipositor lobes characteristic of grass-feeding noctuids that insert their eggs into tight crevices between the leaf sheath and the stem. However, these perceived similarities may show only that the many species included in *Acrapex* are members of a marsh-dwelling, grass-feeding guild, being the products of an evolution with multiple convergences, rather than that they are in the same genus.

Moths of this genus are deceptively similar to certain other amphipyrine noctuids in the American fauna, such as species of *Chortodes* Tutt (=*Hypocoena* Hampson), especially *Chortodes defecta* (Grote), or *Spartiniphaga panatela* (Smith); but the genitalia show little to confirm such a relationship. The male genitalia of *A. relicta* show more similarity to those of *Chortodes defecta* than do those of other species of *Acrapex* that I have examined or seen figured in the literature (e.g., Holloway 1979, Janse 1937–39, Zimmerman 1958), but they still differ from those of *Chortodes* in the shape of the valve, vesica, and the presence of a long ampulla. Holloway (1989: 129) included *Acrapex* as one of several Old World tropical species groups or subgenera within *Sesamia* Guenée *sensu lato*. In treating the Japanese fauna, Sugi (*in* Inoue et al. 1982) listed *Acrapex* near *Archanara* Walker and various other genera that do not occur in the New World but which superficially resemble *Chortodes, Spartiniphaga, Mammifrontia* Barnes and Lindsey, and *Benjaminiola* Strand.

Acrapex relicta Ferguson, new species
(Figs. 1–7)

Diagnosis. A small, slender, narrow-winged, amphipyrine noctuid, about the color of dead grass, with a small white discal spot shaded proximally and sometimes also distally with blackish scales in a manner that may in part give the appearance of a dark central dot. Somewhat similar in color and pattern to *Archanara oblonga* (Grote) (e.g., Covell 1984: pl. 25, fig. 8) but no more than half the size, with a more oblique outer margin on the forewing, a more delicate form, and a slender body about like that of *Amolita fessa* Grote. Closest in appearance to *Chortodes defecta* (Grote) in the North American fauna but again smaller, only about ⅔ the size, less inclined to be yellowish, with relatively prominent black and white discal spots, and a much more southern distribution. Seen from southern Virginia and the Carolinas only; rarely collected and local, probably confined to a specific host in wet, freshwater, grassy habitats. Very close in appearance to *Acrapex azumai* Sugi (1970:221, figs. 16 & 31; *in* Inoue et al. 1982: pl. 185, figs. 25–27), described from Okinawa in the Ryukyu Islands. This is the first record of a species of *Acrapex* from the Western Hemisphere.

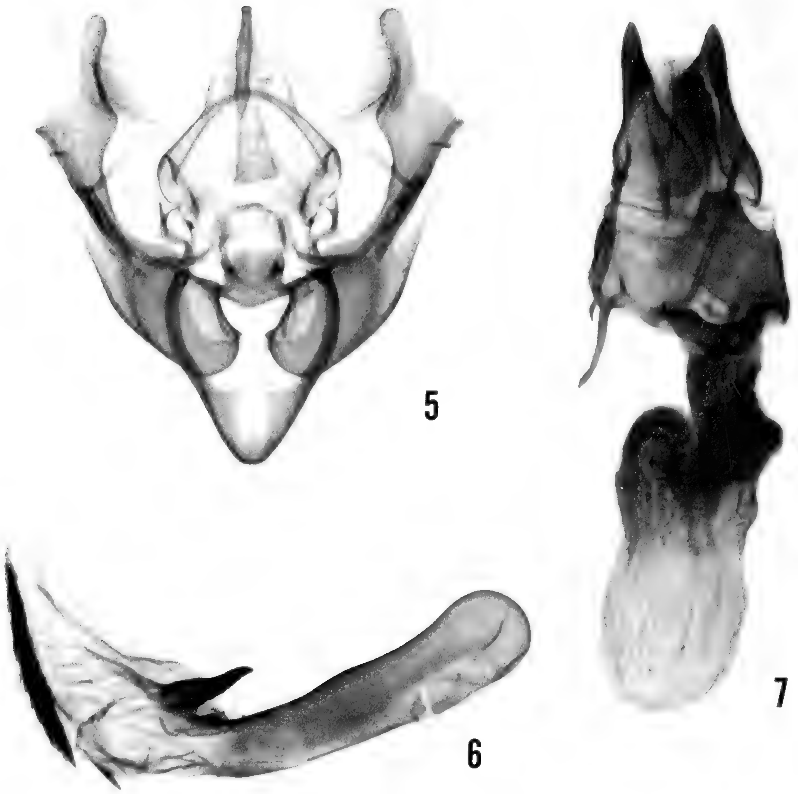
Further description. Antenna of both sexes simple, that of male heavily ciliate, with length of setae almost equal to thickness of shaft. Palpi of both sexes slender, nearly cylindrical, exceeding front by ⅓ their length, middle segment 2-1/2 times length of apical segment, pale brown, shaded with dark brown to black laterally and apically. Front convex, narrower than width of eye, with dark, glossy, smooth, closely appressed scales on lower half, and transverse crest of longer, dark-brown scales on upper half (worn off in most specimens). Tongue well developed. Legs normal, rough scaled, light brown; tibia

FIGS. 1–4. *Acrapex relicta*. Fig. 1, paratype ♀, Wedge Plantation, McClellanville, South Carolina, 3 June 1978, D. C. Ferguson; Fig. 2, holotype ♂; Fig. 3, paratype ♂ from type locality, 6 June 1971, R. B. Dominick & C. R. Edwards; Fig. 4, paratype ♀ from Dismal Swamp, Virginia, 8–9 June 1974, Don & Mignon Davis. About twice natural size.

short, length about equal to that of first tarsal segment, with length of epiphysis about ⅔ length of tibia. Vestiture of thorax pale brown, with a few interspersed darker scales on patagium and tegula; vestiture of abdomen pale brown, without dorsal tufts. Forewing elongated, outer margin evenly convex, tornal angle rounded, apex rounded; pale brown, with very weak basal, antemedial, medial, and postmedial lines consisting of irregular, incomplete rows of blackish scales; small, black, basal dot present, except in worn specimens; outer margin with distinct, black, terminal line, interrupted at vein endings; discal spot whitish, transversely elongated, preceded near its posterior end by a contrasting blackish spot or short dash that may reappear as a few dark scales on opposite (distal) side; a few light-reddish scales in median area; veins toward middle of subterminal area outlined with black, and their interspaces often with longitudinal reddish- or gray-brown streaks. Overall aspect usually shows a subtle, dark, longitudinal streak from base to outer margin near apex, interrupted just beyond middle by discal spot; fringes pale brown. Hindwing hardly darker than forewing, but gray brown rather than straw colored; fringes nearly concolorous. Underside of forewing suffused with gray brown, of hindwing paler with diffuse discal spot and a diffuse, partial, postmedial band in some specimens; both wings beneath with weak, dark, terminal band, that of forewing broken into spots. Length of forewing: holotype ♂, 8.5 mm; other males (n = 5), 7.5–10.0 mm; females (n = 3), 8.5–10.0 mm.

Male genitalia (Figs. 5, 6). General form distinctive, as illustrated. Juxta with two raised, pointed sclerites, one on each side; ampulla long, slender, produced for half its length beyond costa of valve; articulation between tegumen and vinculum expanded and complex, composed of two slender, somewhat helical, sclerotized loops; transtilla complete, semi-sclerotized. Aedeagus with one large toothlike cornutus on vesica, connected to end of aedeagal tube by a ridged bar of sclerotin bearing 3 or 4 small dentate processes; an unattached, medium-sized cornutus surmounting a small lobe on vesica; and, more distad, a conspicuous longitudinal strip of many closely set cornuti. Eighth segment delicate but with sclerites of characteristic shape in both sternum and tergum that stain red with eosinY.

Female genitalia (Fig. 7). Eighth sternum consisting largely of a sclerotized postostial



FIGS. 5–7. Genitalia of *Acrapex relicta*. Fig. 5, ♂ genitalia of specimen shown in Fig. 3; Fig. 6, aedeagus of same specimen; Fig. 7, ♀ genitalia of paratype from type locality, collected 3 June 1973.

plate of characteristic shape, as illustrated; ostium, ductus bursae, and proximal part of bursa copulatrix also sclerotized, the latter strongly rugose; signum a slender, delicate, straight, longitudinal band on ventral surface of membranous part of corpus bursae; ductus seminalis slender, arising from a sclerotized posterior lobe of corpus bursae to left of ductus bursae; ovipositor lobes massive, sclerotized, acutely conical, with their pointed tips slightly compressed laterally and usually visible without dissection.

Types. Holotype ♂ (Fig. 1), Wedge Plantation, McClellanville, Charleston Co., South Carolina, 2 June 1978, at light, D. C. Ferguson. Paratypes: 1 ♀, same locality and collector, 3 June 1978; 1 ♂, same locality, 6 June 1971, at light, R. B. Dominick and Charles R. Edwards; 3 ♂♂, same locality, 17 June 1971, 31 May 1973, 3 June 1973, R. B. Dominick; 1 ♀, same locality and collector, 3 June 1973; 1 ♂, Cartaret Co., North Carolina, 10 June 1972, J. Bolling Sullivan; 1 ♀, Lake Drummond, Dismal Swamp, Nansemond Co., Virginia, 8–9 June 1974, Don and Mignon Davis. Two other males from the type locality, collected 15 June 1971 and 24 May 1976, and in The Wedge Plantation Collection, Richard B. Dominick Laboratory, University of South Carolina, at McClellanville, were seen by me and are paratypes by definition, although not labeled. The holotype and most paratypes are in the collection of the U.S. National Museum of Natural History. The North Carolina paratype is in the collection of J. B. Sullivan, Beaufort, N.C.

Distribution. Known only from three sites: The Wedge Plantation, on the south bank of the South Santee River, Charleston Co., South Carolina; near Beaufort, Cartaret Co., just south of Cape Hatteras, North Carolina; and the Great Dismal Swamp, near the North Carolina border in southeastern Virginia.

Early stages. Unknown. The larva of the doubtfully congeneric *Acrapex exanimis* (Meyrick) in Hawaii is a stem borer in species of *Panicum*, and the adults deposit egg clusters behind the grass leafsheaths (Zimmerman 1958:325). This would explain the bladelike modification of the ovipositor. It is likely that all species of the genus have similar feeding habits, as indeed is suggested for *A. relicta* by its crambiform appearance and apparent association with grassy, freshwater marshes.

DISCUSSION

Acrapex exanimis, described from Hawaii, was thought by Zimmerman (1958:324) to have been introduced, but it is not known to have been collected elsewhere. Zimmerman considered it closely related to *A. exsanguis* Lower, an Australian species. It is not closely related to the American species, which more nearly resembles *A. azumai* Sugi, from Okinawa. Specimens of *A. azumai* and of other closely related but unidentified species from Taiwan and the Philippines in the U.S. National Museum of Natural History closely resemble *A. relicta* superficially, but their genitalia are different. The females are all much alike in having the same type of rigid, pointed, conical or flattened ovipositor lobes.

I considered the possibility that *Acrapex relicta* might be an African or western Pacific species introduced to America by man, but its seemingly specialized occurrence only in remote, isolated, southeastern habitats inhabited by many other endemics suggests that it is native. It appears to be of Asian affinity and, therefore, is most likely another of the many Miocene relicts showing the East Asian-eastern North American pattern of disjunction typical of the temperate-zone biota of the two regions.

ACKNOWLEDGMENTS

I thank the following for reviewing this paper: G. L. Godfrey, Illinois Natural History Survey, Champaign, Illinois; E. H. Metzler, Columbus, Ohio; A. S. Menke, Systematic Entomology Laboratory, USDA; and especially J. E. Rawlins, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, who checked my conclusions in great detail by examining all of the Old World species of *Acrapex* and many of their relatives in the collections of The Natural History Museum, London, and the Carnegie Museum. A colleague, R. W. Poole, was also the source of helpful information. I am similarly indebted to those who collected and made available additional specimens; namely, J. B. Sullivan, Beaufort, North Carolina; D. R. Davis, National Museum of Natural History, Washington, D. C.; and the late R. B. Dominick of The Wedge Plantation (type locality). I prepared the illustrations.

LITERATURE CITED

COVELL, C. V. 1984. A field guide to the moths of eastern North America. Houghton Mifflin, Boston. 496 pp., 64 pls.

HAMPSON, G. F. 1894. *In* Blandford, W. T. (ed.), The fauna of British India, including Ceylon and Burma. Taylor and Francis, London. Moths, vol. 2:i–xxii, 1–609, figures 1–325.

——— 1910. Catalogue of the Lepidoptera Phalaenae in the British Museum. Trustees of the British Museum, London. Vol. 9:xv + 552 pp., pls. 137–147.

HOLLOWAY, J. D. 1979. A survey of the Lepidoptera, biogeography, and ecology of New Caledonia. W. Junk Publishers, The Hague. xii + 588 pp., 153 figs., 87 pls.

——— 1989. The moths of Borneo, pt. 12, Noctuidae (in part). The Malayan nature Society and Southdene Sdn. Bhd., Kuala Lumpur. 226 pp., 404 figs., 8 col. pls.

INOUE, H., S. SUGI, H. HUROKO, S. MORIUTI & A. KAWABE. 1982. Moths of Japan. Kodansha Company Ltd., Tokyo. Vol. 1: 966 pp.; vol. 2: 552 pp., 392 pls.

JANSE, A. J. T. 1937–39. The moths of South Africa. Vol. 3, Cymatophoridae, Callidulidae, and Noctuidae (partim). Published by the author, Pretoria. 435 pp., illus.

SUGI, S. 1970. The Noctuidae of the Ryukyu Islands. Part 1, Trifidae (Lepidoptera). Tinea 8:213–229, 5 pls.

WALKER, F. 1866. List of the specimens of lepidopterous insects in the collection of the British Museum. Printed by order of the Trustees of the British Museum by Edward Newman, London. 35:1535–2040.

ZIMMERMAN, E. C. 1958. Insects of Hawaii. Vol. 7, Macrolepidoptera. Univ. of Hawaii Press, Honolulu. 542 pp., illus.

Received for publication 18 March 1991; revised and accepted 14 June 1991.

Journal of the Lepidopterists' Society
45(3), 1991, 215–221

OVIPOSITION BY *DANAUS PLEXIPPUS* (NYMPHALIDAE: DANAINAE) ON *ASCLEPIAS VIRIDIS* IN NORTHERN FLORIDA

TONYA VAN HOOK
Department of Entomology and Nematology, University of Florida,
Gainesville, Florida 32601

AND

MYRON P. ZALUCKI
Department of Entomology, The University of Queensland,
Brisbane, Queensland, Australia 4072

ABSTRACT. Female monarch butterflies, *Danaus plexippus* L. (Danainae), remigrating in spring from overwintering sites in Mexico encounter and oviposit on three species of *Asclepias*, *A. humistrata* Walt., *A. asperula capricornu* (Woods.) Woods., and *A. viridis* Walt. (Asclepiadaceae), in the southeastern U.S.A. These plants are relatively high, but quite variable, in gross cardiac glycoside (CG) concentration, both within and among species. We compared CG concentration between plants in a single stand of *A. viridis* with and without immatures (eggs and larvae) of *D. plexippus*. Plants with immatures showed an intermediate CG concentration (280 μg/0.1 g DW), with lower variability (SD = 104, N = 20), than plants without immatures (314 ± 176, N = 10). This study supports previous findings that females oviposit preferentially on plants with intermediate CG content in single species stands. Other studies indicate that it is on these plants that sequestration by larvae of CGs is maximal.

Additional key words: Asclepiadaceae, cardiac glycosides, immature distribution.

Monarch butterflies, *Danaus plexippus* L. (Nymphalidae: Danainae), remigrating from overwintering sites in Mexico in early spring encounter and oviposit on primarily three species of *Asclepias* in the southeastern U.S.A. These species, A. *humistrata*, A. *viridis*, and A. *asperula capricornu*, all have relatively high concentrations of cardenolides, or cardiac glycosides (CG) (Malcolm & Brower 1989).

Monarchs breed in the southeastern United States for one to two generations before high temperatures apparently force them to continue migrating northward (Malcolm et al. 1987, 1991). One consequence of this northward colonization is the use of a larval host, A. *syriaca* L., that is relatively low and variable in CG concentration. Because monarchs sequester CG's, which make them unpalatable to potential predators, they would be better protected if they utilized plants higher in CG's. Thus butterflies feeding as larvae on A. *syriaca* may be relatively palatable (Malcolm et al. 1988).

The relationship between female oviposition site selection to the CG content of the larval food plant is unclear (see Oyeyele & Zalucki 1990, for a review). Brower (1961) found more monarch immatures on A. *humistrata*, which is high in CG content, than on A. *tuberosa rolfsii*

(Britton) Woodson, which is very low in CG content, at a site where the two plant species co-occur. However, direct observation of ovipositing monarchs in two very different populations (on *A. fruticosa* L. in Australia and *A. humistrata* in northern Florida) showed that females selected plants of intermediate CG concentration (Oyeyele & Zalucki 1990, Zalucki et al. 1990). In both studies females showed post-alighting discrimination against plants with very low and those with very high CG concentrations.

In this study, we examined the distribution of immature monarchs on another species of milkweed, *A. viridis*. We analyzed the CG concentration of plants with and without immature monarchs to determine whether females were discriminating among plants based on their CG concentration.

MATERIALS AND METHODS

We sampled 30 *A. viridis* plants in a limestone outcropping adjacent to a quarry near Williston, Levy Co. (29°25′N, 82°28′W), in north central Florida on 16 April 1987. All plants were within 20 m of each other, on the northern, eastern, and southern margins of an old quarry. All plants stood out from a low undergrowth of grasses. The stems of all plants sampled were counted, their heights measured and averaged, and each plant's phenological stage was classified using a 3 point scale as flowering (=3), with immature flower buds (=2), not yet flowering (=1). All monarch eggs and larvae were counted and their location on the plants noted. Leaf samples from the same position on all plants (third leaf pair from the top of the northern most stem), were placed in separate labelled bags for CG analysis. We attempted to obtain equal numbers of plants in three categories: (1) without immature monarchs, (2) with eggs only, and (3) with eggs and larvae. We took flower material and leaf material for comparative CG analysis from 4 plants that were in flower and had eggs on them. All plant material was dried for 16 h at 60°C in a forced draft oven and stored in labelled envelopes inside a desiccator until processing. Cardiac glycoside determinations were done within two weeks of collection using a standard spectrophotometric technique (Brower et al. 1975, 1984).

RESULTS AND DISCUSSION

Mean plant phenological stage, size, number of monarch immatures, and cardiac glycoside concentrations are listed in Table 1 for plants in 3 categories: without monarchs, with eggs only, and with eggs and larvae. All but 2 of 31 plants were either flowering (n = 14) or with buds (n = 15). The average plant phenological stage (using a 3 point scale for stage categories) was similar in plants without and with mon-

TABLE 1. Summary of observations made on *Asclepias viridis* at Williston, Florida, showing mean phenological stage (see text for details), size (average height, multiplied by the number of stems), eggs and larvae per plant, and plant CG concentration. Plants have been grouped as without immature monarchs, with eggs only, and with eggs and larvae. (Values in brackets are standard deviations.)

Parameter	Plant monarch status		
	Without monarchs	Eggs only	Eggs & larvae
N	11*	9	11
Phenological stage	2.2 [0.75]	2.8 [0.44]	2.8 [0.40]
Size (cm)	73 [42.6]	255 [150.7]	257 [201.3]
Eggs	—	1.2	1.8
Larvae	—	—	2.7
CG concentration (μg/0.1 g DW)	314 [176]	265 [127]	294 [86]

* One plant sample lost for CG analysis.

archs (Table 1). Plants with eggs only, and those with eggs and larvae, did not differ in size (Table 1), but those without eggs were markedly smaller than the rest ($P < 0.05$, t-test). Among plants with eggs only, eggs were distributed evenly; 7 plants had 1 egg each and 2 had 2 eggs. Plants with eggs and larvae had the following dispersion: one plant had 9 eggs and 4 larvae, another had 1 egg and 8 larvae. The remaining plants had (in sampling order): 0, 3, 0, 0, 2, 0, 1, 0, and 2 eggs, and a corresponding larval distribution of: 1, 1, 1, 1, 3, 1, 3, 2, 2. Larvae ranged in age from first (I) to third (III) instar with the following age distribution: 6I, 13II, and 8III.

There was a strong correlation between eggs, larvae, and total immatures per plant and plant size ($r = 0.73$, 0.45, and 0.71, $N = 30$, $P < 0.05$, respectively). There was no relationship between plant size (number of stems multiplied by the average height) and CG concentration ($r = 0.14$, $P > 0.05$). These results are very similar to those obtained by Cohen and Brower (1982) for a small sample ($N = 9$) of *A. humistrata*. However, it is difficult to infer a relationship between oviposition and larval food plant CG levels based on the pattern of distribution of immatures in the absence of direct observations of oviposition (Zalucki et al. 1989).

Based on observational data, Oyeyele and Zalucki (1990) and Zalucki et al. (1990) found that females were more likely to lay eggs on plants of intermediate CG concentration and reject lower and higher CG concentration plants. Therefore we predict that the CG frequency distribution of plants with immatures should have a smaller variance than plants without immatures. In making this prediction we are assuming that: (1) CG levels do not change rapidly in response to larval feeding, and (2) that all plants without immatures could have been sampled by adults. The latter seems reasonable as all plants were exposed, relatively

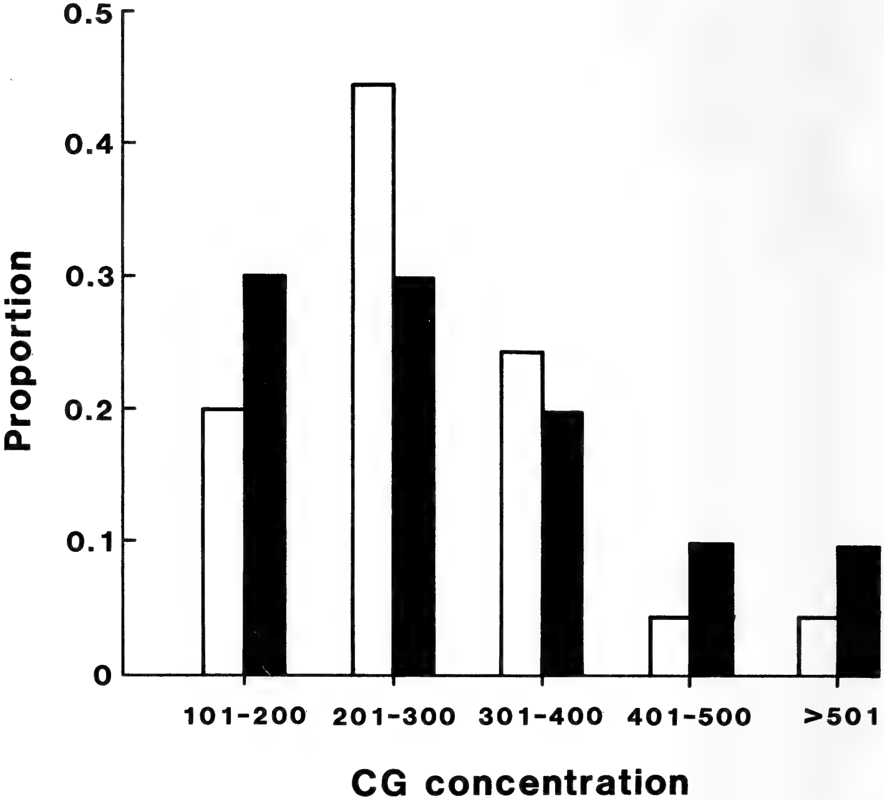


FIG. 1. Distribution of plant cardiac glycosides expressed as ranges of CG concentration (μg/0.1 g DW), in plants without (solid bars) and with (open) immature monarchs ($\bar{x}$ without = 314; $\bar{x}$ with = 280 μg/0.1 g DW).

close to each other (ca. 0.5 to 1.5 m apart), and our sampling included virtually all (ca. 80%) of the plants in the area.

Although the mean cardenolide content was lower in plants with eggs and immatures than those without (Table 1), the differences were not significant ($P > 0.05$). However, the distribution of CG concentration among plants with immatures was less variable than among plants without (F ratio test, $F_{10,20} = 2.863$, $P < 0.05$).

The frequency distribution of CG's in plants with immatures is contained within the distribution of plants without immatures (Fig. 1), with most immatures (70%) being found on plants with CG concentrations in the range 201–400 μg/0.1 g dry weight (DW). This supports findings by Oyeyle and Zalucki (1990) and Zalucki et al. (1989, 1990) that females select plants of intermediate levels of CG concentration for oviposition.

TABLE 2. Cardiac glycoside (CG) concentrations (μg/0.1 g DW) recorded in *Ascelpias viridis* by various authors.

Location	CG concentration				Reference
	N	$\bar{x}$	SD	Range	
Florida	7	478	136	316–676	Malcolm and Brower 1986
Florida	18	376	203	148–972	Malcolm and Brower 1989
Louisiana	60	245	70	95–432	Lynch and Martin 1987
Florida	30	292	130	106–730	This study

Many eggs (19 out of 29) were found on the inflorescenses of *A. viridis*. We measured CG concentration in leaves and inflorescenses from the same plant. For 4 plants with immatures the inflorescenses had an average CG level of only 42% of the leaf sample readings. The CG values (in μg/0.1 g DW) for leaf vs. flower samples for each plant were: 332 vs. 116, 206 vs. 16, 106 vs. 88, and 159 vs. 67. This suggests that monarchs are ovipositing on plant parts with a lower CG concentration. Similar observations were made on *A. linaria* Cav. in Mexico, a very high CG plant (1400 μg/0.1 g DW); immatures were found on plants, and on plant parts (including inflorescenses), with the lowest CG concentrations (L. P. Brower & M. P. Zalucki, unpubl. data). However, it should be noted that the inflorescences of *A. viridis* are also much softer than the leaves, and females may be assessing the 'quality' of plant parts on the basis of texture rather than on CG concentration.

Our results for CG concentration in *A. viridis* are within the range of those published by Lynch and Martin (1987) and Malcolm and Brower (1986, 1989) (Table 2). Although *A. viridis* is generally a high CG plant, the range in CG concentration (95–972 μg/0.1 g DW) is considerable (Table 2). Such variation could be due to many factors, including plant part sampled, seasonal effects, and method of CG determination between labs. Because we sampled leaves from the same position on each plant, differences between plants presumably must be due to differences primarily in genotype, age, phenological stage, and localized soil and moisture conditions. Our results indicate that the pattern of occurrence of immature monarchs on *A. viridis* plants is similar to those found in more extensive studies on other milkweed species (Oyeyele & Zalucki 1990, Zalucki et al. 1989, 1990). Namely, plants in the intermediate CG concentration category are more likely to support monarchs than are plants with either very low or very high CG concentrations.

The plants on which immatures are found have CG concentrations at which sequestration is maximal and the resultant adults have the highest CG level obtainable, given the logarithmic relationship between plant CG and the adult CG level (Malcolm & Brower 1989, Nelson 1991). To demonstrate an oviposition preference based on CG concentration, further work on *A. viridis* is needed, in which ovipositing females are followed and plants accepted and rejected are assayed for CG concentration.

ACKNOWLEDGMENTS

We thank Lincoln Brower for providing facilities and for constructive comments on the manuscript, Steve Malcolm for his encouragement, and Jocelyn Campbell for typing. This research was supported by NSF grant # BSR-8500416, with L. P. Brower as Principal Investigator. M. P. Zalucki was on study leave from the University of Queensland.

LITERATURE CITED

BROWER, L. P. 1961. Studies on the migration of the monarch butterfly I. Breeding populations of *Danaus plexippus* and *D. gilippus berenice* in south central Florida. Ecology 43:549–552.

BROWER, L. P., M. EDMONDS & C. M. MOFFITT. 1975. Cardenolide content and palatability of a population of *Danaus chrysippus* butterflies from West Africa. J. Entomol. 49:183–196.

BROWER, L. P., J. N. SEIBER, C. J. NELSON, S. P. LYNCH, M. P. HOGARD & J. A. COHEN. 1984. Plant determined variation in cardenolide content and thin-layer chromatography profiles of monarch butterflies, *Danaus plexippus* reared on milkweed plants in California, 3: *Asclepias californica*. J. Chem. Ecol. 10:1823–1857.

COHEN, J. A. & L. P. BROWER. 1982. Oviposition and larval success of wild monarch butterflies (Lepidoptera: Danaidae) in relation to host plant size and cardenolide concentration. J. Kans. Entomol. Soc. 55:343–348.

LYNCH, S. P. & R. A. MARTIN. 1987. Cardenolide content and thin-layer chromatography profiles of monarch butterflies, *Danaus plexippus* L., and their larval host-plant milkweed, *Asclepias viridis* Walt., in northwestern Louisiana. J. Chem. Ecol. 13:47–70.

MALCOLM, S. B. & L. P. BROWER. 1986. Selective oviposition by monarch butterflies *Danaus plexippus* L. in a mixed stand of clepias curassavica L. and *A. incarnata* L. in South Florida. J. Lepid. Soc. 40:255–263.

MALCOLM S. B. & L. P. BROWER. 1989. Evolutionary and ecological implications of cardenolide sequestration in the monarch butterfly. Experientia 45:284–295.

MALCOLM, S. B., B. J. COCKRELL & L. P. BROWER. 1987. Monarch butterfly voltinism; effects of temperature constraints at different latitudes. Oikos 49:77–82.

MALCOLM, S. B., B. J. COCKRELL & L. P. BROWER. 1988. Cardenolide fingerprint of monarch butterflies reared on common milkweed, *Asclepias syriaca* L. J. Chem. Ecol. 15:819–853.

MALCOLM, S. B., B. J. COCKRELL & L. P. BROWER. 1991. Spring recolonization of eastern North America by the monarch butterfly: successive brood or single sweep migration? *In* Malcolm, S. B., and M. P. Zalucki (eds.), The biology and conservation of the monarch butterfly. Natural History Museum of Los Angeles County, Contributions in Science, *in press*.

NELSON, C. 1991. A model for cardenolide and cardenolide glycoside storage by the monarch butterfly *Danaus plexippus* (L.). *In* Malcolm, S. B., and M. P. Zalucki (eds.), The biology and conservation of the monarch butterfly. Natural History Museum of Los Angeles County, Contributions in Science, *in press*.

OYEYELE, S. V. & M. P. ZALUCKI. 1990. Cardiac glycosides and oviposition by *Danaus plexippus* on *Asclepias fruticosa* in south-east Queensland (Australia), with notes on the effect of plant nitrogen content. Ecol. Entomol. 15:177–185.

ZALUCKI, M. P., OYEYELE, S. V. & P. VOWLES. 1989. Selective oviposition by *Danaus plexippus* (L.) (Lepidoptera: Nymphalidae) in a mixed stand of *Asclepias fruticosa* and *A. curassavica* in Southeast Queensland. J. Aust. Entomol. Soc. 28:141–146.
ZALUCKI, M. P., L. P. BROWER & S. B. MALCOLM. 1990. Oviposition by *Danaus plexippus* in relation to cardenolide content of three *Asclepias* species in the south-eastern U.S.A. Ecol. Entomol. 15:231–240.

Received for publication 17 July 1990; revised and accepted 17 July 1991.

PROFILES

Journal of the Lepidopterists' Society
45(3), 1991, 222–225

THE CLARKE/SHEPPARD/TURNER GENETIC COLLECTION OF BUTTERFLIES AT THE NATURAL HISTORY MUSEUM, LONDON

Additional key words: *Papilio, Hypolimnas, Heliconius,* mimicry.

This collection consists of 132 drawers of specimens from the investigations of genetics of Lepidoptera that the late P. M. Sheppard and I started about 40 years ago. This work deals with the genetics of a number of species and of particular importance has been a study of mimicry in swallowtail butterflies. In 1982, the collection was accepted for permanent storage by the British Museum (Natural History), now called the Natural History Museum. The collection is active, as my colleagues and I continue to expand on four decades of genetic research.

The butterflies in the drawers (ca. 5000 specimens total) are those paired in genetic crosses and their progeny. With them are explanations of the experiments, and locality maps. Alongside the cabinets are bound copies of the relevant reprints of papers published on these experiments. Also accompanying the collection is the early correspondence between P. M. Sheppard and me when the work was begun in the 1950s. To guide those interested in studying the collection, I have prepared a descriptive catalog: *Guide to the Clarke/Sheppard/Turner Genetic Collection of Butterflies*. Originally written in 1982, it was updated in 1987 (after J. R. G. Turner joined as collaborator in 1986), and most recently in October 1990 (3rd Updating). The *Guide* briefly describes the history of the collection and summarizes the experiments, by species, in chronological order. The *Guide* also contains a glossary of 40 genetic terms and an Appendix that discusses special aspects of genetic work on three moth species. A visitors' record book completes the collection.

SUMMARY OF THE COLLECTION

The sequence of the following list of species studied roughly corresponds to the order in which we did the work. There are approximately 40 specimens in each of the 132 drawers.

Main Collection: Butterflies

***Papilio machaon* group:** 6 drawers (#1–6); 21 reprints (1952–86). Includes *P. machaon, P. polyxenes* (*asterias*), *P. machaon lapponicus,* *P. brevicauda, P. hospiton, P. m. saharae, P. m. hippocrates, P. maackii, P. zelicaon,* and *P. rudkini.*

***Papilio glaucus* group and its close relatives:** 9 drawers (#7–15); 12 reprints (1955–91). Includes *P. glaucus, P. rutulus, P. eurymedon,* and *P. multicaudatus.*

***Papilio polytes* and its mimicry:** 11 drawers (#16–26); 2 reprints (1972). Includes hybrids with other species.

***Papilio dardanus* and its mimicry:** 32 drawers (#27–59); 21 reprints (1936–91). Includes relationships to *P. demodocus, P. constantinus, P. phorcas,* and *P. humbloti.*

Papilio aegeus: 2 drawers (#61–62); 1 reprint (1985).

Hypolimnas bolina: 18 drawers (#63–80); 7 reprints (1975–89). Includes its status as a mimic and all female broods.

***Papilio memnon* and its mimicry:** 44 drawers (#81–124); 9 reprints (1967–82).

Chilasa clytia: partial drawer (#125); 1 reprint (1967). Genetics of the two mimetic forms of the Sri Lankan subspecies *lankeswara.*

Danaus plexippus: partial drawer (#125); 1 reprint (1980). Genetics of a new mutant.

Danaus chrysippus: 1 drawer (#126); 1 reprint (1973). Genetics of crosses from Australia and Sierra Leone.

Appendix: Moths

Biston betularia: 2 drawers (#127–128); 6 reprints (1976–90). A 29-year study of the frequency of form *carbonaria* in the Wirral.

Lymantria dispar: 3 drawers (#129–131); 7 reprints (1980–91). A reassessment (with E. B. Ford) of the work of Goldschmidt; with suggestions regarding pest control in the USA.

Panaxia dominula: 1 drawer (#132); 2 reprints (1990–91). Samples from the rediscovered colony on the Wirral Way.

A BRIEF HISTORY OF THE COLLECTION

In 1946, after the war, where I had spent in Australia the last of my six years in the Navy, my boyhood interest in breeding butterflies was reawakened, and I discovered the technique of hand-mating swallowtail butterflies, and thereby was able to breed *Papilio machaon.* In this species I first studied the brown/green pupal coloration in collaboration (by post) with Dr. J. P. Knudsen of Oglethorpe University, Georgia. In September 1952 he sent me some pupae of the black American Swallowtail *Papilio polyxenes* (*asterias*) and on 4 October I was successful in hand-mating a female to a *P. machaon* male, from Malta (*P. machaon gorganus*) and this led to the publication of our first paper "A hybrid swallowtail" (Clarke, C. A. & J. P. Knudsen 1953, *Entomologist's Record and Journal of Variation* 65:76–80).

In October 1952 I was lucky enough to get in touch with a young (age 32) geneticist, Dr. P. M. Sheppard, who was working in E. B. Ford's department at the University of Oxford. He advertised for pupae of *machaon*, and in the early correspondence with him I mentioned that I had larvae of *polyxenes* × *machaon* cross, and sent him some eggs. He was keenly interested, and we arranged to meet at the Mitre Hotel in Oxford on 7 December 1952. This early correspondence with Philip Sheppard is with the collection.

We soon turned our attention to the study of mimicry in *Papilio glaucus* and *Papilio dardanus* and kept in touch over the breeding work, which was done at my home near Liverpool. In 1956 Philip came to Liverpool as senior lecturer in genetics (later becoming professor) and subsequently we worked together both on butterflies and on Man until his death in 1976. The story of the research is outlined in the biographical memoir (1977) I wrote for him for the Royal Society, of which copies are both with the letters and with our joint reprints (Sir Cyril Clarke 1977, Philip Macdonald Sheppard 1921–1976, *Biographical Memoirs of Fellows of the Royal Society* 23:465–499).

In 1974, two years before he died, Philip was awarded the Royal Society's Darwin Medal. This is given biennially for work of acknowledged distinction in the broad area of biology in which Charles Darwin worked, notably in evolution and population biology. Sixteen years later (1990) I was awarded the Royal Society's Buchanan medal "in recognition of distinguished original research in the broad area of medical sciences". In my case this was in the prevention of Rh haemolytic disease of the newborn, and arose from a study of butterfly genetics, particularly of *Papilio memnon*.

In 1986 Dr. John R. G. Turner, then aged 45, and Reader in Evolutionary Genetics at Leeds University (later, 1987, Professor) agreed to collaborate in the running and future care of the collection, which is now known as the *Clarke/Sheppard/Turner Genetic Collection of Butterflies*. John, with his knowledge of butterfly genetics, his Liverpool background, and his training by E. B. Ford, was an admirable choice for continuing the important genetic experiments documented by this collection. It is our intention that, over the next few years, the three and a half thousand *Heliconius* (chiefly *melpomene* and *erato*) bred by Sheppard and Turner, in collaboration with K. S. Brown Jr., W. W. Benson, and others, will be added to the collection.

Much of the work documented by the collection was made possible by generous grants from the Nuffield Foundation to the University of Liverpool, where most of the breeding was done. Transfer of the col-

lection to the Natural History Museum in 1982 (then called the BMNH) was supported by an Emeritus Fellowship from the Leverhulme Trust to Sir Cyril Clarke.

USE OF THE COLLECTION

The collection can be visited by application to Mr. R. I. Vane-Wright (direct line 071 938 9341) or Mr. Phillip Ackery (direct line 071 938 9346) both in the Department of Entomology at the Natural History Museum, and I am often in London and could probably meet anyone interested there (home telephone 051 625 8811). Mrs. Alison Gill goes to the NHM frequently to act as curator of this collection; she can be reached at her address: Tideway, The Warren, Mapledurham, Near Reading, RG4 7TQ (telephone 0734 479 126). A limited number of copies of the *Guide* are available to interested researchers in exchange for postage.

SIR CYRIL A. CLARKE, *KBE, FRS, President, Royal Entomological Society of London, and Emeritus Professor of Medicine and Honorary Nuffield Senior Research Fellow, Department of Genetics and Microbiology, University of Liverpool L69 3BX, England.*

Received for publication 9 January 1991; revised and accepted 8 July 1991.

GENERAL NOTES

Journal of the Lepidopterists' Society
45(3), 1991, 226–231

CATOCALA (NOCTUIDAE) TAKEN AT SHENANDOAH NATIONAL PARK, VIRGINIA,WITH COMPARATIVE NOTES ON ADULT FLIGHT PHENOLOGIES IN EASTERN NORTH AMERICA

Additional key words: light trap, collecting methods, Lepidoptera.

In this paper we provide an initial list of *Catocala* species captured in light traps at Shenandoah National Park, Page County, Virginia, and compare our results with those published recently for New England (Sargent, T. D. 1977, J. Lepid. Soc. 31:1–16) and Tennessee (Miller, W. A. 1977, J. Lepid. Soc. 31:197–202). We also compare these trap records to historical sampling data from several other sites in eastern North America, and test the conventional wisdom that different *Catocala* species fly in a largely predictable sequence throughout the summer, irrespective of where one collects.

Our *Catocala* records are drawn from 1989 light trap surveys for Lepidoptera in Shenandoah National Park, which were undertaken to monitor the impact on non-target insects of aerially applied *Bacillus thuringiensis* (*Bt*). Nine portable light traps ("General Purpose Black Light Trap" of O. B. Enterprises, Oregon, Wisconsin) were used to capture adult insects in both *Bt* and untreated sites within Shenandoah National Park. Each trap was outfitted with a 15-watt fluorescent black light bulb and powered by a 12-volt gel-cell battery. A custom designed solar switch activated each trap system at dusk and turned it off at dawn. A combination of ethyl acetate and DDVP (*Vapona* strips) was used to kill trapped insects. Labelling of specimens was done in the field, and the material was stored frozen for subsequent sorting, identification, and counting. Each trap was usually (but not always) operated only one night per week during the period 12 May to 3 October 1989, with insects being removed from the traps as early as possible on the following morning. All traps were spaced at least 200 m apart, and insofar as possible were placed in sites with similar aspect (facing northwest) and elevation (ca. 1000 m). Full details of the spraying and trapping regimes as they relate to the *Bt* work will be presented elsewhere.

Table 1 lists the *Catocala* captured in all nine traps, by species and week of sampling. A total of 1034 individuals was collected, representing 23 species. The earliest capture date was 26 June, and the last date was 2 October. As is usually the case with *Catocala* light trap samples (see Sargent, T. D. 1976, *Legion of Night*, Univ. Mass. Press, Amherst, Massachusetts, 222 pp.), only a few species comprised the majority of our captures, with over two-thirds of all specimens being *C. cerogama* Gueneé, *ilia* Cramer, *palaeogama* Gueneé, and *lineella* Grote (see Gall, L. F. 1989, Psyche 97:121–129 for re-elevation of *lineella* to species rank, and other taxonomic decisions regarding the "*amica* Hübner complex").

The total of 23 *Catocala* species for 1989 at Shenandoah is similar to yearly totals recorded at light traps in New England: between 26–35 species in Washington, Litchfield County, Connecticut, during the period 1961–1973; 29–30 species in West Hatfield, Hampshire County, Massachusetts, 1969–1973; and 24–30 species in Leverett, Franklin County, Massachusetts, 1970–1973 (see appendices in Sargent 1976, *op. cit.*). Miller (1977, *op. cit.*) did not present yearly totals for Celina, Clay County, Tennessee, but 41 was his cumulative species total for the period 1970–1976 at that locality. For the New England localities, the cumulative species totals were 39, 37, and 33, respectively, and it seems certain from these comparative data and field experience in Virginia (including knowledge of available local *Catocala* larval foodplants) that the cumulative species total for Shenandoah National Park can be expected to eventually exceed 30.

At Shenandoah, different *Catocala* species clearly flew at different times of the year, and for all species but *cerogama* the two sexes seemed to have similar flight seasons (the

①

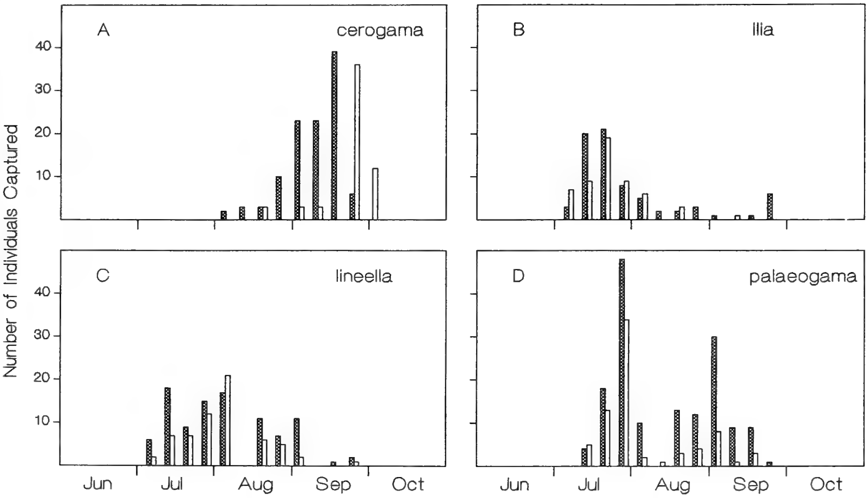


Fig. 1. Seasonal abundance profiles for the four most common *Catocala* listed in Table 1. Hatched bars, males; open bars, females.

②

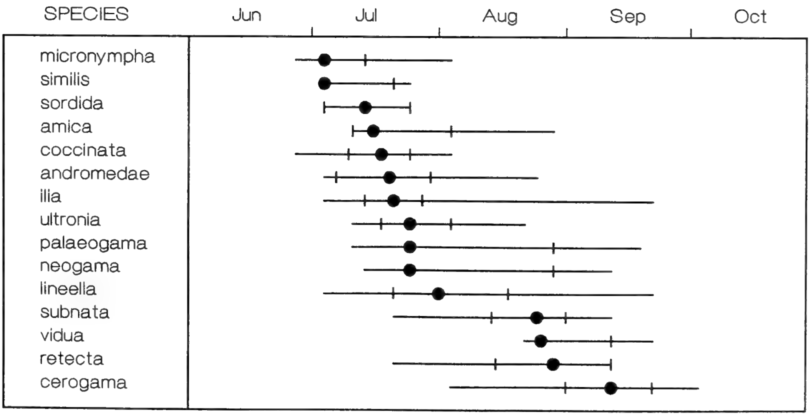


Fig. 2. Seasonal occurence of *Catocala* listed in Table 1 having 10 or more total captures. Ends of horizontal lines represent first and last capture dates; vertical hatch marks, first and third quartiles; solid circles, median capture dates. Species ordered vertically by increasing median capture date. Modeled after Fig. 4 of Sargent (1977). See text for discussion and statistical analysis.

TABLE 1. *Catocala* species collected in Shenandoah National Park, Page County, Virginia at UV light traps during 1989.

Catocala species	26 Jun thru 02 Jul	03 Jul thru 09 Jul	10 Jul thru 16 Jul	17 Jul thru 23 Jul	24 Jul thru 30 Jul	31 Jul thru 06 Aug	07 Aug thru 13 Aug
amica Hbn.	0	0	7	1	2	2	0
andromedae Gn.	0	7	4	3	4	5	0
blandula Hlst.	0	2	0	1	4	0	0
cara Gn.	0	0	0	1	0	0	0
cerogama Gn.	0	0	0	0	0	2	3
coccinata Grt.	1	25	12	15	15	11	0
epione Dru.	0	0	2	1	1	1	0
flebilis Grt.	0	0	0	0	0	0	0
ilia Cram.	0	10	29	40	17	11	2
judith Stkr.	0	0	0	0	0	1	0
lacrymosa Gn.	0	0	0	0	0	0	0
lineella Grt.	0	8	25	16	27	38	0
micronympha Gn.	3	48	7	5	11	2	0
nebulosa Edw.	0	0	0	0	1	0	0
neogama J. E. Sm.	0	0	1	0	6	0	0
palaeogama Gn.	0	0	9	31	82	12	1
relicta Wlkr.	0	0	0	0	0	0	0
retecta Grt.	0	0	0	1	0	1	0
similis Edw.	0	7	0	3	1	0	0
sordida Grt.	0	4	4	0	3	0	0
subnata Edw.	0	0	0	1	4	3	2
ultronia Hbn.	0	0	2	6	6	3	0
vidua J. E. Sm.	0	0	0	0	0	0	0
Totals	4	111	102	125	184	92	8

cerogama males were captured earlier than the females); these patterns can be seen in the seasonal histograms for the four most common species (Fig. 1a–d). To quantify these trends, an analysis of variance (ANOVA) was performed with date of capture as the dependent variable and sex and species as independent, using those species from Table 1 for which both males and females were captured. The ANOVA revealed a significant species effect ($F = 86.24$, df = 17/992, $P < 0.01$), a non-significant sex effect ($F = 0.91$, df = 1/992, $P = 0.34$), and a significant sex by species interaction ($F = 2.84$, df = 17/992, $P < 0.01$), with that interaction being traceable to *cerogama* ($F = 0.77$, df = 16/807, $P = 0.72$ without it).

Fig. 2 presents flight phenologies at Shenandoah National Park in 1989 for the 15 *Catocala* species having 10 or more captures, with species ordered vertically by increasing median capture date. Our Fig. 2 is modeled after Fig. 4 of Sargent (1977, *op. cit.*), which shows the same information for 30 *Catocala* species at Washington, Connecticut.

Miller (1977, *op. cit.*) did not present median capture dates for Celina, Tennessee, but the dates of his first captures are available for comparisons with the Shenandoah and Washington data. In addition, dates of first captures are given in the literature for: the 1877–1881 seasons at Frankford, Philadelphia County, Pennsylvania (Johnson, J. S. 1882, Can. Entomol. 14:59–60); the 1877 season at Centre, Albany County, New York (Bailey, J. S. 1877, Can. Entomol. 9:215–218); and the 1911–1913 seasons at Louisiana, Pike County, Missouri (Rowley, R. R. & L. Berry 1914, Entomol. News 25:157–167). Table 2 presents the first and median capture dates at all six localities, when determinable, for the 34 species that are present at two or more localities. All available species are used from the Frankford and Louisiana lists (where total captures are not stated), whereas

TABLE 1. Continued.

14 Aug thru 20 Aug	21 Aug thru 27 Aug	28 Aug thru 03 Sep	04 Sep thru 10 Sep	11 Sep thru 17 Sep	18 Sep thru 24 Sep	25 Sep thru 01 Oct	02 Oct thru 08 Oct	Totals
0	0	2	0	0	0	0	0	14
0	1	0	0	0	0	0	0	24
0	0	0	0	0	0	0	0	7
0	0	0	0	0	0	0	0	1
6	10	26	26	39	42	12	21	187
0	0	0	0	0	0	0	0	79
1	1	0	0	0	0	0	0	7
0	1	1	0	1	0	0	0	3
5	3	1	1	1	6	0	0	126
0	0	0	0	0	0	0	0	1
0	0	0	0	0	1	0	0	1
17	12	13	0	1	3	0	0	160
0	0	0	0	0	0	0	0	76
0	0	0	0	1	0	0	0	2
1	0	2	0	2	0	0	0	12
16	16	38	10	12	1	0	0	228
0	0	0	0	1	0	0	0	1
1	2	3	0	3	0	0	0	11
0	0	0	0	0	0	0	0	11
0	0	0	0	0	0	0	0	11
2	12	8	5	3	0	0	0	40
4	1	0	0	0	0	0	0	22
0	6	0	1	1	2	0	0	10
53	65	94	43	65	55	12	21	1034

only those species having 10 or more total captures are used from the other four localities. Because *amica* was distinguished from *lineella* only at Shenandoah National Park, these two species are omitted from Table 2.

Distinctive species-specific patterns of adult seasonality are evident in Table 2, and these patterns appear to be geographically consistent, despite differences in the overall timing of *Catocala* flight from locality to locality. For example, in the three recent samples, *micronympha* Gueneé flies earlier than *andromedae* Gueneé, which in turn flies earlier than *retecta* Grote—and all capture dates for these three species are earliest at Celina, intermediate at Shenandoah National Park, and latest at Washington.

In order to quantify these geographical similarities in flight phenologies, the data in Table 2 were treated as nine column vectors, and these were tested against one another for association using Spearman rank correlation. Each of the 36 possible comparisons among the nine vectors yielded a positive rank correlation—the values ranging from $r = +0.50$ through $r = +0.96$, with 32 of 36 being significantly positive ($P < 0.01$ for twenty two, $P < 0.05$ for ten). This clearly establishes that the order in which different *Catocala* species fly during the season is consistent at all six localities.

Note that light trapping was the sole collecting method used at Shenandoah National Park and Washington; artificial bait was the only method at Centre; "tree tapping" was used exclusively at Frankford and Louisiana; and a combination of light, bait, and tapping was used at Celina. Artifical bait is known to attract certain species of *Catocala* better than others (e.g., Kellogg, C. & T. D. Sargent 1972, J. Lepid. Soc. 26:35–49), and there is also some indication that phenologies derived from bait captures may at times differ from phenologies derived from other collecting methods (unpublished field data of L. F.

TABLE 2. Dates of first and median capture for 34 *Catocala* species collected in Washington, Litchfield County, Connecticut (CT, data from Sargent 1976); Shenandoah National Park, Page County, Virginia (VA, data from present paper); Centre, Albany County, New York (NY, data from Bailey 1877); Celina, Clay County, Tennessee (TN, data from Miller 1977); Frankford, Philadelphia County, Pennsylvania (PA, data from Johnson 1882); and Louisiana, Pike County, Missouri (MO, data from Rowley & Berry 1914). Species ordered vertically by increasing first capture date at Washington, Connecticut (when possible). See text for discussion and statistical analysis.

	Earliest capture date						Median capture date		
Catocala species	CT	VA	NY	TN	PA	MO	CT	VA	NY
blandula Hlst.	7/05	—	7/07	—	—	6/21	7/13	—	7/19
micronympha Gn.	7/05	6/26	7/20	6/22	—	—	7/20	7/03	7/25
coccinata Gr.	7/06	6/26	—	—	—	6/28	7/18	7/17	—
andromedae Gn.	7/08	7/03	—	6/23	—	—	8/02	7/19	—
unijuga Wlkr.	7/08	—	7/07	—	—	—	8/22	—	8/07
epione Dr.	7/09	—	7/09	6/21	7/10	6/21	8/02	—	7/24
ilia Cram.	7/10	7/03	7/07	6/20	7/01	6/20	8/17	7/20	7/20
antinympha Hb.	7/11	—	7/11	—	—	—	8/02	—	—
ultronia Hb.	7/11	7/10	7/11	6/23	7/08	6/21	8/04	7/24	7/23
grynea Cram.	7/12	—	7/17	—	7/01	7/13	8/06	—	7/23
praeclara Gr. & Rob.	7/13	—	7/12	—	—	—	8/02	—	7/30
palaeogama Gn.	7/16	7/10	7/20	7/05	7/11	7/03	8/02	7/24	8/10
concumbens Wlkr.	7/19	—	7/14	—	—	—	8/25	—	—
dejecta Stkr.	7/19	—	—	6/24	—	6/28	8/03	—	—
serena Edw.	7/19	—	—	—	7/11	—	8/11	—	—
judith Stkr.	7/21	—	—	6/25	7/09	—	8/03	—	—
residua Gr.	7/25	—	7/25	7/04	—	7/06	8/19	—	8/07
subnata Gr.	7/26	7/20	—	7/05	7/14	—	8/10	8/24	—
parta Gn.	7/29	—	—	—	7/21	6/28	9/12	—	—
retecta Gr.	7/30	7/20	7/30	7/05	7/19	—	9/02	8/28	8/29
neogama J. E. Sm.	7/31	7/13	—	7/05	7/10	7/06	9/06	7/24	—
insolabilis Gn.	—	—	—	7/04	7/08	7/05	—	—	—
cerogama Gn.	—	8/03	7/25	7/04	8/08	7/19	—	9/11	—
nebulosa Edw.	—	—	—	7/05	—	7/05	—	—	—
lacrymosa Gn.	—	—	—	7/16	—	7/13	—	—	—
piatrix Gr.	—	—	—	—	8/10	8/07	—	—	—
flebilis Gr.	8/02	—	—	7/05	7/26	8/02	8/27	—	—
obscura Stkr.	8/08	—	—	7/04	7/10	—	9/06	—	—
cara Gn.	8/10	—	7/31	—	8/06	7/12	9/13	—	8/10
habilis Gr.	8/11	—	7/30	7/31	7/25	7/19	9/14	—	8/16
angusi Gr.	—	—	—	7/31	—	7/29	—	—	—
amatrix Hb.	—	—	—	—	8/09	7/28	—	—	—
vidua J. E. Sm.	—	8/21	8/18	8/01	8/09	7/31	—	8/25	8/19
robinsoni Gr.	—	—	—	—	8/10	8/16	—	—	—

Gall and D. F. Schweitzer). An attempt was therefore made to modify the Celina phenologies to reflect largely the results of light trapping and tree tapping, by deleting six species for which bait accounted for more than half of all captures (*cerogama, ilia, obscura* Strecker, *residua* Grote, *retecta*, and *vidua* J. E. Smith), and repeating the analyses. Because the correlations involving Celina remained significant upon retesting ($r = +0.62$ to $r = +0.83$, $P < 0.05$ for all), the bait and light/tapping phenologies at Celina appear not to have differed appreciably.

These results corroborate the conventional wisdom relied upon by *Catocala* collectors for years—namely, that relative adult flight periods for different species are predictable, irrespective of regional differences in the overall timing of *Catocala* flight. It is especially noteworthy that the phenological correlations hold across six geographically distant localities that have only partially overlapping assemblages of *Catocala* species and their larval foodplants. In light of the considerable research on *Catocala* adult and larval communities conducted primarily in New England (see Sargent 1976, *op. cit.*; Gall, L. F. 1987, Oikos 49:172–176, and 1991a–c, J. Res. Lepid. 29, *in press*), this consistency in phenologies suggests that a number of the ecological paradigms drawn from the New England work will be applicable to *Catocala* faunas elsewhere in deciduous forests of eastern North America.

Light trap sampling in 1989 was conducted under permit number NRSP-N-121 to JWP from the Shenandoah National Park, and we thank Richard Potts and David Haskell for help in securing the research permit, and for continued technical and administrative assistance at Shenandoah.

LAWRENCE F. GALL, *Entomology Division, Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06511,* JOHN W. PEACOCK, *USDA Forest Service, 51 Mill Pond Road, Hamden, Connecticut 06514,* AND STEPHEN W. BULLINGTON, *Department of Entomology, Virginia Tech, Blacksburg, Virginia 24061.*

Received for publication 22 February 1991; revised and accepted 23 July 1991.

Journal of the Lepidopterists' Society
45(3), 1991, 231–233

HAWK MOTHS (SPHINGIDAE) IN THE WHITLEY COLLECTION FROM WALKER COUNTY, TEXAS

Additional key words: phenology, zoogeography.

Surprisingly little is known of the hawk moths (Sphingidae) of Texas. R. W. Hodges (1971, Sphingoidea, Fasicle 21, The moths of America north of Mexico, Wedge Entomol. Found. & E. W. Classey Ltd., London, 158 pp.) reported records of many species from Texas, although few specific localities were provided. The bibliography in Hodges (*op. cit.*) included no publications that list and analyze the sphingid fauna of any part of Texas, although two publications cited by Hodges discuss the sphingids of neighboring Arkansas (Freeman, H. A. 1938, Field & Lab. 6:33–43; Selman, C. A. & H. E. Barton 1971, Arkansas Acad. Sci. Proc. 25:56–58).

Here I report on a collection of sphingids from Walker County in east central Texas that is part of the Michael Whitley collection, now in the the Entomology Collection of the Houston Museum of Natural Science (HMNS). Most specimens were collected from 10 July 1971 to 19 May 1987 approximately 13 km SW of Huntsville or on the outskirts of Huntsville itself (Walker County). Specimens were collected at white light, UV light, fruit baits, and by casual daylight collecting. All specimens were collected by Michael Whitley and his family.

The climate of Walker County (data from Huntsville), is humid, warm temperate. Mean annual temperature is 19.4°C and mean annual precipitation is 1123 mm. Typically, 101 days a year have a daily maximum temperature above 32.2°C and 26 days have a daily mimimum temperature below 0°C. The growing season averages 265 days (7 March to 27 November). Rainfall averages over 65 mm for each month, but warm season thunderstorms produce slight precipitation peaks in April/May and September. On average, 65 days a year experience at least 2.5 mm of precipitation; snow is uncommon.

Winds are generally from the south or southeast, but northerly winds predominate in January.

Walker County contains 1540 km^2 with gently rolling topography, most of which is naturally forested land. Although Walker County is generally included in the southeastern forested region (Warner, S. R. 1926, Proc. & Trans. Texas Acad. Sci. 26:83–97; Pessin, L. J. 1933, Ecology 14:1–14), vegetational types can be easily and accurately subdivided into pine forest, post oak forest, blackland prairie, and bottomland hardwoods (Warner, *op. cit.*). Much of the eastern and southeastern portions of Walker County are included within Sam Houston National Forest, where management for pine silviculture has drastically reduced the hardwood components of the natural communities.

Walker County straddles the ecotone between the East Texas Pineywoods (dominated by species of *Pinus*: Pinaceae, *Quercus*: Fagaceae, and *Carya*: Juglandaceae) and the Oak Hickory Savannah/Forest (dominated by *Quercus, Carya* and *Juniperus*: Pinaceae). Although sphingids are a vagile group and extra-limital dispersal is common, the sphingid fauna of Walker County illustrates the transition of a fauna from the mesic and hydric woodlands typical of the Austroriparian Biotic Province to the humid and subhumid prairies, savannahs, and woodlands of the Texan Biotic Province (Blair, W. F. 1950, Texas J. Sci. 2:93–117).

The 419 specimens of sphingids in the Whitley collection represent 26 species (Table 1). My survey of all sphingid records in Texas has produced a list of 82 species (R. W. Neck, unpubl. data). The majority of the Texas species not known from Walker County are southwestern or subtropical forms that normally are found no farther east or north than western or southern Texas, respectively. Additional species not represented in Whitley's Walker Co. collections include a number of truly tropical forms that periodically migrate far northward of their breeding ranges.

Several species in the Whitley collection were taken at both UV-light traps and fruit baits, depending upon the season. Generally only males were attracted to light, but both sexes of *Sphecodina abbotii* (Swainson) and *Darapsa pholus* (Cramer) were attracted to fruit. *Amphion floridensis* B. P. Clark was collected at both watermelon and banana bait, but not at UV light traps. *Hyles lineata* (Fabricius), a species known to fly at all times of the day (Freeman, *op. cit.*), was collected during daylight and at UV-light but not at bait.

Although this collection does not provide a complete representation of the flight phenology of the sphingids of Walker County, the data are sufficient to allow preliminary comparison with published studies in adjacent states. Local voltinism probably is controlled largely by ambient climatic regimes but also may be modified by the nutritive value of suitable food plants at various times of the year. In general, the voltinism pattern in eastern Texas resembles those of Arkansas and Kansas. Some of the observed differences may be the result of the phenology of collection efforts, e.g., *H. lineata* certainly occurs more often than the observed records of March and May. Seasonal occurrence of sphingids in tropical areas generally is related directly to rainfall periods (Owen, D. F. 1969, Proc. Royal Ento. Soc. London A44:162–168; Stradling, D. G., C. J. Legg, & F. D. Bennett 1983, Bull. Entomol. Res. 73:201–232). The spring and fall peaks of species richness in eastern Texas (Table 1) are not related solely to precipitation, which is relatively equal in all months, but occur during relatively cool periods during the growing season when reduced evaporation rates prevail. Both cold-season deciduousness in winter and warm-season moisture stress in summer eliminate or reduce, respectively, sphingid activity in eastern Texas.

An interesting departure from previously published phenology is the long flight period of *Paonias myops* (J. E. Smith) in Walker County (March/April, July, and September); Hodges (*op. cit.*, p. 86) reported that *P. myops* "seems to be single brooded." The single July and single September specimens of *P. myops* in the HMNS collection could indicate a very long-lived adult stage, an anomalous emergence time due to unusual climate regimes, or a partial second brood in this species. Unfortunately, Freeman (*op. cit.*) did not report the seasonal occurrence of *P. myops* in Arkansas, although he recorded it from six counties.

TABLE 1. Sphingidae from Walker Co., Texas in the Whitley Collection (HMNS), with months of collection. Letters refer to months from March (M) to September (S). Number in parentheses is number of individuals for each species.

Species name	M	A	M	J	J	A	S
Agrius cingulata (7)						X	X
Manduca sexta (15)						X	X
Manduca quinquemaculata (4)					X	X	X
Manduca rustica (38)					X	X	X
Manduca jasminearum (1)						X	
Dolba hyloeus (9)		X	X			X	X
Ceratomia amyntor (4)						X	X
Ceratomia undulosa (16)	X	X	X		X	X	X
Ceratomia catalpae (3)	X					X	
Ceratomia hageni (19)	X	X	X	X		X	X
Paratrea plebeja (25)	X	X	X			X	X
Smerinthus jamaicensis (17)	X	X			X	X	X
Paonias excaecatus (28)	X	X	X			X	X
Paonias myops (9)	X	X			X		X
Laothoe juglandis (11)	X	X		X		X	X
Pachysphinx modesta (7)	X	X				X	X
Hemaris diffinis (2)						X	X
Eumorpha pandorus (3)					X		X
Eumorpha fasciata (36)						X	X
Sphecodina abbotii (8)	X			X			
Deidamia inscripta (21)	X	X					
Amphion floridensis (62)	X				X	X	
Darapsa myron (31)	X	X	X	X	X	X	X
Darapsa pholus (16)	X	X	X		X	X	
Xylophanes tersa (16)			X	X	X	X	X
Hyles lineata (11)	X		X				
Total species—26 (419)	15	12	9	5	10	21	19

The Whitley collection of 26 species of sphingids contains mostly species representative of the southeastern United States, which generally occur to the west only in localized populations. Interesting is the absence in this collection is of any of the widely-dispersing tropical species that are found regularly in southern Texas and that are occasionally collected far north of their normal range, e.g., species of the genera *Errinyis* and *Aellopos*. Of the 82 species of sphingids known from Texas, 57 species are likely to be encountered in Walker Co., Texas. Clearly, additional collecting is required before the sphingid fauna of this area is known completely.

I thank Michael Whitley and members of his family for their efforts in the collection and documentation of these specimens. Doug Stine assisted with efforts to catalogue this collection and produce this manuscript. This article is Contribution No. 1, Houston Museum of Natural Science, Entomology Series.

RAYMOND W. NECK, *Houston Museum of Natural Science, One Hermann Circle Drive, Houston, Texas 77030.*

Received for publication 30 October 1989; revised and accepted 28 June 1991.

Journal of the Lepidopterists' Society
45(3), 1991, 234–236

RAPID COLONIZATION OF THE WESTERN UNITED STATES BY THE PALEARCTIC MOTH, *AGONOPTERIX ALSTROEMERIANA* (OECOPHORIDAE)

Additional key words: Apiaceae, *Conium*, Gelechioidea, introduced insect.

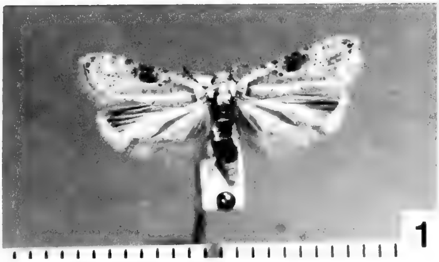
Larvae of *Agonopterix alstroemeriana* (Clerck) (Oecophoridae) (Figs. 1, 2), which live in conspicuous leaf rolls on Poison Hemlock (*Conium maculatum* L., Apiaceae =Umbelliferae), were discovered in Tompkins County, New York (Berenbaum, M. & S. Passoa 1983, J. Lepid. Soc. 37:38). The species was assumed to have recently immigrated to North America because no records were known before 1973 (Hodges, R. W. 1974, Moths of America north of Mexico, fasc. 6.2, Gelechioidea, Oecophoridae, 142 pp.). The earliest record we have seen is 24 June 1973, at Elm St. Ext. Coy Glen near Ithaca, Tompkins Co., New York. However, one might expect a new colonist to appear near a port of entry or major international airport, such as Buffalo, Erie, the New York City area, or along the St. Lawrence River, rather than 300 km inland. Hence, *A. alstroemeriana* populations may have existed elsewhere in the northeastern U.S.A. prior to discovery in the Ithaca area. There are lengthy gaps in the record of establishment and spread of other introduced moths in populous North American regions of both coasts (Powell, J. A. & J. M. Burns 1971, Psyche 78:38; Powell, J. A. 1989, Pan-Pacific Entomol. 64:98).

Nevertheless, there are numerous records documenting the amazingly synchronous appearance of *A. alstroemeriana* in widespread parts of the western Nearctic. The species was detected in California, Oregon, and Utah in 1983. During that season it appeared on both sides of San Francisco Bay, at Berkeley and San Bruno Mountain, localities that had been regularly sampled during the preceding several years by Powell and R. L. Langston. So rapid was the spread of this species throughout the western U.S. that we can reconstruct neither direction of expansion nor avenue of entry. We suspect this moth invaded the western Nearctic by direct introduction, either from Europe or from the northeastern U.S. Overland expansion of its range from the east seems unlikely because a survey of *Conium maculatum* insects in Illinois during several seasons (1986–89) by Passoa failed to reveal larvae of *A. alstroemeriana,* and we did not find any records in the midwest states prior to collection of an adult near Columbus, Ohio, in June, 1990, by Powell. The records suggest colonizations in the Columbia River (Oregon) area, the Puget Sound (Washington) area, or both, and independently in the San Francisco Bay area.

Moths of the genus *Agonopterix* characteristically are secretive, hiding in dark corners and crevices, rather than flying to lights when disturbed. The larvae feed in spring and early summer, adult emergence occurs soon thereafter, and the moths aestivate and hibernate prior to oviposition in early spring. Hence, on the Pacific Coast, adults of *A. alstroemeriana* may be encountered during any month between late June and March. Their habits and longevity therefore make them likely candidates for transport by man as stowaways on ships, trucks, etc., during aestivation or hibernation.

By 1987, *A. alstroemeriana* occurred throughout many non-arid parts of the west, in Colorado, Utah, Idaho, Washington, Oregon, and northern California (Fig. 3), following its hostplant, which has been a widely naturalized weed for many decades (Robbins, W. W. 1940, Calif. Agr. Exp. Sta. Bull. 637). R. D. Goeden and D. W. Ricker (1982, Ann. Entomol. Soc. Amer. 75:173) did not find this moth in their extensive survey of insects feeding on *Conium maculatum* in southern California during 1978 and 1979, and we do not know of any collections subsequently (through 1990), although colonization there is probable. We have not seen records of *A. alstroemeriana* in Canada, but establishment around Vancouver and southern Ontario is likely.

Western U.S. material examined.—CALIFORNIA: Alameda Co.: Albany VII-5-85, I-30-86 (J. W. Brown, UCB); Aquatic Park, Berkeley V-22-83, larvae on *Conium maculatum* (P. Neyman, UCB); north Berkeley III-10-84 and subsequent dates, at light (J. Powell, UCB); Strawberry Cyn., Berkeley Hills VI-27-87 (S. Passoa, SPC), Fairmount Ridge SE



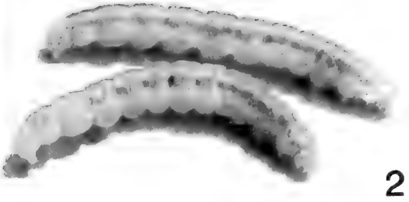


FIG. 1. Adult of *Agonopterix alstroemeriana*, Berkeley, California (scale bar in mm).
FIG. 2. Final instar larvae of *A. alstroemeriana*, Hooper, Whitman Co., Washington.

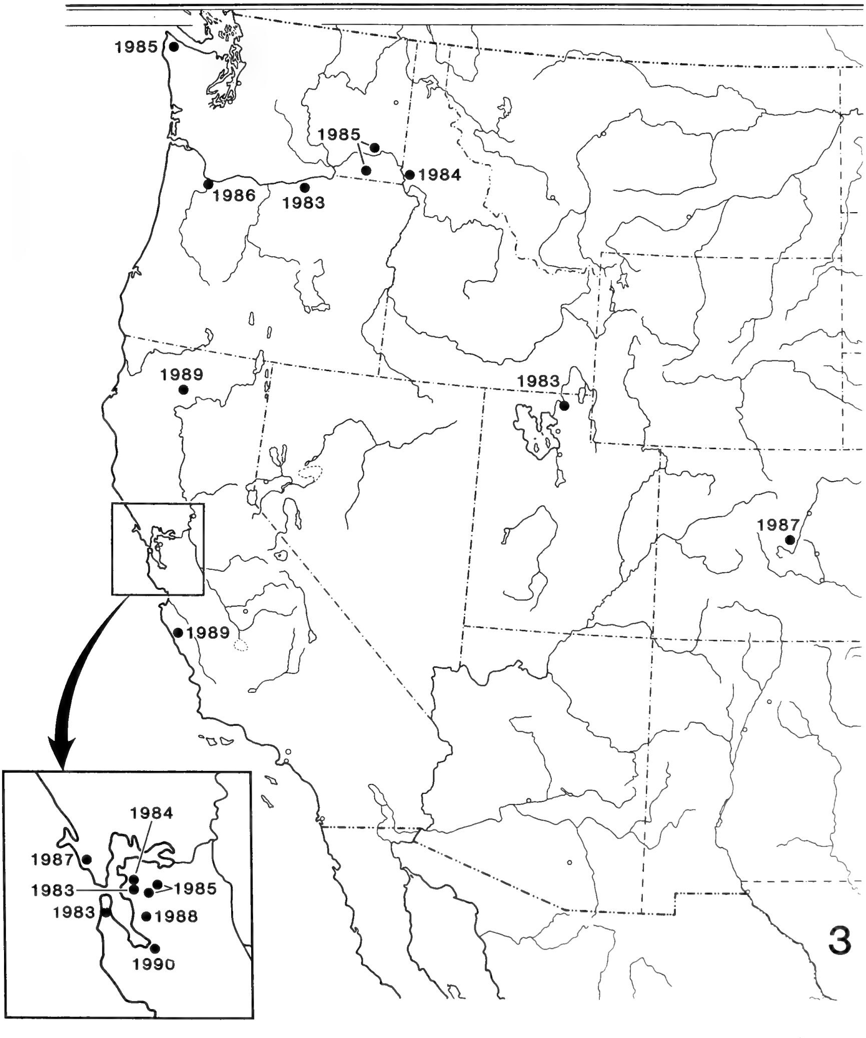


FIG. 3. Locality records for *Agonopterix alstroemeriana* in the western United States, with year of first capture.

of San Leandro II-10-88 (Powell, UCB). Contra Costa Co.: Orinda VII-3/11-85 (C. D. MacNeill, OM); Russell Reserve N of Lafayette X-22-85 (Brown & Powell, UCB). Marin Co.: Audubon Cyn. nr. Bolinas V-17-87, larvae on *C. maculatum* (R. Peterson, photo UCB.) Monterey Co.: Big Creek Reserve X-7 to XI-10-89 (F. Arias, BCR, UCB). San Mateo Co.: San Bruno Mt. XI-28-83 and later dates (R. Langston, CAS, RLC) and reared from larvae on *C. maculatum* IV-86 (JAP 86D1), V-86 (JAP 86E12), III-87 (JAP 87C56) (J. De Benedictis, UCB). Santa Clara Co.: nr. Milpitas IV-25-90, larvae on *C. maculatum* (L. Spahr, UCB). Siskiyou Co.: Mt. Shasta City VI-9-89, larvae on *C. maculatum* (B. Villegas, CDFA). COLORADO: No. Platte, 6600′ [1980 m] Jefferson Co. VIII-20-87, at light (P. A. Opler, UCB). IDAHO: 5 mi. [8 km] SW Cul de Sac, Nez Perce Co. VII-10-84, reared from *C. maculatum* (F. Merickel, USNM). OREGON: Morrow Co. VI-14-83 (no collr. given, USNM). Multnomah Co.: Hayden Isl., Portland IX-19-86 (Powell, UCB), UTAH: Cache Co.: Hyrum St. Park VIII-5-86 (Passoa, SPC); Logan X-1-83 (D. Veirs, UCB). WASHINGTON: Walla Walla Co.: Walla Walla VI-6-85, reared from *C. maculatum* (no collr. given, USNM). Whatcom Co.: Blaine V-30-85, larvae on *C. maculatum* (Passoa, SPC). Whitman Co.: Hooper V-30-85, larvae on *C. maculatum* (S. Passoa, UCB). (CAS = California Academy of Sciences, San Francisco; CDFA = Calif. Dept. Food & Agric., Sacramento; OM = Oakland Museum, Oakland, California; RLC = R. Langston collection, Kensington, California; SPC = S. Passoa Collection, Reynoldsburg, Ohio; UCB = Essig Museum of Entomology, U. Calif. Berkeley; USNM = U.S. National Museum of Nat. Hist., Washington, D.C.).

Cooperation by authorities of the above named collections enabled use of specimens in their care. We also thank J. M. Burch, USDA, APHIS, Moorestown, New Jersey, for review and suggestions on the manuscript. The map was drawn by Tina Jordan.

J. A. POWELL, *Department of Entomological Sciences, University of California, Berkeley, California, 94720* and S. PASSOA, United States *Department of Agriculture (USDA), Animal and Plant Health Inspection Service (APHIS), Plant Protection and Quarantine (PPQ), Reynoldsburg, Ohio 43068.*

Received for publication 1 April 1991; revised and accepted 13 June 1991.

Journal of the Lepidopterists' Society
45(3), 1991, 236–238

COLD HARDINESS OF *HYALOPHORA EURYALUS KASLOENSIS* (SATURNIIDAE) FROM THE OKANAGAN VALLEY, BRITISH COLUMBIA

Additional key words: supercooling, freezing tolerance, overwintering, cocoons.

Overwintering temperate zone insects that are not freezing tolerant (able to survive formation of ice in extracellular body fluids) must avoid freezing to survive. They do so by lowering the freezing point of their body fluids (supercooling), as low as −53°C in some species (Somme, L. 1982, Comp. Biochem. Physiol. 73A:519–543), with the aid of biochemical antifreezes such as sugar alcohols and thermal hysteresis proteins. Also, to avoid freezing, some insects seek sheltered microhabitats or construct elaborate cocoons, or both, in preparation for overwintering; such activities may also provide protection from predators while the overwintering insect is immobile (Danks, H. V. 1978, Can. Entomol. 110:1167–1205). The three species (*sensu* Lemaire, C. 1978, The Attacidae of America. Attacinae, Edition C. Lemaire, 42 Boulevard Victor Hugo, Neuilly-sur-Seine, France, pp. 114–125) of the North American genus *Hyalophora* Duncan (Saturniidae) are large univoltine moths that overwinter as diapausing pupae within well-constructed double cocoons. The well-known species *H. cecropia* (L.) has been the subject of a variety of ecological, behavioral, and physiological studies and is known to be freezing tolerant (e.g., Asahina, E. & K. Tanno 1966, Low Temp. Sci. Ser. B. 24:25–34). In contrast, *H. euryalus* (Boisduval), native to the Pacific coast and western mountains from Baja California to British Columbia, has not been well studied. The form known as *H. euryalus kasloensis* (Cockerell) is found in the interior of British Columbia and in northern Washington and Idaho (Ferguson, D. C., *in* Dominick, R. B. et al. 1972, The moths of America north of Mexico, fasc. 20.2B, Bombycoidea (in part)) but its geographic range has not been clearly defined. Although the taxonomic status of *H. e. kasloensis* has yet to be firmly established, the form is herein considered distinct (*cf*. Morewood, W. D. 1991, J. Entomol. Soc. Brit. Columbia 88, *in press*).

In May 1988 a small captive colony of *H. e. kasloensis* was established from an adult female collected at Kelowna, in B.C.'s Okanagan Valley, and larvae were reared indoors on cuttings of *Ceanothus sanguineus* Pursh (Rhamnaceae) under ambient conditions in the Okanagan Valley. The colony was maintained and enlarged by mating several reared females with wild males in the Okanagan in 1989 and 1990 using mating cages constructed from coffee cans, as described by T. A. Miller and W. J. Cooper (1976, J. Lepid. Soc. 30: 95–104). Larvae were reared on *C. sanguineus* in the Okanagan during the summer of 1989 and on *Rhamnus purshiana* DC. (Rhamnaceae) in Victoria, B.C., during the summer of 1990. Pupae were overwintered outdoors in Victoria each year.

In mid-January 1990, 16 pupae (6 male, 10 female) were removed from their cocoons and cooled at a continuous rate of 0.3°C per minute from 0 to −30°C using the materials and methods described by L. M. Humble and R. A. Ring (1985, Cryo-Letters 6:59–66). Freezing of the pupae was indicated by the release of the heat of fusion, detected via thermocouples in contact with the pupal case. The temperature at which the pupae froze, their supercooling point, was −21.0 ± 0.40°C (mean ± SE); males and females did not differ significantly (−20.2 ± 0.49°C for males versus −21.5 ± 0.52°C for females; $t_{(2)13} = 1.8482$, $0.05 < P < 0.10$). These pupae were cooled further to −30°C to ensure that they had frozen, and they were immediately returned to outdoor temperatures (between 0 and 10°C at that time). Only one of the pupae that had been frozen failed to produce an adult in the spring of 1990 (this adult emerged on 4 July 1991). The others emerged successfully (even one that had been accidentally dropped 5 May, splitting the pupal case!) between 25 May and 11 June, with a distinct peak of emergence on 29 May. This pattern corresponded very closely with that of 33 pupae that had not been frozen, including 15 that had been removed from their cocoons shortly after pupation in August and 4 that failed to produce adults in the spring of 1990 (two of these adults emerged on 27 June 1991, the other two on 3 and 7 July 1991). It is not uncommon for a small proportion of an insect population to remain in diapause for more than one year (Danks, H. V. 1987, Insect dormancy: An ecological perspective, Biological Survey of Canada (Terrestrial Arthropods), pp. 179–184). Although overall fecundity was not assessed, one female that had been frozen mated with a sibling male and laid at least 134 eggs, of which 121 (90%) hatched.

In September 1990 all pupae were removed from their cocoons for weighing, as part of a separate study, and were placed in small plastic boxes lined with paper towels for overwintering. In early January 1991 three groups of seven male and eight female pupae each were placed directly into a freezer and held at −30 ± 2°C. One group was removed after 24 h, another after seven days, and the last after four weeks. In each case the pupae were returned directly to outdoor temperatures, which varied between 0 and 10°C. Two pupae in each group died and had desiccated by spring whereas two pupae that had been frozen for seven days failed to produce adults (but may do so after another year of diapause, see above); all of the remaining pupae produced adults between 15 June and 13 July 1991. In the control group of 17 pupae that were not frozen, one died, one failed to produce an adult, and the remainder all produced adults between 18 June and 1 July 1991. Three matings were obtained between males and females that had both been frozen for four weeks as pupae. These females laid 156, 113, and 118 eggs after mating, of which 111 (71%), 92 (81%), and 113 (96%) hatched, respectively. These data compare favorably with the results of two matings between adults from the control group wherein the females laid 105 and 91 eggs after mating, of which 98 (93%) and 63 (69%) hatched, respectively.

Thus, *H. e. kasloensis* is capable of moderate supercooling during pupal diapause and is also tolerant of freezing below the supercooling point and may remain frozen for up to four weeks without adverse effects on subsequent survival and fecundity. Such a level of cold hardiness would be ample for winter survival in the Okanagan Valley where, at Penticton for example, the average daily minimum temperature for the coldest month of the year was −5.9°C and the absolute minimum temperature was −26.7°C during a 19 year period (Meteorological Office 1980, Tables of temperature, relative humidity, precipitation and sunshine for the world, Part 1 North America and Greenland, HMSO, London, p. 14). In contrast with *H. cecropia,* whose larvae enter a wandering phase prior to selecting a cocoon spinning site (Scarbrough, A. G., J. G. Sternburg & G. P. Waldbauer 1977, J. Lepid. Soc. 31:153–166), over 80% (n = 76) of the *H. e. kasloensis* larvae reared during the summer of 1989 simply spun their cocoons attached to twigs amongst the foliage on which they had been feeding (those that did wander may have been responding to overcrowded conditions). If this represents normal behavior for these larvae then most overwintering pupae would be exposed to extremes in ambient air temperature. However, the level of cold hardiness demonstrated in this study indicates that the pupae are well able to survive such extremes even without the thermal buffer provided by the double-walled cocoon and its trapped air spaces. *H. e. kasloensis* pupae may overwinter primarily in the supercooled state but also must freeze commonly enough that their ability to survive freezing has been maintained and this ability would obviate any protection from freezing provided by the cocoon. On the other hand, the cocoon represents a considerable investment of energy and material reserves and must therefore be of great importance for overwintering survival.

A variety of factors, including mechanical damage, mold, predators, and parasitoids, probably all contribute to the importance of the protective barrier provided by the cocoon. For example, F. L. Marsh (1937, Ecology 18:106–112) reported that the primary parasitoid of *H. cecropia, Gambrus* (= *Spilocryptus*) *extrematis* (Cresson) (Hymenoptera: Ichneumonidae), laid eggs only during the period of cocoon spinning even though adult parasitoids were present both before and after this period. This would suggest that active larvae are either unsuitable as hosts or are mobile enough to avoid attack and that the completed cocoon provides an effective barrier against entomophagous arthropods. Overwintering *H. cecropia* pupae suffer heavy predation by woodpeckers (Picidae) when their cocoons are spun high in trees (Waldbauer, G. P. & J. G. Sternburg 1967, Ecology 48: 312–315). Also, deermice (*Peromyscus* spp.) (Muridae: Cricetinae) may open cocoons spun close to the ground; however, house mice (*Mus musculus*) (Muridae: Murinae) will eat bare pupae but will not open cocoons (Scarbrough, A. G., G. P. Waldbauer & J. G. Sternburg 1972, Oecologia 10:137–144). Many other potential predators are probably prevented from feeding on saturniid pupae by the presence of sturdy cocoons. Surveys of cocoon sites and winter mortality would help to clarify the role of the cocoon and spinning site in winter survival of *H. e. kasloensis.*

Thanks to T. J. Simonson for invaluable assistance in collecting adults and rearing larvae in 1988 and 1989, and to M. Gardiner for mating moths and collecting eggs in the spring of 1990. Thanks also to H. V. Danks, R. A. Ring, and two anonymous reviewers of the manuscript for helpful comments.

Voucher specimens (one male, one female) have been deposited at the Royal British Columbia Museum, Victoria (catalogue numbers ENT990-1800 and ENT990-1801).

W. D. MOREWOOD, *Department of Biology, University of Victoria, P.O. Box 1700, Victoria, British Columbia V8W 2Y2, Canada.*

Received for publication 5 July 1990; revised and accepted 6 August 1991.

Journal of the Lepidopterists' Society
45(3), 1991, 239–240

OVIPOSITION BEHAVIOR AND NECTAR SOURCES OF THE PAWNEE MONTANE SKIPPER, *HESPERIA LEONARDUS MONTANA* (HESPERIIDAE)

Additional key words: Colorado, threatened, *Bouteloua gracilis, Liatris punctata, Aster laevis.*

The pawnee montane skipper, *Hesperia leonardus montana* (Skinner) (Hesperiidae), was listed as threatened under the Endangered Species Act of 1973 on 25 September 1987 (Millar, J. L. 1987, Endangered and threatened wildlife and plants. Final rule to determine pawnee montane skipper (*Hesperia leonardus montana*) to be threatened species, 50 CFR 17, Vol. 52, No. 188, 5 pp.). The systematics and basic ecology of *H. leonardus* have been described by J. A. Scott and R. E. Stanford (1982, J. Res. Lepid. 20: 18–35). Intensive surveys during 1985 and 1986 confirmed that *H. l. montana* is restricted to an area of about 97.5 km² in the South Platte River drainage SW of Denver, Colorado; this area includes the location of the proposed Two Forks Dam and Reservoir on the South Platte River (Keenan, L. C., R. E. Stanford, S. L. Ellis, & B. A. Drummond 1986, Status report on: Pawnee montane skipper, Denver Water Dept., Denver, Colorado, 49 pp.).

S. L. Ellis (1986, Pawnee montane skipper 1986 field studies, ERT, Res. Eng. Co., Fort Collins, Colorado, Doc. D198: 82 pp.) showed that the occurrence of *H. leonardus montana* is positively correlated with the presence of *Liatris punctata* Hooker (Asteraceae), a favored nectar plant. Ellis also showed that blue grama grass, *Bouteloua gracilis* (H.B.K.)

TABLE 1. Observations of preoviposition behavior (POP), oviposition (OP), and ova attached to plants (OVA) of *Hesperia leonardus montana* in 1987. All observations were on *Bouteloua gracilis*. Time is Mountain Daylight Time.

Date	Study site	POP	OP	OVA	Elevation (m)	Time
8/21	West Creek	—	1	1	2060	1220
9/2	Sphinx Park	2	0	0	2060	1100
9/3	Swan Ranch	—	1	1	2060	1100
9/8	Sphinx Park	1	—	—	2060	1300
9/10	Dome Rock	—	—	2	2060	1100
9/10	Sphinx Park	—	—	1	2060	
9/10	Foxton	—	1	1	1939	1215
9/10	Kennedy Gulch	—	—	2	2030	
9/10	Sugar Creek	—	—	1	2181	
9/10	Oxyoke	—	—	1	1969	
9/10	Wigwam	—	—	1	2090	
9/10	Lone Rock	—	—	1	2030	
9/10	Horse Creek	—	—	1	2131	
9/11	Wigwam Creek	—	1	1	2266	
9/15	Buffalo Creek	—	—	1	2090	
9/18	Sugar Creek	—	1	1	2060	
9/21	Deckers Camp	1	—	—	2060	
9/22–10/2		—	—	—		
	Totals	4	5	15		
	Mean elevation				2069 m	
	Range in elevation				327 m	

TABLE 2. Nectar plants visited by adult *Hesperia leonardus montana* in August and September 1987 (VC = very common, C = common, O = occasional, R = rare).

Species (family)	Frequency of use
Liatris punctata Hooker (Asteraceae)	VC
Aster laevis L. (Asteraceae)	VC
Carduus nutans L. (Asteraceae)	C
Chrysopsis villosa (Pursh) Nuttall (Asteraceae)	O
Helianthus sp. (Asteraceae)	O
Aster porteri Gray (Asteraceae)	O
Heliomeris multiflora Nuttall (Asteraceae)	R
Senecio spartoides Torrey & Gray (Asteraceae)	R
Monarda fistulosa L. (Lamiaceae)	R
Geranium caespitosum James (Geraniaceae)	R

Lag. (Poacae), the only known larval food plant, covers about 1–3% of the ground in the skipper's habitat. During August and September 1987 we surveyed *H. l. montana* habitat in Jefferson and Douglas counties, Colorado, to determine if oviposition occurred on plants other than *Bouteloua gracilis*, to record time and elevational range of oviposition, and to identify nectar plants used by this skipper. These baseline data were collected for use in future monitoring of the effects of inundation of a portion of the skipper's habitat by the proposed Two Forks Dam and Reservoir Project. The results of the oviposition survey are presented in Table 1.

The first adult *H. l. montana* observed in 1987 was on 6 August and the last adult was seen on 29 September. Our observations of preoviposition behavior (n = 4), oviposition (n = 5), and ova found on plants (n = 15) support the report (Ellis *op. cit.*) that *Bouteloua gracilis* is the only grass on which oviposition takes place. During ovipositions, we observed the female flutter from base to base of clumps of *B. gracilis*, land on a clump, arch her abdomen, and place a single egg on the underside of a leaf blade about 3–8 cm above the ground. *Bouteloua gracilis* clumps chosen for oviposition were 7.6 to 10 cm in basal diameter and located on south-facing slopes between 1939 and 2266 m elevation. Oviposition took from 3 to 15 seconds to complete and occurred between 1100 h and 1300 h MDT (n = 3). We collected four clumps of *B. gracilis* on which we observed eggs being laid. Eggs on these four clumps hatched after 8, 19, 21, and 42 days, respectively.

Hesperia leonardus montana was observed nectaring on 10 species of plants. The most commonly visited species during August and through 10 September was *Liatris punctata*. After 10 September we noticed a marked shift to *Aster laevis* L. (Asteraceae). *Carduus nutans* L. (Asteraceae) was also a commonly visited nectar source late in the season. Other species were visited only occasionally or rarely (Table 2).

This study was commissioned by the Denver Board of Water Commissioners as part of the Environmental Impact Assessment for the proposed Two Forks Dam and Reservoir Project.

ROBERT L. WOOLEY, *P.O. Box 144, Silver Lake, Oregon 97638;* LEWIS C. KEENAN, *P. O. Box 1029, Arvada, Colorado 80010;* MARK N. NELSON, *2356 Cherry Street, Denver, Colorado 80207;* AND RAY E. STANFORD, *720 Fairfax St., Denver, Colorado 80220.*

Received for publication 25 January 1990; revised 30 July 1991; accepted 7 August 1991.

Journal of the Lepidopterists' Society
45(3), 1991, 241–243

A COMPARISON OF FOUR METHODS TO EVALUATE BUTTERFLY ABUNDANCE, USING A TROPICAL COMMUNITY

Additional key words: neotropics, Costa Rica, line-transect method, relative abundance.

In recent years, several transect methods to evaluate the abundance of butterflies have been proposed (Pollard, E. 1977, Biol. Conserv. 12:115–134; Feltwell, J. 1982, Proc. Trans. Br. Entomol. Nat. Hist. Soc. 15:17–24), but to our knowledge there has been no attempt to compare experimentally their usefulness in relation to the availability of time and resources. Herein, we present the results of an experiment in which modifications of four of those methods were applied, simultaneously, to a community of neotropical butterflies.

The study area was a 30-year old secondary forest (Moist Premontane Tropical Forest in the Holdridge System; Holdridge, L. R. 1974, Life zone ecology. Tropical Science Center, San José, Costa Rica, 206 pp.) located in San Pedro de Montes de Oca, Costa Rica (elevation 1200 m, annual precipitation 2000 mm, mean annual temperature 20.5°C). Censuses were taken from 0900 h to 1100 h on sunny mornings during the dry season of 1989, a time selected because weather conditions were excellent for butterfly activity. The experiment was replicated 13 times (13–25 February 1989).

Transect censuses involve counting butterflies while walking, usually along a trail (90 m long, in our case). For all the methods mentioned below, a steady walking speed is assumed, although occasional stops to take notes or to corroborate taxonomic identifications are allowed. We found that a small tape recorder is better than the usual note pad, as it eliminates the need to stop for writing and allows the observer to look constantly for butterflies.

We used the following methods (details in Pollard *op. cit.*; Feltwell *op. cit.*; Southwood, T. R. E. 1978, Ecological methods, Chapman and Hall, London, 524 pp.): **(1) King:** all individuals seen are counted and the distance at which each individual is first seen is recorded; for butterflies, identification beyond 5 m is unreliable and thus we used that distance as a maximum; **(2) Sides:** all individuals seen within a pre-defined distance but only at both sides of the observer are counted (we selected a predefined distance of 5 m and counted butterflies on both sides of the trail); **(3) Pollard:** all individuals seen in front of the observer at a range of 5 m or less are counted; **(4) Dowes:** all individuals seen to the right of the observer within a range of 5 m are counted.

Note that the last three methods actually are variants of the classical method of King. By applying the King method along with recording both the distance and the direction of the observation, one person can obtain simultaneously the kind of data required by all four methods. Nevertheless, the methods may be somewhat different due to non-independence, and for that reason method names appear in quotes in Table 4. To maximize consistency V.N. made all counts in our study. Density (individuals/m^2) was calculated independently according to the area actually covered by each method (Table 4). Family identifications were based on field guides of B. D'Abrera (1984, Butterflies of South America, Hill Press, Victoria, Australia, 256 pp.) and P. J. DeVries (1989, The butterflies of Costa Rica, Princeton Univ. Press, 327 pp.). Although we were primarily interested in comparing methods and not in species determinations (or in measuring actual population sizes), we collected vouchers which we deposited in the Natural History Museum (London).

The distance at which butterflies were first seen varied by taxon (family or subfamily) (Kruskal-Wallis AOV, $P < 0.01$; Table 1). Taxon was not correlated with frequency of identification according to the relative position of the observer (Contingency Chi-square $= 9.9$, $P > 0.05$; Table 2). More individuals were seen in front of the observer than on either side (Chi-square, $P < 0.01$; Table 3).

The method of King produced significantly higher counts than the other methods (Kruskal-Wallis AOV, $P < 0.01$; Table 4), which in turn did not differ significantly among themselves (Tukey Non Parametric Test). Although the King method apparently samples

TABLE 1. Distances (m) at which individuals were first seen according to taxon. Distance values for all families range from 0.25 to 5 m.

Family/subfamily	Mean	SD
Nymphalinae	1.1	0.9
Satyrinae	1.2	1.0
Ithomiinae	1.3	1.1
Pieridae	1.9	1.3
Heliconiinae	2.1	1.5

TABLE 2. Relation between taxon and direction in which individuals were first seen (left, front, or right of the observer) for all observations.

Family/subfamily	Left	Front	Right
Ithomiinae	53	77	46
Satyrinae	32	75	44
Pieridae	19	18	16
Heliconiinae	10	14	9
Nymphalinae	4	2	5
Total	118	186	120

TABLE 3. Relation between distance (m) and direction in which individuals were first seen, in number of cases.

Distance	Left	Front	Right
1	20	79	29
1–1.9	46	68	50
2–2.9	23	15	12
3–3.9	21	15	18
4–5	8	10	11
Total	118	187	120

TABLE 4. Density of butterflies in a neotropical secondary forest (individuals/m^2) × 100 according to four methods. Each row represents one day.

King	"Sides"	"Pollard"	"Dowes"
1.4	1.4	2.9	1.3
20	1.6	4	2
19.2	2.7	4	3.1
21.7	3.8	5.6	4
13.3	2.7	3.9	3.1
16.2	3	5.2	2.9
12.1	2.1	4	2.7
14.9	2	4	2
20	2	4.1	1.6
9	1.8	3.9	0.9
10.1	0.9	2.1	0
14	3.1	4.7	2.9
3.1	0.9	1.6	0.9

more of the population, it may have more error (e.g., counting individuals multiple times). When the sampling time is limited, the method of Dowes is recommended because it is simpler and its results are similar to those of the "sides" and Pollard methods. Future work should (1) test the effect of non-independence of methods applied simultaneously and (2) use a population of known size to evaluate the accuracy of each method.

We thank T. C. Emmel, J. Feltwell, P. Hanson, L. F. Jirón, and one anonymous reviewer for comments on the manuscript.

VANESSA NIELSEN, *Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica,* AND JULIÁN MONGE-NÁJERA, *Museo de Zoología, Universidad de Costa Rica, San José, Costa Rica.*

Received for publication 18 March 1991; revised and accepted 28 June 1991.

BOOK REVIEW

Journal of the Lepidopterists' Society
45(3), 1991, 243–244

PRIMITIVE GHOST MOTHS. Morphology and Taxonomy of the Australian Genus *Fraus* Walker (Lepidoptera: Hepialidae *s. lat.*) (Monographs on Australian Lepidoptera, Volume 1), by Ebbe S. Nielsen and Niels P. Kristensen. 1989. CSIRO, East Melbourne, Victoria, Australia. Distributed by Apollo Books, Lundbyvej 36, DK-5700 Svendborg, Denmark. xii + 206 pp. with 435 figures. Hard cover, 17.5 × 25.5 cm, ISBN-0-643-04999-1; DKK 378 (about. $57 U.S.)

The Hepialidae are phylogenetically and biologically distinct outliers that sit near the very base of the evolutionary tree that has at its tips some 150,000 species of butterflies and moths. Hepialids are arguably the most interesting and popular of the ancient lepidopteran lineages, being noteworthy for their diversity, often beautiful coloration, and comparatively enormous size (at least one of these "microleps" has a wingspan that may exceed 250 mm!). Their peculiar flight and courtship habits—from which their common name the "ghost moths" obtains—also have garnered them a great deal of attention from a range of naturalists. Further, they stand as biological record holders in being among the most fecund non-social herbivores as well as candidates for the most polyphagous (even omnivorous!) Lepidoptera.

Primitive Ghost Moths is the first volume in a new monographic series on the Australian Lepidoptera recently initiated by E. S. Nielsen. In this work Nielsen and Kristensen revise what is believed to be the most primitive hepialid genus, *Fraus* Walker (hence the book's title), a genus of 25 species endemic to Australia and Tasmania. The authors review thoroughly the morphology and taxonomy of the genus and survey all available biological data.

The first 100 pages are given to a morphological review that is exceptionally detailed and will be of use to all entomologists concerned with lepidopteran anatomy. Emphasis is placed on the skeletal structure, visceral anatomy, and musculature of the head, thoraco-abdominal articulation, and genitalia segments. This first chapter is generously supplied with 222 line drawings and photomicrographs. The tissue sections are very clearly stained. Even more impressive are the electron scanning micrographs of sections that have secondarily had the embedding material (paraplast) dissolved away. The numerous scanning electron micrographs of the external anatomy are used effectively throughout. The first 85 pages treat the structure of adults, with the remainder given to the egg, larval, and pupal stages. One cannot help but be struck by the fact that there is perhaps more information on moth morphology here than in John L. Eaton's mistitled book *Lepidop-*

teran Anatomy (1988, John Wiley & Sons, New York, 257 pp.; reviewed in *J. Lepid. Soc.* 43:338–339)—a work limited to the morphology of *Manduca sexta.*

The larval and pupal descriptions are based on examination of a single species, *Fraus simulans*, an occasional pest of turf in southeastern Australia and Tasmania. Although the larval SEM's are rather dirty (perhaps an effort might have been made to collect fresher material or to sonicate more thoroughly the material used), there is more detail in these figures than in any previous publication on the immature stages of this family. Figures 216 and 217 showing the branched microtrichea in the larval spiracles are especially striking. The authors claim that the larval antenna is two-segmented, yet the normal condition within the Lepidoptera is for the antennae to be interpreted as being three-segmented. No SEM's of the pupal stage are given, although detailed line drawings are presented. One comment made by the authors with which I fully concur is that the pupal stage promises to be a rich (and presently underexplored) source of characters for defining phylogenetic interrelationships within the family.

One of the most significant findings of the anatomical studies is a reinterpretation of the tegumen. Rather than being derived from dorsum IX as in other Lepidoptera, the authors make the case that the hepialoid "tegumen" is a derivative of the lateroventral wall of segment X. In addition, Nielsen and Kristsensen note that the ventral nerve cord of *Fraus* is strikingly different from the condition reported for other (higher) Hepialidae.

The second chapter on biology is short and adds little to previously published literature on the genus. Much of the discussion is taken from a paper by R. J. Hardy (1973, The biology of *Fraus simulans* Walker (Lepidoptera: Hepialidae), J. Aust. Entomol. Soc. 30: 113–120). Chapter 3 on diversity and distribution is also brief, mostly given to listings of species found in various regions and habitats about Australia and to ten photographs of *Fraus* localities in Australia and Tasmania. There is little discussion or synthesis likely to be of interest to biogeographers working outside Australia. The fourth chapter examines the phylogenetic position of *Fraus* within the Exoporia and the interspecific relationships within the genus.

The final chapter is a thorough taxonomic revision of the 25 members of the genus. Seventeen new species are described; keys to both males and females are provided, along with black and white photomicrographs of the adult male and female, male genitalia, and female genitalia and subanal plate for each species. The photographs of adults appear a little overexposed and might have benefited from a higher contrast printing, whereas those of the genitalic structures are outstanding and provide for ready interpretation. Label data and distribution maps are also given.

Technical and production aspects of the book are very good. The print is clear and figures have reproduced well onto the semi-gloss white paper. The work is handsomely supplied with 435 figures, all of which are clearly captioned or labeled, almost none of which are redundant. The text is generally well written, but I found many of the descriptive sections tedious, especially passages where eight or more sentences in a paragraph began with "The . . ." (e.g., p. 21). I ran across very few typos or editorial problems. The cardboard used for the cover is prone to warpage, such as in both my copies.

Even after a quick glance through this monograph, there will be little doubt as to why Nielsen and Kristsensen are so highly regarded. They have set a new standard for those preparing revisionary works. Although the book's audience will certainly be limited because of its focus on a single rather obscure and uncolorful genus of Australian moths, the detail provided in the morphological section will make the book a must for all interested in anatomy of Lepidoptera or in the evolution of the order. And because *Fraus* represents a basal lepidopteran lineage, those studying ordinal relationships among insects may also want to own a copy.

With Nielsen as the editor-in-chief of Monographs on Australian Lepidoptera, all can expect subsequent contributions to be outstanding. I am already looking forward to forthcoming publications in this series.

DAVID L. WAGNER, *Ecology and Evolutionary Biology, U-Box 43, University of Connecticut, Storrs, Connecticut 06269-3042.*

Date of Issue (Vol. 45, No. 3): 5 December 1991

NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of Lepidoptera study. Categories are Articles, Profiles, 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 111 in Volume 44(2). *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 submit manuscripts in *triplicate*, typewritten, *entirely double-spaced*, with wide margins, on one side only of white, letter-sized paper. Prepare manuscripts according to the following instructions, and submit them flat, not folded.

Abstract: An informative abstract should precede the text of Articles and Profiles.

Key Words: Up to five key words or terms not in the title should accompany Articles, Profiles, General Notes, and Technical Comments.

Text: Contributors should write with precision, clarity, and economy, and should use the active voice and first person whenever appropriate. Titles should be explicit, descriptive, and as short as possible. The first mention of a plant or animal in the text should include the *full scientific name* with *author*, and *family*. Measurements should be given in metric units; times in terms of the 24-hour clock (0930 h, not 9:30 AM). Underline only where *italics* are intended.

Literature Cited: References in the text of Articles and Profiles should be given as Sheppard (1959) or (Sheppard 1959, 1961a, 1961b) and listed alphabetically under the heading LITERATURE CITED, in the following format without underlining:

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

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

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

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.

Tables: Tables should be numbered consecutively in Arabic numerals. Headings for tables should not be capitalized. Tabular material must be typed *on separate sheets*, and placed following the main text, with the approximate desired position indicated in the text. Vertical lines as well as vertical writing should be avoided.

Voucher specimens: When appropriate, manuscripts must name a public repository where specimens documenting identity of organisms can be found. Kinds of reports that require vouchering include life histories, host associations, immature morphology, and experimental enquiries.

Proofs: The edited manuscript and galley proofs will be mailed to the author for correction of printer's errors. Excessive author's changes at this time will be charged to authors at the rate of $2 per line. A purchase order for reprints will accompany proofs.

Page charges: For authors affiliated with institutions, page charges are $20 per *Journal* page. For unaffiliated authors, page charges are $10 per *Journal* page with a $50 maximum. Authors of Book Reviews and Obituaries are exempt from page charges. Authors unable to pay page charges for reasons such as difficulties with foreign exchange should apply to the editor for free publication.

Correspondence: Address all matters relating to the *Journal* to the editor.

PRINTED BY THE ALLEN PRESS, INC., LAWRENCE, KANSAS 66044 U.S.A.

CONTENTS

PROFILES

GENERAL NOTES

BOOK REVIEW

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

e 45 1991 Number 4

ISSN 0024-0966

JOURNAL
of the
LEPIDOPTERISTS' SOCIETY

Published quarterly by THE LEPIDOPTERISTS' SOCIETY
Publié par LA SOCIÉTÉ DES LÉPIDOPTÉRISTES
Herausgegeben von DER GESELLSCHAFT DER LEPIDOPTEROLOGEN
Publicado por LA SOCIEDAD DE LOS LEPIDOPTERISTAS

19 May 1992

THE LEPIDOPTERISTS' SOCIETY

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.

Active members—annual dues $25.00
Student members—annual dues $15.00
Sustaining members—annual dues $35.00
Life members—single sum $500.00
Institutional subscriptions—annual $40.00

Send remittances, payable to *The Lepidopterists' Society*, to: Fay H. Karpuleon, Treasurer, 1521 Blanchard, Mishawaka, Indiana 46544, U.S.A.; and address changes to: Julian P. Donahue, Natural History Museum, 900 Exposition Blvd., Los Angeles, California 90007-4057 U.S.A. For information about the Society, contact: William D. Winter, Secretary, 257 Common St., Dedham, Massachusetts 02026-4020, U.S.A. (617-326-2634). To order back issues of the *Journal, News,* and *Memoirs,* write for availability and prices to the Publications Coordinator: Ronald Leuschner, 1900 John St., Manhattan Beach, California 90266-2608, U.S.A.

Journal of the Lepidopterists' Society (ISSN 0024-0966) is published quarterly for $40.00 (institutional subscription) and $25.00 (active member rate) by the Lepidopterists' Society, % Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, California 90007-4057. Second-class postage paid at Los Angeles, California and additional mailing offices. POSTMASTER: Send address changes to the Lepidopterists' Society, % Natural History Museum, 900 Exposition Blvd., Los Angeles, California 90007-4057.

Cover illustration: Courtship dance of *Scythris flaviventrella* (Scythrididae), which involves mutual touching of the forelegs and antennae while vibrating the wings; male (on left) is extending his abdomen toward female just prior to copulation (see page 348). Original drawing by Pietro Passerin d'Entrèves.

JOURNAL OF
THE LEPIDOPTERISTS' SOCIETY

Volume 45 1991 Number 4

Journal of the Lepidopterists' Society
45(4), 1991, 245–258

PAPILIO CANADENSIS AND *P. GLAUCUS* (PAPILIONIDAE) ARE DISTINCT SPECIES

ROBERT H. HAGEN,[1] ROBERT C. LEDERHOUSE, J. L. BOSSART AND J. MARK SCRIBER

Department of Entomology, Michigan State University, East Lansing, Michigan 48824

ABSTRACT. *Papilio canadensis* Rothschild & Jordan is recognized as a distinct species, not a subspecies of *P. glaucus* L., on the basis of physiological and genetic differences despite great similarity in adult appearance of these two taxa. Interspecific hybrids are found in a well-marked zone where the ranges of the species come into contact. The ecological or genetic factors that maintain species integrity despite this natural hybridization are as yet uncertain.

Additional key words: diapause, electrophoresis, hybrid zone, Michigan, Great Lakes region.

In their revision of American Papilionidae, Rothschild and Jordan (1906) described a northern subspecies of *Papilio glaucus* L., *P. g. canadensis*, distinguishable from *P. g. glaucus* by differences in the details of wing color pattern and by its smaller size. Although evidence was scanty, Rothschild and Jordan suggested that *glaucus* and *canadensis* "completely intergrade" in the Great Lakes region. Presumably, the parapatric distribution of these two taxa was a major factor in their decision to treat *canadensis* as a subspecies of *P. glaucus*.

Despite the morphological similarity between *P. glaucus* and *canadensis* adults and the occurrence of natural hybridization, our recent studies lead us to conclude that *canadensis* does warrant recognition as a distinct species. Three lines of evidence support our interpretation: first, there is significant differentiation between *glaucus* and *canadensis* in characters besides adult morphology; second, there appears to be a closer phylogenetic relationship between *glaucus* and *P. alexiares* Hoppfer than between *glaucus* and *canadensis*; and third, intergra-

---

[1] Current address: Department of Entomology, Haworth Hall, University of Kansas, Lawrence, Kansas 66045.

dation between *glaucus* and *canadensis* is restricted to a narrow hybrid zone. We discuss this evidence and its implications below.

In contrast to *canadensis*, another currently recognized subspecies of *P. glaucus*, *P. g. australis* Maynard, appears to fully intergrade morphologically and genetically with *P. g. glaucus* in the southeastern United States (Hagen & Scriber 1991, R. C. Lederhouse, J. L. Bossart & J. M. Scriber unpubl.). We suggest that *australis* should be treated as only a form of *P. glaucus*. A more complete discussion of relationships between *australis* and typical *glaucus* populations is in preparation (R. C. Lederhouse, J. L. Bossart & J. M. Scriber unpubl.). In addition, our studies provide no evidence whatsoever to justify resurrection of an Alaskan subspecies, *arcticus* Skinner; all specimens from Fairbanks, Alaska, that we have examined are clearly *P. canadensis*.

Papilio canadensis **Rothschild & Jordan, new status**

Papilio glaucus canadensis Rothschild & Jordan (1906).

Diagnostic characters for the species are discussed below, and include those which have been used previously for the subspecies.

DIAGNOSTIC CHARACTERS

Color Pattern and Morphology

Overall similarity of adults characterizes taxa within species groups of *Papilio* and contributes to frequent uncertainties in species-level taxonomy of Papilionidae (Rothschild & Jordan 1906, Munroe 1961, Sperling 1987, 1990). Two features of the wing pattern originally noted by Rothschild and Jordan appear to be fairly reliable characters for distinguishing adult *glaucus* and *canadensis*, along with overall size.

The first feature is the form of the forewing underside submarginal spots (Luebke et al. 1988). In *P. glaucus* the yellow spots centered in each cell are distinct; in *P. canadensis*, the spots form a nearly continuous yellow band with black pigment confined to a narrow line of scales at each vein. The yellow band in *canadensis* is similar to that on the forewing underside of *P. rutulus* Lucas. However, both *canadensis* and *glaucus* can be distinguished from *rutulus* by the presence of orange in the first submarginal spot of the hindwing (Rothschild & Jordan 1906).

The second diagnostic feature for *canadensis* is the width of the black band along the anal margin of the hindwing (Scriber 1982). For *P. glaucus* males, widths are in the range 10 to 50 percent of the width from wing margin to the CuA2 vein; whereas for *P. canadensis* males, the range is 50 to 90 percent (Scriber 1982, R. Hagen, unpubl. data). The width of the black band is greater in females than males, though the relative difference between species persists.

Smaller adult size is a third criterion useful for distinguishing specimens of *P. canadensis* from *P. glaucus*. Luebke et al. (1988) estimated size from the forewing chord length (FCL), the distance from wing apex to base: FCL for male *P. canadensis* ranged from 41 to 50 mm (median = 45 mm; n = 91); FCL for male *P. glaucus* ranged from 46 to 59 mm (median = 54 mm; n = 72). (Females were not measured in this study.) In both species the upper limits to size appear to be determined by intrinsic developmental constraints, but variation in larval food plant quality can produce wide variation among individuals below this limit; thus, small *P. glaucus* may be similar in size to *P. canadensis*.

Use of wing pattern characters for species diagnosis also must be tempered with caution. Adult *P. glaucus* that diapaused as pupae have greater anal band widths than individuals that did not undergo diapause, and more closely resemble *P. canadensis* adults in other wing pattern features (Scriber 1990). This effect undoubtedly contributes to similarity between *P. canadensis* and "spring brood" (i.e., overwintered) *P. glaucus*, noted by Rothschild and Jordan (1906) and discussed at length by Clark and Clark (1951). It is even possible that some early season individuals collected within the range of *P. glaucus* may be *P. canadensis*, or hybrids (Scriber 1990).

At least one larval character appears useful for distinguishing *glaucus* and *canadensis*. Very young larvae (1st or 2nd instar) of *canadensis* possess three transverse white bands on the dorsal side, whereas *glaucus* larvae have only a single, central, band (Fig. 1). A possible difference in the mature larvae (4th and 5th instar) is the presence of a distinct pale yellow or white pigment around the dorsal anal tubercles of *canadensis* that is fainter or absent in *glaucus* larvae. However, we are uncertain of the reliability of this character difference. The form and color of the metathoracic "eyespots" of mature larvae do not differ between *glaucus* and *canadensis*, though they differ markedly from those of *P. eurymedon* Lucas, *P. rutulus*, and *P. multicaudatus* Kirby larvae (Brower 1959).

Male genitalia of *glaucus* and *canadensis* cannot be distinguished by shape, independent of overall size (Brower 1959). Female genitalia and internal morphology have yet to receive careful study.

Diapause

The most striking differences between *glaucus* and *canadensis* involve physiological and developmental characters (Table 1).

Populations of *canadensis* and *glaucus* differ in the control of pupal diapause (Scriber 1982, Hagen & Lederhouse 1985, Rockey et al. 1987a, Hagen & Scriber 1989). In *P. glaucus*, diapause appears to be determined environmentally: larvae that experience long daylength, good

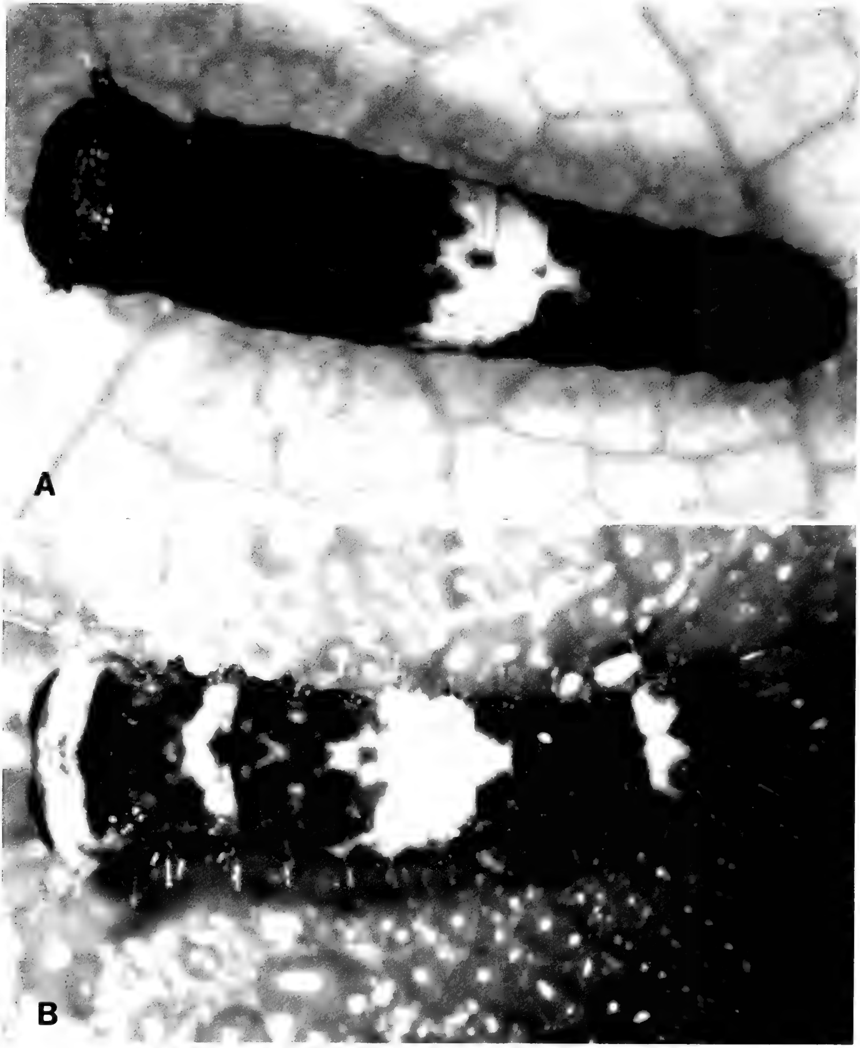


FIG. 1. First instar larvae of (A) *P. glaucus*, from Lawrence County, Ohio and (B) *P. canadensis*, from Cheboygan County, Michigan, showing diagnostic banding patterns (reared June–July 1991).

quality food, and perhaps warm temperatures are much more likely to develop directly into adults, without diapause, than are larvae that experience short days, poor food, or low temperatures. Under standard rearing conditions of 16 h light : 8 h dark, the proportion of larvae developing directly decreases among populations of *P. glaucus* with increasing latitude (Hagen & Lederhouse 1985, Rockey et al. 1987a).

TABLE 1. Summary of physiological and biochemical differences between *P. glaucus* and *P. canadensis*, and their modes of inheritance, if known. See text for fuller explanation.

Character	*P. glaucus*	*P. canadensis*	Inheritance	Reference
(Physiological/Developmental)				
Environmental determination of pupal diapause	yes	no	X-linked	1, 2
Lower lethal temperature for diapausing pupae	−23°C	−23 to −27°C	?	3
Larval survival on aspen foliage	very low	high	polygenic	4, 5, 6
Larval survival on birch foliage	low	high	polygenic	5, 7
Larval survival on tuliptree foliage	high	very low	polygenic	4, 5
Polymorphism for female color	present	absent	Y-linked	8, 9
Suppression of melanic color	absent	present	X-linked	1, 9, 10
(Biochemical)				
Hexokinase (*Hk*) alleles	"100"	"110"	autosomal	11
Lactate dehydrogenase (*Ldh*) alleles	"100"	"80," "40"	X-linked	1, 7, 11
6-Phosphogluconate dehydrogenase (*Pgd*) alleles	"100," "50"	"125," "80," "150"	X-linked	1, 7, 11

1. Hagen and Scriber (1989); 2. Rockey et al. (1987a); 3. Kukal et al. in press; 4. Scriber (1986); 5. Scriber (1988); 6. Scriber et al. 1989; 7. Hagen 1990; 8. Clarke and Sheppard (1962); 9. J. M. Scriber, R. H. Hagen and R. C. Lederhouse, unpublished; 10. Scriber et al. (1987); 11. Hagen and Scriber 1991.

This pattern is presumably an adaptive response to latitudinal variation in day length, similar to that shown by many other insects (Tauber et al. 1986).

In *P. canadensis*, however, pupal diapause appears to be obligate: regardless of rearing conditions, all individuals enter pupal diapause (Rockey et al. 1987a). The genetic basis for obligate diapause is an X-linked, recessive allele present in *P. canadensis* (Rockey et al. 1987b, Hagen & Scriber 1989). (The sex chromosomes of males are here denoted as XX; those of females as XY.)

The obligate diapause allele of *P. canadensis* has an obvious benefit for individuals of this species, since the growing season throughout its range is too short to permit more than one generation to develop successfully each year (Hagen & Lederhouse 1985, Scriber 1988). The obligate diapause allele would be highly disadvantageous for *P. glaucus*, because *glaucus* occurs in areas where the growing season should permit two or more generations per year.

Differences in the regulation of diapause induction are accompanied by differences in the cold tolerance of diapausing pupae (Table 1: Kukal et al. in press). Diapausing *P. canadensis* pupae are capable of surviving lower temperatures than are *P. glaucus* pupae. The species also differ in primary metabolism: labelled glucose injected into diapausing pupae is converted to different compounds in each species (Kukal et al. in press). The genetics of cold tolerance and pupal physiology have not been studied in these species.

Larval Food Plant Use

Larval food plant use by *P. glaucus* and *P. canadensis* also differs (Table 1: Scriber 1988). Laboratory studies have revealed that *P. glaucus* larvae develop poorly on foliage from aspen (*Populus* spp.: Salicaceae) or birch (*Betula* spp.: Betulaceae), good hosts for *P. canadensis.* Conversely, *P. canadensis* larvae are unable to grow on foliage from tuliptree (*Liriodendron tulipifera* L.: Magnoliaceae), an important host for *P. glaucus.*

These reciprocal inabilities are due to differences in the larval detoxication systems of each species. Lindroth et al. (1988) showed that *P. canadensis* larvae possess high levels of a specific esterase enabling detoxication of a glycoside present in extracts of trembling aspen (*Populus tremuloides* Michx.) foliage. Larvae of *P. glaucus* lack this esterase activity and are poisoned by the glycoside; esterase activity is heritable (Scriber et al. 1989). Extracts of tuliptree foliage are similarly toxic to *P. canadensis* larvae, but are tolerated by *P. glaucus* (Lindroth et al. 1986). The toxic components in tuliptree have not yet been characterized, but clearly differ from those present in aspen.

Mimicry

As noted by Rothschild and Jordan (1906), mimetic (black or dark brown) females occur as a polymorphism only in *glaucus*; *canadensis* females are always yellow. The expression of this polymorphism in *P. glaucus* is determined by genes on both the X and Y chromosome (Hagen & Scriber 1989). The phenotypic polymorphism in *P. glaucus* results from a genetic polymorphism at the Y-linked locus (Clarke & Sheppard 1962). Thus, in *P. glaucus,* yellow females produce yellow daughters and black females produce black daughters. (Both produce yellow sons, since males do not carry the Y chromosome.)

However, an X-linked gene is also required for expression of the mimetic form (Hagen & Scriber 1989). A female who inherits the Y-linked allele for black color from her mother but also inherits the X-linked "suppressor" allele from her father will be yellow. The X-linked suppressor allele appears to have no effect on the yellow phenotype of males or of females that inherit the Y-linked yellow allele.

Genetic analysis of *P. glaucus* and *P. canadensis* hybrids suggests that *P. canadensis* populations lack the Y-linked allele for black color and may be fixed for the X-linked suppressor allele (J. M. Scriber, R. H. Hagen & R. C. Lederhouse unpubl.). Conversely, *P. glaucus* populations appear to lack the X-linked suppressor allele.

Biochemical and Molecular Characters

Papilio glaucus and *P. canadensis* show fixed genetic differences at three enzyme loci detected by allozyme electrophoresis: Hexokinase (*Hk*), Lactate dehydrogenase (*Ldh*), and 6-Phosphogluconate dehydrogenase (*Pgd*) (Table 1: Hagen & Scriber 1989, Hagen 1990, Hagen & Scriber 1991). The distribution of allele frequencies at these loci in samples of butterflies collected from Michigan are given in Table 2 and shown in Fig. 2 (discussed below). Differences between the species may represent either chance fixation of neutral variants or the results of natural selection favoring different enzymes in each species.

Analysis of 26 allozyme loci, including the three noted above, yielded an estimate of genetic identity (Nei 1972) also consistent with species-level differentiation between *glaucus* and *canadensis* (Hagen & Scriber 1991). The estimate, 0.86, was lower than that between *P. eurymedon* and *P. rutulus* (0.91), and the same as that between *P. glaucus* and *P. alexiares*. A similar range of genetic identities was reported by Sperling (1987) for North American species of the *Papilio machaon* species group. The allozyme data gave no support for the proposal (Scott 1986) that *P. rutulus* is conspecific with *P. canadensis* or *P. glaucus*.

The mitochondrial DNA's of *P. glaucus* and *P. canadensis* also differ (F. Sperling & R. Hagen unpubl.).

DISCUSSION

Phylogenetic Evidence

A phylogenetic analysis of tiger swallowtails using allozyme loci gave strongest support for a monophyletic lineage consisting of *P. glaucus* and *P. alexiares* (Hagen & Scriber 1991). The characters most clearly supporting this lineage were *Hk* and *Ldh*. In both cases, *P. glaucus* and *P. alexiares* share a form of the enzyme that differs from that present in all other *P. glaucus* group taxa.

Papilio glaucus and *P. alexiares* also uniquely share the mimetic female form (Beutelspacher-Baigts & Howe 1984). Analysis of interspecific hybrids between *P. glaucus* and *P. alexiares* indicates that genetic control of female color is similar in the two species (Scriber et al. 1988[89]). It appears likely that presence of mimetic females is a derived character within the *P. glaucus* species group (Scriber et al. 1990).

The "Haldane Effect" is a commonly observed consequence of in-

TABLE 2. Allele frequencies for *Ldh*, *Pgd*, and *Hk* allozyme loci from Michigan samples, separated by county. Counties are listed from north (*P. canadensis* range) to south (*P. glaucus* range), as shown in Fig. 2. N = number of males scored for each locus. Alleles at each locus are named according to enzyme mobility relative to the most common allele in *P. glaucus* (named the "100" allele: Hagen & Scriber 1989, Hagen & Scriber 1991). The *canadensis* alleles for *Ldh* are "80" and "40"; for *Pgd*, "125," "80," and "150"; and for *Hk*, "110." *Hk* was not scored from some samples ("—"). (Electrophoretic methods discussed in Hagen & Scriber 1989 and Hagen & Scriber 1991.)

	LDH				PGD	
County	N	100	80	40	N	100
1. Ontonagon	20	0.0	0.95	0.05	20	0.0
2. Gogebic	2	0.0	1.00	0.0	2	0.0
3. Iron	25	0.0	1.00	0.0	25	0.0
4. Dickinson	10	0.0	1.00	0.0	10	0.0
5. Luce	32	0.0	1.00	0.0	30	0.0
6. Mackinac	8	0.0	1.00	0.0	8	0.0
7. Emmet	28	0.0	1.00	0.0	28	0.0
8. Antrim	18	0.0	0.89	0.11	18	0.0
9. Otsego	16	0.0	0.88	0.12	16	0.0
10. Manistee	16	0.0	0.88	0.12	16	0.0
11. Roscommon	10	0.0	0.70	0.30	10	0.0
12. Ogemaw	2	0.0	1.00	0.0	2	0.0
13. Gladwin	6	0.0	1.00	0.0	6	0.17
14. Newago	24	0.0	1.00	0.0	24	0.0
15. Isabella	34	0.0	0.85	0.15	34	0.0
16. Allegan	24	0.92	0.08	0.0	24	0.96
17. Ingham	61	0.85	0.13	0.02	61	0.93
18. Jackson	4	1.00	0.0	0.0	4	1.00
19. Washtenaw	29	0.93	0.07	0.0	29	1.00
20. St. Joseph	24	1.00	0.0	0.0	24	0.96
21. Lenawee	34	1.00	0.0	0.0	35	0.94

terspecific hybridization (Haldane 1922, Coyne & Orr 1989). In the *P. glaucus* group, the Haldane Effect has been observed when *P. glaucus* females are hand-paired to males of *P. eurymedon*, *P. rutulus*, and *P. multicaudatus*, taking the form of reduced viability of female hybrid offspring (Scriber et al. 1990). The effect was not observed among hybrid offspring of *P. glaucus* females and *P. alexiares* males (Scriber et al. 1988[89]).

A significant Haldane Effect does occur among hybrid offspring of *P. glaucus* females and *P. canadensis* males. A total of 568 male and 370 female offspring eclosed successfully from 39 hybrid families reared in our laboratory from 1983–88 (39.4% female: Hagen & Scriber in press). There was a significant bias against female hybrids in these families: in 25 families more males than females eclosed, in three an equal number eclosed, and in only 11 did fewer males than females eclose (P = 0.026; Wilcoxon test). Backcrosses of hybrid males to *P.*

TABLE 2. Extended.

PGD				HK		
50	125	80	150	N	100	110
0.0	0.80	0.05	0.15	—		
0.0	1.00	0.0	0.0	—		
0.0	0.88	0.12	0.0	—		
0.0	0.90	0.10	0.0	10	0.0	1.00
0.0	0.87	0.10	0.03	—		
0.0	0.75	0.13	0.12	6	0.0	1.00
0.0	0.80	0.14	0.06	26	0.0	1.00
0.0	0.94	0.06	0.0	—		
0.0	0.94	0.06	0.0	—		
0.0	0.94	0.06	0.0	8	0.13	0.87
0.0	0.90	0.10	0.0	—		
0.0	0.50	0.0	0.50	—		
0.0	0.83	0.0	0.0	2	0.0	1.00
0.0	0.88	0.12	0.0	6	0.0	1.00
0.0	0.91	0.03	0.06	4	0.0	1.00
0.0	0.04	0.0	0.0	—		
0.01	0.06	0.0	0.0	39	0.95	0.05
0.0	0.0	0.0	0.0	4	1.00	0.0
0.0	0.0	0.0	0.0	22	0.73	0.27
0.0	0.04	0.0	0.0	—		
0.03	0.03	0.0	0.0	28	0.93	0.07

glaucus females also resulted in significantly lower eclosion success of female progeny (Hagen & Scriber 1989, in press).

Hybrid offspring from the reciprocal cross (*P. canadensis* female with *P. glaucus* male) did not show the Haldane Effect: from 35 families reared over the same interval, a total of 284 male and 300 female offspring eclosed (51.4% female: Hagen & Scriber in press). In 14 families more males eclosed, in seven families an equal number of males and females eclosed, and in 14 families fewer males eclosed ($P = 0.829$; Wilcoxon test). The same absence of Haldane Effect was observed in reciprocal crosses when *P. glaucus* males were paired with *P. eurymedon* or *P. rutulus* females (Scriber et al. 1990).

These observations raise a new question about the status of *P. alexiares* in relation to *P. glaucus* (Hagen & Scriber 1991). For the present, it seems preferable to retain species designation for *alexiares*, given the lack of information on interactions between *glaucus* and *alexiares* in

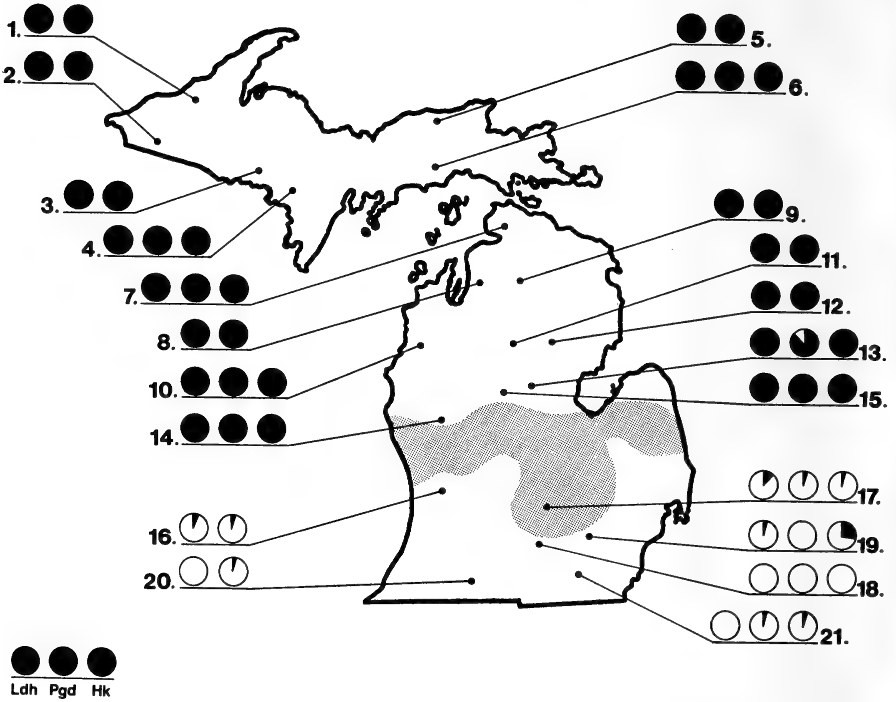


FIG. 2. Proportion of all *canadensis* alleles for *Ldh*, *Pgd*, and *Hk* loci in samples of butterflies from Michigan counties. The number next to each set of circles corresponds to a county listed in Table 2. *Hk* was not scored for samples from all counties; only 2 circles are shown in those cases. Filled circle = 100% *canadensis*; open circle = 0% *canadensis* (=100% *glaucus*); intermediate frequencies of *canadensis* alleles are indicated by the proportion of each circle filled. Sample sizes are given in Table 2, along with frequencies for the separate *canadensis* and *glaucus* alleles. The shaded region indicates the position of 1400–1500°C seasonal isotherm in Michigan, the predicted northern limit for a multivoltine life cycle.

northeastern Mexico, where they are reported to be sympatric (Beutelspacher-Baigts & Howe 1984).

The Hybrid Zone Between *glaucus* and *canadensis*

Evidence of natural hybridization between *glaucus* and *canadensis* has come from studies of morphology (Rothschild & Jordan 1906, Luebke et al. 1988), host plant use (Scriber 1986, 1988, Hagen 1990); inheritance of mimetic female color (Scriber et al. 1987, J. M. Scriber, R. H. Hagen & R. C. Lederhouse unpubl.) and allozyme electrophoresis (Hagen 1990). However, hybridization is confined to a relatively narrow zone between 41 and 44°N latitude, extending from New England through the Great Lakes region. The position of the hybrid zone appears to track closely the seasonal degree-day isotherm corresponding to the predicted northern limit for a multivoltine lifecycle in *P. glaucus* (Scriber 1982, 1983, 1988, Hagen 1990).

The narrowness of the hybrid zone is demonstrated best by allozyme characters, since their frequencies can be estimated more easily than frequencies of physiological or developmental characters. Allele frequencies for *Hk, Ldh,* and *Pgd* from samples of males collected in Michigan from 1986–89 are given in Table 2, grouped by county. The county locations are shown in Fig. 2.

The sharp transition in frequencies for all three loci in Michigan coincides with the predicted northern limits to a multivoltine life cycle. Laboratory experiments have shown that successful completion of two generations by *P. glaucus* or *P. canadensis* requires a minimum of 1400 to 1500°C "degree-days" above a threshold of 10°C, on good larval hosts (Hagen & Lederhouse 1985). The shaded band in Fig. 2 indicates the position of this 1400–1500°C band based on a 20 year (1950–70) average of climatic data (J. M. Scriber unpublished data).

Conclusions

Because there is no geographic barrier to prevent dispersal of *P. glaucus* and *P. canadensis* across the hybrid zone, maintenance of the sharp boundary between them must be attributed to more subtle factors that prevent extensive interbreeding or the establishment of sympatric populations. One possible factor may be inability of *P. glaucus* to adapt to the univoltine lifecycle that is essential for survival north of the hybrid zone (Hagen & Lederhouse 1985, Rockey et al. 1987a). This could prevent northward extension of *P. glaucus*' range, but would not prevent *P. canadensis* from extending its range further south.

Another possibility is disruption of development in the offspring of interspecies matings: for example, that which is responsible for the Haldane Effect observed in laboratory-generated hybrids. However, this too may be only a partial barrier, since we have evidence of developmental disruption affecting female offspring in only one direction of hybridization. Additional possibilities include differential mate preference by males or females of the two species, or differing tolerances for extremes of high—or low—temperature encountered on either side of the hybrid zone.

It is probable that a combination of factors will turn out to be responsible for maintaining the species' identities. The range boundary between *P. glaucus* and *P. canadensis* coincides with a complex ecotone between boreal coniferous forest and temperate deciduous forest (Braun 1974, Curtis 1959). This ecotone coincides with a climatic transition between northern areas dominated by relatively cool, dry arctic air masses and southern areas dominated by warmer, wetter tropical air masses (Bryson & Hare 1974). It also coincides generally with the southern margins of Pleistocene continental glaciation and thus represents a transition in topography and history of occupancy by animals and plants (Braun 1974).

The range limits of a variety of animal taxa coincide with this ecotone (Remington 1968, Scriber & Hainze 1987). Among the best-known examples from Lepidoptera are subspecies of the admiral butterfly, *Limenitis arthemis arthemis* Drury and *L. a. astyanax* Fabricius (Nymphalidae) (Platt & Brower 1968, Waldbauer et al. 1988). We strongly suspect that similar patterns of geographic differentiation occur frequently among eastern North American Lepidoptera. Tiger swallowtails may be atypical only in that they have received the intensive study necessary to detect it.

ACKNOWLEDGMENTS

We are grateful to Matt Ayres, Wade Hazel, James Nitao, Felix Sperling, and Fred Stehr for valuable discussion and criticism at various stages in preparation of this manuscript. For collecting assistance in Michigan, we also thank Jim Bess, Dave Biddinger, Charley Chilcote, Mark Evans, Bruce Giebink, Ted Herig, Mo Nielsen, Virginia Scott, and Mark Stehr. Doozie Snider cheerfully assisted with allozyme electrophoresis in the laboratory. The research contributing to this manuscript was funded by the Michigan State University Agricultural Experiment Station (Projects 8051, 8072, and 1644) and Graduate School (AURIG), NSF grants (BSR 8306060, BSR 87-18448, BSR 87-02332, and BSR 88-01184), and USDA-CRGO (87-CRCR-1-2851).

LITERATURE CITED

BEUTELSPACHER-BAIGTS, C. R. & W. H. HOWE. 1984. Mariposas de Mexico. Fasc. 1. La Prensa Medica Mexicana, S.A. Mexico, D.F. 127 pp.

BRAUN, E. L. 1974. Deciduous forests of eastern North America. (Reprint of 1950 ed.) Free Press, New York. 596 pp.

BROWER, L. P. 1959. Speciation in butterflies of the *Papilio glaucus* group. I. Morphological relationships and hybridization. Evolution 13:40–63.

BRYSON, R. A. & F. K. HARE. 1974. The climates of North America, pp. 1-47. *In* Bryson, R. A. & F. K. Hare (eds.), Climates of North America (World survey of climatology, Vol. 11). Elsevier, Amsterdam. 420 pp.

CLARK, A. H. & L. F. CLARK. 1951. The butterflies of Virginia. Smithsonian Misc. Coll. 116 (7):1–239.

CLARKE, C. A. & P. M. SHEPPARD. 1962. The genetics of the mimetic butterfly *Papilio glaucus*. Ecology 43:159–161.

COYNE, J. A. & H. A. ORR. 1989. Two rules of speciation, pp. 180–207. *In* Otte, D. & J. A. Endler (eds.), Speciation and its consequences. Sinauer Assoc., Sunderland, Massachusetts. 679 pp.

CURTIS, J. T. 1959. The vegetation of Wisconsin. Univ. of Wisconsin Press, Madison. 655 pp.

HAGEN, R. H. 1990. Population structure and host use in hybridizing subspecies of *Papilio glaucus* (Lepidoptera: Papilionidae). Evolution 44:1914–1930.

HAGEN, R. H. & R. C. LEDERHOUSE. 1985. Polymodal emergence of the tiger swallowtail, *Papilio glaucus* (Lepidoptera: Papilionidae): Source of a false second generation in New York state. Ecol. Entomol. 10:19–28.

HAGEN, R. H. & J. M. SCRIBER. 1989. Sex-linked diapause, color and allozyme loci in *Papilio glaucus*: Linkage analysis and significance in a hybrid zone. J. Heredity 80: 179–185.

——— 1991. Systematics of the *Papilio glaucus* and *P. troilus* species groups (Lepidoptera: Papilionidae): Inferences from allozymes. Ann. Entomol. Soc. Am. 84:380–395.

——— (in press). Sex chromosomes and speciation in tiger swallowtails. *In* Scriber, J. M., Y. Tsubaki & R. C. Lederhouse (eds.), The ecology and evolutionary biology of the Papilionidae. Scientific Publishers, Gainesville, Florida.

HALDANE, J. B. S. 1922. Sex-ratio and unisexual sterility in hybrid animals. J. Genetics 12:101–109.

KUKAL, O., M. P. AYRES & J. M. SCRIBER. Cold tolerance of pupae in relation to the distribution of swallowtail butterflies. Can. J. Zool. In press.

LINDROTH, R. L., J. M. SCRIBER & M. T. S. HSIA. 1986. Differential response of tiger swallowtail subspecies to secondary metabolites from tulip tree and quaking aspen leaves. Oecologia (Berl.) 70:13–19.

——— 1988. Chemical ecology of the tiger swallowtail: Mediation of host use by phenolic glycosides. Ecology 69:814–822.

LUEBKE, H. J., J. M. SCRIBER & B. S. YANDELL. 1988. Use of multivariate discriminate analysis of male wing morphometrics to delineate the Wisconsin hybrid zone for *Papilio glaucus glaucus* and *P. g. canadensis*. Amer. Midl. Nat. 119:366–379.

MUNROE, E. 1961. The generic classification of the Papilionidae. Can. Entomol. Suppl. 17:1–51.

NEI, M. 1972. Genetic distance between populations. Am. Nat. 106:283–292.

PLATT, A. P. & L. P. BROWER. 1968. Mimetic versus disruptive coloration in intergrading populations of *Limenitis arthemis* and *astyanax* butterflies. Evolution 22:699–718.

REMINGTON, C. L. 1968. Suture-zones of hybrid interaction between recently joined biotas. Evol. Biol. 2:321–428.

ROCKEY, S. J., J. H. HAINZE & J. M. SCRIBER. 1987a. A latitudinal and obligatory diapause response in three subspecies of the eastern tiger swallowtail, *Papilio glaucus* (Lepidoptera: Papilionidae). Amer. Midl. Nat. 118:162–168.

——— 1987b. Evidence of a sex-linked diapause response in *Papilio glaucus* subspecies and their hybrids. Physiol. Entomol. 12:181–184.

ROTHSCHILD, W. & K. JORDAN. 1906. A revision of the American papilios. Novitates Zool. 13:411–744.

SCOTT, J. A. 1986. The butterflies of North America. Stanford Univ. Press, Stanford, California. 583 pp.

SCRIBER, J. M. 1982. Foodplants and speciation in the *Papilio glaucus* group, pp. 307–314. *In* Visser, J. H. & A. K. Minks (eds.), Proceedings 5th international symposium on insect-plant relationships. Pudoc, Wageningen, Netherlands. 464 pp.

——— 1983. The evolution of feeding specialization, physiological efficiency, and host races in selected Papilionidae and Saturniidae, pp. 373–412. *In* Denno, R. F. & M. S. McClure (eds.), Variable plants and herbivores in natural and managed systems. Academic Press, New York. 717 pp.

——— 1986. Allelochemicals and alimentary ecology: Heterosis in a hybrid zone?, pp. 43–71. *In* Brattsten, L. B. & S. Ahmad (eds.), Molecular aspects of insect-plant associations. Plenum, New York. 346 pp.

——— 1988. Tale of the tiger: Beringial biogeography, binomial classification and breakfast choices in the *Papilio glaucus* complex of butterflies, pp. 241–301. *In* Spencer, K. (ed.), Chemical mediation of coevolution. Academic Press, San Diego, California. 609 pp.

——— 1990. Interaction of introgression from *Papilio glaucus canadensis* and diapause in producing 'spring form' eastern tiger swallowtail butterflies, *Papilio glaucus* (Lepidoptera: Papilionidae). Great Lakes Entomol. 23:127–138.

SCRIBER, J. M., R. V. DOWELL, R. C. LEDERHOUSE & R. H. HAGEN. 1990. Female color and sex ratio in hybrids between *Papilio glaucus* and *P. eurymedon*, *P. rutulus*, and *P. multicaudatus* (Papilionidae). J. Lepid. Soc. 44:229–244.

SCRIBER, J. M., M. H. EVANS & R. C. LEDERHOUSE. 1988(89). Hybridization of the Mexican tiger swallowtail, *Papilio alexiares garcia* (Lepidoptera: Papilionidae) with other *P. glaucus* group species and survival of pure and hybrid larvae on potential host plants. J. Res. Lepid. 27:222–232.

SCRIBER, J. M., M. H. EVANS & D. RITLAND. 1987. Hybridization as a causal mechanism of mixed color broods and unusual color morphs of female offspring in the eastern tiger swallowtail butterfly, *Papilio glaucus*, pp. 119–134. *In* Huettel, M. (ed.), Evolutionary genetics of invertebrate behavior. Univ. Florida, Gainesville. 335 pp.

SCRIBER, J. M. & J. H. HAINZE. 1987. Geographic invasion and abundance as facilitated by different host plant utilization abilities, pp. 433–468. *In* Barbosa, P. & J. C. Schultz (eds.), Insect outbreaks: Ecological and evolutionary processes. Academic Press, New York. 578 pp.

SCRIBER, J. M., R. L. LINDROTH & J. NITAO. 1989. Differential toxicity of a phenolic glycoside from quaking aspen to *Papilio glaucus* butterfly subspecies, hybrids and backcrosses. Oecologia 81:186–191.

SPERLING, F. A. H. 1987. Evolution of the *Papilio machaon* species group in western Canada. Quaest. Entomol. 23:198–315.

——— 1990. Natural hybrids of *Papilio* (Insecta: Lepidoptera): Poor taxonomy or interesting evolutionary problem? Can. J. Zool. 68:1790–1799.

TAUBER, M. J., C. A. TAUBER & S. MASAKI. 1986. Seasonal adaptations of insects. Oxford Univ. Press, New York. 411 pp.

WALDBAUER, G. P., J. B. STERNBURG & A. W. GHENT. 1988. Lakes Michigan and Huron limit gene flow between the subspecies of the butterfly *Limenitis arthemis*. Can. J. Zool. 66:1790–1795.

Received for publication 26 May 1990; revised and accepted 24 July 1991.

Journal of the Lepidopterists' Society
45(4), 1991, 259-271

PAPILIO HOMERUS (PAPILIONIDAE) IN JAMAICA, WEST INDIES: FIELD OBSERVATIONS AND DESCRIPTION OF IMMATURE STAGES

THOMAS W. TURNER[1]
12 Kingfishers Cove, Safety Harbor, Florida 34695

ABSTRACT. The life history and immature stages of *Papilio homerus* Fabricius are described from material collected in eastern Jamaica. The butterfly is now present in two small, isolated populations, each associated with the distribution of primary larval foodplants which are endemic species of *Hernandia* (Hernandiaceae) located in the last remaining areas of humid, virgin rainforest. Field observations of larval and adult behavior are also reported.

Additional key words: rainforest, Hernandiaceae, endemic species, adult behavior, taxonomy.

Papilio homerus Fabricius (Papilionidae) is the largest swallowtail species in the New World. It is endemic to Jamaica where it inhabits wet, primary forests. Only brief accounts of the immature stages have been published: Gosse (1879) described the egg and larva, Panton (1893) the mature larva, Taylor (1894) the larva and pupa, and Swainson (1901) the larva. However, as Brown and Heineman (1972) noted, none provided a complete description of the immature stages. Walker (1945) and Avinoff (in Brown & Heineman 1972) provided fragmented accounts of adult behavior. Wells et al. (1983) and Collins and Morris (1985) summarized the life history and ecology from data provided, in part, from the study reported here. Based on observations from 1962 to 1980, this paper reports the results of the first long-term study of *Papilio homerus*, describes all immature stages, and provides information on foodplants, population distribution, predation, and daily and seasonal behavior of adults in their natural environment.

MATERIALS AND METHODS

Rearing Observations

From 1968 to 1970, immature stages were collected from Corn Puss Gap in eastern Jamaica and taken to the Entomology Laboratory, University of the West Indies, Mona, for detailed study. Eggs and first and second instars were placed in small, round, plastic containers (5 × 3 cm); all other larvae were placed in larger plastic containers (25 × 10 cm). Moisture was provided by placing damp tissue paper in the container lids. Larvae were fed with leaves of *Hernandia catalpaefolia* Britton & Harris and *H. jamaicensis* Britton & Harris (Hernandiaceae)

---

[1] Research Associate, Division of Lepidoptera Research, University of Florida, Gainesville, Florida.

obtained from potted seedlings or from cuttings collected from the native habitat. Containers were cleaned daily. Before pupation, larvae were transferred to cylindrical screened cages (18 × 60 cm) with the foodplant in jars of water. Twigs were added to provide additional pupation sites. Plastic bags, placed over the cages to maintain high humidity, were left open at the bottom for ventilation. After pupation, all leaves were removed from the cages. All stages were kept in a shaded insectary at 25–30°C. Daylength varied between 12.0 and 13.25 h.

Eggs, first and second instars, and head capsules were measured with an ocular micrometer. All other measurements were made with a caliper or metric ruler. Samples of each stage were preserved in Dietrich's solution and larval head capsules were collected after each molt. Twenty-three eggs, 51 larvae, and 7 pupae were studied. Nomenclature of the immature stages largely follows Peterson (1962).

Study Area and Field Observations

Based on information from literature and museum specimen records, I visited all localities where the butterfly had been collected previously and other potentially suitable localities. I spent a total of 123 days in the field.

The main study area in the east was centered around Corn Puss Gap (elev. 600 m), where the Blue Mountains and John Crow Mountains meet, in primary tropical forest with a high canopy (30 m). The steep terrain has numerous streams and waterfalls. On the north side of the Gap, the forest is continuous; on the south side, it is fragmented due to previous logging operations, subsistence farming, and major landslides along a road from Bath to the Gap, which has become impassable. Low clouds cover this area for extended periods, particularly from September to mid-April. Over the study period, 47 days were spent observing *P. homerus* in this locality and 39 days were spent searching for the butterfly in the surrounding mountain ranges.

The western study area was between Elderslie and Quickstep (elev. 450 m) in the Cockpit Country in primary tropical forest. The terrain consists of numerous small limestone hills with steep sides, separated by narrow valleys. The forest is fragmented from logging, subsistence farming, and continuing road construction. Twenty days were spent studying this population and searching surrounding localities.

The third area visited was on and around Mount Diablo (elev. 300–1000 m) in central Jamaica where the butterfly was last collected in 1925. This area is generally more accessible by road and consists of small fragments of primary forest on steep limestone, extensive secondary forest, pastureland, and plantations of Caribbean Pine (*Pinus caribaea* Morelot, Pinaceae) and Blue Mahoe (*Hibiscus elatus* SW., Malvaceae). Seventeen days were spent searching all former known localities of the butterfly and investigating other nearby areas.

The average annual rainfall at Corn Puss Gap and in the Cockpit Country is over 5000 mm, with slightly less rainfall occurring on Mt. Diablo. All areas had high humidity and frequent mists. Average daytime summer temperatures in all three areas were 25°C under the canopy to 30°C in open areas. Winter temperatures were lower, especially in the eastern study area, and ranged from 13°C to 29°C. Generally, localities had to be reached on foot. Most trips lasted one day; occasionally, 2–5 days were spent camping at one locality.

I collected foodplants and identified them at the Herbarium, Department of Botany, University of the West Indies. Observations of adults were made with wide angle binoculars (12 × 50 objectives). On each trip, I was able to recognize individual butterflies by noting unique patterns of wing damage. On one-day trips, observations were made between 0900 h and 1600 h (EST); on camping trips, between 0600 h and 1800 h. I observed a total of 103 adults and captured 23 males and 9 females. All specimens were released except eight males.

Voucher specimens of all stages have been deposited at the Allyn Museum of Entomology, Sarasota, Florida.

RESULTS AND DISCUSSION

Descriptions of Life Stages

EGG (Fig. 1A). Egg spherical 1.45–1.54 mm in height (mean 1.50); 1.73–1.77 mm wide at the widest diameter (mean 1.75) (n = 23). Base approximately 1.5 mm wide, attached to leaf by a distinct layer of basal cement. Color, pale green when first deposited. The micropyle is finely knobbed with droplets of liquid creating a white frosting. This frosting is lost after five days, after which the egg becomes pale yellow. A paler spot, the larval head, develops on top; this spot gradually darkens, and after two additional days, becomes light brown. On the eighth day, this marking becomes dark brown before the larva hatches.

The larva cuts a lateral slit below the micropyle and enlarges this to a tear-drop shape before emerging. The chorion is subsequently eaten except for the basal portion.

LARVA. Head measurements for all instars are presented in Table 1.

First instar (Fig. 1B, C): Head brown, darkening to black with 5 short, black, simple setae on each hemisphere in the ocellar region. Thorax and abdomen light brown, becoming black; last two abdominal segments predominantly white.

First thoracic segment with mid-dorsal osmeterial pit. Osmeterium brown, used with reluctance and producing little discernable scent. There is a simple seta on either side of the mid-dorsum; a single, dark brown scolus dorsolaterally bearing 2 terminal, and 14 peripheral, black setae, and a verucca at the base of the scolus bearing 5 black setae. Second and third thoracic segments and the first abdominal segment are similar to each other. Each has a single, simple, black seta on either side of the mid-dorsum, and has scoli dorsolaterally, each with one terminal and seven peripheral brown setae, tipped with black. Bases of scoli on the third thoracic segment are ringed with white. There are veruccae at the base of each dorsolateral scolus bearing simple black setae; two setae on each verucca on the first abdominal segment, and four to five setae on each verucca on the second and third abdominal segments.

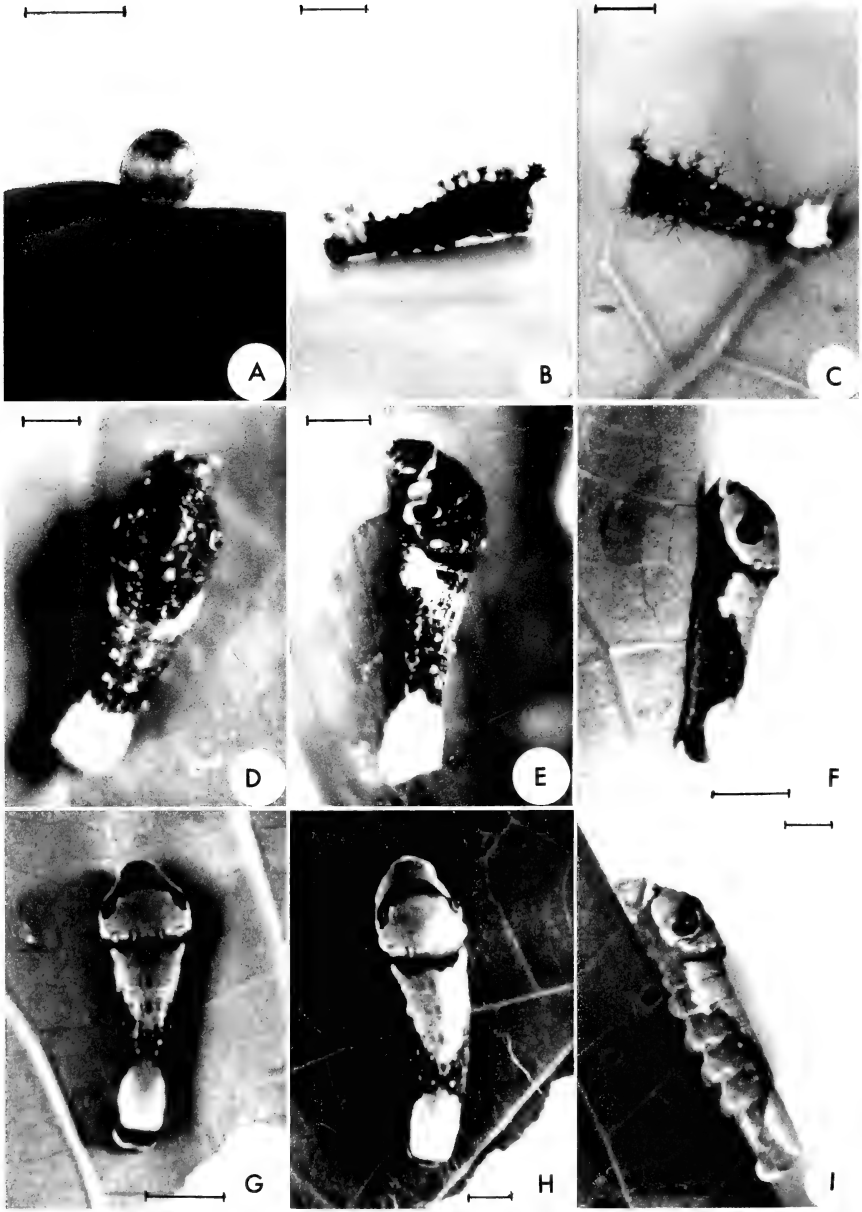


FIG. 1. *Papilio homerus*. A, Egg; B–I, Larva: B, First instar, lateral aspect; C, First instar, dorsal aspect; D, Second instar; E, Third instar; F, Fourth instar, lateral aspect; G, Fourth instar, dorsal aspect; H, Fifth instar, dorsal aspect; I, Fifth instar, lateral aspect. Scale bars: A–C = 0.25 cm; D–E = 0.50 cm; F–I = 1.0 cm.

TABLE 1. Measurements in mm of larval head widths of *Papilio homerus*.

Instar no.	n	Range	Mean	SD
1	13	0.8–1.2	1.00	0.04
2	11	1.7–2.2	1.95	0.01
3	10	2.8–3.0	2.90	0.03
4	9	3.9–4.4	4.10	0.08
5	8	5.7–6.4	6.05	0.09

Abdominal segments 2 to 7 each with a pair of short dorsolateral scoli bearing five setae; a part of base of each scolus is white. Laterodorsally on each of these segments is a single black seta with a brown base. Abdominal segments 2 to 4 pigmented laterally with a white diagonal saddle-like marking with a brownish center. Mid-dorsum becomes light brown posteriorly. Last two segments white and slightly larger than preceding abdominal segments. Each of these two segments with a simple black seta near the mid-dorsum, and white scoli dorsolaterally and laterally, each scolus with one central and seven peripheral white setae with black tips. At base of each lateral scolus, an additional simple seta. Ventral regions, prolegs, and claspers brown; anal region gray. This first stadium lasts 5 days, and the larva grows from 4.0 mm to ca. 9.0 mm in length.

Second instar (Fig. 1D): Head dark brown to black with 5 simple black seta in the ocellar region. Osmeterium and anterior portion of first thoracic segment brown. Anterior segments enlarged to form a mostly black anterior hump which narrows to a brown mid-abdominal region. There is a small scolus with short black setae laterally on the first, and dorsolaterally on the last two abdominal segments. All other major scoli reduced to tubercles that become light brown and ringed with blue as larva grows. Lateral tubercles on the third thoracic segment are the most prominent. Posterior abdominal segments black, except for the last two, which are slightly larger than those preceding and are white dorsally. All darker areas of the larva dotted with fine, circular to ovate, dark spots with lighter peripheral rings. There are white patches laterally between the second and fourth abdominal segments, and a pair of white dorsolateral spots on the last thoracic segment as well as on the first, fourth, fifth and sixth abdominal segments. There are simple black setae laterally on all legs, prolegs, and claspers. The larva is ca. 15.0 mm in length at end of second instar, which lasts 5 days.

Third instar (Fig. 1E): Head light brown. Anterior region of first thoracic segment white and forms ridge above head. Area around osmeterial pits light brown. Osmeterium brown, with a turpenoid scent when extruded.

Anterior segments enlarged to form broad hump ca. 10.0 mm wide, narrowing to an abdomen only half as wide and with only slightly enlarged terminal segments. Basic larval coloration remains dark gray to black, with a darker diamond pattern along mid-dorsum. A broad, white, lateral stripe on thorax tapers to an end on third segment. Immediately above this stripe on third segment, tubercle is black basally and light brown terminally, ringed with a blue crescent dorsally, and subtended ventrally by a separate brown crescent, producing a prominent eye-spot.

Abdominal markings similar to those of previous instar, but segments six and seven have some white coloration dorsally, which merges into the last two segments, which are entirely white. Terminal segment bears two white dorsolateral prominences. Sublateral region brown. I observed larvae drinking water from leaf surfaces. Larva is ca. 26.0 mm long at the end of third instar, which lasts an average of 9 days.

Fourth instar (Fig. 1F, G): When first molted, larva retains coloration and markings of third instar. After ca. 18 hours most areas that were previously white become light green; after approximately 84 hours they become darker green edged with greenish yellow. Head pale brown and withdrawn into thoracic segments. Region around osmeterial pit green; osmeterium brick red. Remaining dorsal, lateral, and ventral regions gray to black. Anterior thoracic and abdominal segments greatly enlarged compared with the relatively narrow posterior region which ends bluntly. Tubercles on third thoracic segment now form very conspicuous eye-spots with a brown dorsal band between. Along the posterior edge of the anterior hump is a white band broken by two blue spots on each side of the dorsum. Anterior portion of abdomen marked with a gray-and-white-flecked saddle across dorsum, with some green coloration mid-dorsally. There are blue spots laterodorsally and laterally on the fifth segment and laterally on the sixth. There are three conspicuous green patches laterally on the seventh segment. Terminal segments white dorsally, with some green mid-dorsally. Spiracles edged with light brown. Claspers gray. Fourth instar lasts an average of 10 days and the larva grows to ca. 40.0 mm in length.

Fifth instar (Fig. 1H, I): Markings and color same as at end of fourth instar. After feeding for 16–24 days, larvae reach 64.0 to 70.0 mm in length. Head gray-brown with major epicranial sutures lighter. Prothorax with first annulation dark brown. Osmeterium brick red when extended. Remainder of thorax green dorsally, except for conspicuous lateral eye-spots at end of a thick, brown band that crosses the dorsum. Other than the green dorsal and lateral markings, larva brown. Crotchets of prolegs arranged in uniserial, triordinal, transverse bands.

Pre-pupa: Larva ceases feeding and all green pigmented areas turn dull green and then yellowish; brown areas become black and all blue spots become pale blue. Just before pupation, larva turns dark gray. Approximately 48 hours after spinning the cremastal pad and thoracic girdle, the larva pupates.

PUPA (Fig. 2A, B). Pupa dull gray immediately after shedding larval skin, then develops into one of three color forms: gray, brown, or brown mixed with green. Each pupal form bears a series of white spots that become prominent a few hours later. Of 7 pupae reared, 5 were brown and 2 were gray. Three pupae were observed in the field: two were suspended on branches of *Hernandia* overhanging streams and were gray; the third pupated on a brown stem of a green fern and was brown mixed with green.

Pupae are 31 to 40 mm in length. Head 6.0–9.5 mm in width; width at wing base 9.0–12.0 mm; maximum width 12.0–18.5 mm across pupal wings. There are small projections on the frontal prominence and at base of the wing-cases. There is a median, blunt, thoracic projection anterior of the wings. Thoracic region dorsoventrally flattened, but not markedly. Abdomen roughly circular in cross section. Between thorax and abdomen, pupa is bent at an angle of approximately 120°. Dorsally, head region marked with a pinkish brown spot anterior of the frontal prominence and with a pair of white dorsolateral spots just behind this prominence. Mid-thoracic region pinkish brown with a faint V-shaped marking. Wing-cases usually have a dark, gray-brown median marking. Abdomen has two pairs of raised, white spots dorsolaterally on the second segment and an additional pair laterodorsally on the third segment behind the wing-cases. Ground color varies and is usually tan brown or dark gray. A third color form is tan brown with extensive areas of lime green on the thorax, abdomen and wing-cases. Pupal stage lasts 10–14 days. Diapause has not been recorded. Adults emerge between 0300 h and 0900 h ($n = 6$, of which 5 were males).

The life cycle takes 64–74 days from egg to adult ($n = 6$).

ADULT (Fig. 2C, D). Both males (FWL = 72.0–76.0; $\bar{x} = 74.5$; $n = 15$) and females (FWL = 74.0–80.0; $\bar{x} = 77.3$; $n = 15$) black with large yellow bands on each wing dorsally. A less conspicuous row of light blue spots occurs distal of the yellow band on the hindwings, which also possess prominent, spatulate, black tails. Females similar to males, but with ground color less intense and yellow and blue markings more intensely colored. Peripheral red markings on hindwings more prominent in the female. Undersides of both sexes similar to uppersides but with ground color predominantly reddish brown rather than black. The Homerus Swallowtail is unmistakable in flight and can be easily identified at a distance. Adult lifespan is unknown.

Field Observations

Papilio homerus was located only in the eastern and western study areas and was not seen on Mount Diablo, although previously it had

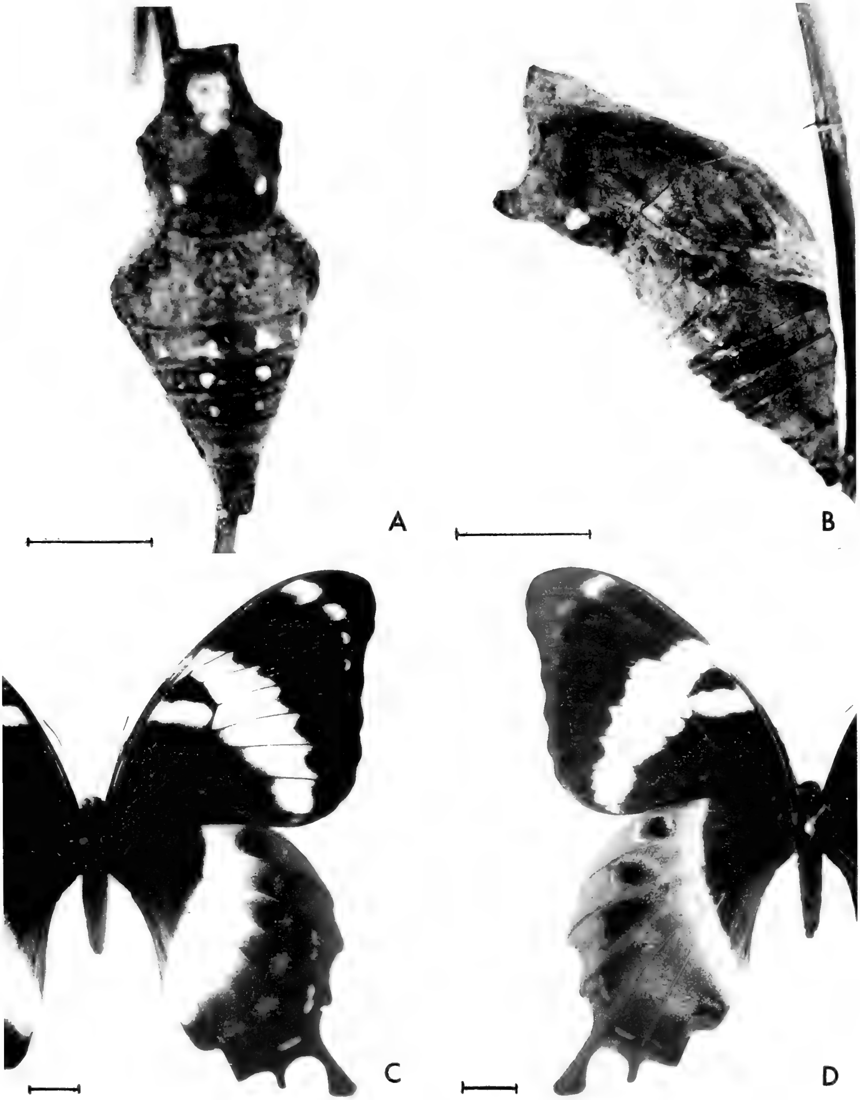


FIG. 2. *Papilio homerus*. A, Pupa, dorsal aspect; B, Pupa, lateral aspect; C, Adult male, dorsal aspect; D, Adult male, ventral aspect. Scale bars = 1.0 cm.

been collected from all three areas (Fig. 3). What once was probably a single population, occupying the central forests of Jamaica, now appears to be divided into two small isolated populations referred to as the eastern and western populations. The central population apparently

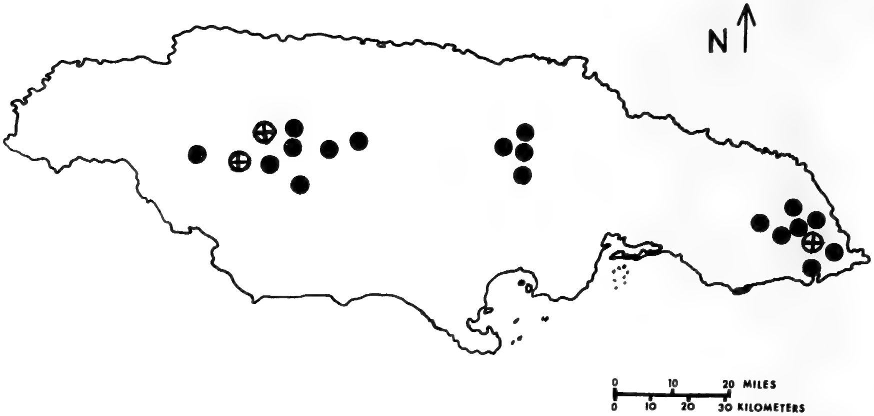


FIG. 3. Past and present distribution of *Papilio homerus* in Jamaica showing the decline of the eastern and western populations. The last recorded capture from the central population was ca. 1925. ⊕ Breeding populations located 1962–1980. ● Collecting localities recorded before 1962; no adults located 1962–1980.

no longer exists. The last capture of this butterfly from the Mount Diablo area was about 1925 (Kaye 1926).

Larval Foodplants

Hernandia catalpaefolia, *H. jamaicensis*, and *Ocotea* sp. (Lauraceae) were recorded as larval foodplants. *Hernandia catalpaefolia*, an endemic species of Hernandiaceae with affinities to Lauraceae, is locally common where the eastern population of *P. homerus* occurs. The local names for this plant are "water mahoe" and "water wood" and should not be confused with the unrelated "blue mahoe" (*Hibiscus elatus*) or "seaside mahoe" (*Thespesia populnea* (L.) Solander ex. Correa), which belong to the Malvaceae and are not larval foodplants. A number of early records of larval foodplants are incorrect, largely due to confusion over colloquial plant names. Kaye (1926) correctly identified *H. catalpaefolia* as a larval foodplant.

I observed one *P. homerus* ovipositing on *H. jamaicensis* in the southwestern region of the Cockpit Country in October 1971. Six eggs were deposited, at intervals of about one every 30 seconds, on the upper surfaces of older leaves at approximately 1400 h. *Hernandia jamaicensis* is an endemic species known locally as "popnut," "pumpkin wood," or "suck axe," and is locally common where the western population of *P. homerus* occurs. This is the first record of *H. jamaicensis* as a foodplant for *P. homerus*. In August 1969, I observed a female lay 14 eggs between 1500 and 1600 h on one tree of *Ocotea* sp. (tentatively identified as *O. leucoxylon* (SW.) Gómez maza) (Lauraceae) at Corn

Puss Gap. Lewis (1949) also observed oviposition on *Ocotea* in the Cockpit Country. Another potential larval foodplant is *Hernandia sonora* L., which was introduced into early forestry cultivations in Jamaica and is recorded at Moneague in the northern foothills on Mt. Diablo (C. D. Adams pers. comm.). The present status of this introduction is not known. *Ocotea* sp. also occurs on Mt. Diablo and either plant could have been the host plant for the central population.

Larval Behavior

All eggs collected in the field (n = 23) were found on *H. catalpaefolia* and were oviposited 1–3 m above the ground on the top of older leaves rather than on terminal shoots. Eggs were laid singly, but up to 5 eggs of different ages were often found on the same leaf. Two collected eggs failed to hatch due to unknown causes, but no parasitism was observed. On three occasions, between 1000 and 1400 h, I observed a large ant remove a total of seven eggs from a foodplant leaf.

Larvae were usually solitary, but occasionally four to five larvae (fourth and fifth instars) were collected resting on a silken mat spun on top of a single leaf often positioned beneath other overhanging leaves. Larvae in the first three instars fed on mature leaves; in the final two instars, larvae fed on younger leaves. Larvae were reluctant to extrude osmeteria even when disturbed, although when extruded, osmeteria emitted a mildly pungent, turpenoid scent. Although larval coloration appears to mimic bird or lizard excrement in the first three and early fourth instar, larvae of all ages were subject to predation from birds. On three occasions, between 1000 and 1400 h, I observed a species of *Elaena* (Tyrannidae) take first, second, or third instars (a total of four) from small marked plants on which the black and white larvae were resting, exposed on tops of leaves. On one occasion, at 1300 h, I watched an oriole, *Icterus* sp. (Icteridae) take green fourth (n = 2) and fifth (n = 3) instars from the tops of leaves of a sapling.

Adult Behavior

Papilio homerus was observed flying as early as 0900 h in sunny weather. Density of vegetation, steep terrain, and narrow trails often made capture or prolonged observation of adults difficult. Usually no more than three different individuals were observed on days with favorable weather conditions, but each individual was often sighted several times. Most observations were less than a minute in duration, but observations for longer periods were often possible while adults were sunning, circling, feeding, or ovipositing.

Single adults made short flights from the forest to a sunlit area and selected a large leaf, often that of *Cecropia peltata* L. (Moraceae), on which they settled and remained, for as long as 35 min, with wings outspread. This behavior was also noted by Walker (1945) and Avinoff (in Brown & Heineman 1972). After sunning, the butterfly ascended to the forest canopy or flew to clearings in search of nectar sources. Species of *Cissus* (Vitaceae), *Mecranium* (Melastomaceae), *Lantana* (Verbenaceae), *Asclepias* (Asclepiadaceae), *Bidens* (Asteraceae), and a malvaceous shrub were recorded as nectar sources. *Cissus* provided the main nectar resource at Corn Puss Gap where there are few plants flowering at any one time. Walker (1945) also reported adults feeding on *Cissus*. In addition, Lewis (1947) recorded *Spathodia* (Bignoniaceae) as a nectar source. Adults spent less than a minute visiting each flowering plant near the ground, but *Cissus* vines hanging from other trees presented a long array of small flowers that were visited briefly or occasionally for up to 10 min. All specimens caught while nectaring were males (n = 4).

By 1000 h, some adults started circling slowly, high above the canopy, in the natural horseshoe-shaped amphitheaters delineated by the forest where mountain streams flow over cliffs. The same individuals, identified by distinct wing damage, occupied this territory for as long as four hours at a time without nectaring and returned to the same location on consecutive days. When captured, these individuals were found to be males (n = 6). Females were collected flying along stream beds (n = 5) and along intersecting clearings in the forest, under the canopy, where larval foodplants grew (n = 5). Males were also captured under the canopy (n = 7) or descending or ascending streams (n = 10).

Predation of adults by birds was also observed. Loggerhead flycatchers (*Tolmarchus* sp., Tyrannidae) attacked adults either when the butterflies were resting on top of foliage with wings outstretched (n = 7) or in flight (n = 13). Adults that escaped from such attacks usually sustained noticeable wing damage. Beak damage from unidentified birds is also evident on some museum specimens (n = 24). Adults of both sexes emitted a strongly perfumed, turpenoid scent when handled. This scent was similar, but not identical, to that emitted from larval osmeteria and appears to emanate from the thoracic segments. Courtship and mating were not observed. Oviposition occurred between 1000 and 1600 h (n = 12).

Three overlapping broods were identified at Corn Puss Gap between April and October: mid-April to June, June to mid-August, and August to October. Immature stages have been collected between August and December at lower elevations, representing two broods: August to mid-October and October to December.

At ca. 1300 h, adults started flying down the mountain slopes, usually following streams and flying in groups about 4 m above the stream bed. This daily flight was spectacular when the species was abundant. In 1962, as many as 18 individuals were counted in 1.5 h descending a stream just south of the Gap. Six of these were captured and all were males. By 1500 h this flight was largely over and adults were rarely seen after this time. Avinoff (in Brown & Heineman 1972) noted seeing adults flying as late as 1800 h but did not specify where these observations were made. When populations were small, this daily movement was less noticeable. No large-scale daily movement was seen between 1969 and 1980.

In addition to the local daily migrations observed in summer near Corn Puss Gap (elev. 600 m), the eastern population also exhibits seasonal vertical movement.

Corn Puss Gap was visited in all months of the year, but *P. homerus* was not seen at this locality from January through March. Adults were first seen in April when ovipositing on *Hernandia* was also observed. Their numbers increased in May and June but most (73%) of the adults were seen during July and August. Only six individuals were seen from September through December during the entire study.

In September, minimum temperatures in the Corn Puss Gap area fall below 20°C, there are heavy daily rains, and the forest is shrouded in low cloud. The reduction in numbers of adults coincides with these weather changes. In April, after the minimum temperature has risen above 20°C and the cloud cover lifts, adults again can be found in this area.

Papilio homerus was found along tributaries of the Plantain Garden River, southeast of the Gap, and along tributaries of the Rio Grande, northeast of the Gap at elevations as low as 220 m. Adults have been collected in these lower localities in most months of the year. My records of 37 individuals observed in the Rio Grande Valley show that 73% were collected from September through March. Immature stages were seen from August through December.

Comparison with Related Species

Papilio homerus belongs to the tribe Papilioninii, the fluted swallowtails. Collins and Morris (1985), summarizing earlier authorities, list Central American species that are morphologically similar to *P. homerus*. These include *P. birchalli* Hewitson in the *scamander* species-group and *P. victorinus* Doubleday, *P. garamas* Geyer, and *P. abderus* Hopffer in the *homerus* species-group.

Like *P. homerus*, the adults of these species usually can be seen flying over the canopy in humid cloud forests and females oviposit on species of Hernandiaceae and Lauraceae. Eggs are laid singly, often on saplings, are similar in size, though not in color to *P. homerus,* and larvae emerge after a development of time of about eight days.

The immature stages of *P. victorinus* are described in part by Muyshondt et al. (1976), Young (1984), DeVries (1987), and Comstock and Vasquez (1961). The sites of oviposition both dorsally and ventrally on young and mature *Hernandia* leaves, the relatively equal size of dorsal setae, color pattern, ready use of osmeteria in the first instar, and erect pupae with dorsal and lateral longitudinal markings all differ significantly from *P. homerus.* However, the third instar of both species appear similar in shape, color, and behavior. The fifth instar of *P. homerus, P. victorinus,* and *P. birchalli* also show similarities. They are mostly green dorsally with an enlarged thoracic region bearing spectacled eyespots, and a darker "crossed" mark mid-abdominally. The pupa of *P. birchalli* (DeVries 1987) is also said to be "similar to *thoas* only much rounder, with larger abdomen and rounded head area". This description also could be applied to the pupa of *P. homerus* but there is no mention of the very distinctive white dorsal spots as found on *P. homerus.* Beutelspacher (1980) states that the mature larva of *P. garamus* is similar to that of *P. homerus,* but sufficient details have not yet been published for a detailed comparison. K. S. Brown Jr. (pers. comm.) regards *P. garamas* and *P. abderus* as conspecific. He has made comparisons of all the adults and immature stages discussed here, and is of the opinion that *P. garamas* is probably a near relative of *P. homerus* but that *P. homerus* should be considered distinct.

Determining the degree of affinity of *P. homerus,* which has been isolated on Jamaica, to related species in Central and South America may prove difficult because of hybridization between several of those species and subspecies. Additional life history information is needed to help clarify these affinities.

ACKNOWLEDGMENTS

The author thanks I. Goodbody for making available facilities of the Zoology Department, University of the West Indies, C. D. Adams for identifying larval foodplants and related species, T. C. Emmel for valuable discussions, T. H. Farr, Institute of Jamaica and D. Hopwood for assistance with field work, and the reviewers for their comments on the manuscript.

LITERATURE CITED

BEUTELSPACHER, C. R. 1980. Mariposas diurnas del Valle de Mexico. Edificiones cientificas L.P.M.M. Mexico Registro de Cámara Nacional de la Industria Editorial No. 00106. p. 31.

BROWN, F. M. & B. HEINEMAN. 1972. Jamaica and its butterflies. E. W. Classey Ltd., London. 478 pp.

COLLINS, N. M. & M. G. MORRIS. 1985. Threatened swallowtail butterflies of the world. The IUCN Red Data Book. IUCN, Gland and Cambridge. 401 pp.

COMSTOCK, J. A. & L. VASQUEZ. 1961. Estadios de los ciclos biologicos en lepidopteros Mexicanos. Ann. Inst. Biol., U.N.A. Mexico 31:349–448.

DEVRIES, P. J. 1987. The butterflies of Costa Rica and their natural history. Princeton Univ. Press, Princeton. 327 pp.

GOSSE, P. H. 1879. On *Papilio homerus,* its ovum and larva. Proc. Entomol. Soc. Lond. 1879:lv–lviii.

KAYE, W. J. 1926. The butterflies of Jamaica. Trans Entomol. Soc. Lond. 73:455–504.

LEWIS, C. B. 1947. Butterfly notes and records. Natural History Notes, Institute of Jamaica 3(29–30):91.

——— 1949. Butterfly notes. Natural History Notes, Institute of Jamaica 4(39):48.

MUYSHONDT, A., A. MUYSHONDT JR. & P. MUYSHONDT. 1976. Notas sobre la biologica de lepidopteros de El Salvador. I. Rev. Soc. Mex. Lepid. 2:77–90.

PANTON, E. S. 1893. A description of the larva of *Papilio homerus*. J. Inst. Jamaica 1: 375–376.

PETERSON, A. 1962. Larvae of Insects. Lepidoptera and Hymenoptera. Part 1. 4th edition. Edwards Brothers Inc., Ann Arbor, Michigan. 315 pp.

SWAINSON, E. M. 1901. Notes on lepidopterous larvae from Jamaica. J. New York Entomol. Soc. 9:77–82.

TAYLOR, C. B. 1894. The description of the larva and pupa of *Papilio homerus* Fabricius. Trans. Entomol. Soc. Lond. 42:409–410.

WALKER, D. J. 1945. *Papilio homerus*. Natural History Notes, Institute of Jamaica 2(22–24):161–163.

WELLS, S. M., R. M. PYLE & N. M. COLLINS. 1983. The IUCN Invertebrate Red Data Book. IUCN, Cambridge and Gland. 632 pp.

YOUNG, A. M. 1984. Notes on the natural history of *Papilio victorinus* Doubl. (Papilionidae) in northeastern Costa Rica. J. Lepid. Soc. 38:237–242.

Received for publication 16 September 1988; revised 7 August 1991; accepted 29 August 1991.

Journal of the Lepidopterists' Society
45(4), 1991, 272–290

THE STATUS OF SILVERY BLUE SUBSPECIES (*GLAUCOPSYCHE LYGDAMUS LYGDAMUS* AND *G. L. COUPERI*: LYCAENIDAE) IN NEW YORK

ROBERT DIRIG

Bailey Hortorium Herbarium, 462 Mann Library,
Cornell University, Ithaca, New York 14853

AND

JOHN F. CRYAN

New York State Department of Environmental Conservation, 1 Hunterspoint Plaza,
47-40 Twenty-first Street, Long Island City, New York 11101

ABSTRACT. Two subspecies of the Silvery Blue (*Glaucopsyche lygdamus*, Lycaenidae) are recorded from New York. The nominate subspecies was reported from central New York through 1969, but has not been seen from 1970–1991. Adults flew in May, and larvae fed on native Wood Vetch (*Vicia caroliniana*, Fabaceae) on steep, naturally unstable, southwest-facing shale banks. *Glaucopsyche lygdamus couperi* is reported for the first time from northern New York (and Vermont), where its larvae feed on planted or naturalized Tufted Vetch (*Vicia cracca*), and adults fly in June on weedy road banks. This butterfly is spreading south using vetch-lined highway corridors. The two entities exhibit marked ecological and phenotypic contrasts in New York.

Additional key words: Fabaceae, *Vicia cracca*, *Vicia caroliniana*, range expansion, rare species.

The Silvery Blue, *Glaucopsyche lygdamus* (Doubleday) (Lycaenidae), has been considered rare and local in New York, where the nominate subspecies reaches its northern limit (Klots 1951, Shapiro 1974, Opler & Krizek 1984). Literature references and specimens are scanty, and almost nothing has been published about its natural history in New York. Scudder (1889) said that ssp. *lygdamus* was "known from the upper waters of the Susquehanna [River]," but gave no details. Forbes (1928, 1960) reported the "type race" from Ithaca, Tompkins County, and Binghamton, Broome County, suggesting in 1928 that it was "probably a leguminous feeder," and in the later paper listing *Lathyrus* sp. and *Vicia caroliniana* Walt. (Fabaceae) as larval foodplants without specifically referring to New York populations. Shapiro (1974) discussed the nominate subspecies, stating that its foodplants were "unreported in New York," and noting that "its reputed hosts, *Lathyrus* and *Vicia*, are widespread" in the state. Shapiro (*loc. cit.*) also suggested that *G. l. couperi* Grote, although "unrecorded for New York . . . , probably occurs in the northernmost counties, since it is common in nearby Quebec."

In 1977 we began to search for ssp. *lygdamus* at former and potential localities in the Finger Lakes region of central New York. Correspondence and conversations with the late Laurence R. Rupert (see biographical notes in Dirig & Cryan 1986), who discovered the population at Horseheads, and with John G. Franclemont, who observed the butterfly at Ithaca in the 1930's, elicited unpublished life history information and detailed habitat notes for the typical subspecies. In 1984 we discovered *G. l. couperi* in northern New York, where it appears to be moving south along vetch-lined highway corridors in much the same way that the Inornate Ringlet (*Coenonympha inornata* W. H. Edwards, Satyridae) has since the early 1970's (Shapiro 1974, Dirig 1977, authors' unpubl. data 1973–present). This paper presents historical information on the nominate subspecies in central New York and observations of the recently discovered *G. l. couperi* population in the northern part of the state.

Forbes (1960) used the vernacular names "Southern Silvery Blue" (SSB) for the nominate (Appalachian, eastern United States) subspecies of *Glaucopsyche lygdamus,* and "Northern Silvery Blue" (NSB) for subspecies *couperi* (which occurs in Canada and along the United States border in the northeastern part of North America) (Fig. 1). We retain these common names throughout this paper, abbreviated as shown. In older literature, the SSB was known as subspecies *nittanyensis* F. Chermock. Miller and Brown (1981) and Hodges et al. (1983) regarded *nittanyensis* as a synonym of the nominate subspecies.

New York specimens of these two butterflies are quite distinct (Fig. 2). SSB's are significantly smaller (see Discussion). Dorsal wing surfaces of SSB males are paler silvery blue than those of the NSB. SSB females have much narrower dark wing borders dorsally than NSB's, and the forewing apices are more rounded in SSB's. The ventral wing surfaces are browner and have larger black spots with relatively very narrow white rims in the SSB, in contrast to a greyer ventral ground color with coarser scaling basally and much smaller dark spots with wider white margins in the NSB (Fig. 2). Klots (1951) made similar observations regarding these two entities. The SSB is rare and local, perhaps now extirpated, in New York, whereas the NSB is common and becoming widespread.

Lepidoptera names follow Ferris (1989); plant nomenclature follows Mitchell (1986).

THE SOUTHERN SILVERY BLUE IN CENTRAL NEW YORK

Historical Distribution

Table 1 presents available New York records of the SSB. The butterfly was univoltine with a May–early June flight season. Few New York specimens exist, most from the Horseheads locality. The butterfly has been reported from five contiguous counties (Fig. 3).

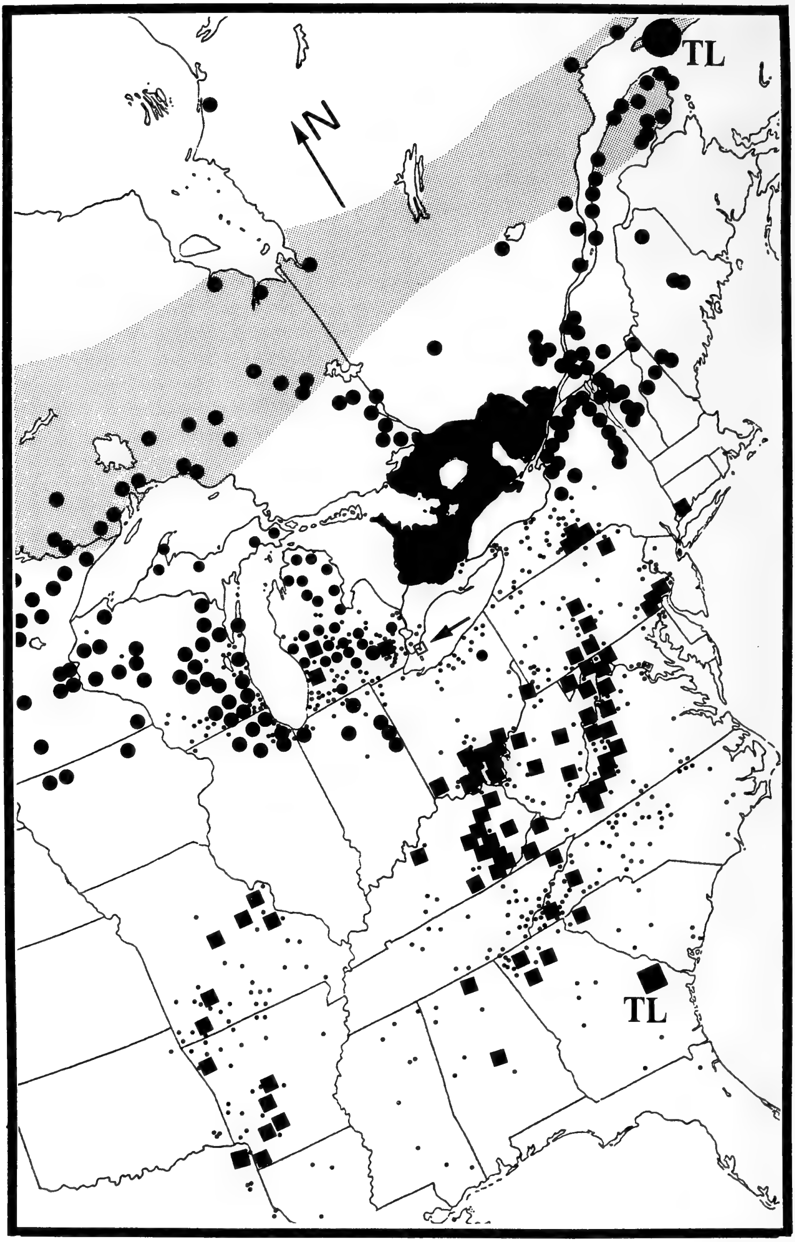


FIG. 1. The Silvery Blue Butterfly (*Glaucopsyche lygdamus*) in eastern North America. Grey shaded area (top) is the range of ssp. *couperi* shown by Scudder (1889). Large black circles and the solid black area in southern Ontario are the known distribution of ssp. *couperi* through 1991, based on literature, specimens, and correspondence. Smaller black circles in Michigan and Ohio are records of unknown subspecies, after Opler (1983)

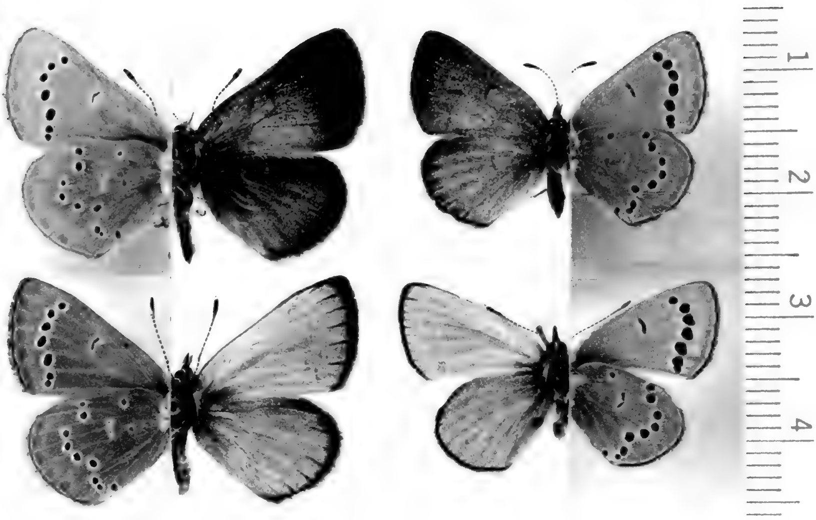


FIG. 2. New York specimens of *Glaucopsyche lygdamus*. LEFT: ssp. *couperi* from Ogdensburg, 4 June 1984 (Dirig collection). RIGHT: the nominate subspecies from Horseheads collected by L. R. Rupert, female on 19 May 1947 (CUIC), male on 2 May 1949 (Dirig collection). Females at top, males at bottom, venters of same specimens, scale numbers in centimeters. (Photos by Kent Loeffler.)

Habitat

Since the SSB is restricted to a specific natural situation in New York, we present descriptions of two known habitats below.

Laurence R. Rupert described the Horseheads locality of this rare butterfly thus (letter, 19 February 1977): "[T]he spot . . . is very small. . . . The butterflies were quite common along a stretch of the roadway that was very rocky and quite barren. It was steep, with no trees of any size, and few bushes. There was a rangy species of *Vicia* growing there . . . [with] pale lavender [flowers]." Following specific directions Rupert supplied elsewhere in this letter, we visited the site during the SSB flight season on 6 May 1977; and revisited it with Rupert on 7 August 1977.

←

and David C. Iftner and John V. Calhoun's unpublished Ohio distribution map. Black squares are localities of the typical subspecies, after Opler (1983) and Iftner and Calhoun's Ohio map. Open square (arrow) at Point Pelee, Ontario, is a record of the typical subspecies, interpreted as an immigrant by Wormington (1983). Largest black circle and square labelled "TL" are type localities of ssp. *couperi* on Anticosti Island and nominate *lygdamus* in Georgia. Smallest dots are records of *Vicia caroliniana* based on ca. 1275 specimens from 21 herbaria.

TABLE 1. Records of the Southern Silvery Blue [*Glaucopsyche lygdamus lygdamus* (Doubleday)] in central New York, at the northern limit of its range. CUIC = Cornell University Insect Collection, AMNH = American Museum of Natural History, USNM = United States National Museum, Smithsonian Institution. Specimens marked with an asterisk (*) show apparent introgression with *G. l. couperi* Grote.

Broome County, Town of Binghamton

Binghamton, May, before 1926 (Forbes 1928).
Binghamton, Asylum Hill, June, A. B. Klots, 2 males, AMNH.

Chemung County, Town of Horseheads

Horseheads, 12 May 1947, 3 males, CUIC, USNM; 19 May 1947, 2 males, 2 females, CUIC; 4 May 1948, 2 males, CUIC; 2 May 1949, 6 males, 1 female, USNM, authors' collections; all collected by L. R. Rupert.
Elmira, 14 June 1907, E. I. Huntington, female and male, AMNH.

Cortland County, Town of Harford

Beam Road Barrens, 14 May 1968, A. M. Shapiro, female, CUIC*.

Tioga County

Unspecified locality, between 1840 and 1982 (Opler 1983).

Tompkins County

Town of Caroline, Besemer, 16 May 1969, A. M. Shapiro, 2 males, CUIC*.
Town of Ithaca, Ithaca, 17 May 1914, J. R. Eyer, female, CUIC (Forbes 1928).
Town of Ithaca, Sixmile Creek, 1930's, J. G. Franclemont.
"Ithaca, McLean Bog" (which is 27 km northeast of the city), 4 May 1937, E. J. Gerberg, female, AMNH.

Unspecified

"New York," M. Rothke, male, AMNH.

The Horseheads population was found on the east (southwest-facing) bank of a dirt road east of State Rt. 17 and south of Latta Brook Rd. The road spiralled up a wooded hill of 50° slope from its base at elevation 275 m to 380 m at the site. A steeper 70° slope continued on the east side of the road to the summit at 460 m. The soil consisted largely of 4- to 5-cm-long, angular grey shale fragments which were naturally unstable on such a declivity. (Walking off the road in the area caused the stony flakes to slide dangerously at each step.) Latta Brook flows into Newton Creek around the base of the hill, within the upper Susquehanna River tributary system.

FLORA: In bloom on 6 May 1977 were *Anemonella thalictroides* (L.) Spach. and *Thalictrum dioicum* L. (Ranunculaceae); *Polygala paucifolia* Willd. (Polygalaceae); *Arabis lyrata* L. (Brassicaceae); *Phlox subulata* L. (Polemoniaceae); *Antennaria plantaginifolia* (L.) Richards (Asteraceae); and *Vicia caroliniana*. Some of these may have served as nectar sources for SSB's in the past, and *V. caroliniana* was the presumed larval foodplant.

On 7 August 1977, additional plants were noted. Trees included *Acer rubrum* L. (Aceraceae); *Quercus velutina* Lam. (Fagaceae); *Carya glabra* (Mill.) Sweet (Juglandaceae); and *Prunus serotina* Ehrh. (Rosaceae). Smaller trees and shrubs were *Corylus americana* Walt. and *Carpinus caroliniana* Walt. (Betulaceae); *Hamamelis virginiana*

L. (Hamamelidaceae); *Sassafras albidum* (Nutt.) Nees (Lauraceae); *Diervilla lonicera* Mill. and *Viburnum acerifolium* L. (Caprifoliaceae); *Vaccinium pallidum* Ait. (Ericaceae); *Amelanchier arborea* (Michx. f.) Fern. (Rosaceae); and sprouts of *Castanea dentata* (Marsh.) Borkh. (Fagaceae). *Smilacina racemosa* (L.) Desf. (Liliaceae); *Pteridium aquilinum* (L.) Kuhn (Cyatheaceae); *Asplenium platyneuron* (L.) BSP. and *Dryopteris marginalis* (L.) Gray (Aspleniaceae); *Geranium maculatum* L. (Geraniaceae); *Achillea millefolium* L. and *Solidago* sp. (Asteraceae), composed the herb layer. Herbarium specimens collected from this locality were deposited in the Bailey Hortorium Herbarium (BH) at Cornell University.

Rupert indicated that the area was much more densely grown over in 1977 than when he had last visited it about 30 years before. He stressed that "the place where I found the butterflies was quite limited, . . . a southwest-facing bank, very stony and *with little vegetation at the time*" [our italics] (letter, 15 June 1977).

The SSB also occurred on an exposed bank in the Sixmile Creek gorge at Ithaca, at least through the late 1930's (John G. Franclemont pers. comm. 1977). The site is a steep, stony, southwest-facing promontory with a 60° slope, rising from 165 m elevation in the stream bed to 200 m at its wooded summit. The butterflies occurred at the sunny base of the hill, and were easily discovered along the footpath edging the creek.

FLORA: Plants growing at the Sixmile Creek site in 1986 included *Vicia caroliniana*; *Ceanothus americanus* L. (Rhamnaceae); *Hamamelis virginiana*; *Pteridium aquilinum*; *Helianthus divaricatus* L., *Solidago nemoralis* Ait., *S. caesia* L., and *Aster patens* Ait. (Asteraceae); and *Vitis* sp. (Vitaceae). Flora along the path and bedrock outcrops at the base of the slope included saplings of *Fagus grandifolia* Ehrh. (Fagaceae); *Platanus occidentalis* L. (Platanaceae); *Tsuga canadensis* (L.) Carr. and *Pinus strobus* L. (Pinaceae); *Acer saccharum* Marsh. (Aceraceae); *Tilia americana* L. (Tiliaceae); *Fraxinus americana* L. (Oleaceae); and *Rhus typhina* L. (Anacardiaceae). An open space of only 10 × 30 m at the base of the slope implies that the butterflies were intensely local. Soil on the unstable part of the slope, where *Vicia caroliniana* was growing, was mixed with sliding, angular grey shale fragments. We expect that this area was more open and much less disturbed half a century ago, when the butterflies were there.

Other patches of *Vicia caroliniana* occurred upstream in similar, steep, unstable, exposed situations. *Taenidia integerrima* (L.) Drude and *Zizia aptera* (Gray) Fern. (Apiaceae), and *Hepatica nobilis* Mill., var. *obtusa* (Pursh) Steyerm. (Ranunculaceae), have also been associated with *V. caroliniana* at additional sites in Tompkins and Schuyler counties (herbarium specimens in BH).

The SSB thus occupied an essentially pristine habitat remote from human access and disturbance—yet naturally in a state of flux. Such relatively warm microclimates are not surprising at the northern outposts of this southern butterfly. The great fragility and vulnerability of its habitats are apparent. They are, in fact, a northern approximation of the mid-Appalachian shale barrens communities described by Keener (1983), where this butterfly thrives (Opler & Krizek 1984).

Larval Foodplant

Wood or Carolina Vetch (*Vicia caroliniana*) is the only known larval host of the SSB (Opler & Krizek 1984). This native perennial legume

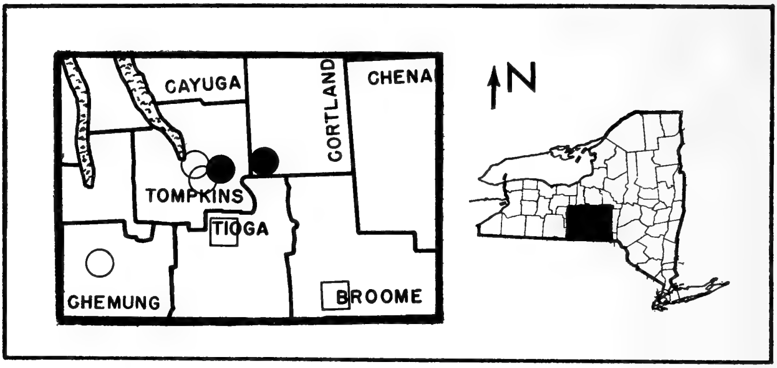


FIG. 3. Historic distribution of the Southern Silvery Blue (*Glaucopsyche lygdamus lygdamus*) in central New York, based on literature and specimen records (Table 1). Black circles are specimens from the 1960's; open circles represent populations believed to be extinct; open squares are populations of unknown status.

occurs spottily throughout the Finger Lakes, the upper Susquehanna River tributaries (near Horseheads), the Genesee River system west of the Finger Lakes, and in the Allegheny and Niagara River systems in western New York (Fig. 4). The greatest number of records come from Ithaca and Chemung County, perhaps due to more extensive botanical exploration of these regions. Wood Vetch ranges from New York and southern Ontario to Wisconsin, and south to Georgia, Alabama, Mississippi, Louisiana, Oklahoma, and northeastern Texas (Fernald 1950, and specimens loaned to us) (Fig. 1). Distribution of the SSB follows the vetch in mountainous or dissected topography from New York and southwestern Connecticut through Pennsylvania, Ohio, West Virginia, Virginia, Maryland, Kentucky, Tennessee, and the Carolinas to Georgia and Alabama (Opler 1983, and specimens examined by us), and west to Missouri (Heitzman & Heitzman 1987), Arkansas, and Texas (Karpuleon 1970) (Fig. 1).

This beautiful plant blooms in May in New York. The 1-cm-long corolla is white, marked with lavender on the keel. Plants average 0.3–0.5 m long, but may reach 1.5 m. They are weak-stemmed and sprawling, loosely held by forked tendrils that terminate the compound leaves, and often grow in large masses. Thus they are conspicuous and easily found in the steep open habitats where they grow. SSB larvae feed on flowers and developing seed pods (Opler & Krizek 1984). The flight season of the butterfly, early to mid-May, coincides precisely with the bloom season of the foodplant, and finding the insect implies the nearby occurrence of its host. The best search strategy is to seek blooming plants and then look for butterflies around them.

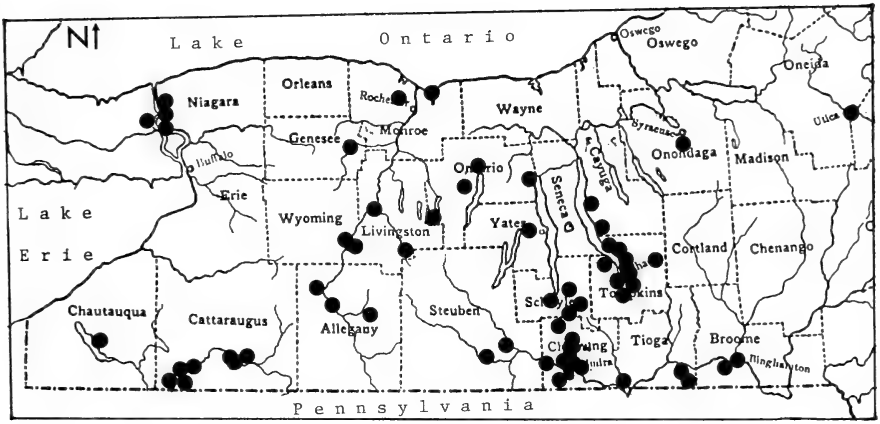


FIG. 4. Known New York distribution of Wood Vetch (*Vicia caroliniana*), larval host of the Southern Silvery Blue. Not shown is a station on Staten Island (Richmond County).

Basal parts of the vetch may remain green throughout the winter (13 cm of a 30-cm-long stem still green, late March 1986), and new shoots appear in early spring (9 April 1977, 23–30 March 1986, at Sixmile Creek, Ithaca). Plants have seeded by mid-July at the same site. Thorough botanical descriptions were given by Fernald (1950) and Gleason (1952). Newcomb (1977) published a good picture for field use (apically rounded leaflets are distinctive).

Reports of "*Lathyrus*" (Forbes 1960, Shapiro 1974) as a SSB foodplant in New York are almost certainly in error, referring to records of *G. l. couperi* or the several western subspecies of this butterfly (Ferris 1989).

Status

No living individuals of the SSB are known from New York since 1968–69 (Table 1). We have done field work annually in central New York between 1968–1991, but have not seen this butterfly.

Trees and shrubs have grown to large size at Rupert's Horseheads locality, changing its character since the late 1940's. Whereas Wood Vetch grew in an 8-m-long solid patch along the east bank of the road 30 years ago (according to Rupert), we found only a dozen plants there in 1977. Vegetational succession may have crowded or shaded out the vetch—and thus the butterfly. We explored this entire hill, looking for more vetch, but found none in 1977. The butterfly is almost certainly gone from this locality.

Wood Vetch still occurs in the Sixmile Creek gorge, but the butterfly is certainly gone from the place where Franclemont observed it 50 years ago, at least since 1968. This bank is small with less than a dozen vetch plants at present, and a hiking trail at its base has had heavy traffic in recent years.

The SSB may still occur in New York. The remoteness and wide separation of its habitats, especially in recent decades, would make colonization of new areas difficult. A careful survey is needed to determine if this butterfly merits an official "threatened," "endangered," or "extirpated" classification by the New York State Department of Environmental Conservation and the New York Natural Heritage Program. Any extant or new populations should be reported to the Director, New York Natural Heritage Program, 700 Troy-Schenectady Road, Latham, New York 12110-2400, and specimens deposited in museums. Populations are probably quite small; only a few specimens should be collected.

THE NORTHERN SILVERY BLUE IN NORTHERN NEW YORK

Locality Records

While visiting Ottawa, Ontario, in early June 1984, we saw the NSB for the first time. Ross A. Layberry, our host, suggested that we check for the butterfly in northern New York, since it was known in southern Ontario nearly to the United States border.

Re-entering New York at Ogdensburg, St. Lawrence County, we immediately found NSB's on the road banks (state record). We continued south through St. Lawrence and Jefferson counties, discovering NSB's everywhere we looked within the 88-km span between Ogdensburg and Watertown (sites 1–6, Fig. 5). We were surprised, on 29 May 1985, to find two males as far south as Glens Falls, Warren County (site 7, Fig. 5), 200 km south of the Canadian border and but 70 km north of Albany in the upper Hudson River valley. On 31 May–1 June 1985, we found NSB's at nine additional sites in Warren, Essex, Clinton, Jefferson, and Lewis counties (sites 8–16, Fig. 5). Field work in 1986–87 disclosed the butterfly in Franklin and Saratoga counties as well (sites 17–24, Fig. 5). A very early specimen was collected at Cicero, Onondaga County, on 5 May 1991 by David P. Shaw (site 25, Fig. 5). Voucher specimens are in the authors' collections, Cornell University Insect Collection (CUIC), American Museum of Natural History (AMNH), and United States National Museum, Smithsonian Institution (USNM).

Habitat

Site 1 in St. Lawrence County (Fig. 5) was located on the eastern half of Ford St. (extension), between its junctions with Rts. 37-812 and Proctor Ave. in Ogdensburg. The site is typical, and a brief description

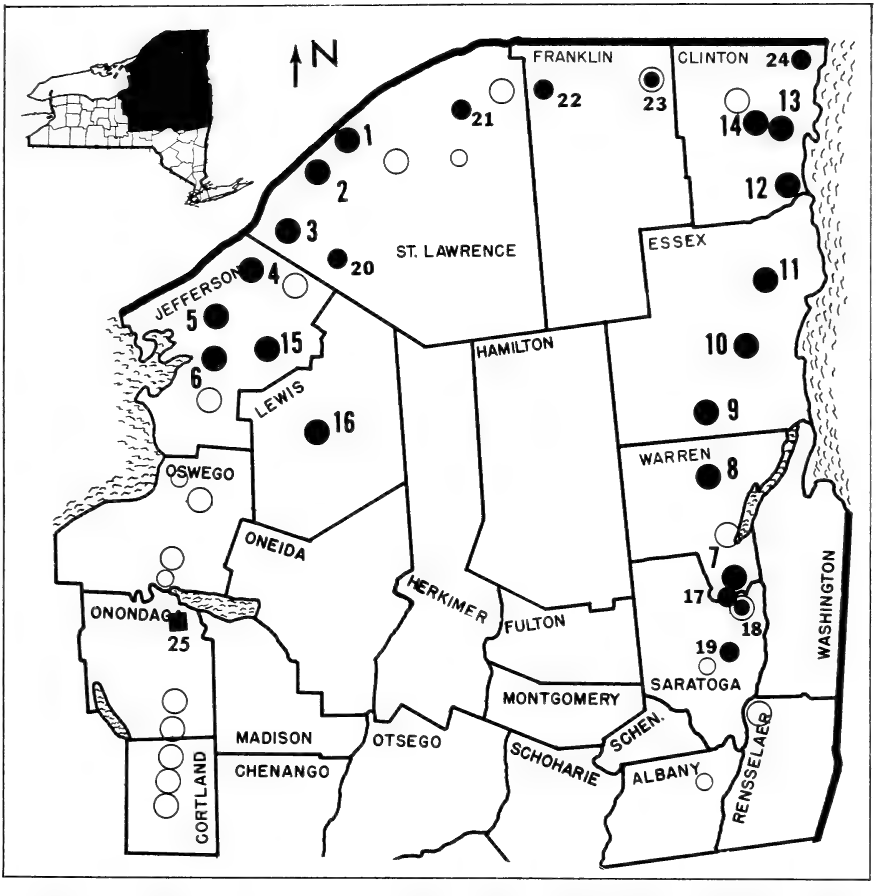


FIG. 5. Distribution of the Northern Silvery Blue (*Glaucopsyche lygdamus couperi*) in New York through 1988 (with an additional 1991 site). Black circles 1–6 from 1984, 7–16 from 1985. Open circles of same size are places the butterfly was not found in 1984–85. Smaller black circles 17–19 are 1986 records, 20–24 from 1987 (including 18 and 23 in areas where the butterfly was not previously found). Smaller open circles are sites without the butterfly in 1986–87. Black square is site 25, 1991. All sites documented by specimens.

may be helpful to others who seek this butterfly in New York or elsewhere at similar latitudes. The paved two-lane road had shoulders as wide as the lanes leading to a shallow sandy ditch, with open sunny banks eventually grading into shrubs and large trees.

FLORA: On 4 June 1984, blooming roadside herbs included **Stellaria graminea* L. and **Lychnis flos-cuculi* L. (Caryophyllaceae); *Potentilla canadensis* L. and *Fragaria virginiana* Mill. (Rosaceae); *Sisyrinchium montanum* Greene (Iridaceae); **Taraxacum officinale* Weber *ex* Wiggers (Asteraceae); **Barbarea vulgaris* R. Br. (Brassicaceae); **Medicago lupulina* L. (Fabaceae); and several Poaceae. Other herbs, not in bloom, were

Euthamia graminifolia (L.) Nutt. *ex* Cass. and *Solidago* spp. (Asteraceae); *Equisetum arvense* L. (Equisetaceae); **Hypericum perforatum* L. (Clusiaceae); **Daucus carota* L. and **Pastinaca sativa* L. (Apiaceae); **Ranunculus acris* L. (Ranunculaceae); **Trifolium pratense* L. and **T. hybridum* L. (Fabaceae); *Asclepias syriaca* L. (Asclepiadaceae); and *Galium* sp. (Rubiaceae). *Typha angustifolia* L. (Typhaceae); **Lythrum salicaria* L. (Lythraceae); and **Rumex crispus* L. (Polygonaceae), grew in a wet part of the ditch. **Tragopogon* sp. (Asteraceae), and **Vicia cracca* L. (Fabaceae), were fully budded, at the onset of bloom, the vetch abundant on both sides of the highway. Shrubs, woody vines, and tree saplings on the road banks included *Toxicodendron radicans* (L.) Kuntze and *Rhus typhina* L. (Anacardiaceae); *Cornus sericea* L. (Cornaceae); *Vitis* sp. (Vitaceae); *Ulmus americana* L. (Ulmaceae); *Populus tremuloides* Michx. and *Salix* sp. (Salicaceae); *Spiraea latifolia* (Ait.) Borkh. and flowering **Malus pumila* Mill. and *Aronia melanocarpa* (Michx.) Ell. (Rosaceae). Plants marked with an asterisk (*) in this list are exotic. All are common roadside plants in this part of the Northeast.

All other sites are similar to site 1 except site 6, which is in alvar vegetation on limestone pavement, and sites 7, 12, and 17–19, which are in disturbed pine barrens vegetation on glacial sand deposits.

Associated Butterflies

The following were observed or collected flying with the NSB (Fig. 5 sites indicated). The NSB's season coincides with full spring flights of many common species.

HESPERIIDAE: *Thorybes bathyllus* (J.E. Smith), 9; *T. pylades* (Scudder), 6, 7, 9; *Erynnis icelus* (Scudder & Burgess), 1, 7; *E. juvenalis* (Fabricius), 1, 6, 7; *E. martialis* (Scudder), 7; *Carterocephalus palaemon mandan* (W. H. Edwards), 1, 9, 23; *Thymelicus lineola* (Ochsenheimer), 7, 9, 17; *Hesperia metea* Scudder, 7; *H. sassacus* Harris, 6, 7; *Polites peckius* (W. Kirby), 7; *P. themistocles* (Latrielle), 6, 7; *P. mystic* (W. H. Edwards), 6, 7, 9, 17; *Poanes hobomok* (Harris), 1, 6, 7, 9, 17, 20; *Atrytonopsis hianna* (Scudder), 7; *Amblyscirtes hegon* (Scudder), 7, 9, 10; and *A. vialis* (W. H. Edwards), 7, 9.

PAPILIONIDAE: *Papilio polyxenes asterius* (Stoll), 1, 7; *Pterourus glaucus* (Linnaeus), 1, 7, 9, 10; *P. troilus* (Linnaeus), 7.

PIERIDAE: *Pieris rapae* (Linnaeus), 7, 9, 25; *Colias philodice* Godart, 1, 7–9, 24.

LYCAENIDAE: *Feniseca tarquinius* (Fabricius), 7; *Lycaena phlaeas americana* (Harris), 6–9; *Incisalia polia* (Cook & Watson), 6; *I. niphon* (Hübner), 7; *Everes comyntas* (Godart), 7, 17; *Celastrina argiolus ladon* (Cramer) complex, 6, 7, 9, 25; and *Lycaeides melissa samuelis* Nabokov, 7.

NYMPHALIDAE: *Clossiana selene myrina* (Cramer), 7; *Charidryas harrisii* (Scudder), 9; *Phyciodes tharos* (Drury) complex, 1, 6, 7, 20–22; *Polygonia interrogationis* (Fabricius), 9; *P. comma* (Harris), 25; *Vanessa virginiensis* (Drury), 1, 6, 7, 9; *V. atalanta rubria* (Fruhstorfer), 7; *Basilarchia arthemis* (Drury), 21; and *B. archippus* (Cramer), 7.

SATYRIDAE: *Megisto cymela* (Cramer), 6, 7, 9; *Coenonympha inornata,* all sites.

Coenonympha inornata was the most consistently associated butterfly. Site 7 (Glens Falls Sand Plain) is the only known place in New York where *G. l. couperi* and *L. m. samuelis* are sympatric. Voucher specimens of associated butterflies are in CUIC and the authors' collections.

Life History

Flight season. We encountered mostly fresh males in 1984–85, suggesting the onset of the flight season. Of 84 specimens collected on 31

May–1 June 1985, 5 were worn males (sites 7, 9), 63 were fresh males (all sites), and 16 were fresh females (sites 9, 11, 15). We made no attempt to collect more males than females, simply keeping the butterflies we caught. On 1 June 1985 we sampled the very beginning of the flight season across the northern part of the Adirondacks (Clinton, Franklin, and St. Lawrence counties), where cold, drizzly, windy weather and high elevation probably caused the flight season to commence a few days later than in the lowlands. Flights of fresh butterflies were observed on 27 May 1986 (sites 1, 6), 2 June 1987 (sites 20–24), 6 June 1987 (site 9), and 5 May 1991 (site 25). Layberry et al. (1982) indicated a univoltine spring flight for this butterfly from early May to mid-July (extreme limits), with the peak flight from 25 May to 25 June at Ottawa. We expect that the flight season continues throughout June, peaking in the middle of the month, in northern New York.

Adult feeding. NSB's were observed nectaring at these plants (Fig. 5 sites in parentheses): *Stellaria graminea* (1); *Sisyrinchium montanum* (1); *Aronia melanocarpa* (1); *Potentilla canadensis* (1, 10); *Barbarea vulgaris* (5); *Hieracium caespitosum* Dumort (Asteraceae) (9); *Vicia cracca* (9, 22); *Arabis glabra* (L.) Bernh. (Brassicaceae) (9); *Fragaria virginiana* (10); *Comandra umbellata* (L.) Nutt. (Santalaceae) (6); *Rubus idaeus* L. and *R. allegheniensis* Porter *ex* Bailey (Rosaceae) (both 9); and *Euphorbia esula* L. (Euphorbiaceae) (6, 15). Males were also observed puddling (1, 6, 9).

Behavior. Basking with widespread wings was frequent in both sexes. Nectaring males held their wings at a 45° angle (sites 9, 11). [Basking positions are very similar to those of the Karner Blue (*L. m. samuelis*).] Adults flew 0.3–0.6 m above roadside foliage with a slow weaving movement also reminiscent of the Karner Blue (site 1). Males patrolled along shaded edges of open, flower-filled spaces, investigating other Blues; one patrolling male aggressively bumped a much larger nectaring *Vanessa virginiensis* (site 9). Adults were much more active (in perfect weather conditions) after 1315 h (site 9). Adults roosted with wings closed in grasses [*Bromus inermis* Leyss. (Poaceae)] and short shrubs (1-m-tall *Rhus typhina*) on steep banks during windy and cloudy periods (site 11). Resting butterflies were flushed in very blustery weather (site 14) or late in the day (1850 h, site 16). Flight ended by 1830 h. A mating pair found at 1245 h on 6 June 1987 (site 9) was photographed from a few cm away (Fig. 6).

Predators. A fresh male showed a bird beak mark across the left forewing apex (site 1).

Larval foodplant. Scudder (1889) suspected *Vicia cracca* to be the foodplant in Canada. This is the apparent larval host in New York, since it was always present, butterflies seemed closely associated with

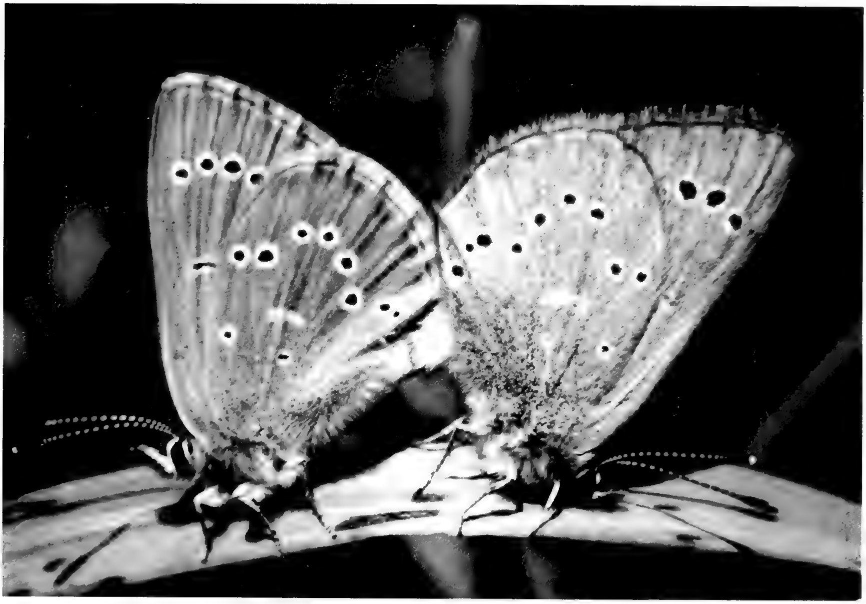


FIG. 6. Mating pair of Northern Silvery Blues (*Glaucopsyche lygdamus couperi*), fresh female at left, slightly worn male at right, 1245 h, 6 June 1987 (site 9), specimens in CUIC.

the plants, and we saw a female oviposit on it (site 9). Herbarium specimens of this vetch were deposited in BH from several sites.

Vicia cracca is a perennial legume with sprawling stems to 1 m long (usually half that length) bearing alternate, tendril-terminated compound leaves. The crowded blue-violet flowers are borne in long-peduncled, one-sided racemes along the stem. Newcomb (1977) published an excellent illustration for field use (note narrow, apically pointed leaflets). These plants are stronger-stemmed than *V. caroliniana*, and are often held firmly over other plants by their forked tendrils. Plants are just starting to bloom, and average 30–40 cm long, during the NSB flight season. Layberry et al. (1982) reported that NSB larvae fed on the flowers of the host, and Ebner (1970) mentioned myrmecophily in Wisconsin.

Vicia cracca occurs in sunny, disturbed habitats, and has been widely naturalized from Europe throughout eastern North America (Fernald 1950). Gleason (1952) interpreted it as native in the northern part of its range. It is "sometimes used as a cover crop" in northern New York, and due to its "aggressive nature, . . . may escape from cultivation to roadsides" (Norman W. Hummel Jr., letter, 24 March 1986). Adjacent plants were connected by rhizomes at site 9, where vetch entirely covered roadside slopes. Tufted Vetch has been well established throughout northern New York since early in this century, at least (13 specimens from seven counties in BH dated 1899–1930).

Layberry et al. (1982) listed *V. cracca, Melilotus alba* Desr. *ex* Lam., and *Medicago sativa* L. as larval hosts at Ottawa. Leblanc (1985) also mentioned *Lathyrus* sp. and *Astragalus* sp. as foodplants in Quebec (all Fabaceae).

Oviposition and rearing. We observed a worn female oviposit on *V. cracca* at 1214 h on 6 June 1987 (site 9), and a captive female from this locality laid two eggs on vetch four days later. The newly laid egg was bright green, fading to greyish-white (matching the villosity of the vetch) one minute later. It was placed on a very young inflorescence bud in the wild. One ovum laid in confinement was similarly placed; another was glued on a leaf base. Ova hatched by 20 June, but the tiny larvae were impossible to see without magnification, and were lost. Rearing the NSB is difficult. Females are not easy to feed, and oviposition is almost impossible to achieve in captivity. Cut vetch dessicates quickly; potted vetch plants would facilitate rearing. The captive female that laid was kept during six days in a variety of tight transparent enclosures containing *V. cracca* plants, set on a table near a south-facing window. The two setups that worked (one egg each) were a glass jar 25 cm high and 15 cm in diameter, and a large plastic box (30 × 30 × 45 cm).

Range Expansion

A century ago, Scudder (1889) mapped the southern limit of *G. l. couperi* at 500 km north of New York in Ontario (Fig. 1). The butterfly had been reported from the eastern tip of the Gaspé Peninsula at that time, and Scudder (*loc. cit.*) suggested that "it may occur in the extreme northern portions" of the United States. Layberry et al. (1982) regarded it "the commonest Lycaenid" of the Ottawa District, 450 km south of Scudder's southern limit, 94 years later, and Layberry (pers. comm., June 1984) said it was generally distributed in Ontario and Quebec south to the St. Lawrence River. Shapiro (1974) also indicated that it was "common" in Quebec, and Leblanc (1985) mapped its wide distribution in that province.

The NSB has only recently entered New England, being found in Maine as early as 1967 (C. F. dos Passos specimens in AMNH). Its spread in Maine has been reported by Grey (1975) and Winter (1977, 1980). We found it in southwestern Maine in 1988 (Fig. 1). Opler (1983) and Opler & Krizek (1984) included Maine in their NSB range depictions. Warren Kiel and Jim Holmes have reported this butterfly from northern New Hampshire since 1986 (Winter 1988–91), the later reports mentioning spread in New Hampshire and oviposition on *Vicia.* We found it throughout the northern half of Vermont (state record) and in west-central New Hampshire on 3–4 June 1987. And James D. Hedbor reported it from Colchester, Vermont, in 1989 (Winter 1988–91) (Fig. 1).

This butterfly entered New York perhaps as late as 1980. Shapiro (1974) and O'Brien (1983) did not report the NSB in northern New York. We did not find it until 1984, in spite of field work there at the proper season since 1975. Lack of Adirondack Mountain region records probably reflects lack of search. Being of northern affinity, it is likely that the NSB will be found at higher elevations shortly, if it is not there already. We expect it in Oswego, Oneida, Herkimer, Hamilton, Fulton, Montgomery, Schenectady, Washington, and Albany counties (Fig. 5) within a few years.

The range of *G. l. couperi* has thus expanded south 750 km in the last century! In New York and Vermont, movement is along weedy roadsides where *Vicia cracca* grows abundantly; Rothschild and Farrell (1983:13–14) described similar movements along "butterfly highways" in Britain. At sites 3 and 4 (Fig. 5) we observed large numbers of this butterfly flying in vetch-filled fields abutting roadsides. We expect that the NSB uses highways as habitat corridors from one such locus to the next.

Method of movement is unknown, but these are possibilities: (1) Two butterflies were seen flying from one side of the road to the other (site 1). Females flying across highways might get inside a parked or moving automobile and be transported for kilometers this way, perhaps until the vehicle stopped. (2) New York road verges are usually mowed in early summer, and larvae or pupae on vetch plants, as well as vetch seeds, might be dragged and dispersed along roadsides in this fashion. (3) Where butterflies occur in hayfields, larvae or pupae could be transported in bales of hay; Burns (1966) suggested that *Thymelicus lineola* has been spread in North America this way. (4) Individual butterflies undoubtedly move along the roadways, perhaps for several kilometers in the course of their lives, the females laying eggs en route. We encountered such vanguards in 1986 in Saratoga County (sites 18–19). (5) Butterflies may be blown for some distance by winds.

The reason for such a dramatic range expansion is unknown. If Gleason's (1952) belief that *V. cracca* is native in eastern Canada is correct, then the widespread naturalization of this legume throughout the Northeast in the last century surely has opened up large zones of formerly unavailable habitat which the butterflies are now exploiting.

DISCUSSION

The SSB is clearly a monophagous butterfly, limited by (1) a very specific habitat, (2) a single foodplant, (3) bloom season of the foodplant, and (4) human disturbance. Thus it (1) occurs in intensely local, widely-spaced populations, and is rare and vulnerable; (2) feeds only on a native, perennial foodplant; (3) is univoltine with an adult flight season coincident with bloom season of the host in May, and larvae specialized to feed on inflorescences and developing legumes; and (4) occurs in remote, pristine sites which are extremely sensitive to human activity, with mostly native plants (*Achillea millefolium* was the only naturalized plant noticed at Horseheads).

The NSB, in contrast, is oligophagous at Ottawa. Of the four limits mentioned above for the SSB, only bloom season of the foodplant is applicable to the NSB. This results in univoltinism, highly correlated host bloom and butterfly flight seasons in June, and larval feeding on flowers and fruits of an at least partly naturalized, perennial foodplant (*V. cracca*). [*Medicago sativa* and *Melilotus alba* (Layberry et al. 1982) are also both naturalized from Europe. The first is perennial, the second annual or biennial (Fernald 1950). *Lathyrus* and *Astragalus* (Leblanc 1985) are mostly native perennials in Quebec (Fernald 1950).] The NSB is, however, (1) not limited to a specific habitat, occurring in New York in hayfields (sites 3–4), on roadsides (many sites), in pine barrens (sites 7, 12, 17–19), and on limestone pavement (site 6). It can therefore be expected to become generally distributed. It is (2) not limited to a single host, and feeds on non-native plants, some of which are not perennial. Finally, (4) it is encouraged by human disturbance, thriving in weedy places with a high percentage of introduced plants (see site 1 description). These two butterflies are ecologically very different. The habitat of the SSB is as restricted as that of the Northern Metalmark, *Calephelis borealis* (Grote & Robinson) (Riodinidae), and Bog Elfin, *Incisalia lanoraieensis* Sheppard (Lycaenidae), whereas the NSB closely resembles North American *Thymelicus lineola*, a widespread generalist, in habitat choice. NSB and SSB flight seasons are also temporally separated.

Moreover, New York specimens of these two butterflies only superficially resemble one another (see Fig. 2 and introductory section). They also differ in size. SSB specimens measured ($N = 11$) had a mean forewing length (base to tip) of 12.81 mm ($SE = 0.72$), in contrast to a mean forewing length of 14.48 mm ($SE = 0.35$) in NSB specimens ($N = 20$). Student's t-test analysis of these indicated a highly significant difference ($t = 6.91$, $df = 29$, $P < 0.005$). The SSB and NSB are highly differentiated, phenotypically and ecologically, in New York.

Shapiro's specimens from 1968–69 (Table 1) have the rounded forewing apices and dorsal coloring of the SSB, and were caught during its season. However, their habitats were characterized by Shapiro (1974) as "fencerows, pasture land, brush," and seem reminiscent of *couperi* localities to the north. Shapiro's three specimens (mean forewing length 12.67 mm) are slightly smaller than Ithaca and Horseheads SSB's, but their wing venters resemble NSB's. They show apparent introgression with *couperi*. In fact, Shapiro (1974) mentioned that "a few Ithaca-area specimens show a phenotypic transition" between nominate *lygdamus* and *couperi*, probably referring to these specimens. A similar situation occurs throughout Michigan, according to W. H. Wagner Jr. (letter, 27 July 1988): "Southern Michigan has fairly typical *lygdamus*, but some individuals show the influence of *couperi*, having much reduced spots on the hind wing underside. In northern Michigan, there is more resemblance to typical *couperi*, but . . . many individuals . . . look like typical *lygdamus*. Way up north, near Lake Nipigon, you get 'pure' *couperi*, with no individuals resembling typical *lygdamus*." If *couperi* continues its southward progression in the Northeast, a "blend zone" similar to that of *Cercyonis pegala pegala* (Fabricius) and *C. p. nephele* (W. Kirby) (Satyridae) and *Basilarchia arthemis arthemis* (Drury) and *B. a. astyanax* (Fabricius) (Nymphalidae) may develop as *couperi* collides with the SSB in Pennsylvania.

The phenotypic differences and marked ecological contrasts of these two butterflies suggest that they may be two species, isolated for millenia, that still can interbreed when secondary contact occurs. Fertility of these offspring is unknown. Careful field and laboratory studies are needed to establish the true status of these two taxa.

ACKNOWLEDGMENTS

In addition to those already mentioned, we thank these people for assistance with this project: M. Deane Bowers, Adelaide E. Briggs, Anne Bruneau, Robert T. Clausen, Edward A. Cope, Charles V. Covell Jr., Matthew F. J. Dirig, William J. Dress, W. Heitzmann, Ronald W. Hodges, E. Richard Hoebeke, Peter A. Hyypio, John Ingram, Fay H. Karpuleon, Bente S. King, James K. Liebherr, Melissa Luckow, Mogens C. Nielsen, Kevin C. Nixon, L. L. Pechuman, Daniel Potter, John E. Rawlins, Charles L. Remington, Frederick H. Rindge, Robert K. Robbins, Brian Scholtens, Arthur M. Shapiro, Margaret H. Stone, Adrienne Venables, F. Robert Wesley, Ernest Williams, and William D. Winter Jr. Curators of the following herbaria kindly loaned *Vicia caroliniana* specimens used in compiling the range of this plant in Fig. 1 (acronyms from Holmgren et al. 1990); BKL, BUF, CAN, CM, F, HUH, MASS, MICH, MIN, MO, NYS, OS, PH, SYRF, TRT, UCS, US, VT, WIS, YU. John V. Freudenstein assisted with statistics. Warren H. Wagner Jr. shared information on *G. lygdamus* subspecies in Michigan, and Irwin Leeuw sent a sample of Indiana and Michigan specimens. Charles J. Sheviak graciously supplied *V. caroliniana* records kept at the NYS herbarium, and Ross A. Layberry provided NSB distributional data for eastern Canada. Boyce A. Drummond, John V. Freudenstein, Paul A. Opler, Warren H. Wagner Jr., and two anonymous reviewers read an early draft of this paper, making many valuable suggestions.

LITERATURE CITED

BURNS, J. M. 1966. Expanding distribution and evolutionary potential of *Thymelicus lineola* (Lepidoptera: Hesperiidae), an introduced skipper, with special reference to its appearance in British Columbia. Can. Entomol. 98:859–866.

DIRIG, R. 1977. Labelling and storing an insect collection. N.Y.S. Coll. of Agric. and Life Sci., Cornell Univ. 4-H Members' Guide M-6-7:1–21.

DIRIG, R. & J. F. CRYAN. 1986. Obituary, Laurence Remington Rupert (1902–1978). J. Lepid. Soc. 40:242–245.

EBNER, J. A. 1970. The butterflies of Wisconsin. Milwaukee Public Mus. Pop. Sci. Handbook 12:i–x, 1–205.

FERNALD, M. L. 1950. Gray's manual of botany, eighth (centennial) edition—illustrated, a handbook of the flowering plants and ferns of the central and northeastern United States and adjacent Canada. American Book Co., New York. lxiv + 1632 pp.

FERRIS, C. D. (ed.). 1989. Supplement to: A catalogue-checklist of the butterflies of America north of Mexico. Lepid. Soc. Mem. 3:i–viii, 1–103.

FORBES, W. T. M. 1928. Order Lepidoptera, pp. 532–687. *In* Leonard, M. D. (ed.), A list of the insects of New York, with a list of spiders and certain other allied groups. Cornell Univ. Agric. Expt. Sta. Mem. 101:1–1121 + map.

——— 1960. Lepidoptera of New York and neighboring states, part IV, Agaristidae through Nymphalidae, including butterflies. Cornell Univ. Agric. Expt. Sta. Mem. 371:1–188.

GLEASON, H. A. 1952. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. Vol. 2. Published for the New York Bot. Gard. by Hafner Press, a division of Macmillan Publishing Co., New York. iv + 655 pp.

GREY, P. 1975. Zone 7, Northeast, pp. 13–15. *In* 1974 field season summary. News Lepid. Soc. No. 2–3, 1 June.

HEITZMAN, J. R. & J. E. HEITZMAN. 1987. Butterflies and moths of Missouri. Missouri Dept. of Conservation, Jefferson City, Missouri. viii + 385 pp.

HODGES, R. W., T. DOMINICK, D. R. DAVIS, D. C. FERGUSON, J. G. FRANCLEMONT, E. G. MUNROE & J. A. POWELL. 1983. Check list of the Lepidoptera of America north of Mexico, including Greenland. E. W. Classey Ltd. & The Wedge Entomological Research Foundation, London. xxiv + 284 pp.

HOLMGREN, P. K., N. H. HOLMGREN & L. C. BARNETT. 1990. Index herbariorum, part I, the herbaria of the world, 8th ed. Regnum Vegetabile, published and distributed for the Internat. Assoc. for Plant Taxon. by the New York Bot. Gard., Bronx. 693 pp.

KARPULEON, F. H. 1970. *Glaucopsyche lygdamus* in Arkansas and Texas. Mid-Continent Lepidoptera Series [1](12):11–12.

KEENER, C. S. 1983. Distribution and biohistory of the endemic flora of the mid-Appalachian shale barrens. Bot. Rev. 49:65–115.

KLOTS, A. B. 1951. A field guide to the butterflies of North America, east of the Great Plains. The Peterson Field Guide Series No. 4. Houghton Mifflin Co., Boston. xvi + 349 pp.

LAYBERRY, R. A., J. D. LAFONTAINE & P. W. HALL. 1982. Butterflies of the Ottawa District. Trail & Landscape 16(1):3–59.

LEBLANC, A. 1985. Les Lycenides (Lepidoptera: Lycaenidae) du Quebec. Assoc. des Entomol. Amateurs du Quebec. Fabreries, Suppl. 4:1–66.

MILLER, L. D. & F. M. BROWN. 1981. A catalogue-checklist of the butterflies of America north of Mexico. Lepid. Soc. Mem. 2:i–viii, 1–280.

MITCHELL, R. S. 1986. A checklist of New York State plants. N.Y.S. Mus. Bull. 458:i–x, 1–272.

NEWCOMB, L. 1977. Newcomb's wildflower guide, an ingenious new key system for quick, positive field identification of the wildflowers, flowering shrubs and vines of northeastern and north-central North America. Little, Brown and Co., Boston. xxii + 490 pp.

O'BRIEN, M. F. 1983. New butterfly distribution records for northern New York. J. Lepid. Soc. 37:92–94.

OPLER, P. A. 1983. County atlas of eastern United States butterflies (1840–1982). Privately printed, Washington, D.C. 90 unnumbered pp.

OPLER, P. A. & G. O. KRIZEK. 1984. Butterflies east of the Great Plains, an illustrated natural history. Johns Hopkins Univ. Press, Baltimore. xviii + 294 pp.

ROTHSCHILD, M. & C. FARRELL. 1983. The butterfly gardener. Michael Joseph Ltd. and Rainbird Publ. Group Ltd., London. 128 pp.

SCUDDER, S. H. 1889. The butterflies of the eastern United States and Canada with special reference to New England. 3 vols. Cambridge, Massachusetts, published by the author. 1958 pp. + 89 plates + maps.

SHAPIRO, A. M. 1974. Butterflies and skippers of New York State. Search Agric. Entomol. (Ithaca) 12, vol. 4, No. 3:1–60.

WINTER, W. D., JR. 1977. Zone 7, Northeast, pp. 14–15, 18–19. *In* Field Summary 1976. News Lepid. Soc. No. 2, Mar–Apr.

——— 1980. Zone 7, Northeast, pp. 23–24. *In* 1979 season summary. News Lepid. Soc. No. 2, Mar–Apr.

——— 1988–1991. Zone 10, Northeast. *In* 1987–1990 season summaries. News Lepid. Soc. No. 2, Mar–Apr issues.

WORMINGTON, A. 1983. The butterflies of Point Pelee National Park, Ontario. Ontario Field Biol. 37(1):1–26.

Received for publication 24 May 1991; revised and accepted 7 September 1991.

Journal of the Lepidopterists' Society
45(4), 1991, 291–295

A NEW SPECIES OF *AMBLYSCIRTES* FROM MEXICO (HESPERIIDAE)

HUGH AVERY FREEMAN
1605 Lewis Drive, Garland, Texas 75041

ABSTRACT. *Amblyscirtes brocki* is described from Sonora, Chihuahua, Coahuila, and Oaxaca, Mexico, the type series consisting of 42 males and 14 females. This new species is differentiated from other species of *Amblyscirtes* primarily by characters of size, color and maculation. Holotype and genitalia of a paratype are illustrated.

Additional key words: *Amblyscirtes brocki, A. elissa, A. exoteria, A. folia, A. immaculatus.*

Jim P. Brock, Tucson, Arizona, sent me some skippers for determination that he and Douglas Mullins, Pat Savage, Mike Smith, and R. E. Wells had collected in Sonora, Mexico. At about the same time I received from John Kemner, Dripping Springs, Texas, some specimens of *Amblyscirtes* that he had collected in Coahuila and Oaxaca, Mexico. After closely examining all specimens of *Amblyscirtes* that Brock had sent, I found that they were the same as those from Kemner and represent a new species that is described here.

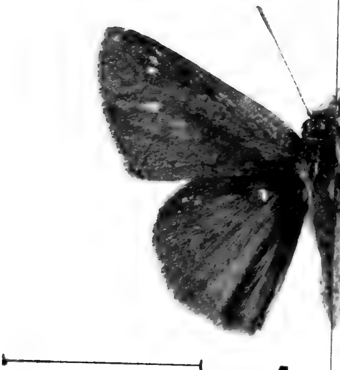
Amblyscirtes brocki Freeman, new species
(Figs. 1–3)

Male upper side (Fig. 1). Primaries: dark brown, overscaled with golden scales; usually a small, opaque, sordid yellow spot in space 3 and another in space 6, the other apical spots in spaces 7 and 8 faint or absent; when all apical spots are present they form a straight line directed from space 8 toward the outer angle; a narrow, tripartite, brown stigma, forms a curve from inside the origin of vein 3 to vein 1; fringe light brown, faintly checkered, darker brown at vein endings. Secondaries: dark brown, heavily overscaled with golden scales, especially the discal area; fringe pale brown, some specimens being slightly checkered as on the primaries.

Male under side (Fig. 2). Primaries: brown, with golden overscaling restricted to the discal and postdiscal areas forward of the cubitus and the apical area near the termen with gray overscaling; spots as above, but better defined and some specimens have faint spots in spaces 2, 4, and 5; fringe light brown, very faintly checkered. Secondaries: brown, overscaled with gray scales, some of the specimens from Oaxaca with golden scaling in space 2A–3A; a faint, curved band of gray, discal spots extends from space 2 to space 7, but may be absent in some specimens; fringe light brown, may be faintly checkered.

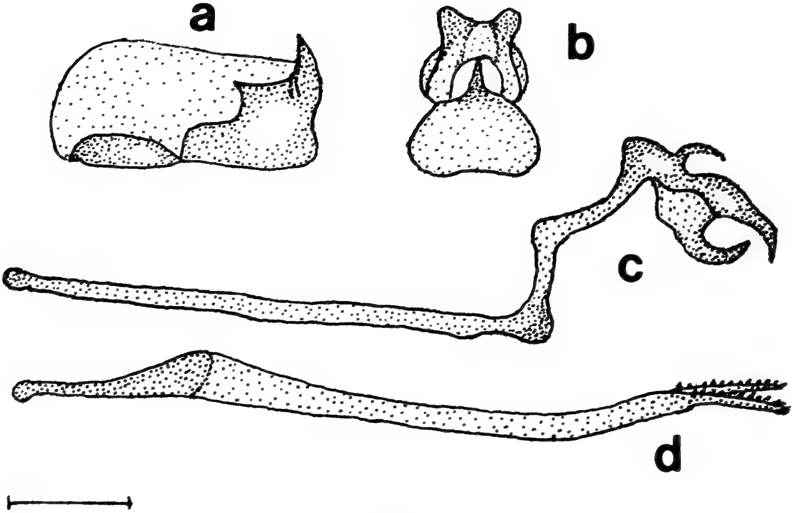
Body. Thorax: dark brown, heavily overscaled with golden hairs on the upper side, lighter beneath due to some tan scales present. Abdomen: dark brown above, lighter beneath. Head: dark brown, covered with light brown and black hairs. Palpi: first and second segments short and broad, covered with brown and black hairs above; third segment bare and fairly short; under side lighter due to numerous white, hair-like scales and only a few black ones. Legs: brown. Antennae: both shaft and club dark brown above; underside of shaft prominently checkered white between segments; club sordid white at base; apiculus black. Nudum count: 10.

Wing measurements. Holotype. Primaries: base to apex, 13 mm; apex to outer angle, 8.5 mm; outer angle to base, 11 mm. Secondaries: base to end of vein 3, 9 mm; center of costa to anal angle, 9 mm. Total expanse: 26 mm. Total expanse of male paratypes: $\bar{x} = 26$ mm ($n = 41$). Total expanse of female paratypes: $\bar{x} = 26$ mm ($n = 14$).



1

2



3

Female. Very similar to male except there is usually a minute dot in space 2, slightly basad from the spot in space 3, on the upper side of the primaries, which is usually also present on the under side. Apical spots are usually better developed and form a straight line directed to the outer angle.

Types. Holotype, male, MEXICO.—Sonora: Trinidad-Yecora Road, 16 km NW Yecora, 21 July 1985 (leg. Jim P. Brock), in the American Museum of Natural History, New York. There are 41 male and 14 female paratypes collected by the following: Jim P. Brock, MEXICO.—Sonora: Trinidad-Yecora Road, 8 km W Yecora, 21 July 1985, 3 males; Santa Rosa-Yecora Road, 8 km NW Yecora, 28–29 July 1987, 8 males, 4 females; 8 km W Yecora, plateau edge, 28 June 1987, 1 female; Creek at ca. 1500 m elev., Trinidad-Yecora Road, 9 km W Yecora, 31 July 1984, 1 female; 21 km E El Novillo, 11 Aug. 1985, 1 female; Trinidad-Yecora Road, 16 km W Yecora, 22 July 1985, 1 female; 10 km W Yecora, 31 July 1984, 1 male; 6 km NW Huicoche, 12–13 July 1989, 2 males, 1 female; —Chihuahua: 6.2 km NE Chinacas, 10–11 July 1989, 2 males, 1 female. Pat Savage, MEXICO.—Sonora: Plateau 16 km E Santa Rosa on Santa Rosa-Yecora Road, 28–29 July 1987, 7 males, 2 females. Douglas D. Mullins, MEXICO.—Sonora: new Rt. 16, W edge Sierra Plateau, 24 July 1988, 1 male. R. E. Wells, MEXICO.—Chihuahua: Hwy. 127, ca. 75 km SW Creel, 23–24 July 1989, 1 male, 1 female. Mike Smith, MEXICO.—Sonora: Santa Rosa-Yecora Road, ca. 8 km N Yecora at plateau edge, 28 June 1987, 1 male, 1 female. John Kemner, MEXICO.—Coahuila: near Los Lirios, San Rafael, elev. ca. 2280 m, 6 July 1988, 1 male; Oaxaca: 8 km N city of Oaxaca, elev. ca. 1800 m, 10 July 1988, 1 male; 22 July 1988, 1 male; 23 Aug. 1988, 1 male; 14 Aug. 1989, 1 male; 15 Aug. 1989, 1 male; 17 Aug. 1989, 1 male; 18 Aug. 1989, 1 male; 23 Aug. 1989, 1 male; 1 Aug. 1990, 1 male; Oaxaca: 16 km N city of Oaxaca, elev. ca. 2100 m, 24 May 1990, 3 males. In the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, there are 2 males with the label, "Mexico: Chihuahua, 1 July. Townsend". Paratypes will be placed in the following museums and collections: four, American Museum of Natural History, New York; four, United States National Museum, Washington, D.C.; four, The Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; four, Allyn Museum of Entomology, Sarasota, Florida; four, Natural History Museum of Los Angeles County, Los Angeles, California; 10, Jim P. Brock, Tucson, Arizona; two, Douglas D. Mullins, Tucson, Arizona; nine, Pat Savage, Saint George, Utah; two, R. E. Wells, Jackson, California; two, Mike Smith, Sacramento, California. The rest will remain for the present in my collection (HAF).

Etymology. I take pleasure in naming this new species for my good friend Jim P. Brock, Tucson, Arizona, who collected part of the type series and has furnished me with many skippers from Arizona and Sonora, Mexico.

Diagnosis

This new species does not seem to be closely related to any of the other species of *Amblyscirtes*, although it does fit into the portion of species that have stigmas. I follow Evans (1955) in making a distinction

---

←

FIGS. 1–3. **1, 2** (scale line = 1 cm), Upper side (Fig. 1) and under side (Fig. 2) of *Amblyscirtes brocki* Freeman, holotype, male, Mexico.—Sonora: Trinidad-Yecora Road, 16 km NW Yecora, 21 July 1985 (*leg.* Jim P. Brock) in the American Museum of Natural History, New York; **3** (scale line = 1 mm), *Amblyscirtes brocki*, male genitalia of paratype (Genitalia Vial-H-941) same location and collector as holotype, 28–29 July 1987 (HAF collection). a) right valva in lateral view of interior; b) uncus, gnathos, tegumen dorsal view; c) uncus, gnathos, tegumen, vinculum, saccus in lateral view; d) aedeagus in lateral view.

between the terms stigma and brand or brands, found on the primaries of males in certain species of Hesperiidae. The term stigma applies to the specialized patch of tubular scales and androconia extending between and sometimes crossing the veins, whereas the term brand or brands applies to the same type of specialized patch or patches that extend parallel with the vein or veins. The following species of *Amblyscirtes* have a tripartite stigma: *exoteria* (Herrich-Schaffer 1869), *folia* Godman (1900), *patriciae* (Bell 1959), *raphaeli* Freeman 1973, *immaculatus* Freeman 1970. Superficially, on the upper side, *A. brocki* slightly resembles a small specimen of *immaculatus* Freeman (Freeman 1970 illustrates the holotype and genitalia of a paratype); *brocki* primaries average, from base to apex, 13 mm, whereas *immaculatus* averages 18 mm; the wings on the upper side of *brocki* are dark brown, heavily overscaled with golden scales, whereas *immaculatus* is a lighter brown, overscaled with gray scales; the faint maculation is similar in both species; on the under side of the secondaries *brocki* has a faint, curved band of gray discal spots, extending from space 2 to space 7, slightly resembling the maculation of *Amblyscirtes oslari* (Skinner 1899), whereas *immaculatus* usually has three indistinct, sordid white discal spots and a faint cell spot. Some *brocki* females could be confused with females of *Amblyscirtes fluonia* Godman 1900, although the arrangement of the apical spots will easily separate the two species: *fluonia* has these spots forming a slight curve directed toward the end of vein 3, and the spot in space 3, if present, is never more distinct than the spot in space 2, whereas *brocki* has the apical spots forming a straight line directed toward the outer angle and the spot in space 3 is always more distinct that the spot in space 2. Members of true *Amblyscirtes* have very similar male genitalia, especially in the long saccus and aedeagus and basic shape of the valva, with the differences being small but always distinct. Some of the basic differences in *Amblyscirtes* genitalia are well illustrated in Burns (1990).

I have found that certain species of *Amblyscirtes* and *Piruna* that have an extensive range in Mexico have better developed maculation in the more northern part than in the southern. Specimens of *Amblyscirtes elissa* Godman 1900, from Arizona and Sonora, Mexico, have well developed maculation, whereas specimens from Guerrero, Oaxaca, and Chiapas, Mexico, are almost immaculate on the upper side, especially males. *Piruna polingii* (Barnes 1900) and *P. brunnea* (Scudder 1872) exhibit this same variation of reduced maculation in their southern range. The specimens of *A. brocki* from Sonora, Chihuahua, and Coahuila all have the spot in space 3 and space 6 on the upper side of the primaries present, whereas the specimens that John Kemner collected in Oaxaca have these spots faint or absent.

ACKNOWLEDGMENTS

I thank Frederick H. Rindge of the American Museum of Natural History, New York, for making the photographs of the holotype used in this article, and John M. Burns of the National Museum of Natural History, Washington, D.C., and Stephen R. Steinhauser of the Allyn Museum of Entomology, Sarasota, Florida, for helpful comments on the manuscript. Thanks also to Jim P. Brock and Douglas D. Mullins of Tucson, Arizona, and Pat Savage of Saint George, Utah, for their loan of specimens, and to John Kemner of Dripping Springs, Texas, for collecting many fine species of Hesperiidae in Mexico for my study.

LITERATURE CITED

BURNS, J. M. 1990. *Amblyscirtes*: Problems with species, species groups, the limits of the genus, and genus groups beyond—A look at what is wrong with the skipper classification of Evans (Hesperiidae). J. Lepid. Soc. 44:11–27.

EVANS, W. H. 1955. A catalogue of the American Hesperiidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part IV. Hesperiinae and Megathyminae. British Museum, London. 499 pp., pls. 54–88.

FREEMAN, H. A. 1970. A new genus and eight new species of Mexican Hesperiidae. J. N.Y. Entomol. Soc. 78:88–99.

Received for publication 29 April 1991; revised and accepted 29 August 1991.

Journal of the Lepidopterists' Society
45(4), 1991, 296–347

FOODPLANT ASSOCIATIONS OF THE URANIINAE (URANIIDAE) AND THEIR SYSTEMATIC, EVOLUTIONARY, AND ECOLOGICAL SIGNIFICANCE

DAVID C. LEES

Flat 6, 23 Normanton Road, South Croydon, Surrey, CR2 7AE, United Kingdom

AND

NEAL G. SMITH

Smithsonian Tropical Research Institute, Unit 0948, APO AA34002-0948 U.S.A.

ABSTRACT. Larval and adult foodplant records for the moth subfamily Uraniinae (*sensu* Sick 1937) are reviewed. Reliable larval foodplant records for all seven genera include only the genera *Omphalea* L., *Endospermum* Benth., and *Suregada* Roxb. ex Rottl. (Euphorbiaceae), and this specialization on Euphorbiaceae supports Sick's concept of Uraniinae (based on metathoracic and tympanal morphology) as a monophyletic group. Whereas *Omphalea* is known to be fed on only by larvae of the three strictly day-flying genera (*Urania* Fabricius, *Chrysiridia* Hübner, and *Alcides* Hübner), *Endospermum* is a recorded foodplant for *Alcides* and three primarily nocturnal genera (*Lyssa* Hübner, *Urapteroides* Moore, and *Cyphura* Warren). The latter two genera have been traditionally included in the Microniinae, as has been *Urapteritra* Viette, whose larval foodplant *Suregada* is reported here for the first time. Some ecological and evolutionary aspects of uraniine larval foodplant specialization are discussed. A putative phylogeny of Uraniinae based on published hearing organ and larval morphology is presented, and the phylogenetic significance of larval foodplant relationships evaluated. Adult foodplants (nectar resources) for the diurnal uraniines are summarized, and the possibility of their role in the moths' reproductive or predator defense ecology is briefly discussed.

Additional key words: Microniinae, *Omphalea, Endospermum, Suregada,* Euphorbiaceae.

SYSTEMATICS OF THE URANIIDAE

Diurnal members of the uraniid subfamily Uraniinae are renowned for their iridescent colors, rivalling the most exquisite butterflies. There are approximately 50 described species in 7 genera, distributed throughout the tropics: *Urania* ca. 6 spp., *Chrysiridia* 2 spp., *Alcides* ca. 7 spp., *Lyssa* ca. 7 spp., *Urapteritra* ca. 8 spp., *Urapteroides* 3 spp., and *Cyphura* ca. 15 spp. (D. C. Lees, unpubl. data). Although there are no modern cladistic studies of the subfamily, Sick (1937) provided a basis for the generic arrangement of the group and its subfamilial relationships. Only two genera of the Uraniinae *sensu* Sick have been revised: *Lyssa* (Altena 1953) [=*Nyctalemon* Dalm.—see Fletcher 1979:121] and *Urapteritra* (Viette 1972). Viette separated *Urapteritra* from *Urapteroides* (Gaede 1926–30) on the basis of distinct genitalic differences and on the absence in *Urapteritra* of the stalked condition in the veins CuA_1 and M_3 of both sets of wings, which is present in both *Urapteroides* (Hampson 1895) and *Cyphura* (Westwood 1894). Traditionally, Uraniidae has been placed in the superfamily Geometroidea; males and females of the Geometridae possess a pair of tympanal organs on the first abdominal sternite (=sternite 2; abdominal sternite 1 is absent). However, there is a clear sexual dimorphism in the position of these organs in uraniines: although they occur in females on the anterior of abdominal sternite 2, in males they are found laterally at the junction of abdominal tergites 2 and 3 (Eltringham 1924b, Kennel & Eggers 1933, Sick 1937, Minet 1983), a synapomorphy with the Microniinae and the Epiplemidae *sensu auct.*

Following the suggestions of Sick (1937), Minet (1983, 1986) redefined the Uraniidae and erected a separate superfamily for them, the Uranioidea, reducing the Epiplemidae (ca. 700 spp. worldwide) to the rank of subfamily along with the Uraniinae and Microniinae (=Acropterinae of Sick). (Later, Minet (1991:87) returned the Uraniidae to a revised Geometroidea along with the Sematuridae and the Geometridae.) Minet (1983) concurs with Sick (1937) that the Indo-Australasian genera *Urapteroides* and *Cyphura* (conventionally regarded as microniines) are best placed in the Uraniinae based on tympanal and thoracic morphology.

Characters. Sick's three uraniid subfamilies form a monophyletic group defined by the synapomorphies in Table 1. The Microniinae *sensu auct.* (including *Cyphura* and *Urapteroides*) are all delicate conspicuous whitish moths with pointed wing apices, oblique dark cross-striations, and predator-deflection markings on the hindwing tails. The frenulum is absent or vestigial (both microniines and uraniines appear to substitute the conventional type of wing-coupling with expansion of the humeral angle of the hindwing, allowing a looser amplexiform coupling method: Common 1970:849–851). Although this "gestalt" concept of Microniinae may seem appealing, the patterns are very likely to be homoplasious anti-predator adaptations. Color patterns remarkably similar to those of various Microniinae *sensu auct.* reoccur in (a) the Neotropical Epipleminae, e.g., *Aorista* Warr., *Meleaba* Wkr., and *Psamathia* Wkr. (=*Micronioides* Mesm.); (b) an Old World epiplemine (*Epiplema himala* Btlr.); (c) the Old World Geometridae (e.g., *Ourapteryx* Leach); and (d) the Neotropical oxytenid genus *Asthenidia* Westwood. Microniinae is Paleotropical, whereas Epipleminae and Uraniinae are pantropical.

Posture. Resting posture often is phylogenetically distinctive within the Lepidoptera. All uraniids possess a generally splayed-out day-time resting position, apparently the plesiomorphic condition within the group, but wing posture varies among uraniid subfamilies. The epiplemines, with cryptic coloration, are distinct in folding the hindwings alongside the abdomen, and frequently warp the forewings rather than extending them flat (Gaede 1926–30:390, Common 1970, Sugi 1987).

TABLE 1. Characters defining the Uraniidae (*sensu* Sick 1937 & Minet 1983) and its constituent subfamilies.

	Refs.†
Apomorphies defining Uraniidae	
1. Females with a unique conformation of tympanic cases and tympana, deriving from the first abdominal sternite (sternite 2) where they are anterior-laterally situated	1, 2, 3
2. Males with a unique conformation of hearing organs, with tympana, tympanic projections, countertympana, and tympanic cavities deriving from abdominal tergites 2 & 3	1, 2, 3
3. Females with scolopal body of scoloparium inverted	3, 4
4. Presence of a spiniform endosclerite ("Coxalzapfen") from the metathoracic epimeron next to the secondary arm of the furca	3, 4
Other characters [plesiomorphies?]	
5. Forewing vein R_5 sharing a common stalk with M_1 or joined at the base with M_1 (also occurs in epicopeids)	3, 5, 6
6. Forewing vein R_5 well separated from R_1–R_4	3, 7
7. Larvae with full complement of prolegs (=16 legs)	5
8. Larvae without secondary setae; primary setae on tubercles	8, 9, 10
9. Eggs domed/spherical ("upright"), with projecting ribs	6, 11
Apomorphies defining Uraniinae	
1. Metathoracic epimerons of females modified into ±concave, oval covers in front of or laterally over abdominal tympana	3, 4
2. Known larval foodplants in the Euphorbiaceae (all genera specialists on *Omphalea/Endospermum/Suregada*, plants with polyhydroxy alkaloids)	12
Other characters [loss/reduction/absence characters]	
3. Mesothoracic anepisterna reduced or absent	3, 13
4. Female metacoxa *not* covered with projecting scales [scales form protective covers over tympana in Epipleminae and Microniinae]	3, 4
5. Strengthening conjunctiva between female intersegmental thoracic-abdominal membrane and tympanum less extended than in Epipleminae and Microniinae	4
6. Hindwing frenulum lost	12
Apomorphies defining Microniinae (sensu Acropterinae of Sick 1937)	
1. Angle of countertympanum to tympanum in males obtuse, ca. 120° [note: angle acute, ca. 60–80° in Uraniinae and ca. 45° in Epipleminae; ca. 100° in *Decetia*]	3, 4
2. Known larval foodplants in the Asclepiadaceae (*Dregia volubilis* Benth. ex Hook for *Acropteris ciniferaria* (Walker) in Sri Lanka and *Marsdenia tomentosa* C. Morr. & Decne for *A.* cf. *sparsaria* (Walker) in Taiwan [note: Olacaceae (*Olax wightiana* Wall) recorded for *Decetia subobscurata* Walker in India]	14, 15
Other characters [loss/reduction character]	
3. Frenulum absent or vestigial [note: frenulum present in *Decetia* Wkr. and *Paradecetia* Swinhoe]	3, 7
Characters defining Epipleminae [clear autapomorphies unknown]	3
1. Male tympanum separated posteriorly from countertympanum by a sclerified arm (in Uraniinae/Microniinae by a narrow membranous strip)	3
2. Frenulum and retinaculum present (best developed in males)	3

TABLE 1. Continued.

	Refs.†
3. Hindwing humeral angle weakly expanded with humeral vein vestigial/absent in contrast to Uraniinae and Microniinae	3, 7
4. Hindwing vein 3A present or atrophied	3
5. Larval foodplants include Rubiaceae, Caprifoliaceae, Oleaceae, Daphniphyllaceae, Bignoniaceae, and Verbenaceae (just as in Sphingidae)	8, 16

† References: 1. Eltringham 1924b; 2. Kennel & Eggers 1933; 3. Minet 1983; 4. Sick 1937; 5. Hampson 1895:110–113; 6. Minet 1986; 7. Common 1970:849–851; 1990:381–385; 8. Holloway et al. 1987:171–172; 9. Kühn 1887; 10. Moore 1884–87:398–403, pl. 186; 11. Macleay 1834; 12. Current paper; 13. Brock 1971; 14. T. R. D. Bell 1901 MS; 15. J. Rawlins, pers. comm.; 16. Sugi 1987.

Members of the *Decetia* group are also drab, but their resting posture has not been described. The remainder of the Microniinae and the Uraniinae (*sensu stricto*) extend the wings flat, but appear to differ in alighting behavior. Microniines have a labored, conspicuous flight, normally crepuscular or nocturnal. They are easily disturbed by day, after which they flutter slowly for a short distance before alighting again, on or often underneath a leaf (Gaede 1933:97; Bell 1901 MS; D. C. Lees, pers. obs. for *Aploschema* Warren and *Acropteris* Geyer in Cameroon). Uraniines generally alight on top of a leaf, then reverse their position so that the head points downward, a tactic that confuses predators by drawing attention to the hindwing tails (Seitz 1940:829). Microniines and uraniines also may be aposematic, relying for protection by day on their bright contrasting colors, even at rest. For example, *Urapteritra* spp. in Madagascar may rest on top of leaves and are disinclined to move even when disturbed (J. Minet, pers. comm.). A clear exception is the genus *Lyssa*, which has a more cryptic brown coloration with disruptive white bands and rests in dark places or under leaves (Altena 1953:40–41). The nocturnal roosting posture of uraniines is also generally spread-out, with forewings slightly lowered over hindwings, observed in *Urapteritra fasciata* (Mabille) (D. C. Lees, pers. obs.) and *Urania fulgens* Wkr. (N. G. Smith, pers. obs.). However, *Chrysiridia* spp. [and reportedly "microniines" (Gaede 1933:97)] rest at night with wings held vertically over the back like many butterflies (D. C. Lees, pers. obs.; Lucas 1876).

Foodplants. Foodplant records are useful in evaluating the phylogenetic relationships, based on morphological characters, of the uraniid subfamilies and the seven genera placed in the Uraniinae in this paper. Although foodplant records strongly support the monophyly of the Uraniinae *sensu* Sick (Table 1), the Epipleminae *sensu auct.* (for which Minet 1983 can find no convincing autapomorphies) and Microniinae *sensu* Minet appear more vulnerable taxa: more detailed morphological studies ultimately may prove them to be paraphyletic. Epipleminae are apparently associated with a suite of hostplants also found within the Sphingidae (Table 1). The inclusion of *Decetia* Wkr. and *Paradecetia* Swh. among the microniines (Minet 1983) on the basis of tympanal characters alone (Table 1) is questionable (see also Sick 1937) because it ignores their distinctive wing-shape, which is different from the rest of the microniines; the pectinated antennae in *Decetia*; the presence of a well-developed hindwing frenulum; and a foodplant record on Olacaceae for *Decetia*, contrasting with apparent specialization on milkweeds (Asclepiadaceae) in the case of the microniine genus *Acropteris* (Table 1). Although the female tympana of *Decetia* have yet to be described (see Sick 1937), the appropriate solution may be the erection of a new uraniid subfamily for *Decetia* and *Paradecetia* (along with *Auzea* Walker).

LARVAL FOODPLANT RECORDS FOR THE URANIINAE

Uraniine foodplant records, widely dispersed in the literature, are summarized in Table 2, together with all known unpublished records. *Omphalea* L. (Euphorbiaceae) was first reported as the larval foodplant of *Urania* by Macleay (1834) and as that of *Chrysiridia* by Camboué (1889, 1892). Our review indicates that the genera *Urania* and *Chrysiridia* are specialists feeding exclusively on this pantropical plant genus (see Table 2). Furthermore, *Alcides metaurus* (Hopffer 1856) (=*A. zodiaca* (Butler 1869), synonomy as yet unpublished) from Queensland, North Australia, recently has been reported to feed on the *Omphalea* species endemic to the region (Coleman & Monteith 1981). *Endospermum* Benth. (Euphorbiaceae) was first reported as a uraniine foodplant for *Urapteroides* by Browne (1937), for *Lyssa* by Szent-Ivany and Carver (1967), and for *Alcides* by Coleman and Monteith (1981), and has subsequently proved to be a widespread uraniine foodplant in the Indo-Australasian region (Table 2).

The larval foodplant of the genus *Urapteritra* is reported here for the first time. Larvae of two species were discovered in Madagascar in January 1991 feeding on two different species of *Suregada* Roxb. ex Rottl. (=*Gelonium* Roxb. ex Willd.) (Euphorbiaceae) (Table 2).

Records of other purported uraniine foodplants are widespread in the literature. None have been confirmed to date. *Mangifera indica* L. (Anacardiaceae) was incorrectly stated as the larval foodplant of *C. rhipheus* (Boisduval 1833, Sganzin & Boisduval 1873; but see Guenée 1877, Mabille 1889), and of the closely related *C. croesus* from East Africa (Pinhey 1975:79, and subsequently by Sevastopulo 1981; but see Sevastopulo 1986). It is likely that mango flowers are a nectar resource for adult *Chrysiridia* (see Table 8), as may be flowers of *Terminalia catappa* L. (Combretaceae) (T. Grant, pers. comm.), also unconvincingly reported as a larval foodplant by Pinhey. *Chrysiridia rhipheus*, like *Urania* spp., characteristically engages in territorial behavior alighting upside down on leaves of mango trees (Lucas 1869), and perhaps on foliage of other adult nectar sources; such behavior may have misled some authors (e.g., E. Pinhey, pers. comm.). *Eugenia malaccensis* L. (Myrtaceae) has been reported more than once as the larval foodplant of *Lyssa zampa* (Btlr.) and *Urapteroides astheniata* (Gn.) (Corbett & Dover 1927, reiterated by Altena 1953:38 and Barlow 1982:136). This is now recognized as a transcription mistake for *E.* (*Endospermum*) *malaccense* Benth. (syn. *E. diadenum* (Miq.) Airy Shaw) (Y. P. Tho, pers. comm., H. S. Barlow, pers. comm.). *Pittosporum* sp. (Pittosporaceae) has been reported as an *Alcides* foodplant by Szent-Ivany and Carver (1967), a record which should also be treated with caution in the absence of confirmation (Coleman & Monteith 1981). See Table 2, note 10, as regards a vague record of a palm as a *Lyssa* foodplant (Boisduval 1874). The description of the larval foodplant of a *Lyssa* sp. from N.E. Sulawesi (Kühn 1887) is too imprecise for certain identification (but see Table 2, note 9).

GEOGRAPHICAL DISTRIBUTION OF URANIINE LARVAL FOODPLANTS

Because of the apparent high degree of specialization of uraniines on their euphorbiaceous foodplants, it is of value to summarize the available botanical information on the species and their distribution (Tables 3, 4, 6). This has potential for pinpointing the gaps in knowledge of uraniine foodplant relationships, and, by comparison with data on moth distribution, might reveal if other foodplants are likely to be involved.

Omphalea, a genus of trees and large canopy-spreading lianas with about 16 species (Table 3), at least two of which are sometimes cultivated for their edible seeds in the Neotropics (Gillespie 1990), has so far been found to be the larval foodplant for seven species within three uraniine genera (Table 2). Eight species of *Omphalea* are known in the Neotropics, from Mexico to Amazonian South America and the atlantic coastal forests of Brazil, and sporadically through the Greater and Lesser Antilles. An additional eight species have a relict distribution in the Paleotropics, occurring in Tanzania, Madagascar, Queensland, New Guinea, the Bismarck Archipelago, Solomon Is., Sulawesi, Philippines, Borneo, Malaysia, Thailand, Laos, and Myanmair [Burma] (Gillespie 1990), including a new species discovered during recent fieldwork in Madagascar (Gillespie, unpubl. data). Cladistic analyses suggest that the Neotropical and Afrotropical species form a monophyletic group defined by a unique set of male floral characters, whereas the three Indo-Australasian species form a more plesiomorphic clade (Gillespie 1988, 1990). The disjunct distribution of the day-flying uraniines, which

TABLE 2. Larval foodplant records for the Uraniinae⊗. Confirmed rearings: locality in bold. Records bracketed with arrows denote the foodplant is one of 2 or 3 spp. (see notes). Locality abbreviations: Cub = Cuba; Jam = Jamaica; Mex = Mexico; Pan = Panama; Amaz = Amazonian S. America; Trin = Trinidad; Mad = Madagascar; NG = New Guinea (PNG = Papua New Guinea); NQd = North Queensland, North Australia; Phil = Philippines; pMal = peninsular Malaysia; Thai = Thailand; Sol = Solomons.

Moth taxon†‡	**Larval foodplants*** (Confirmed foodplants in bold) Species (Family—aceae)										
	Omphalea oppositifolia (Euphorbi-)	*O. triandra*	***O. hypoleuca***	***O. trichotoma***	***O. oleifera***	***O. diandra***	***O. palmata***	***O.* sp. nov.**	***O. occidentalis***	***O. queenslandiae***	***Endospermum macrophyllum*** (Euphorbi-)
Urania	•	•	•	a	•	•	•	•	•	•	•
boisduvalii	•	•	•	b	•	•	•	•	•	•	•
(Guérin)	•	•	b	•	•	•	•	•	•	•	•
U. sloanus	•	c	•	•	•	•	•	•	•	•	•
(Cramer)											
U. poeyi	•	•	•	d	•	•	•	•	•	•	•
(H.-S.)											
U. fulgens	•	•	•	•	b	e	•	•	•	•	•
Walker	•	•	•	•	b	e	•	•	•	•	•
U. leilus	•	•	•	•	•	f	•	•	•	•	•
(L.)	•	•	•	•	•	g	•	•	•	•	•
Chrysiridia	h	•	•	•	•	•	•	•	•	•	•
rhipheus	•	•	•	•	•	•	i	•	•	•	•
(Drury)	•	•	•	•	•	•	•	•	i	•	•
	•	•	•	•	•	•	•	i	•	•	•
Alcides	•	•	•	•	•	•	•	•	•	•	•
agathysus	•	•	•	•	•	•	•	•	•	•	•
(Kirsch.)[3]											
A. metaurus	•	•	•	•	•	•	•	•	•	l	•
(Hopffer)[5]	•	•	•	•	•	•	•	•	•	•	•
	•	•	•	•	•	•	•	•	•	•	•
Lyssa macleayi	•	•	•	•	•	•	•	•	•	•	•
(Montrouzier)	•	•	•	•	•	•	•	•	•	•	•
	•	•	•	•	•	•	•	•	•	•	•
L. ?macleayi[6]	•	•	•	•	•	•	•	•	•	•	•
L. monoetius	•	•	•	•	•	•	•	•	•	•	•
(Hopffer)[9]											
L. zampa docile	•	•	•	•	•	•	•	•	•	•	•
(Butler)[11]											
L. zampa zampa	•	•	•	•	•	•	•	•	•	•	•
(Butler)											
Urapteroides	•	•	•	•	•	•	•	•	•	•	•
astheniata	•	•	•	•	•	•	•	•	•	•	•
(Guenée)	•	•	•	•	•	•	•	•	•	•	•

TABLE 2. Extended.

E. medullosum	***E. myrmecophilum***	*E. labios*	***E. moluccanum***	***E. diadenum***	*E.* sp.	***Suregada boiviniana*** (Euphorbi-)	***S. decidua***	*Quisqualis indica* (Combret-)	*Pittosporum* sp. (Pittospor-)	"Palm" (Arec-)	**Rearing locality†**
•	•	•	•	•	•	•	•	•	•	•	**Cub: W**^{1}
•	•	•	•	•	•	•	•	•	•	•	**Cub: NW, Matanzas**
•	•	•	•	•	•	•	•	•	•	•	**Cub: W, Mogotes**
•	•	•	•	•	•	•	•	•	•	•	Jam: N, Ocho Rios
•	•	•	•	•	•	•	•	•	•	•	**Cub: E, Punta Maisi**^{2}
•	•	•	•	•	•	•	•	•	•	•	**Mex: Veracruz**
•	•	•	•	•	•	•	•	•	•	•	**Pan: N & S**
•	•	•	•	•	•	•	•	•	•	•	**Amaz: Surinam**
•	•	•	•	•	•	•	•	•	•	•	**Trin**
•	•	•	•	•	•	•	•	•	•	•	**Mad: E**
•	•	•	•	•	•	•	•	•		•	**Mad: W, Lac Bemamba**
•	•	•	•	•	•	•	•	•	•	•	**Mad: W, Bemaraha**
•	•	•	•	•	•	•	•	•	•	•	**Mad: NW, Ankarana**
•	<	j	>	•	•	•	•	•	•	•	**PNG: E, Sogeri**^{8}
•	•	•	•	•	•	•	•	•	k	•	PNG: E, Rouna Falls, Port Moresby^4
•	•	•	•	•	•	•	•	•	•	•	**NQd: upper Mulgrave R.**
•	j	•	•	•	•	•	•	•	•	•	**NQd: Bamaga, Cp. York**
j	•	•	•	•	•	•	•	•	•	•	**NQd: Mission Beach)**
•	•	<	k	>	•	•	•	•	•	•	PNG: E, Brown R.^{7}
•	<	j	>	•	•	•	•	•	•	•	**PNG: E, Sogeri**^{8};
j	•	•	•	•	•	•	•	•	•	•	**NQd: Cape Tribulation**
•	j	•	•	•	•	•	•	•	•	•	**NQd: Cape York**
•	•	•	•	•	•	•	•	•	•	m	Phil^{10}
•	•	•	•	n	•	•	•	•	•	•	**pMal: Selangor**
•	•	•	•	•	•	•	•	o	•	•	Thai: Bangkok^{12}
•	•	•	•	p	•	•	•	•	•	•	**pMal: Selangor**
•	•	<	q	>	•	•	•	•	•	•	Sol^{13}
r	•	•	•	•	•	•	•	•	•	•	**NQd: Cape Tribulation**

TABLE 2. Continued.

Moth taxon†‡	**Larval foodplants*** (Confirmed foodplants in bold) Species (Family—aceae)	***Omphalea oppositifolia*** (Euphorbi-)	*O. triandra*	***O. hypoleuca***	***O. trichotoma***	***O. oleifera***	***O. diandra***	***O. palmata***	***O.* sp. nov.**	***O. occidentalis***	***O. queenslandiae***	***Endospermum macrophyllum*** (Euphorbi-)
U. anerces (Meyrick)		•	•	•	•	•	•	•	•	•	•	s
Cyphura semi-obsoleta Warr.		•	•	•	•	•	•	•	•	•	•	•
Urapteritra fasciata (Mabille)		•	•	•	•	•	•	•	•	•	•	•
U. ?piperita (Oberthur)[14]		•	•	•	•	•	•	•	•	•	•	•

⊗ In captivity, *Urania* larvae will feed on other species of *Omphalea* tested (N. G. Smith, D. C. Lees, pers. obs.); these records are all from the wild.

* See Tables 3, 4 and 5 for authors of plant names.

† Notes (superscripts):

1. As "*O. triandra* Linn.," which does not occur in Cuba; however, Macleay's illustration clearly shows the hostplant to be *O. trichotoma*.
2. Voucher photographs show *Urania* larvae hanging down on threads (Fig. 1A); larvae are not *U. boisduvalii* and by elimination are assumed to be *U. poeyi*.
3. There is a color figure of *A. agathyrsus* larvae descending from an unspecified tree in Lae, Papua New Guinea, in D'Abrera (1974:60).
4. An *E. moluccanum* specimen in the Rijksherbarium, Leiden, was originally identified as a *Pittosporum* sp., so it is perhaps conceivable that such a misidentification could have been made in this case.
5. There are 3 larvae of *A. metaurus* collected by A. S. Meek in the BMNH collection, and, as they were collected at Cedar Bay, S. of Cooktown, it is likely they were reared on *E. medullosum* rather than one of the other two recorded foodplants.
6. The identity of the population of *Lyssa* in North Queensland, not recognized by Altena (1953), requires clarification, and is here referred to as *L. ?macleayi*. Previously it has been referred to in the literature as *L. patroclus* (Coleman & Monteith 1981), but the figure in D'Abrera (1974:60) resembles *L. macleayi*. Altena (1955: 13–14) was in any case unsure that the two taxa deserve specific status.
7. The moth host is described as "*L. patroclus goldiei* Drc.," referable to *L. macleayi macleayi* (see Altena 1953: 15). This foodplant is described as "*Endospermum* sp. nov. (Hoogland 1967, pers. comm.)," which is most likely to be referable to *E. labios* Schodde 1967, although there does exist a collection of *E. myrmecophilum* from Brown R. (see Table 6).
8. Ray Straatman reared his uraniines at Sogeri on a myrmecophilous species that he called "*E. formicarum*" (syn. *E. moluccanum*) (R. Straatman, pers. comm.), but Monteith and Wood (1987) suggest this was *E. myrmecophilum*.
9. Kühn (1887) describes and figures a larva of *Lyssa* "*patroclus*" from Tombugu, N. Sulawesi, which might be either *L. monoetius celebensis* or *L. zampa dilutus* (Altena 1953). The foodplant is described briefly as "an abundant shrub in mangrove swamp with glabrous blue-green bark, and simple ovate, acuminate leaves, the younger ones large hand[-sized?] and trifid." *Endospermum peltatum* Merr. in N.E. Sulawesi has non-peltate

almost exactly corresponds to the range of the Neotropical, Afrotropical, and Australasian (but not the Malesian) *Omphalea* species, is suggestive of a very specialized and ancient relationship, perhaps even predating the final break-up of Gondwanaland in the mid-late Cretaceous, ca. 100–65 million years BP (Coleman & Monteith 1981). Although a vi-

TABLE 2. Continued.

E. medullosum	***E. myrmecophilum***	*E. labios*	***E. moluccanum***	***E. diadenum***	*E.* sp.	***Suregada boiviniana*** (Euphorbi-)	***S. decidua***	*Quisqualis indica* (Combret-)	*Pittosporum* sp. (Pittospor-)	"Palm" (Arec-)	**Rearing locality†**
•	•	•	•	•	•	•	•	•	•	•	**Fiji**
•	•	•	•	•	q	•	•	•	•	•	NG
•	•	•	•	•	•	i	•	•	•	•	**Mad: E, Perinet**
•	•	•	•	•	•	•	t	•	•	•	**Mad: SW, Beza Mahafaly, nr. Betioky**

(acuminate) as well as peltate leaves, occurring in wet forest including swamps (Schaeffer 1971); however, younger divided leaves are not described. [A species of *Suregada*, *S. racemulosa* (Merr.) Croiz. (? =*S. trifida* (Elm.) Croiz.) has appropriately shaped leaves but is known only from the Philippines].

10. The record states only that a larva of this species that was lightly hairy with 16 feet was reared by Lorquin on "une espèce de palmier (qu'entendit-il par ce nom?)".
11. The descriptions given of *L.* ?*zampa docile* larvae by Corbett & Dover (1927) mention the absence of hairs and tubercles, and are thus suspect. The two paintings (dorsal and lateral view) on which the descriptions were based, apparently held in the Department of Agriculture at Kuala Lumpur (Altena 1953:26, 37), have not been examined.
12. A voucher slide shows a reared *L. zampa zampa* adult resting on *Quisqualis indica* leaves, but the larvae were described as "orange, with long hairs", and the observer agreed they did not resemble the illustration of a *L. zampa* (or *L. monoetius*) larva in Kühn (1887). This shows short hairs on raised tubercles, as does a preserved larva of *L.* ?*macleayi* from Mission Beach, reared by D. Kitchin (see Fig. 1E). Thus this record requires confirmation.
13. As "*E. myrmicaria*"; *E. myrmecophilum* does not occur in the Solomons (Schaeffer 1971), so the record probably refers to one of the other two ant mutualist species (see Table 4).
14. *Urapteritra piperita* and *U. falcifera* (Weymer) are the two sympatric species; of these, the former has been recorded from Betioky (Viette 1972).

‡ References: a. Macleay 1834; b. N. G. Smith, pers. obs.; c. Gosse 1881; d. L. J. Gillespie, pers. comm.; e. N. G. Smith, Smiths. Inst. Res. rep. No. 7, Winter 1974; Smith 1982; f. Hofmann 1881; g. Guppy 1907; h. Camboué 1889, 1892; Eltringham 1924a; Catala 1940; i. D. C. Lees, pers. obs.; j. Monteith & Wood 1987; k. Szent-Ivany & Carver 1967; l. Coleman & Monteith 1981; m. Boisduval 1874; n. Y. P. Tho, pers. comm. [see also Barlow 1982]; o. A. R. Pittaway, pers. comm.; p. Browne 1937, 1938, 1940 [see also Corbett & Dover 1927]; q. CAB Int. Inst. of Entomol. economic card index, Natural History Museum, South Kensington; r. G. Monteith, pers. comm.; reared from pupa by D. Kitchin; s. Robinson 1975:315; t. L. L. Holloway, pers. comm., photographs of larvae and hostplant (Fig. 1G).

cariance explanation for the distributions seems sufficient, the possibility of more recent long-distance dispersal of moths or plants cannot be ruled out: the moths are renowned for their population explosions and migratory abilities and at least two *Omphalea* spp. are reported to disperse their seeds on ocean currents (Guppy 1917, Johnston 1949).

Endospermum, some species of which are of minor economic importance as a tropical softwood, has so far been found to be a host for seven species in four uraniine genera (Table 2). *Endospermum* is wide-

TABLE 3. Distribution of *Omphalea* species worldwide and the uraniine species that feed on them or are sympatric. Confirmed foodplants shown in bold. Arranged systematically (Gillespie 1990). Abbreviations: Pa = Sect. Palminerviae Pax & K. Hoffm.; Pe = Sect. Penninerviae Pax & K. Hoffm.; l = liana; t = tree/shrub. Locality abbreviations additional to Table 2: Braz = Brazil; Hisp = Hispaniola; Guat = Guatemala; Hond = Honduras; Tanz = Tanzania; CAm = Central America; IJ = Irian Jaya; Bis = Bismarck Arch. (NI = New Ireland); Myan = Myanmar [Burma]; Bor = Borneo; Sing = Singapore; Sul = Sulawesi. Italics signifies foodplant record as well as sympatry.

Plant species (Bold print: confirmed foodplant)	**Uraniine species***‡ (Uraniines confirmed to feed on *Omphalea* in bold)															**Known distribution of plant: (Ref.)**† (Bold print: diurnal uraniine sympatric)
	Urania boisduvalii Guérin	*U. sloanus* (Cramer)	***U. poeyi* Gundlach**	***U. fulgens* Walker**	***U. leilus* (L.)**	*U. brasiliensis* (Swainson)	***Chrysiridia rhipheus* (Drury)**	*C. croesus* (Gerstaecker)	*Alcides latona* (Druce)	*A. aurora* Salvin & Godman	*A. orontes* (L.)*	*A. cydnus* (Felder)	*A. aruus* (Felder)*	***A. metaurus* (Hopffer)**	*A. agathyrsus* (Kirsch)	
Omphalea brasiliensis Muell. Arg. (Pe; l)	• • •	• • •	• • •	• • •	• • •	a a a	• • •	• • •	• • •	• • •	• • •	• • •	• • •	• • •	• • •	**Braz: atlantic rainforest, Bahia (Salvador & Vitória) to Espirito Santo (Linhares):** (1)
O. oppositifolia (Willd.) Gillespie [=*O. biglandulosa* (Pers.) Baill.] (Pe; t)	•	•	•	•	•	•	*b*	•	•	•	•	•	•	•	•	**Mad: E rainforest, scattered small populations from Antongil Bay S. to Fianarantsoa:** (2)
O. triandra L. (Pe; t)	• •	*c* •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	• •	**Jam:** wet forest on limestone: (2); Haiti (introduced): (3)
O. ekmanii Alain (Pe; t)					No *Urania* records											Hisp (Rep. Dominicana): cloud forest, La Vega & Banao: (3)
O. hypoleuca Grisebach (Pa; t)	*d*	•	•	•	•	•	•	•	•	•	•	•	•	•	•	**Cub: limestone Mogotes in west, Pinar del Rio:** (4)

TABLE 3. Continued.

Plant species (Bold print: confirmed foodplant)	**Uraniine species*‡** (Uraniines confirmed to feed on *Omphalea* in bold)															**Known distribution of plant: (Ref.)†** (Bold print: diurnal uraniine sympatric)
	Urania boisduvalii Guérin	*U. sloanus* (Cramer)	***U. poeyi* Gundlach**	***U. fulgens* Walker**	***U. leilus* (L.)**	*U. brasiliensis* (Swainson)	***Chrysiridia rhipheus* (Drury)**	*C. croesus* (Gerstaecker)	*Alcides latona* (Druce)	*A. aurora* Salvin & Godman	*A. orontes* (L.)*	*A. cydnus* (Felder)	*A. aruus* (Felder)*	***A. metaurus* (Hopffer)**	*A. agathyrsus* (Kirsch)	
O. commutata Muell.	No *Urania* records															Hisp (Haiti): Gonaives I.: (2)
Arg. (Pa; t)																
O. trichotoma	*d*	•	•	•	•	•	•	•	•	•	•	•	•	•	•	**Cub: coastal limestone, N/NW,**
Muell. Arg. (Pa; t)	•	•	*e*	•	•	•	•	•	•	•	•	•	•	•	•	**extreme E:** (4)
O. oleifera Hemsley	•	•	•	*f*	•	•	•	•	•	•	•	•	•	•	•	**S Mex to Guat:** (2);
[=*O. cardiophylla*	•	•	•	*f*	•	•	•	•	•	•	•	•	•	•	•	**El Salvador:** (2, 16)
Hemsley] (Pa; t)																
O. diandra L.	•	•	•	*f*	•	•	•	•	•	•	•	•	•	•	•	**Hond S through lowland CAm:**
																(2);
[=*O. megacarpa*	•	•	•	•	*g*	•	•	•	•	•	•	•	•	•	•	**Amaz:** (2);
Hemsley] (Pa; l)	•	•	•	•	*h*	•	•	•	•	•	•	•	•	•	•	**Trin** & Tobago: (2);
				Urania not known to be a resident												Grenada, cultivated: (2);
				Urania not known to be a resident												Guadeloupe & Martinique: (2);
				Urania not known to be a resident												St. Kitts, St. Vincent: (5)
	•	i	•	•	•	•	•	•	•	•	•	•	•	•	•	**Jam:** (6) (extinct?);
	•	•	d	•	•	•	•	•	•	•	•	•	•	•	•	**Cub: NE near Baracoa:** (7)
O. mansfeldiana	•	•	•	•	•	•	•	g	•	•	•	•	•	•	•	**SE Tanz: Lindi & Selous:**
Mildbraed (Pa; l)	•	•	•	•	•	•	•	j	•	•	•	•	•	•	•	Ebenda, Rufiji R., Kilwa: (8)

TABLE 3. Continued.

Plant species (Bold print: confirmed foodplant)	**Uraniine species*‡** (Uraniines confirmed to feed on *Omphalea* in bold)															Known distribution of plant: (Ref.)† (Bold print: diurnal uraniine sympatric)
	Urania boisduvalii Guérin	*U. sloanus* (Cramer)	***U. poeyi* Gundlach**	***U. fulgens* Walker**	***U. leilus* (L.)**	*U. brasiliensis* (Swainson)	***Chrysiridia rhipheus* (Drury)**	*C. croesus* (Gerstaecker)	*Alcides latona* (Druce)	*A. aurora* Salvin & Godman	*A. orontes* (L.)*	*A. cydnus* (Felder)	*A. aruus* (Felder)*	***A. metaurus* (Hopffer)**	*A. agathyrsus* (Kirsch)	
***O.* sp. nov.** (Pa; t)	•	•	•	•	•	•	b	•	•	•	•	•	•	•	•	**Mad: NW/N: limestone karst, Ankarana;**
	•	•	•	•	•	•	*b*	•	•	•	•	•	•	•	•	Montagne des Francais (E of Antsiranana): (9)
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
***O. palmata* Léandri** (Pa; t)	•	•	•	•	•	•	b	•	•	•	•	•	•	•	•	**Mad: (W/NW): limestone karst,**
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Ankarafantsika,
	•	•	•	•	•	•	b	•	•	•	•	•	•	•	•	**Bemaraha** and deciduous
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	forest on sand, Trangahy,
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Manambolo R., **sublittoral**
	•	•	•	•	•	•	*b*	•	•	•	•	•	•	•	•	**forest W/SW Antsalova:** (10)
O. occidentalis Léandri (Pa; t)	•	•	•	•	•	•	b	•	•	•	•	•	•	•	•	**Mad: (W/NW): limestone karst,**
	•	•	•	•	•	•	*b*	•	•	•	•	•	•	•	•	**Bemaraha,**
	•	•	•	•	•	•	k	•	•	•	•	•	•	•	•	**Namoroka** and dry
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	sandy forest (Tsiempihy): (10)
O. queenslandiae Bailey (Pa; l/(t))	•	•	•	•	•	•	•	•	•	•	•	•	•	*l*	•	**NQd: Atherton/Cairns/ Innisfail rainforest:** (11)
O. papuana Pax & K.	•	•	•	•	•	•	•	•	•	•	•	•	•	l	•	**NQd: Iron Range (Cp. York):** (2);

TABLE 3. Continued.

Plant species (Bold print: confirmed foodplant)	**Uraniine species***‡ (Uraniines confirmed to feed on *Omphalea* in bold)															**Known distribution of plant: (Ref.)†** (Bold print: diurnal uraniine sympatric)
	Urania boisduvali Guérin	*U. sloanus* (Cramer)	***U. poeyi* Gundlach**	***U. fulgens* Walker**	***U. leilus* (L.)**	*U. brasiliensis* (Swainson)	***Chrysiridia rhipheus* (Drury)**	*C. croesus* (Gerstaecker)	*Alcides latona* (Druce)	*A. aurora* Salvin & Godman	*A. orontes* (L.)*	*A. cydnus* (Felder)	*A. aruus* (Felder)*	***A. metaurus* (Hopffer)**	*A. agathyrsus* (Kirsch)	
Hoffm. (Pa; l) [=*Neomphalea gageana* Pax & K. Hoffm., =*N. papuana* Gage]	•	•	•	•	•	•	•	•	•	•	•	g	•	•	g	**NG: PNG, IJ;**
	•	•	•	•	•	•	•	•	•	g	•	•	•	•	•	**Bis (NI);**
	•	•	•	•	•	•	•	•	g	•	•	•	•	•	•	**Sol: Guadalcanal,** Treasury Is.: (12)
O. bracteata (Blanco) Merr. (Pe; (l/(t))	No diurnal uraniine is sympatric; *Lyssa* & *Urapteroides* are not known to feed on *Omphalea*															Flores (?); N/C Sul, Phil, Bor, Sing, pMal, Thai, Laos, Myan: (13)
[=*O. sargentii* Merr. (Pe; l)]																[Bor]:(14)
[=*O. malayana* Merr. (Pe; t)]																[pMal, Phil: Luzon, Bor: Sarawak]: (14)
[=*O. grandifolia* Merr. (Pe; t)]																[Phil: Luzon, Panay]: (15)

* Diurnal uraniines are recorded from the following main areas where *Omphalea* is not (excluding likely migrant records; subscripts refer to refs. below): *Urania boisduvali*: Holguin Province, NE Cuba$_{d}$; *Alcides* spp.: Maluku, see table; *A. metaurus*, extreme N Cape York (G. B. Monteith, pers. comm.); *Chrysiridia croesus*: Zanzibar$_{j}$.

† References: *Omphalea* distribution: 1. Müller-Argovensis 1873–74:514–515; K. S. Brown, Jr., pers. comm.; 2. Gillespie 1990; 3. Liogier 1971, 1986:178–181; 4. Leon & Alain 1953; 5. Adams 1972; 6. Hemsley 1885, Adams 1972; 7. D. C. Lees, pers. obs.: Havana Botanic Garden Herbarium; 8. Mildbraed 1936; Volleson 1980; Radcliffe-Smith 1987:371–373; 9: L. J. Gillespie, pers. comm.; 10. Léandri 1938, 1954; D. C. Lees, pers. obs.; 11. Airy Shaw 1980b:661; 12. Airy Shaw 1980a:177–8; 1966; 1969; 13. Airy Shaw 1971:310–1; 1975:180–1, 1982: 31; 1983:39; 14. Airy Shaw 1975:180–1; 15. Airy Shaw 1983:39; 16. F. Serrano, pers. comm.

‡ References: uraniine distribution (italics signify foodplant record as well as being sympatric): a. K. S. Brown, Jr., pers. comm.; b. D. C. Lees, pers. obs. in Madagascar; c. Gosse 1851, 1880, 1881; d. Instituto de Ecologia y Systematica, Habana, Cuba; e. L. J. Gillespie, pers. comm.; f. N. G. Smith, pers. obs. g. National Collection, Natural History Museum, South Kensington; h. Guppy 1907; i. Townsend 1893; j. J. Kielland, J. Kingdon & W. B. Hynd, pers. comm.; k. R. Paulian, pers. comm.; l. Coleman & Monteith 1981.

spread in the Indo-Australasian region with approximately 13 species (Table 4), all trees, distributed from Assam east to southern China, south through Malaysia and the Philippines, to New Guinea and North Australia (Schaeffer 1971). The genus also occurs in the Andaman Islands and Sumatra as well as the New Hebrides and Fiji (Gowers 1976; Scheaffer 1971). There is a good correspondence between the overall range of *Urapteroides* spp. and *Lyssa* spp. with that of *Endospermum* (compare maps in Altena 1953 for *Lyssa* spp. and Schaeffer 1971 for *Endospermum* spp.—data are summarized in Table 4). Within its known range, *Endospermum* is uncollected from a number of island groups (mainly in the Papuan region) on which uraniines are known to occur (Franken 1984, Gowers 1976); these are listed in Table 4. Strikingly, both uraniine moths and *Endospermum* are completely absent from the archipelagos of the Lesser Sundas (Bali to the Timor Sea): these islands have a very pronounced dry season (van Steenis 1979). However, uraniines have been consistently reported from outside the range of *Endospermum* from Aru, Kai, and Tanimbar Is., C & S Sulawesi, Java and associated islands, and also from Sri Lanka (*Urapteroides astheniata*: Hampson 1895). The absence of records of *Endospermum* from these areas may be due to botanical undercollecting: remarkably, Java seems to be the only Indonesian island in the entire chain from Sumatra to the S.E. Moluccas with any comprehensive floristic treatment (see van Steenis 1979, Froden 1984). This explanation could also account for the apparent absence of *Omphalea* in the Moluccas.

There is no evidence that *Urapteroides* (or *Lyssa*) spp. feed on *Omphalea*. *Urapteroides* is the most widespread genus of Indo-Australasian Uraniinae, ranging from Assam to Queensland (*U. astheniata*), West Solomons, New Hebrides (*U. hyemalis* (Btlr.)), and Fiji (*U. anerces* Meyr.). This distribution is consistent with specialization on *Endospermum* spp. (Tables 4 and 5) throughout its range, but occurrence outside this range might be explained by adoption of an alternative foodplant or immigration, if not by gaps in floristic knowledge. Present evidence suggests that *Omphalea* does not constitute an alternative foodplant for *Urapteroides* because the larvae have a very characteristic feeding damage pattern (figured by Browne 1937; see also Fig. 1H) complete with a web that usually stays intact on herbarium specimens (often including droppings and occasionally head capsules or ova). An examination of all specimens of *Omphalea* and *Endospermum* in the herbaria of Royal Botanic Gardens (RBG), Kew, and Rijksherbarium, Leiden, revealed that although *Urapteroides*-type webs are fairly common on *Endospermum* spp. (Table 5), no such webs were found on Indo-Australasian *Omphalea* spp. However, records in Table 5 from the New Guinea region and Solomons alternatively might be referable to *Cyphura* spp., should this genus have similar feeding habits.

There are some 35 spp. of *Suregada* (Croizat 1942), entirely Paleotropical in distribution, with 13 spp. in Madagascar (Radcliffe-Smith 1991), eight spp. in Africa (Léonard 1958), including four spp. in East and South Africa (Palgrave 1977:432–434, Radcliffe-Smith 1987) (Table 6) and about 14 spp. in Indo-Australasia (D. C. Lees, pers. obs., Kew Herbarium). There is also a related genus, *Cladogelonium* Léandri (Léandri 1938), endemic to Madagascar, which, as the sister genus of *Suregada* (Radcliffe-Smith, pers. comm.) and being sympatric with *Urapteritra* spp. (Table 6), is a potential foodplant. The distribution of *Urapteritra* is consistent with the range of *Suregada* both in South and East Africa and in Madagascar as evident from museum and herbarium collections (D. C. Lees, unpubl. data; see Table 6). Eight species of *Urapteritra* are known from Madagascar (eastern rainforests and montane forests, western and southwestern dry deciduous forests: Viette 1972). One of these, *U. falcifera*, occurs in coastal eastern South Africa, Kenya, and Tanzania as well as in the southwestern forests of Madagascar. Two specimens of *U. falcifera* (Weymer) in the Natural History Museum, London, were bred by P. J. Leigh at Durban, Natal (where *Suregada* occurs), on an unspecified plant; a blown larval specimen from the same Leigh material exists at the Transvaal Museum in Pretoria, and also lacks foodplant data (C. B. Cottrell, pers. comm.). In Madagascar as in Africa the range of *Urapteritra* is considerably wider and stretches further south than that of the known *Omphalea* species (Table 3). This and the fact that no *Urapteritra* spp. were found recently during extensive fieldwork on Malagasy *Omphalea* species during the rainy season (D. C. Lees, pers. obs.) tends to suggest that *Urapteritra* does not feed on *Omphalea*. Similarly, it seems likely that *Chrysiridia* does not utilize *Suregada*. *Endospermum*, being absent from the Afrotropics, is not a potential natural foodplant of these two genera.

However, the remaining *Suregada* spp., widely distributed from India and South China to Australasia (Airy Shaw 1971, 1975, 1980a, 1980b, 1982, 1983) are potential uraniine foodplants. These are not tabulated here since no revision has been published and none are known to be foodplants. However, it will be of importance to discover whether any Indo-Australasian uraniines feed on the genus. Utilization of *Suregada* could explain some of the gaps mentioned in the distribution of *Endospermum* where uraniines occur. For example, *Lyssa zampa docile* (Butler) is apparently native to W. Java (Altena 1953), whereas *Endospermum* apparently is not (Backer 1963), although it is cultivated in the Bogor Botanical Garden (Schaeffer 1971). However, herbarium

TABLE 4. Distribution of *Endospermum* in Indo-Australasia and the uraniine species that feed on them or are sympatric. Confirmed foodplants shown in bold. *Endospermum* spp. (all trees) arranged in approximate systematic order (Schodde 1967; Schaeffer 1971; Smith 1978, 1981; Airy Shaw 1980a:79; Monteith & Wood 1987). Potentially new unnamed taxa collected from Biak and Numfoor Is., Irian Bay (Schodde 1967:401, Schaeffer 1971:191) not included. *Lyssa* spp. arranged after Altena 1953. Abbreviations: ** = species myrmecophilous (with *Camponotus quadriceps* Smith); * = twigs sometimes hollow but myrmecophily not known; # = inner bark odor foul, mousy; @ = inner bark odor like green beans; ? = identity of moth uncertain; localities not in Tables 2 and 3: Fij = Fiji Is.; Van = Vanuatu [New Hebrides]; NB = New Britain; Malu = Maluku [Moluccas]; Sum = Sumatra; HK = Hong Kong I.; IC = Indochina; pThai = peninsular Thailand; mThai = mainland Thailand. Italics signifies foodplant record as well as sympatry.

Plant species†⊗ (Bold print: confirmed foodplant)	**Uraniine species***‡ (Uraniines confirmed to feed on *Endospermum* in bold)																					**Plant distribution: (Ref.)**† (Bold print: uraniine sympatric)
	Alcides latona (Druce)■	*A. aurora* Salv. & Godm.	*A. orontes* (L.)	*A. cydnus* (Felder)	*A. arus* (Felder)	***A. metaurus*** (Hopffer)	***A. agathyrsus*** (Kirsch)	*Lyssa patroclus* (L.)■	*L. macleayi* (Montrouzier)	*L. toxopeusi* (Altena)	*L. mutata* (Butler)	*L. curvata* (Skinner)	*L. menoetius* (Hopffer)	***L. zampa*** (Butler)	***Urapteroides anerces*** (Meyr.)	*U. hyemalis* (Butler)	***U. astheniata*** (Guenée)	*Cyphura* (Solomons spp.)▲	*Cyphura* (Bismarcks spp.)	***Cyphura*** **(NG spp.)**	*Cyphura* (Maluku spp.)	
Endospermum macrophyllum (Muell. Arg.) Pax & Hoffm.*	•	•	•	•	•	•	•	•	•	•	•	•	•	•	*a*	•	•	•	•	•	•	**Fij: Vanua Levu,**
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	a	•	•	•	•	•	•	**Viti Levu;** Ovalau,
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Taveuni, Kadavu: (1)
E. robbieanum A. C. Smith	•	•	•	•	•	•	•	•	•	•	•	•	•	•	a	•	•	•	•	•	•	**Fij: C. Vanua Levu:** (1)
E. medullosum L. S. Smith @ [?=*E. domatiphorum* Schaeffer, from E/C. PNG]	•	•	•	•	•	•	•	•	•	•	•	b	•	•	•	c	•	•	•	•	•	**Van: SE Efate, Northern Is.:** (2)
	c	•	•	•	•	•	•	•	•	•	b	•	•	•	•	c	c	c	•	•	•	**Sol:** (3),
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Santa Cruz Is.: (4)
	•	•	•	•	•	•	•	?b	•	•	•	•	•	•	•	•	c	•	•	•	•	**Admiralty Is.:** (5)
	•	c	•	•	•	•	•	•	•	b	•	•	•	•	•	•	c	•	c	•	•	**Bis: NB:** (3),
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Normanby I.: (6)
	•	•	•	c	•	•	c	•	b	•	•	•	•	•	•	•	c	•	•	c	•	**NG: PNG,**
	•	•	c	c	d	•	c	•	b	b	•	•	•	•	•	•	c	•	•	c	•	**IJ,**

TABLE 4. Continued.

Plant species†⊗ (Bold print: confirmed foodplant)	**Uraniine species***‡ (Uraniines confirmed to feed on *Endospermum* in bold)																					**Plant distribution: (Ref.)**† (Bold print: uraniine sympatric)
	Alcides latona (Druce)■	*A. aurora* Salv. & Godm.	*A. orontes* (L.)	*A. cydnus* (Felder)	*A. aruus* (Felder)	***A. metaurus*** (Hopffer)	***A. agathyrsus*** (Kirsch)	*Lyssa patroclus* (L.)■	*L. macleayi* (Montrouzier)	*L. toxopeusi* (Altena)	*L. mutata* (Butler)	*L. curvata* (Skinner)	*L. menoetius* (Hopffer)	***L. zampa*** (Butler)	***Urapteroides anerces*** (Meyr.)	*U. hyemalis* (Butler)	***U. astheniata*** (Guenée)	*Cyphura* (Solomons spp.)▲	*Cyphura* (Bismarcks spp.)	***Cyphura* (NG spp.)**	*Cyphura* (Maluku spp.)	
	•	•	•	•	•	•	•	•	e	•	•	•	•	•	•	•	c	•	•	c	•	**Numfoor,**
	•	•	•	•	•	•	•	•	b	•	•	•	•	•	•	•	•	•	•	•	•	**Biak,**
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	c	•	•	•	•	**Yapen,**
	•	•	•	d	•	•	•	•	b	•	•	•	•	•	•	•	•	•	•	•	•	**Salawati Is.:** (5)
	•	•	•	•	•	f	•	•	?*f*	•	•	•	•	•	•	•	*c*	•	•	•	•	**NQd, Iron Range (Claudie R.) S. to Cape Tribulation, Mission Beach:** (7)
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	NQd: N Territory, Daly R. & Channel Point: (7)
E. myrmecophilum L. S. Smith**#@	•	c	•	•	•	•	•	•	•	b	•	•	•	•	•	•	c	•	c	•	•	**Bis: NB:** (8)
	•	•	•	c	•	•	c	•	b	•	•	•	•	•	•	•	c	•	•	c	•	**NG: PNG, E/S:** (3)
	•	•	•	•	•	*f*	•	•	?f	•	•	•	•	•	•	•	•	•	•	g	•	**NQd: N Cape York, Bamaga-Lockerbie rainforest:** (7)
E. labios ssp. *gracilipes* Schodde**@	c	•	•	•	•	•	•	•	•	•	b	•	•	•	•	c	c	c	•	•	•	**Sol,** E at least to
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Santa Isabel I.: (9)
ssp.?	•	c	•	•	•	•	•	•	•	b	•	•	•	•	•	•	c	•	c	•	•	**Bis: NB:** (6)
ssp. *labios* Schodde**#	•	•	•	c	•	•	c	•	b	•	•	•	•	•	•	•	c	•	•	c	•	**NG: PNG [esp. N of C. cordillera],**
	•	•	c	c	d	•	c	•	b	b	•	•	•	•	•	•	c	•	•	c	•	**IJ [esp. N of C. range],**
	•	•	•	d	•	•	•	•	b	•	•	•	•	•	•	•	•	•	•	•	•	**Salawati I.:** (9)

TABLE 4. Continued.

Plant species†⊗ (Bold print: confirmed foodplant)	**Uraniine species***‡ (Uraniines confirmed to feed on *Endospermum* in bold)																					**Plant distribution: (Ref.)**† (Bold print: uraniine sympatric)
	Alcides latona (Druce)■	*A. aurora* Salv. & Godm.	*A. orontes* (L.)	*A. cydnus* (Felder)	*A. aruus* (Felder)	***A. metaurus*** **(Hopffer)**	***A. agathyrsus*** **(Kirsch)**	*Lyssa patroclus* (L.)■	*L. macleayi* (Montrouzier)	*L. toxopeusi* (Altena)	*L. mutata* (Butler)	*L. curvata* (Skinner)	*L. menoetius* (Hopffer)	***L. zampa*** **(Butler)**	***Urapteroides anerces*** **(Meyr.)**	*U. hyemalis* (Butler)	***U. astheniata*** **(Guenée)**	*Cyphura* (Solomons spp.)▲	*Cyphura* (Bismarcks spp.)	***Cyphura*** **(NG spp.)**	*Cyphura* (Maluku spp.)	
E. moluccanum (Teijsm. & Binnend) Kurz**# [=*E. formicrum* Becc.]	c	•	•	•	•	•	•	•	•	•	b	•	•	•	•	c	c	c	•	•	•	**Sol**
	•	c	•	•	•	•	•	•	•	b	•	•	•	•	•	•	c	•	c	•	•	**Bis: NB:** (3),
	•	c	•	•	•	•	•	b	•	b	•	•	•	•	•	•	c	•	c	•	•	**NI:** (6),
	•	•	•	c	•	•	c	•	b	•	•	•	•	•	•	•	c	•	•	c	•	**NG: PNG,**
	•	•	c	c	d	•	c	•	b	b	•	•	•	•	•	•	c	•	•	c	•	**IJ:** (3),
	•	•	•	•	•	•	•	•	b	•	•	•	•	•	•	•	•	•	•	•	•	**Kar-Kar,** Adi I.: (6)
	•	•	•	•	•	•	•	•	e	•	•	•	•	•	•	•	c	•	•	c	•	**Numfoor,**
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	**Biak,**
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	c	•	•	•	•	**Yapen,**
	•	•	•	d	•	•	•	•	b	•	•	•	•	•	•	•	•	•	•	•	•	**Salawati Is.**
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Kofiau Is.,
	•	•	c	•	•	•	•	b	•	•	•	•	•	•	•	•	c	•	•	•	c	**Malu, S: Seram,**
	•	•	c	c	c	•	•	e	•	b	•	•	•	•	•	•	d	•	•	•	c	**Ambon,**
	•	•	c	•	•	•	•	b	•	b	•	•	•	•	•	•	c	•	•	•	c	**Malu, N: Bacan,**
	•	•	•	•	•	•	•	b	•	•	•	•	•	•	•	•	•	•	•	•	h	**Morotai,**
	•	•	•	e	•	•	•	b	•	•	•	•	•	•	•	•	•	•	•	•	•	**Ternate,**
	•	•	c	e	•	•	•	b	•	•	•	•	•	•	•	•	•	•	•	•	h	**Halmahera,**
	•	•	[e]	•	•	•	•	•	•	•	•	•	b	b	•	•	h	•	•	•	•	**Sul, NE,**
	•	•	•	•	•	•	•	•	•	•	•	•	•	e	•	•	•	•	•	•	•	**Talaud Is.:** (3)
E. banghamii Merr.	•	•	•	•	•	•	•	•	•	•	•	•	•	b	•	•	c	•	•	•	•	**Sum, N: Atjeh:** (3)
E. ronaldii Schaeffer	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	**pMal:** P. Tioman: (3)

TABLE 4. Continued.

Plant species†⊗ (Bold print: confirmed foodplant)	**Uraniine species***‡ (Uraniines confirmed to feed on *Endospermum* in bold)																					**Plant distribution: (Ref.)**† (Bold print: uraniine sympatric)
	Alcides latona (Druce)■	*A. aurora* Salv. & Godm.	*A. orontes* (L.)	*A. cydnus* (Felder)	*A. aruus* (Felder)	***A. metaurus*** (Hopffer)	***A. agathyrsus*** (Kirsch)	*Lyssa patroclus* (L.)■	*L. macleayi* (Montrouzier)	*L. toxopeusi* (Altena)	*L. mutata* (Butler)	*L. curvata* (Skinner)	*L. menoetius* (Hopffer)	***L. zampa*** (Butler)	***Urapteroides anerces*** (Meyr.)	*U. hyemalis* (Butler)	***U. astheniata*** (Guenée)	*Cyphura* (Solomons spp.)▲	*Cyphura* (Bismarcks spp.)	***Cyphura*** **(NG spp.)**	*Cyphura* (Maluku spp.)	
E. quadriloculare Pax & K. Hofmann	•	•	•	•	•	•	•	•	•	•	•	•	•	b	•	•	c	•	•	•	•	**Sum, S: Tanjung Ning:** (3)
E. diadenum (Miq.) Airy Shaw	•	•	•	•	•	•	•	•	•	•	•	•	•	b	•	•	c	•	•	•	•	**Sum,**
	•	•	•	•	•	•	•	•	•	•	•	•	•	b	•	•	d	•	•	•	•	**Riau Arch,**
	•	•	•	•	•	•	•	•	•	•	•	•	•	b	•	•	h	•	•	•	•	**Simeulue,** Bangka,
	•	•	•	•	•	•	•	•	•	•	•	•	•	b	•	•	h	•	•	•	•	**Belitung Is.,**
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Natuna Is.,
	•	•	•	•	•	•	•	•	•	•	•	•	b	b	•	•	c	•	•	•	•	**Bor** (throughout),
	•	•	•	•	•	•	•	•	•	•	•	•	•	*i*	•	•	*j*	•	•	•	•	**pMal,**
	•	•	•	•	•	•	•	•	•	•	•	•	•	b	•	•	c	•	•	•	•	**Singapore,**
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	**pThai:** (3)
E. chinense Benth.	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	c	•	•	•	•	**IC: mThai,**
	•	•	•	•	•	•	•	•	•	•	•	•	•	b	•	•	c	•	•	•	•	**Myan, Assam,**
	•	•	•	•	•	•	•	•	•	•	•	•	•	b	•	•	•	•	•	•	•	**Vietnam, N & C,**
	•	•	•	•	•	•	•	•	•	•	•	•	•	b	•	•	•	•	•	•	•	**Hainan I., HK,**
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Shantou I.: (3)
	•	•	•	•	•	•	•	•	•	•	•	•	•	b	•	•	•	•	•	•	•	**S China (Guangdong):** (6)
E. ovatum Merr.	•	•	•	•	•	•	•	•	•	•	•	•	b	b	•	•	c	•	•	•	•	**Phil: Mindanao:** (3)

TABLE 4. Continued.

Plant species†⊗ (Bold print: confirmed foodplant)	**Uraniine species***‡ (Uraniines confirmed to feed on *Endospermum* in bold)																					**Plant distribution: (Ref.)**† (Bold print: uraniine sympatric)
	Alcides latona (Druce)▪	*A. aurora* Salv. & Godm.	*A. orontes* (L.)	*A. cydnus* (Felder)	*A. aruus* (Felder)	***A. metaurus*** **(Hopffer)**	***A. agathyrsus*** **(Kirsch)**	*Lyssa patroclus* (L.)▪	*L. macleayi* (Montrouzier)	*L. toxopeusi* (Altena)	*L. mutata* (Butler)	*L. curvata* (Skinner)	*L. menoetius* (Hopffer)	***L. zampa*** **(Butler)**	***Urapteroides anerces*** **(Meyr.)**	*U. hyemalis* (Butler)	***U. astheniata*** **(Guenée)**	*Cyphura* (Solomons spp.)▴	*Cyphura* (Bismarcks spp.)	***Cyphura*** **(NG spp.)**	*Cyphura* (Maluku spp.)	
E. peltatum Merr.#	•	•	[e]	•	•	•	•	•	•	•	•	•	b	b	•	•	h	•	•	•	•	**Sul, NE:** (3)
	•	•	•	•	•	•	•	•	•	•	•	•	b	b	•	•	c	•	•	•	•	**Phil: Mindanao,**
	•	•	•	•	•	•	•	•	•	•	•	•	b	b	•	•	c	•	•	•	•	**Luzon,** Samar,
	•	•	•	•	•	•	•	•	•	•	•	•	b	b	•	•	c	•	•	•	•	**Bor, N/E,**
	•	•	•	•	•	•	•	•	•	•	•	•	•	b	•	•	c	•	•	•	•	**pMal,**
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	pThai,
	•	•	•	•	•	•	•	•	•	•	•	•	•	b	•	•	c	•	•	•	•	**Andaman Is.:** (3)

* Uraniines recorded for islands where *Endospermum* is not (except Solomons, where *Endospermum* is well distributed): (*Lyssa* data from ref. b below, other data from ref. c below unless otherwise specified by subscripts); Bismarcks: Feni: *Lyssa patroclus* (Lp), *Urapteroides astheniata* (Uas), *Cyphura bifasciata* (Cb); Umboi [Rook]: Uas, Cb; Duke of York Is. [Mioko]: *Alcides aurora*, Lp, Cb; Lavongai [New Hanover]: Uas, Cb, *C. clarissima*; Witu [French I.]: *A. agathyrsus* (Aag), Lp, Uas, Cb; St. Matthias Gp.: *L. macleayi* ssp.?, Cb; E. PNG Is.: Louisade Arch. (Misima [St. Aignan], Tagula [Sudest], Rossel Is.): *A. agathyrsus* ssp.?, *A. cydnus*$_e$, *L. macleayi* ssp.?, Uas; Woodlark Is.: *Lyssa macleayi macleayi* (Lmm), *U. hyemalis* (Uh), Uas; Egum Gp.: Uas; Trobriand Is. (Kiriwina): Lmm$_e$, Uas; D'Entrecasteaux Is.⊗ (Goodenough, Fergusson Is.): Lmm, Uh, Uas, *C. geminia* (Cg), Cb, *C. semiobsoleta*; SW Bismarck Sea Is.: Manam [Vulcan]: Lmm; Irian [Geelvink] Bay Is.: Roon: *L. toxopeusi*, Cg; W. IJ. Is.: Misool: *A. aruus* (Aar); Uas; Waigeo: *A. cydnus* (Ac)$_e$, *A. orontes orontes* (Aoo), Lmm, Uas, Cg; *C. swinhoei*; E. Banda Sea Is.: ARU: Aar, *A. orontes liris* (Aol), Aag, *L. macleayi kotzenbergi* (Lmk), Cg; KAI IS.: Aar$_e$, Lp, Lmm, Cg$_h$; Watubela: Lmm$_e$; Lesser Sundas: TANIMBAR IS. [Timor Laut] (Larat, Yamdena, Selaru): *A. ?cydnus* ssp.?$_h$, Lmk; S. Maluku: Saparua: Aoo$_e$; Lp; Buru: Aol, Lp, Uas, Cg; N. Maluku: Obi: Aol, Lp, Uas, Cg; Gebe: Ac$_e$; Lp, Lmm, Cg, Cp$_h$; Celebesian subregion: SULA MANGOLE: *L. zampa dilutus* (Lzdi); BANGGAI IS.: Lzdi; *L. menoetius celebensis* (Lmc); C/S/W SULAWESI: Lmc; Philippines subregion: Sangihe [Sangir] Is.: *L. menoetius menoetius* (Lme); Palawan: Lme, *L. zampa* ssp.? (Lz?); Bohal: Lme; Lz?; Leyte: Lz?; Cébu: Lz?; Panaon: Lz?; Indochina: Laos: *L. zampa zampa* (Lzz); TAIWAN [Formosa]: Lzz$_e$; Java: W JAVA: *L. zampa docile* (Lzdo); E JAVA: Uas; KARIMONJAWA IS.: Lzdo; Sumatran subregion: Linggai Arch.: Lzdo$_h$, Uas$_h$; Nias: Lzdo; Enggano: Lzdo; Great Nicobar: Uas; [SRI LANKA: Uas (Hampson 1895)]. Islands outside known range of *Endospermum* (Franken 1984, Gowers 1976) in capitals.

⊗ Note: *Endospermum* has been collected in the D'Entrecasteaux Gp. from Normanby I., next to Fergusson I. (Table 4).

▪ *Alcides* & *Lyssa* ssp. comprise (ref. c. unless otherwise indicated by subscript): *A. orontes orontes* (L.) (Maluku & IJ); *A. o. liris* (Fldr.) (similar distribution but not Seram & Ambon); *A. cydnus* (Fldr.) ssp.? (NE PNG); *A. ?c.* ssp.? (Tanimbar)$_h$; *A. agathyrsus* (Kirsch.) ssp.? (Louisade Arch.) *L. macleayi macleayi* (Montrouzier) (NG & islands); *L. m.* ssp.? (Louisade Arch. only); *L. m. kotzenbergi* (Pfeiffer) (Tanimbar, Aru only); *L. ?m.* ssp.? (N Qd, N. Cape York only); *L. menoetius celebensis* (Altena) (NE Sul only); *L. menoetius menoetius* (Hopffer) (N Bor, Phil); *N. m. adspersus* (Altena) (E & S Bor); *L. zampa docile* (Butler) (Malesia); *L. z. z.* (Indochina); *L. z. najabula* (Moore) (Andamans only); *L. z.* ?ssp. (Philippines & ?Salibabu, Talaud only); *L. z. dilutus* (Röber) (NE Sul).

▴ *Cyphura* spp. examined comprise (ref. c. unless otherwise indicated by subscript): Solomons: 1) *C. bifasciata* Warr.; 2) *C. costalis* Btlr.; Bismarcks: Cb; 3) *C. clarissima* Blr.; New Guinea: 4) *C. phantasma* (Fldr.) (Cp) (IJ, PNG, also Japen, Manam, Karkar); 5) *C. geminia* (Cr.) (PNG, IJ, & Irian Bay Is.) (? syn. *C. falka* Swh., *C. pieridaria* Warr., *C. maxima* Strand [also N Qd$_g$]; 6) *C. caudiferaria* (Bdv.) (Cc) (Salawati, IJ, PNG); 7) *C. swinhoei* Rothschild (IJ); 8) *C.* ? new sp. (Numfoor, IJ: Dorey); 9) *C. atramentaria* Warr. (IJ, PNG); 10) *C. multistrigaria* Warr. (IJ, PNG); 11) *C. semiobsoleta* Warr. (IJ, PNG); 12) *C.* sp. nr. *semiobsoleta* (IJ); 13) *C. semialba* Warr. (PNG); 14) *C.* sp. nr. *semialba* (PNG); 15) *C. albisecta* Warr. (PNG); 16) *C. pardata* Warr. (PNG); Maluku: Cb (Halmahera, Morotai, Bacan)$_e$, Cp (Gebe), *C.* ? *geminia* (Halmahera, Bacan, Obi, Buru, Ambon, Seram$_h$, Saparua$_h$, Morotai$_h$, Cc (Halmahera, Bacan, Seram).

specimens of the widely distributed species *Suregada glomerulata* (Bl.) Baill. from Java do show plausible uraniine damage (D. C. Lees, pers. obs.). Although an examination of herbarium specimens of *Suregada* spp. revealed no *Urapteroides*-type larval feeding webs (as in Fig. 1H), a specimen of *S. multiflora* (Juss.) Baill. at RBG, Kew, from Thailand contained a pupal exuvium that may be that of *U. astheniata* (D. C. Lees, unpubl.).

As uraniines do not occur outside the known range of these three euphorbiaceous foodplants, there is presently no unambiguous evidence for other larval foodplants within the group.

SYSTEMATIC AFFINITIES OF LARVAL FOODPLANT GENERA

Caution must always be exercised in championing lepidopteran hosts as plant chemotaxonomists since they might be simply exploiting biochemical homoplasy. The same allelochemicals might have arisen independently within the same family; there are plenty of examples of independent evolution of secondary compounds within unrelated families, e.g., mustard oils exploited worldwide by the pierid genus *Appias* within the Capparales and Euphorbiaceae (*Drypetes*) (D. C. Lees, pers. obs.). It does seem intriguing that all three euphorbiaceous uraniine larval foodplant genera were formerly grouped by Pax and Hoffman (1931) in separate subtribes of the same tribe Geloniae (subfamily Crotonoideae) on the basis of the valvate and imbricate condition of the male calyx. However, these characters are probable plesiomorphies (Gillespie 1990). More recent classifications based on pollen morphology have suggested affinities of *Omphalea* with *Plukenetia* L. in the Acalyphoideae: for example, these two genera share tricolpate pollen (L. J. Gillespie, pers. comm.; Webster 1975, supporting the indications of Croizat 1941 and Punt 1962). Nevertheless, this position is unsatisfactory in certain other respects: e.g., *Omphalea* possesses laticifers, uncharacteristic of Acalyphoideae (Rudall in press). Whereas the taxonomic affinities of *Omphalea* remain debatable, pollen morphology indicates that *Endospermum* has affinities with crotonoid genera such as *Te-*

←

† References: *Endospermum* distribution: 1. Smith 1978, 1981:540–542; 2. Gowers 1976; 3. Schaeffer 1971 and Airy Shaw 1971:258–9, 1975:109–110, 1980a:78–81, 1980b:628–9, 1982:18, 1983:24; 4. Franken 1984:182–3; 5. Airy Shaw 1980a:79; 6. Herbarium, RBG, Kew; 7. Monteith & Wood 1987; 8. Rijksherbarium, Leiden [Lelean & Stevens LAF 51208; NGF 21761, both with ants, but requiring confirmation]; 9. Schodde 1967.

‡ References: uraniine distribution: (italics signifies foodplant record; ? signifies doubt over identity of moth taxa, square brackets express reservation about record) a. Robinson 1975; b. Altena 1953, Semper 1896–1902:597–599; c. National Collection, Natural History Museum, South Kensington including Rothschild collection; d. Rijksmuseum van Natuurlijke Historie, Leiden; e. NHM, South Kensington accessions; f. Monteith & Wood 1987; g. G. B. Monteith, pers. comm.; Common 1990:107, 384); h. Zoölogisch Museum van de Gemeentelijke Universiteit, Amsterdam; i. H. S. Barlow, Y. P. Tho, pers. comm.; j. Browne 1937.

TABLE 5. Herbarium specimens of *Endospermum* showing damage and webs similar to the larval damage of *Urapteroides astheniata* figured by Browne (1937).

Species	Origin	Herbarium†	Specimen ref.
E. macrophyllum	Fij: Nabantini, Serua	RBG	CSIRO S1403/5
E. medullosum	W. Irian Jaya: Biak I.	RL	RL 961292897
*E. medullosum** (as "*E. myrmecophilum*")	N. Qld.: N. Kennedy, Mission Beach (illustrated Fig. 1H)	RBG	B. Hyland 02050
E. myrmecophilum	PNG: Goldie R., Pt. Moresby	RL	R. Pullen 3316
E. myrmecophilum	PNG: Brown R., 8 mi. W. of Karema	RL, RBG	R. Schodde 2665
E. moluccanum	N. Malu: Totedaku, Morotai	RBG	Kostermans 618
E. moluccanum	C. Malu: Ambon	RL	RL 903157173
E. moluccanum	Sol: SE Ranonnga	RL	BSIP 14317
E. moluccanum	Sol: SW Ranonnga	RL, RBG	BSIP 15640
E. "nr. *moluccanum*"	W. Irian Jaya: Sukarnapura	RBG	Kostermans & Soejang 14
E. diadenum	pMal: Forest Research Institute, Kepong, Selangor	RL	FRI 27661
E. diadenum	pMal: Kuala Lumpur, Selangor	RBG	Ridley 3/3/1915
E. diadenum	pMal: Ulu Gombak Forest Reserve, Selangor	RBG	KFN 115660
E. diadenum	Bor: Kuching, Sarawak	RBG	Smythies 12517
E. diadenum	Bor: Kelumpang Forest Reserve, Kunak, Sabah	RBG	SAN 79831
E. diadenum	SE. Bor [Kalimantan Selatan]: Balikpapan, Mentawir	RBG	Saivveur 67
E. "cf. *macrophyllum*"	Bor: Meliau R., Beluran, Sabah	RL	SAN 99872
E. peltatum	pMal: Ulu Langit Forest Reserve. R., Selangor	RL, RBG	KFN 115652
E. peltatum	E. Bor [Kalimantan Timur]: Sangkulirang, E. Kutei	RL, RBG	Kostermans 5854
E. peltatum	Phil: Surigao, Mindanao	RBG	No. 2895

† RL = Rijksherbarium, Leiden; RBG = Royal Botanic Gardens, Kew.
* Monteith & Wood (1987); G. B. Monteith, pers. comm.

trorchidium Poepp. & Endl., *Klaineanthus* Pierre ex Prain (Punt 1962), *Adenocline* Turcz., *Cladogelonium* (Schaeffer 1971), and *Suregada* (Webster 1975). The finding that *Suregada* is a uraniine host appears reassuring because, apart from *Cladogelonium*, it is the most closely related genus placed within the Adenoclineae that occurs in Madagascar (Webster 1975). *Suregada* shares few synapomorphies with *Endospermum* (Gillespie 1990) but more closely related African genera occur outside the range of *Urapteritra*.

FOODPLANT DEFENSES: ECOLOGICAL SIGNIFICANCE FOR URANIINE SPECIALISTS

Ants

Three Australasian species of *Endospermum* (see Table 4) have a mutualistic relationship with a black ant *Camponotus quadriceps* Smith (Monteith & Wood 1987), which inhabits the hollow twigs. This relationship is reflected by the local name of *E. moluccanum* (T. & B.) Kurz in the Solomon Is.: "Ai-Aofia", or "Chief Tree", presumably due to the clearance of surrounding saplings by ants (Whitmore 1966). Uraniine larvae living on foodplants with extrafloral nectaries have adaptations to defend themselves against ants, either by living under a silken web, or by dropping off on a silken line (e.g., see Browne 1937, Gosse 1881; Fig. 1). This silk-line or silk-web behavior, also possessed by epiplemines (Hampson 1895, Holloway et al. 1987), may have facilitated specialization on plants with extrafloral nectaries by ancestral Uraniidae; all *Omphalea* and *Endospermum* spp., in common with many other Euphorbiaceae, possess leaf nectaries attracting ants. Some species of *Suregada* also have secretions exuding from the leaf axils or base of the flower buds (A. Radcliffe-Smith, pers. comm.). An interesting dichotomy occurs in Madagascar. A *Urapteritra* sp. (probably *U. piperita* (Oberthür)) from the S.W. feeds on a *Suregada* species that attracts ants (Table 2, Fig. 1G); this species possesses silk-line and silk-web feeding adaptations (L. L. Holloway, pers. comm.). *Urapteritra fasciata* feeds in the eastern rainforest on another *Suregada* species that lacks ants (Table 2); this species apparently has lost these adaptations, possessing a free-feeding lifestyle in all instars, and using a minimum of silk for attachment (D. C. Lees, pers. obs.).

In concert with silk use, it seems likely that uraniine larvae also possess a chemical deterrent as a primary defense against extrafloral nectary recruits, since visiting ants generally completely ignore uraniine larvae (observed both for *Chrysiridia* and *Urapteritra* in Madagascar: D. C. Lees, pers. obs., L. L. Holloway, pers. comm.). However, the presence of ant recruits and especially ant mutualists in some *Endospermum* spp. probably slows larval maturation and evidently deters oviposition. In North Queensland, plants of *E. myrmecophilum* L. S. Smith devoid of ant mutualists (usually those in open areas) are preferentially laid on and stripped by *Alcides metaurus* (G. B. Monteith, pers. comm.). Extrafloral nectaries of *Omphalea* spp. are also particularly attractive to polistiine wasps (D. C. Lees, pers. obs. in Madagascar), which are effective predators of early instar larvae (N. G. Smith, pers. obs. in Panama).

TABLE 6. Distribution of *Suregada* in the Afrotropics and sympatric uraniines. Confirmed foodplants and moths in bold print. *Suregada* arranged in provisional taxonomic order according to references below; *Urapteritra* arranged after Viette 1972. Abbreviations: ? after ref. = probably sympatric (moth recorded from close to plant collection locality); ? before ref. = identity of moth uncertain; Mad = Madagascar; Moz = Mozambique; SAf = South Africa; Eth = Ethiopia; Som = Somalia; Sud = Sudan; Zai = Zaire; Zam = Zambia; Mal = Malawi; Uga = Uganda; Ken = Kenya; Tan = Tanzania; Zim = Zimbabwe; IvC = Ivory Coast; Gha = Ghana; Nig = Nigeria. Italics signifies foodplant record as well as being sympatric.

Plant species† (Bold print: confirmed foodplant) / **Uraniine species***‡ (Uraniines confirmed to feed on *Suregada* in bold)	***Urapteritra fasciata*** (Mabille)	*U. suavis* (Oberthür)	*U. falcifera* (Weymer)	*U. montana* Viette	*U. malgassaria* (Mabille)	*U. mabillei* Viette	*U. antsianakaria* (Oberthür)	*U. piperita* (Oberthür)	**Plant Distribution**† (Bold print: *Urapteritra* sympatric)
Suregada comorensis (S. Moore) Croizat	•	•	•	•	•	•	•	•	Comoro Is. (only type collection)
S. laurina Baill.	a?	•	•	•	•	a?	•	•	**Mad, E** incl. Sainte Marie. Réunion (cult.)
S. boiviniana Baill.	•	•	•	•	•	•	•	•	Mad, NW: Manongarivo Massif,
	•	•	•	•	a	•	•	•	**Mad, NE:** widely distributed incl.
	•	•	•	•	a?	•	•	•	**Vohimarina,**
	•	•	•	•	•	•	a?	•	**Masoala Peninsula** to
	b	a?	•	•	•	a	•	•	**Mad, E: Analamalazoatra Forest** to
	•	•	•	•	•	•	•	•	Sainte Marie, Tafondro
	•	•	•	•	•	•	•	•	Mad, S: Anadabolava, nr. R. Mandrare
	•	•	•	•	•	•	•	•	Mad, NW: Ankarana, Sambirano to
S. bracteata A. R-Sm.	•	•	•	•	a?	•	•	•	Mad, NE: Maromandia, N of Vohimarina
	•	•	•	•	•	•	•	•	Mad, SE: Fianarantsoa to Ivohibe
S. gaultheriifolia A. R-Sm.	•	•	•	a?	•	•	•	•	Mad, C: Tsinjoarivo, 40 km SE of Ambatolampy

TABLE 6. Continued.

Plant species† (Bold print: confirmed foodplant)	**Uraniine species*‡** (Uraniines confirmed to feed on *Suregada* in bold)								**Plant Distribution†** (Bold print: *Urapteritra* sympatric)
	Urapteritra fasciata (Mabille)	*U. suavis* (Oberthür)	*U. falcifera* (Weymer)	*U. montana* Viette	*U. malgassaria* (Mabille)	*U. mabillei* Viette	*U. antsianakaria* (Oberthür)	*U. piperita* (Oberthür)	
S. adenophora Baill.	•	•	•	•	•	•	•	•	Mad, SE: Vohipeno, Mananjary to
	•	•	•	•	•	•	•	•	Mad, SE: Ft. Dauphin
S. grandifolia A. R-Sm.	•	•	•	•	•	•	•	•	Mad, E: Ambila-Lemaitso
S. nigricaulis A. R-Sm.									**Mad, E: Analamazoatra Forest**
S. eucleoides A. R-Sm.	b	a?	•	•	•	a	•	•	Mad, W: Analavelona Massif (NE Toliara);
	•	•	•	•	•	•	•	•	**Mad, SW: Zombitsy** (E of Sakaraha);
	•	•	a	•	•	•	•	a	Mad, W-C: Isalo Massif
S. capuronii Léandri	•	•	•	•	•	•	•	•	Mad, C: Ihosy to Ivohibe
	•	•	•	•	•	•	•	a?	**Mad, W:** Marosalaza Forest, 50 km **N of Morondava;**
	•	•	•	•	•	•	•	a	**Mad, SW: Sakaraha- Toliara;**
	•	•	a	•	•	•	•	a	Anjamala- **Andranovory;**
	•	•	•	•	•	•	•	a	R. Fiherenana Gorges **NE of Sakaraha;**
	•	•	•	•	•	•	•	•	Ampanihy area
	•	•	•	•	•	•	•	•	Mad, S: Angavo Massif E of Antanimara;
	•	•	•	•	•	•	•	•	E of Ambovombe; Tsimele
S. decidua A. R-Sm.	•	•	•	•	•	•	•	b	**Mad, W: Bemaraha;**
	•	•	•	•	•	•	•	a	**Morondava area** incl.
	•	•	•	•	•	•	•	a	**Andranomena** to N,
	•	•	•	•	•	•	•	•	Mad, SE to Tanambao Forest (R. Maharivo) & S to Morombe
	•	•	•	•	•	•	•	•	**Mad, SW:** Toliara area (incl. lower R. Fiherenana,

TABLE 6. Continued.

Plant species† (Bold print: confirmed foodplant)	**Uraniine species***‡ (Uraniines confirmed to feed on *Suregada* in bold)								**Plant Distribution**† (Bold print: *Urapteritra* sympatric)
	Urapteritra fasciata (Mabille)	*U. suavis* (Oberthür)	*U. falcifera* (Weymer)	*U. montana* Viette	*U. malgassaria* (Mabille)	*U. mabillei* Viette	*U. antsianakaria* (Oberthür)	*U. piperita* (Oberthür)	
	•	•	•	•	•	•	•	•	Mad, R. Manombo & Antseva Forets to N,
	•	•	a	•	•	•	•	a	**Zombitsy** to NE,
	•	•	•	•	•	•	•	a	**Betioky** & district incl.
	•	•	•	•	•	•	•	?*c*	**Beza Mahafaly,**
	•	•	•	•	•	•	•	•	& Ampanihy dist. to SE
S. humberti (Léandri) A. R-Sm.	•	•	•	a?	•	•	•	•	Mad, C-E between Mandritsara and Andilamena
S. perrieri (Léandri) A. R-Sm.	•	•	•	•	•	•	•	•	Mad, SE: R. Anosivolo, 130 km. SE Tana
S. africana (Sonder) Kuntze	•	•	d	•	•	•	•	•	Moz, SW; **SAf, E:**
	•	•	d	•	•	•	•	•	**Natal to Port Elizabeth**
S. procera (Prain) Croizat	•	•	•	•	•	•	•	•	Eth, SW; Som; Sud;
	•	•	•	•	•	•	•	•	Zai; Zam; Mal; Uga;
	•	•	e	•	•	•	•	•	**Ken; Tan; SAf:**
	•	•	e	•	•	•	•	•	**Transvaal, Natal;**
	•	•	d	•	•	•	•	•	**Zim: E;** Moz: W
S. zanzibariensis Baill.	•	•	e	•	•	•	•	•	**Ken; Tan; Zan;**
	•	•	d	•	•	•	•	•	**Pemba; Zim: SE;**
	•	•	e	•	•	•	•	•	**SAf: Natal;**
	•	•	•	•	•	•	•	•	Moz: SW, E incl. is.
S. lithoxyla (Pax & K. Hoffm.)	•	•	e	•	•	•	•	•	**Tan; Ken**

TABLE 6. Continued.

Plant species† (Bold print: confirmed foodplant)	**Uraniine species***‡ (Uraniines confirmed to feed on *Suregada* in bold)								**Plant Distribution**† (Bold print: *Urapteritra* sympatric)
	Urapteritra fasciata (Mabille)	*U. suavis* (Oberthür)	*U. falcifera* (Weymer)	*U. montana* Viette	*U. malgassaria* (Mabille)	*U. mabillei* Viette	*U. antsianakaria* (Oberthür)	*U. piperita* (Oberthür)	
S. croizatiana Léonard	•	•	•	•	•	•	•	•	Zai: Kivu Prov.
S. occidentalis (Hoyle) Croizat	•	•	•	•	•	•	•	•	IvC; Gha; Nig
S. ivorensis (Aubrév. & Pellegr.)	•	•	•	•	•	•	•	•	IvC
S. gossweileri (Moore) Croizat	•	•	•	•	•	•	•	•	Zai: Leopoldville Prov.

* *Urapteritra* spp. have also been collected from the following localities where *Suregada* have not (subscripts refer to references below): *U. malgassaria*: Mad, NE: Ananalova Forest S. of Vohimar$_a$; Farankaraina Forest, Navana, near Maroantsetra$_a$; *U. mabillei*: Mad, E: Tamatave/Alahakato forests$_a$; *U. suavis*: Mad, C: Lake Mantasoa (Andrangoloaka 1389 m.)$_a$; *U. montana*: Mad, C: Antarifady Forest (Ankaratra)$_a$; *U. piperita*: Mad, SW: Ankalirano, Mahafaly plateau$_a$; *U. falcifera*: Ken, Nairobi$_e$; SAf, Transvaal: Hectrospruit$_d$; Limberg (Potgeitersrus dist.)$_d$; "Namaqualand" [=Namibia]$_e$. Note: *Cladogelonium madagascariense* Léandri, a close relative of *Suregada*, has been collected from Tsingy de Bemaraha in W. Madagascar, and Bemarivo R. in the NE (Léandri 1938) and it might be a foodplant of *Urapteritra* (it is sympatric with *U. piperita* in Bemaraha).

† References: *Suregada* nomenclature and distribution: Croizat 1942; Radcliffe-Smith 1991 for Madagascan spp.; Léonard 1958 for West African *Suregada* spp.; Palgrave 1977 for South African spp.; Radcliffe-Smith 1987 for East African spp.

‡ References: *Urapteritra* distribution: a. Viette 1972; b. D. C. Lees, pers. obs. in Madagascar; c. L. L. Holloway, pers. comm.; d. Transvaal Museum (C. B. Cottrell, pers. comm.); e. National Collection, Natural History Museum, South Kensington, including Rothschild Collection.

FIG. 1. Larval stages of Uraniinae. Horizontal bar = ca. 1 cm. **A.** Larva (3rd instar) of *Urania poeyi* showing silk-lining behavior on *Omphalea trichotoma*, Punta Maisi, E. Cuba, Mar 1989, L. J. Gillespie; **B.** Larva (4th instar) of *U. fulgens* on *O. diandra*, Atlantic forest, Panama, Jan 1988, D. C. Lees; **C.** Larva (5th instar) of *U. boisduvalii* on *O. hypoleuca* from Pinar del Rio, W. Cuba, Jun 1989, N. G. Smith; **D.** Larva (4th instar) of

Leaf Shape

Another foodplant defense may be leaf shape. Most species of *Omphalea* and *Endospermum* within the range of diurnal uraniines show a remarkable degree of variation in leaf form; in *Omphalea* deeply divided leaves occur on the same plant and in seedlings (Leon & Alain 1953, Smith in press a), and both peltate and non-peltate leaves occur in *Endospermum* species (Schaeffer 1971). In Madagascar, all four foodplants of *Chrysiridia rhipheus* show such a range of form (D. C. Lees, pers. obs.). In the absence of other obvious specialist herbivores on these plants, it is possible such heterophylly may result from selective pressure by diurnal uraniine females that locate oviposition sites visually (see, e.g., Brown & Lawton 1991). One test of this hypothesis will be to assess leaf morphology of *Omphalea* and *Endospermum* species that occur outside the range of diurnal uraniines (as in Malesia). *Suregada* spp. in Madagascar show no such leaf shape plasticity and *Urapteritra* females there apparently oviposit nocturnally.

Laticifers

A further defense common to both *Omphalea* and *Endospermum* spp. is the presence of laticifers (Rudall in press), which bear latex that is clear or oxidizing reddish but not milky or particularly copious. However, uraniine larvae have not been observed to utilize the leaf vein-cutting behavior (disc-cutting in early instars, midrib trenching in later instars) typical of latex-feeding larvae (Dussourd & Eisner 1987). Early instars instead strip-mine the leaves, eating out the inter-vein mesophyll tissue, whereas later instars of both *Urania* and *Chrysiridia* have been observed to eat, in addition to leaves and fruit, tendrils and young stems bearing latex (N. G. Smith, D. C. Lees, pers. obs.). It would thus appear that later instar uraniine larvae are equipped to deal with the chemical defenses mobilized in the latex and that this latex does not pose a major mechanical problem in terms of mouthpart coagulation. The genus *Suregada* does not possess latex at all (D. C. Lees, pers. obs.), nor laticifers of the non-articulated type typical of Croton-

---

←

Chrysiridia rhipheus on *Omphalea*, sp. nov., Ankarana, NW Madagascar, 2 Dec 1990, L. L. Holloway; **E.** Preserved larva (4th instar) of *Lyssa ?macleayi* from Cape Tribulation, N. Queensland, reared by D. Kitchin 1987 from *Endospermum medullosum*, D. C. Lees; **F.** Larva (5th instar) of *Alcides metaurus* on *Omphalea queenslandiae* from Bamaga, N. Queensland, N. C. Coleman; **G.** Larva (?4th instar) of *Urapteritra ?piperita* on *Suregada decidua* showing protective spinning, Beza Mahafaly, SW Madagascar, 18 Jan 1991, L. L. Holloway; **H.** Silk web spinning with frass typical of *Urapteroides astheniata* on *Endospermum medullosum* specimen AQ 0000126 from North Kennedy, Queensland, 8/10/68 at RBG, Kew, D. C. Lees.

ideae (P. Rudall, pers. comm.), once again raising a question over the phylogenetic position of the genus.

Secondary Plant Compounds

Until recently, examination of *Omphalea* secondary compounds was limited to an analysis of the seed oil of *O. diandra* L., a known purgative (Cash 1908). This oil was found to contain terpenes, sesquiterpenes, acid esters, and palmitic and oleic acids (Freise 1935). Horn et al. (1987) reported that *Omphalea* leaves contain high concentrations of a class of nitrogenous compounds known only since 1976: polyhydroxy alkaloids or alkaloidal glucosidase inhibitors (AGI's) (Fellows 1985, 1989). These compounds have toxic effects on some insect herbivores and antifeedant effects on others (Fellows et al. 1986), and are of considerable interest as they form a series mimicking certain sugars. DMDP (2R,5R-dihydroxymethyl-3R,4R-dihydroxypyrrolidine), resembling fructose, and HNJ (homonojirimycin), an alkaloid previously unknown in nature (Fellows 1989), have been reported from *O. diandra* (Horn et al. 1987, Kite et al. 1988).

AGI's may function in plants as competitive inhibitors of glycosidase synthesis, perhaps blocking the sugar-detecting apparatus of generalist herbivores on palpation (Fellows et al. 1986). They are known to be sequestered selectively by *U. fulgens* adults from the larval foodplant (Kite et al. 1990). Although there is no direct evidence that AGI's are noxious to avian predators, adult *U. fulgens* are rejected by jacamars in feeding trials (P. Chai, pers. comm.).

Strong biochemical similarities between *Omphalea* and *Endospermum*, the two foodplant genera so far examined in detail, suggest a chemical basis for the adoption of a new foodplant genus (Kite et al. 1991). Thus a priority for chemical investigations is to elucidate any differences in the fate of secondary plant compounds between *Lyssa* spp. (large, brown, "nocturnal" moths) and *Alcides* spp. (diurnal, apparently aposematic moths), which feed on the same species of *Endospermum* (Table 4). Preliminary results confirm the presence of AGI's in *Suregada* and in adults of *Urapteritra* (G. C. Kite, pers. comm.).

The apparent "immunity" of diurnal uraniines to predators such as tyrannid flycatchers has not gone unnoticed (Seitz 1913). It has been suggested that the aposematic appearance of adults [perhaps also the late instar larvae] of the three diurnal genera may result from the presence of toxic secondary compounds derived from the larval foodplant (Coleman & Monteith 1981). The mimicry of the New Guinean uraniine *Alcides agathyrsus* (Kirsch) by both sexes of *Papilio laglaizei* Depuiset (Jordan 1897, Poulton 1931) suggests adult toxicity directed towards avian predators in at least one uraniine.

Plant Chemistry and Uraniine Migration

Induced changes in larval foodplant secondary chemistry (Smith in press a) are currently being investigated as a possible ecological correlate of mass migration, a frequently noted behavioral feature in all three genera of diurnal uraniine adults (Smith 1972 for *Urania*), although migration also may occur in nocturnal genera. Captures aboard ships also suggest that *Lyssa* migrates (Altena 1953:39). Both species of the genus *Chrysiridia* have been observed migrating in large numbers (Griveaud 1959, Lucas 1876, Pinhey 1975:79 and pers. comm.), as have populations of *Alcides* sp. in New Britain (P. Jolivet, pers. comm.) and *A. metaurus* in Queensland, which form large roosts on trees at night (King 1826:14, Smithers & Peters 1977). The large biomass of individual uraniine species that fly hundreds of miles in these spectacular mass migrations (Smith 1982, 1983), and the fact that *Urania* and *Chrysiridia* larvae eat *Omphalea* flowers and fruit as well as defoliating entire plants (N. G. Smith, D. C. Lees, pers. obs.), suggest that these moths have a considerable negative impact on the reproduction of their foodplants and on the survival of seedlings (Dirzo 1984). A reduction in growth rate measured over a five year period in *Endospermum diadenum* trees grown in Malaysian timber plots was attributed to the periodic mass herbivory by *Urapteroides astheniata* (Browne 1937, 1938, 1940). Thus attacked plants are likely to respond by changes in secondary compounds or nutrient levels (Smith 1983).

Morphologically and behaviorally distinct migratory and sedentary phases occur in *U. fulgens* (Smith in press b), and Smith (1982:342, 1983:83) proposed that an induced chemical response in the foodplant in response to repeated herbivory by several larval generations might provide the cue for production of migratory morphs. However, artificially simulated mechanical damage to foodplants has produced no clearcut pattern in induction of morph type (Smith 1982, in press a). Nevertheless, in Mexican as well as Central American foodplants of *U. fulgens* (Table 3), some individual plants after a sustained period of damage appear to become toxic to larvae causing high mortality levels (Smith 1982, 1983, R. Dirzo unpubl.). Experiments indicate that density changes are not the sole factor triggering the production of migratory morphs (Smith 1982), but if migratory phases are induced by a nutrient or chemical change, the mechanism remains unknown. There is at present no evidence that AGI's are involved in such a trigger, should one exist at all (Kite et al. 1991).

Although how it is mediated remains unknown, migration in uraniines presumably is selected for as a result of the widely oscillating population dynamics of strictly monophagous genera (Catala 1940:12, 13). Lack of intensive herbivory over long periods may result in lowered moth-induced defenses (Smith 1983:81), allowing buildups in moth populations that culminate in mass local emergences; excessive defoliation would then be a critical factor. Sudden appearances of swarms of fresh individuals have been reported frequently for uraniines (Gosse 1851, Townsend 1893, Browne 1940, Smith 1972, Coleman & Monteith 1981, Smith 1982). Apparent population crashes might result from larval populations reduced by induced chemical defense, but are more likely caused by emigration of adults. Parasitoids, which also might be affected by foodplant allelochemistry, probably also play a role in uraniine population dynamics: tachinid flies, but not Hymenoptera, have been reared from the pupae of *U. fulgens* (Smith in press a) and *Urapteroides astheniata* (Browne 1937), and hymenopteran parasitoids are known for *Chrysiridia rhipheus* (A. Peyriéras, pers. comm.).

EVOLUTION OF DIURNALITY AND FOODPLANT SPECIALIZATION: PHYLOGENETIC HYPOTHESES

An evolutionary hypothesis that is in accord with the phylogeny of Uraniinae based on morphological characters and which explains foodplant exploitation patterns within the Uraniinae is that feeding on *Endospermum,* the only foodplant common to both nocturnal and diurnal uraniines, is plesiomorphic within the group. Once the biochemical leap was made to *Omphalea,* stockpiling of additional (as yet undefined) plant secondary compounds sequestered in the adult stage may have predisposed the moths (presumably through avian selection) to become obligately diurnal. Such a sequence has been suggested to have occurred within the Arctiidae (Rothschild et al. 1979:313, 314).

Diurnality

The term obligate diurnality for the three brightly colored genera is applied here because they have been observed in captivity and in the wild to be quiescent throughout the night, roosting nocturnally *en masse* during migrations (N. G. Smith, pers. obs. for *Urania*; D. C. Lees, pers. obs. for *Chrysiridia*; Eltringham 1924a, Catala 1940:12, Paulian 1951: 58, Coleman & Monteith 1981). However, crepuscular activity has been reported for *Alcides* (Boisduval 1874) and *Urania* (Skutch 1970) and both *Urania* and *Chrysiridia* females oviposit in late afternoon or into dusk (Smith in press a, Alayo & Hernandez 1981, D. C. Lees, pers. obs. in Madagascar). As in the Arctiidae (Rothschild et al. 1979:313), nocturnality is best considered a plesiomorphy for the Uraniidae. Most if not all epiplemines, microniines, and uraniines, apart from the obligately diurnal uraniine genera, appear to be nocturnal or crepuscular or both. *Lyssa* spp. do not seem to be exclusively nocturnal. Although individuals are frequently attracted to lights at night (Altena 1953), *L.*

zampa in Malaysia frequently may be seen flying spontaneously in the forest during the day (J. D. Weintraub, pers. comm.), behavior also recorded for *L. patroclus* (L.) (Altena 1953). One species, *L. mutata* (Btlr.) from the Solomon Is., which possesses a sheen of iridescent purple scales on the wings, has been observed flying freely at midday in a forest clearing, and being attacked by birds (Carpenter 1937). Conversely, the diurnal species *U. fulgens* (or *U. poeyi* H.-S.) occasionally has been observed coming to lights at night in Jamaica (Lewis 1944, 1945, Brown & Heineman 1972:12, T. Turner, unpubl.). *Cyphura* and *Urapteroides* [along with *Urapteritra*] are primarily nocturnal, and so the trend in development of diurnal behavior is in accordance with the morphologically derived cladogram (Fig. 2). However, this interpretation could be criticized on the basis that the hearing organs themselves probably are functionally modified for diurnal, nocturnal, or crepuscular predator evasion.

Uraniine Phylogeny

A phylogeny of the Uraniinae (Fig. 2) was constructed using published morphological (tympanic organ structure and larval morphology) apomorphies summarized in Table 7. Larval foodplants and diurnality have been added to allow interpretation of their roles in the evolution of the group. Larval foodplant patterns are consistent with the morphological data: each generic foodplant relationship need have arisen just once within the Uraniinae, with *Endospermum* the more plesiomorphic relationship within the group (excluding *Urapteritra*). Loss of *Endospermum* as foodplants in *Urania* and *Chrysiridia* can be explained as a simple consequence of vicariance. Note that *Alcides* emerges as the most basal diurnal uraniine, with *Urania* and *Chrysiridia* as sister taxa. The plesiomorphic status of *Alcides* was hinted at by Catala (1940:237, 258), perhaps somewhat unconvincingly on the basis of extensive temperature shock experiments in *C. rhipheus* pupae that produced adult color patterns similar to *Alcides aurora*.

The position of *Urapteritra* is uncertain because nothing has been published on the tympanic organs, although genitalic characters have been examined (Viette 1972). Similarity in wing shape and patterning to *Urapteroides* and *Cyphura* combined with the minor difference in hindwing venation suggests that *Urapteritra* may be basal to the white group of uraniines. As *Suregada* has its greatest species concentration in Indo-Australasia, it seems likely that *Cyphura*, or *Urapteroides*, or both, may feed on *Suregada* in this region. Because *Chrysiridia* does not appear to feed on *Suregada* in Madagascar (D. C. Lees, pers. obs.), this genus seems unlikely to be one of the foodplants of the diurnal clade. It seems more parsimonious to assume that *Suregada* was added

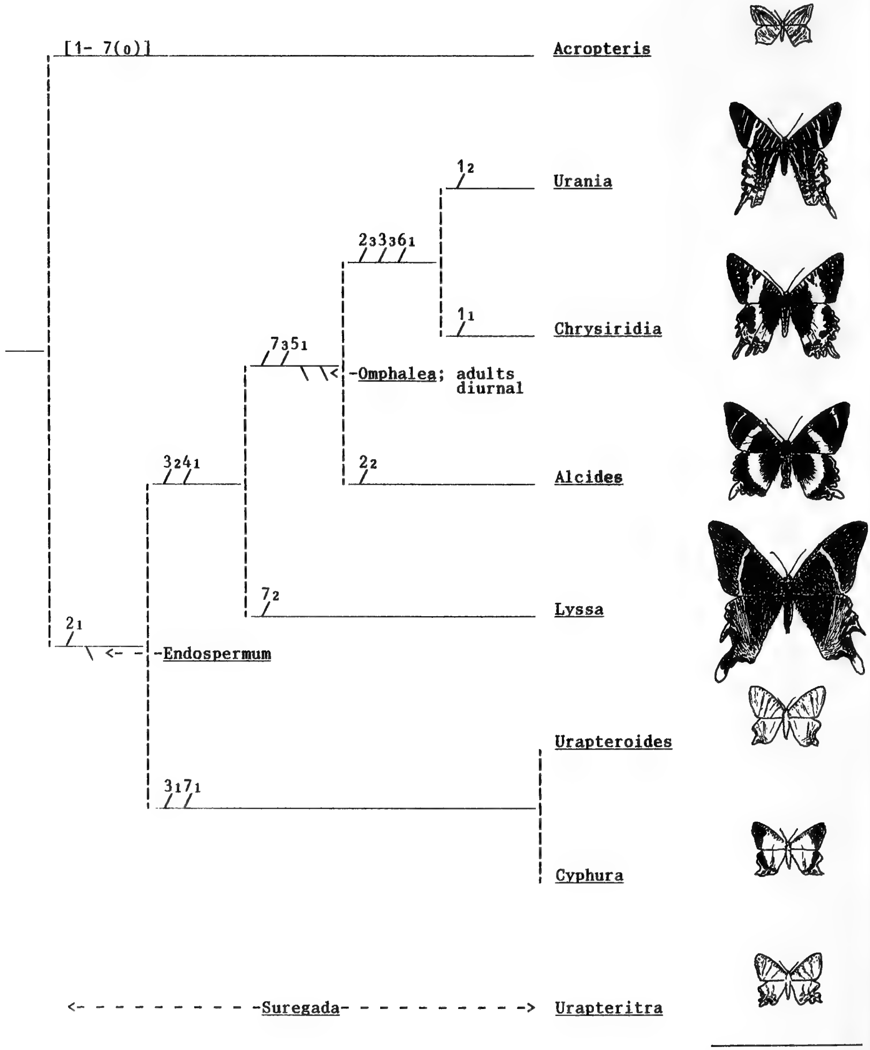


FIG. 2. Phylogeny of the Uraniinae based on larval setal morphology (Bell 1901 MS, Browne 1937, Kühn 1887, Coleman & Monteith 1981, Eltringham 1924a, Guppy 1907) and hearing organ (abdominal and thoracic) morphology (Sick 1937, Minet 1983) (characters 1–7, Table 7). Tree rooted on *Acropteris* (Microniinae) as an outgroup. A computer run using Hennig 86 (J. S. Farris) using the ie option produces one tree, length 14, consistency index 1.00, retention index 1.00. Unordering of multistate characters in the computer run makes no difference to the cladogram topology (characters are arbitrarily numbered). Foodplant associations and adult obligate diurnality are added to this tree. Species drawn as representatives of each genus are: *Acropteris ciniferaria* (Walker), *Urania leilus, Chrysiridia rhipheus, Alcides agathyrsus, Lyssa curvata, Urapteroides astheniata, Cyphura multistrigaria* and *Urapteritra piperita* (*Urapteritra* is not included in the analysis due to absence of published data). Scale bar = 10 cm.

TABLE 7. Character matrix for Fig. 1.

Taxa†	Character number‡ 1	2	3	4	5	6	7
ACRO	0	0	0	0	0	0	0
URAN	2	3	3	1	1	1	3
CHRY	1	3	3	1	1	1	3
ALCI	0	2	2	1	1	0	3
LYSS	0	1	2	1	0	0	2
CYPH	?	1	1	0	0	0	1
URAP	0	1	1	0	0	0	1

† Code: ACRO = *Acropteris* (outgroup); URAN = *Urania*; CHRY = *Chrysiridia*; ALCI = *Alcides*; LYSS = *Lyssa*; CYPH = *Cyphura*; URAP = *Urapteroides*.

‡ Details of characters:

	apomorphy			plesiomorphy
Character state:	3	2	1	0
Character:				
1. Larval last instar spatulate setal state*	—	024 0000 00220	088 6666 66664	All simple.
2. ♀ metathoracic epimeron: devt. type of tympanal cover#	Ventrally lobed LC.	Unlobed LC.	Unlobed AC.	Not developed.
3. ♀ tympanal case: ratio of dorso-ventral height to that of sternite 2	ca. ¼	≤⅛	ca. ⅕	≥⅔
4. ♀ tympanum: depth	—	—	Close to surface.	Relatively sunken.
5. ♀ tympanum: angle to body axis	—	—	Very acute (close to plane of sternite).	Perpendicular.
6. ♀ tympanal cases: 3- and 2-dimensional shape	—	—	Hemispherical; oval.	Flattened; nearly circular.
7. ♂ tympanum: angle to countertympanum	ca. 60°	ca. 70°	ca. 80°	ca. 120°

* Spatulate setal formulae (spatulate setae per segment) are derived from *Urania leilus* (Guppy 1907) and *Chrysiridia rhipheus* (Eltringham 1924a). Other species may differ: indeed in *U. boisduvalii*, the spatulate condition is lost (Macleay 1834), perhaps concomitant with a change to nocturnal feeding behavior (the larva is concealed by day under a web).

= modifications of metathoracic epimerons include central oval areas forming shallowly concave (protective and/or sound-reflective) tympanal covers, either lateral to the tympana, entirely covering the tympanic organs and orientated inwardly (LC) or anterior to the tympana and orientated posteriorly (AC). See Sick (1937) for figures.

to the foodplant repertoire of an independent clade than lost by sympatric ancestors of the diurnal clade. In this respect it is critical to know whether *Lyssa* feeds on *Suregada*: such a discovery might support a change in the topology of the cladogram. The evidence for *Endospermum* as the most plesiomorphic foodplant of the Uraniinae seems the most convincing, as vicariance could also account for its loss by *Urapteritra*.

Although the three known foodplant genera are not closely related enough to provide a useful generic phylogeny, once species phylogenies of each uraniine genus and the foodplant genera are clarified, it will be of interest to compare these trees. For example *Chrysiridia* and *Urania*, sister taxa and the most derived uraniine genera, feed on a monophyletic group of relatively advanced Neotropical and Afrotropical species of *Omphalea* (Gillespie 1990; see Table 3). Also, *Alcides* (at least in Australia) retains the plesiomorphic uraniine foodplant relationship with *Endospermum* as well as feeding on *Omphalea queenslandiae* Bailey, a representative of an apparently plesiomorphic clade of three Indo-australasian *Omphalea* species (Gillespie 1988, 1990, and pers. comm.), which retains the plesiomorphic euphorbiaceous trait of well developed sepal disc glands in the male flower (Airy Shaw 1966, 1969). Although the foodplant relationships of the diurnal genera appear broadly consistent with the phylogeny shown in Fig. 2, it seems at this stage unlikely that parallel cladogenesis at the species level will be demonstrable for individual foodplant genera. For example, there does not seem to be any clearcut pattern of foodplant specialization between penninerved and palmatinerved Afrotropical and Neotropical *Omphalea* species (Table 3). Recent comparisons of phylogenies of phytophagous specialists and their foodplants generally have suggested sequential colonization (Drummond 1986, Miller 1987) rather than parallel cladogenesis or even diffuse coevolution (see Mitter & Brooks 1983) although there are exceptions (Farrell & Mitter 1990).

Biogeography

Biogeographic analysis of the moth/foodplant distributions may be useful to interpret the phylogeny presented in Fig. 2. For example, the absence of nocturnal uraniines in the Neotropics might simply reflect the absence of *Endospermum* or *Suregada* in western Gondwanaland. This perhaps supports an eastern (Australasian) origin for uraniines. As with epiplemines, greatest species concentrations of uraniines are found in Indo-Australasia. A scenario based on vicariance is that ancestral Uraniinae specialized on *Endospermum,* and prior to the final breakup of Gondwanaland the diurnal lineage colonized an ancestral form of *Omphalea* (most likely via an oviposition response to a common allelochemical). Colonization of *Suregada* by an ancestor of *Urapteritra* might have occurred independently before the separation of Australasia with Africa and Madagascar. Evidence for this may be found in the foodplant associations of Australasian species of *Urapteroides, Cyphura,* or both. Vicariance acting on the original colonization of the foodplant genera by the ancestral uraniines seems sufficient without the need to invoke long-distance dispersal, including use of land bridges. One difficulty is that euphorbiaceous pollen is known only from the early Miocene (Muller 1984) whereas the above vicariance explanation requires this foodplant association to be in place not only before the final separation of Africa and South America (ca. 100 mBP) but prior to the separation of Australasia from Africa.

Nevertheless, a Gondwanaland origin for uraniines seems compatible with the present evidence. Altena (1953) suggests that the least derived *Lyssa* species occur to the east of its Indo-Australasian range and the same may be true of *Urapteroides* (D. C. Lees, unpubl.). In this interpretation, both genera apparently managed to bridge the Wallace line to Sulawesi; *Alcides* evidently did not [although two specimens of *A. orontes* (L.), perhaps vagrants, exist in the NHM, South Kensington labelled "N. Celebes": Table 4]. *Alcides* is represented in North and South Maluku [Moluccas] (Table 3), where *Omphalea* has not been recorded, but where it should certainly be checked for. *Endospermum moluccanum* (Teijsm. & Binnend) Kurz is a likely foodplant for *A. aruus* (Felder), *A. orontes* and *A. cydnus* (Felder) (Table 4), but it is interesting that *Alcides* apparently has not managed to colonize the species of *Endospermum* and *Omphalea bracteata* (Blanco) Merr. that occur a little further west in Sulawesi. The lack of a diurnal uraniine within the range of *O. bracteata* (Table 3) might in fact be interpreted as further evidence for the Gondwanaland (eastern) origin of uraniines. Furthermore, it is possible that *Omphalea* is a recent colonist of South-East Asia via seed dispersal on ocean currents since the merging of the Asian and Australian plates. The occurrence of just one variable species of *Omphalea* throughout South-East Asia (Gillespie 1990) supports this hypothesis. Tentative evidence suggests that *Urapteritra* is a relatively recent colonist of East Africa from Madagascar, the center of diversity of *Urapteritra*, since *Suregada* species also occur in West Africa, where *Urapteritra* does not occur (Table 6).

ALTERNATION OF LARVAL FOODPLANTS: IMPLICATIONS FOR CONSERVATION OF MIGRATORY URANIINES

Conservation of uraniines has as much merit on aesthetic grounds as, for example, conservation of papilionids, but has received relatively little attention, despite the fact that the moths are localized in many of the world's most threatened and diverse tropical habitats.

An interesting feature of most diurnal uraniines is their reliance on two or more geographically isolated larval foodplant populations between which they seasonally migrate, often in huge numbers. This certainly includes *Urania fulgens*, *U. boisduvalii* Guérin, *U. poeyi* (H.-S.), *Chrysiridia rhipheus* and *Alcides metaurus* (Table 3). *Chrysiridia rhipheus* in Madagascar is a particularly good example of alternate larval foodplant dependence: adults migrate between populations of three different *Omphalea* species in dry deciduous forest in the west and one rainforest species in the east (Table 3; D. C. Lees, unpubl. data; Griveaud 1959 mentions west–east migrations). Although western foodplant populations (deciduous trees) are protected by reserves in areas on limestone karst, the *Omphalea* species in the east, being the sole evergreen foodplant, is probably crucial to the moth's continued survival, but this species occurs in widely scattered populations mostly outside reserves and is threatened by deforestation (D. C. Lees, unpubl.; Catala 1940:6, 7, 13).

Coupled with the frequently reported wide fluctuations in the size of local populations, dependence on alternate foodplants probably renders island uraniine populations particularly vulnerable to environmental stress (e.g., hurricanes and habitat loss) and, eventually to inbreeding. Sadly, the most spectacular *Urania* species, *U. sloanus* (Cramer) from Jamaica, was last reported as long ago as 1894 or 1895 (Lewis 1944, Perkins 1944) and is likely to be extinct (T. Turner, unpubl.). Although habitat loss in Jamaica may have been a factor in its demise, substantial tracts of primary forest still remain. The reported foodplant of *U. sloanus* on the North coast at Ocho Rios, *Omphalea triandra* L. (Gosse 1881: see Table 3) apparently is still widespread in wet forest on limestone in the island (Adams 1972). However, it is likely that that moth also feeds on *O. diandra*, reported, although not recently, from Portland County (Adams 1972, Hemsley 1885), a former locality for the moth (Townsend 1893). Periodic swarms of moths at flowering trees in the Blue Mountains of Portland were intervened by years of great scarcity (Townsend 1893). The population of *U. sloanus* apparently crashed below a sustainable level, perhaps a victim of loss of one of its larval foodplants.

The insular Cuban endemic *U. boisduvalii* (Smith in press b), whose appearance and morphology indicate long isolation from continental *Urania* populations, may also be at risk; the limestone "Mogote" stacks of Pinar del Rio in Western Cuba, now fortunately a biosphere reserve, appear crucial to its survival, but populations of its alternate foodplant on northern coastal limestone are greatly diminished (N. G. Smith, pers. obs.). The other Cuban species, *U. poeyi*, apparently also uses alternate foodplants because it migrates between localities for *O. diandra* in N.E. Cuba and *O. trichotoma* M.A. in E. Cuba (L. R. Hernandez, pers. comm.). This population probably represents a more recent colonization of the island from Central America; adult specimens and recent photographs of larvae (Fig. 1A; Table 2, ref. 2) suggest it is conspecific with *U. fulgens*. *Urania* specimens taken occasionally in Jamaica this century appear to be migrants, possibly *U. poeyi* from Cuba (Lewis 1944, T. Turner, unpubl., M. J. C. Barnes, pers. comm. with slide). Strikingly, in contrast to Cuba, no *Urania* has been reported for Hispaniola, despite the presence of two endemic and one introduced species of *Omphalea* (Table 3). Perhaps this is due to extinction resulting from loss of larval foodplant; e.g., *O. commutata* M.A. is a casualty of deforestation in Haiti and may survive now only on Gonaives Island (L. J. Gillespie, pers. comm.).

ADULT RESOURCES OF THE URANIINAE AND THEIR ECOLOGICAL SIGNIFICANCE

Many recent studies on the chemical ecology of Lepidoptera have revealed the significance of compounds in adult foods, such as pyrrolizidine alkaloids in nectar of Asteraceae and Boraginaceae, to the reproductive success and anti-predator defense systems of these insects, especially the Danainae, Ithomiinae, Arctiinae, and Ctenuchiinae (Ackery & Vane-Wright 1984, Brown 1984, Boppré 1986, Goss 1977). As a basis for the future study of the chemical ecology of adult uraniines, known adult resources are documented here (Table 8).

Our survey of *Urania*, *Chrysiridia*, and *Alcides* indicates that visual cues play a large role in nectar source selection. All diurnal species prefer white or whitish-yellow flowers. Most flowers visited are also densely filamented, with projecting conspicuous stamens, imparting a "bottle-brush" appearance, particularly those in the Leguminosae: Mimosoideae, Myrtaceae, and Combretaceae, or else are composed of clusters or panicles of small flowers (Table 8). *Urania fulgens* adults are readily attracted to white cotton wool balls soaked in sugar solution, useful to feed them in the laboratory and field. By no means all white flowers elicit a response; the flowers and floral bracts of *Omphalea oppositifolia* in Madagascar are white and showy, but adults of *Chrysiridia rhipheus* were never seen to visit them (D. C. Lees, pers. obs.). *Lyssa* adults appear to be fruit specialists; Ribbe observed them on putrefying bananas (Pfeiffer 1925:127), on which *L. zampa docile* (Btlr.) has also been photographed feeding at night (Yong 1983:13). Semper (1896–1902:598) observed that they come to flowering trees in the evening.

Nectar sources may play an important role in the reproductive or defense ecology of uraniines. Species of the genus *Inga* Scop. (Leguminosae: Mimosaceae), an important nectar resource in the Neotropics, are extremely attractive to *Urania* moths during their short flowering period, as well as to many papilionid, pierid, and heliconiine butterfly species (D. C. Lees, pers. obs.). A sample of moths taken from an *Inga* sp. in Peru showed a predominance of males of *U. leilus* (L.) compared with a *Combretum* sp. flowering nearby (Table 9). This result agrees with observations of migrating *U. fulgens* on an *Inga* sp. filmed in Panama (Table 10) where males constituted about 72–83% of readily sexed individuals. This apparent sex bias in flower-visiting *Urania* has yet to be explained, but may result from differential exploitation of nectar chemicals.

Flowers of at least 13 species of *Inga*, although rich in amino acids, lack pyrrolizidine alkaloids (S. Koptur, pers. comm.). There is at present

TABLE 8. Adult nectar resources of Uraniinae. Arrangement of plant families follows Cronquist (1981); arrangement of genera and species in alphabetical order; flower color observed given (bold print) or obtained from miscellaneous botanical treatments [w = white, y = yellow, o = orange, g = green, p = pink, v = violet, r = red]; S = densely Staminate/filamented flowers; C = flowers in dense Clusters or panicles. Confirmed records shown in bold. Locality abbreviations as in Tables 2, 3, 4 and 6 plus Sur = Surinam; CR = Costa Rica; in cap = captivity (*U. leilus* from Trinidad).

Nectar source Family Species	Color	C/S	*Urania boisduvalii* (Guérin)	*U. sloanus* (Cramer)	*U. fulgens* Walker	*U. leilus* (L.)	*Chrysiridia rhipheus* (Drury)	*C. croesus* (Gerstaecker)	*Alcides metaurus* (Hopffer)	Locality
Lauraceae										
Persea americana **P. Mill**	w-g/y	C	•	•	1	•	•	•	•	Pan
(=*gratissima*)			2	•	•	•	•	•	•	Cub
Ocotea sp.	w		•	3	•	•	•	•	•	Jam
	y	C	•	•	4	•	•	•	•	CR
Theaceae										
Camellia chinensis Kuntze	w + y	S	•	•	•	•	5	•	•	Mad
Capparaceae										
Cleome spinosa Rojas	**w-p**		•	•	•	6	•	•	•	In cap
Rosaceae										
Eriobotrya japonica Lindl.	w	S	•	•	•	•	7	•	•	Mad: 'Tana
Caesalpinaceae										
Pterocarpus ?officinalis Jacq.	y-o	?	•	•	8	•	•	•	•	Pan
Mimosaceae										
***Acacia* spp.**	**w**	S	•	•	•	•	•	•	9	Qld
***Albizia* sp.**	**w**	S	•	•	10	•	•	•	•	Pan

TABLE 8. Continued.

Nectar source			Taxon nectaring†							
Family Species	Color	C/S	*Urania boisduvalii* (Guérin)	*U. sloanus* (Cramer)	*U. fulgens* Walker	*U. leilus* (L.)	*Chrysiridia rhipheus* (Drury)	*C. croesus* (Gerstaecker)	*Alcides metaurus* (Hopffer)	Locality
***Inga* spp.**	**w**	S	•	•	10	•	•	•	•	Pan, CR
Inga quaternata Poepp. & Endl.	**w**	S	•	•	•	6	•	•	•	Peru: Tambopata
Myrtaceae										
Callistemon sp.	**o-r**	S	•	•	•	•	•	•	11	Qld
***Eucalyptus* spp.**	—	S	•	•	•	•	•	•	9	Qld
***Eucalyptus* spp.**	—	S	•	•	•	•	12	•	•	Mad
Eucalyptus ?*saligna* Sm.	w	S	•	•	•	•	7	•	•	Mad
Syzygium rubiginosum Merrill & Perry	w	S	•	•	•	•	•	•	13	Qld
Combretaceae										
Combretum *aubletii* D.C.	**o**	S	•	•	•	14	•	•	•	SAm
Combretum laxum Jacq.	**w-y**	S	•	•	•	6	•	•	•	Peru: Tambopata
Quisqualis indica L.	**r-o/w**	C	•	•	8	•	•	•	•	Pan: Pan City
Terminalia catappa L.	w-y	C	•	•	•	•	•	15	•	Tan: Dar-es-Salaam
			•	•	1	•	•	•	•	Pan
Euphorbiaceae										
Croton glabellus [copalchi]	**w**	S	•	•	4	•	•	•	•	CR
C. panamensis (Klotzsch) M.A.	w	S	•	•	1	•	•	•	•	Pan
Araliaceae										
Cussonia vantsilana Bak.	**w**	?	•	•	•	•	16	•	•	Mad

TABLE 8. Continued.

Nectar source			Taxon nectaring†							
Family Species	Color	C/S	*Urania boisduvalii* (Guérin)	*U. sloanus* (Cramer)	*U. fulgens* Walker	*U. leilus* (L.)	*Chrysiridia rhipheus* (Drury)	*C. croesus* (Gerstaecker)	*Alcides metaurus* (Hopffer)	Locality
Apocynaceae										
Aspidosperma sessiliflorum M.A.	w-y	?	•	•	•	17	•	•	•	Trin
Solanaceae										
Cestrum diurnum L.	w	C	18	•	•	•	•	•	•	Cub
Boraginaceae										
Cordia ?cylindrostachya R. & S.	w	C	•	•	•	19	•	•	•	Trin
Ehretiaceae										
Ehretia tinifolia L.	w	C	18	•	•	•	•	•	•	Cub
Verbenaceae										
Lantana camara L.	**w-p**	C	•	•	•	•	•	20	•	Ken: Mombasa
		C	•	•	•	6	•	•	•	In cap
		C	•	•	•	•	•	•	21	Qld garden
		C	22	•	•	•	•	•	•	Cub
Buddlejaceae										
B. fallowiana Balf & Smith	**v**	C	•	•	•	6	•	•	•	In cap
Buddleia madagascariensis Lam.	**y**	C	•	•	•	6	•	•	•	In cap
Anacardiaceae										
Mangifera indica L.	**w-g**	C	•	•	•	•	•	20	•	Ken: Mombasa
			•	23	•	•	•	•	•	Jam
			22	•	•	•	•	•	•	Cub

TABLE 8. Continued.

Nectar source Family Species	Color	C/S	*Urania boisduvalii* (Guérin)	*U. sloanus* (Cramer)	*U. fulgens* Walker	*U. leilus* (L.)	*Chrysiridia rhipheus* (Drury)	*C. croesus* (Gerstaecker)	*Alcides metaurus* (Hopffer)	Locality
			Taxon nectaring†							
Rubiaceae										
Ixora sp.	o-r	•	•	•	•	17	•	•	•	Trin
Asteraceae										
Eupatorium pauciflorum Rafin	w	C	•	•	•	1	•	•	•	Sur: Paramaribe
Arecaceae										
Roystonea regia O. F. Cook	w-y	C	22	•	•	•	•	•	•	Cub: Pinar del Rio

† References: 1. N. G. Smith, pers. obs.; 2. Gundlach 1881:284–285; 3. Gosse 1851; 4. Skutch 1970 (author notes that nearby yellow flowers of *Cassia spectabilis* and red trumpets of *Spathodea campanulata* ignored); 5. B. Jaosolo, pers. comm.; 6. D. C. Lees, pers. obs.; 7. Sibree 1915:110 [as blue-gum and loquat]; 8. Lundy 1953 [as dragon blood tree and rangoon creeper]; 9. G. Sankowsky, pers. comm.; 10. Smith 1982 (*Albizia* as *Leucaena*); Skutch 1970; 11. BBC TV [*Butterflies in Australia*], documentary, Mar. 1989; 12. B. Courtin, pers. comm.; 13. Breeden & Breeden 1970; 14. BBC TV "Through Animal Eyes", Feb. 1985; 15. T. Grant, pers. comm.; Pinhey 1975, pers. comm.; [*Terminalia* and *Mangifera* recorded as larval foodplant-adult foodplants?]; 16. Catala 1940; 17. Quesnel 1975 (author notes that nearby purple flowers of *Lonchocarpus punctatus* [=*L. violaceus* H. B. & K.] ignored); 18. Macleay 1834; 19. Guppy 1907 [as black sage]; 20. D. G. Sevastopulo, pers. comm.; 21. A. S. Wheeler, pers. comm.; 22. L. R. Hernandez, pers. comm.; 23. Gosse 1880; Lewis 1944.

TABLE 9. Numbers of *Urania leilus* at flowers in S. E. Peru (D. C. Lees). Bushes were 5–10 m apart; time of sampling was 0700–1230 h each day (the bushes did not flower synchronously). Only netted individuals were sampled and their sex determined by the presence or absence of a prothoracic leg hair brush borne and extruded only by males. Expected frequencies are shown in parentheses on the basis of equal sex ratios.

Flower	Date	No. males (no. expected)	No. females (no. expected)	Total
Inga ?*quaternata* Poepp. & Endl. (Mimosaceae)	11 Oct 86	7 (4)	1 (4)	8
Combretum laxum Jacq. (Combretaceae)	15 Oct 86	5 (4.5)	4 (4.5)	9
Total		12	5	17

H_0: No. males = no. females at *Inga*.
H_1: No. males > no. females at *Inga*.
Chi-squared (1 tailed, 1 df) = 4.625, $P < 0.025$, H_0 rejected.

no evidence that *Urania* moths use any plant secondary compounds in nectar for defense, despite the fact that their range of nectar sources does include *Eupatorium* (Table 8) and some Boraginaceae, noted pyrrolizidine alkaloid sources (Brown 1984). However, the importance of amino acids in the competitive mating systems of many Lepidoptera is now better understood (Goss 1977, Drummond 1984), and could explain the skewed sex ratios on *Inga*, if males visit *Inga* flowers to replenish proteins transferred to the females during mating. Amino acids such as proline play an important role in flight metabolism of migrating moths, and the presence of multiple spermatophores in the much heavier migrating females (Smith in press a) is consistent with the hypothesis that male investment in reproduction includes a contri-

TABLE 10. Sexes of migrating *Urania fulgens* filmed at the flowers of an *Inga* sp. in Panama (Margarita, Colon Prov.), September 1983 (N. G. Smith). Six samples (A–F) were taken from a 16 mm film (speed 24 frames per minute), total duration 7.4 minutes. Each sample consisted of advancing the film frame by frame until 10 frame samples were counted. The frames with moths the least agitated were counted, and individuals assigned a sex only where at least two of three sexually dimorphic criteria of shape, size, and wing bar coloration (Smith 1982) were clearly visible. Samples A to F are not assumed to be independent. Sex ratio of individuals in the migration appeared to be 1:1.

Sample	No. of males	No. of females	% males	No. not sexed	Total	% males of total
A	211	63	77.0	59	333	63.4
B	116	13	89.9	41	170	68.2
C	168	10	94.4	22	200	84.0
D	119	29	80.4	17	165	72.1
E	228	79	74.3	33	340	67.1
F	268	54	83.2	28	350	76.6
Mean			83.2			71.9

bution of energy for female flight (and thus dispersal ability) as well as for egg production.

Urania males are attracted to urine-soaked sand and sweat from clothes (D. C. Lees, pers. obs. for *U. leilus* in Peru), and *Alcides* spp. in Papua New Guinea participate in puddling behavior, suggesting that salts or nitrogenous compounds or both may be replenished during this activity.

ACKNOWLEDGMENTS

The following individuals generously helped with information, photocopies, slides, and preserved material: Dr. Geoffrey Monteith, Queensland Museum (S. Brisbane); Dr. Tho Yow Pong, F. R. I. M., Malaysia; Dr. Lynn Gillespie, Smithsonian Institution (Washington); Dr. Jeremy Holloway, C. A. B. International Institute of Entomology (London); Prof. C. B. Cottrell (Transvaal Museum), and Dr. Alan Radcliffe-Smith (Royal Botanic Gardens, Kew). Dr. Max Gunther (Peruvian Safaris) helped one author (D. C. Lees) to work at Tambopata Wildlife Reserve. Drafts of the manuscript were greatly improved by comments from Dr. Malcolm Scoble (Natural History Museum, London), Dr. Jason Weintraub (Natural History Museum, London), Dr. Joel Minet (Muséum National D'Histoire Naturelle, Paris), and Dr. Paula Rudall (Royal Botanic Gardens, Kew), who also helped with cladistic analyses. Louise Holloway helped with preparation of prints for the plate. Dr. Gillespie and Dr. Monteith are thanked in particular for permission to use figs. A and F, respectively, in Fig. 1. Work in Madagascar by D. C. Lees was aided by grants from the Royal Entomological Society, the Royal Geographical Society, the Percy Sladen Memorial Trust, and Mr. Steve C. Collins.

LITERATURE CITED

ACKERY, P. R. & R. I. VANE-WRIGHT. 1984. Milkweed butterflies: Their cladistics and biology. British Museum (Natural History), London. 425 pp.

ADAMS, C. D. 1972. Flowering plants of Jamaica. Univ. of the West Indies, Mona, Jamaica. 848 pp.

AIRY SHAW, H. K. 1966. Malaysian and other asiatic Euphorbiaceae. LXXXI. New records for *Omphalea* L.; LXXXII. The genus *Neomphalea* Pax & Hoffm. in Papua. Kew Bull. 20:414–415.

——— 1969. Malesian and other asiatic Euphorbiaceae. CXIX. Notes on *Omphalea* L. and *Neomphalea* Pax & Hoffm. Kew Bull. 23:130–131.

——— 1971. The Euphorbiaceae of Siam. Kew Bull. 26:258–311.

——— 1975. The Euphorbiaceae of Borneo. Kew Bull. Add. Ser. IV. Her Majesty's Stationery Office, London. 245 pp.

——— 1980a. The Euphorbiaceae of New Guinea. Kew Bull. Add. Ser. VIII. Her Majesty's Stationery Office, London. 243 pp.

——— 1980b. The Euphorbiaceae Platylobeae of Australia. Kew Bull. 35:629–689.

——— 1982. The Euphorbiaceae of Central Malesia (Celebes & Moluccas, Lesser Sunda Is.). Kew Bull. 37:1–40.

——— 1983. The Euphorbiaceae of the Philippines. Royal Botanic Gardens, Kew. 56 pp.

ALAYO, P. D. & L. R. HERNANDEZ. 1981. Atlas de las mariposas diurnas de Cuba. Editorial Científico-Téchnica, Ministerio de Cultura, La Habana. 1987 Edition. 148 pp., 49 pl.

ALTENA, C. O. VAN R. 1953. A revision of the genus *Nyctalemon* Dalman, with notes on the biology, distribution and evolution of its species (Lepidoptera: Uraniidae). Zool. Verh. Leiden 19:1–57, 4 pl.

BACKER, C. A. 1963. Flora of Java 1. N.V.P. Noordhoff, Groningen. 648 pp.

BARLOW, H. S. 1982. An introduction to the moths of South-east Asia. Malayan Nature Society, Kuala Lumpur. 305 pp., 50 pl.

BELL, T. R. D. CA. 1901. [Life histories of Indian moths]. Unpublished MS, Natural History Museum, London.

BOISDUVAL, J. B. A. D. DE. 1833. Mémoire sur les Lépidoptères de Madagascar, Bourbon et Maurice. Nouv. Annales des Mus. d'Hist. Nat. Paris 2:149–270, 8 pls.

——— 1874. Monographie des Agaristidées (Lépidoptères). Revue Mag. Zool. 2(3):45.

BOPPRÉ, M. 1986. Insects pharmacophagously utilizing defensive plant chemicals (pyrrolizidine alkaloids). Naturwissenschaften 73:17–26.

BREEDEN, S. & K. BREEDEN. 1970. Tropical Queensland. A natural history of Australia, part I. Collins, Sydney. 262 pp.

BROCK, J. P. 1971. A contribution towards an understanding of the morphology and phylogeny of the ditrysian Lepidoptera. J. Nat. Hist. 5:29–102.

BROWN, F. M. & B. HEINEMAN. 1972. Jamaica and its butterflies. E. W. Classey Ltd., London. 478 pp.

BROWN, K. S., JR. 1984. Adult-obtained dihydropyrrolizidine alkaloids defend ithomiine butterflies against spider predator. Nature 309:707.

BROWN, V. K. & J. H. LAWTON. 1991. Herbivory and the evolution of leaf size and shape. Phil. Trans. R. Soc. (B) 333:265–272.

BROWNE, F. G. 1937. A note on the defoliation of Sendok-sendok (*Endospermum malaccense*). Malay. Forester 6:267–269.

——— 1938. Defoliation of Sendok-sendok. Malay. Forester 7:35.

——— 1940. Defoliation of Sendok-sendok. Malay. Forester 9:38–39.

BUTLER, A. G. 1869. *Nyctalemon zodiaca*, Butler. Entomologist's Mon. Mag. 5:273.

CAMBOUÉ, R. P. 1889. L'*Urania rhipheus* Bdv. Quelques notes sur les états imparfaits ou larvaires. Revue Sci. Nat. Appl. 36:439.

——— 1892. Sur l'*Urania rhipheus*. Congrès International de Zoologie, 2nd session, Moscow:180–184.

CARPENTER, G. D. H. 1937. Further evidence that birds do attack and eat butterflies. Proc. Zool. Soc. Lond. (A) 107:223–247. Pls. 1, 2.

CASH, J. T. 1908. The characters and actions of the seeds of *Omphalea megacarpa* (*diandra*), *Omphalea triandra* and *Garcia nutans* from Trinidad. Pharm. J. (Ser. 4) 27:351–352.

CATALA, R. 1940. Variations expérimentales de *Chrysiridia madagascariensis* Less. (Lep.: Uraniidae). Ph.D. Thesis, Archives du Muséum Nationale de Paris (A), no. 406 (439). 260 pp., 36 pl.

COLEMAN, N. C. & G. B. MONTEITH. 1981. Life history of the north Queensland day-flying moth, *Alcides zodiaca* Butler (Lepidoptera: Uraniidae). N. Qd Nat. 45:2–6.

COMMON, I. F. B. 1970. Lepidoptera (moths and butterflies), pp. 765–866. *In* CSIRO, The insects of Australia (a textbook for students and research workers). Melbourne Univ. Press, Melbourne. 1029 pp.

——— 1990. Moths of Australia. Melbourne University Press. 535 pp., 32 pl.

CORBETT, G. H. & C. DOVER. 1927. Notes on miscellaneous insects of 1926: *Nyctalemon patroclus* L., *Lyssidia achillaria* Hub. and *Micronia astheniata* Guen., Malay. Agric. J. 15:408–419.

CROIZAT, L. 1941. Notes on the Euphorbiaceae II: 1. The systematic position of *Omphalea*. Bull. Bot. Gdns Buitzen. (III) 17:204–208.

——— 1942. Bull. Bot. Gdns Buitzen. (III) 17:212–217.

CRONQUIST, A. 1981. An integrated system of classification of flowering plants. Columbia University Press, New York. 1262 pp.

D'ABRERA, B. 1974. Moths of Australia. Lansdowne Press, Melbourne. 79 pp.

DIRZO, R. 1984. Herbivory: A phytocentric overview, pp. 141–165. *In* Dirzo, R. & J. Sarukhan (eds.), Perspectives on plant population ecology. Sinauer Associates Inc., Sunderland, Massachusetts. 478 pp.

DRUMMOND, B. A. III. 1984. Multiple mating and sperm competition in the Lepidoptera, pp. 291–370. *In* Smith, R. L. (ed.), Sperm competition and the evolution of animal mating systems. Academic Press, London & New York. 687 pp.

——— 1986. Coevolution of ithomiine butterflies and solanaceous plants, pp. 303–327.

In D'Arcy, W. G. (ed.), The Solanaceae: Biology and systematics. Columbia University Press, New York. 603 pp.

DUSSOURD, D. E. & T. EISNER. 1987. Vein-cutting behaviour: Insect counterploy to the latex defense of plants. Science 238:898–901.

ELTRINGHAM, H. 1924a. On the early stages of *Chrysiridia ripheus* Dru. Trans. Entomol. Soc. Lond. [1923]:439–443.

——— 1924b. On the tympanic organ of *Chrysiridia ripheus* Dru. Trans. Entomol. Soc. Lond. [1923]:443–458.

FARRELL, B. & C. MITTER. 1990. Phylogenesis of insect/plant interactions: Have *Phyllobrotica* leaf beetles (Chrysomelidae) and the Lamiales diversified in parallel? Evolution 44:1389–1403.

FELLOWS, L. E. 1985. The sugar-shaped weapons of plants. New Scient. 107(1469): 40–41.

——— 1989. Botany breaks into the candy store. New Scient. 123 (1679):45–48.

FELLOWS, L. E., S. V. EVANS, R. J. NASH & E. A. BELL. 1986. Polyhydroxy plant alkaloids as glycosidase inhibitors and their possible ecological role, pp. 72–78. *In* Green, M. B. & P. A. Hedin, P. A. (eds.), Natural resistance of plants to pests: Roles of allelochemicals. Amer. Chem. Soc. Symp. Ser., no. 296. 243 pp.

FLETCHER, D. S. 1979. Geometroidea. Vol. 3. *In* Nye, I. W. B. (ed.), Generic names of the moths of the world. British Museum (Natural History), London. 243 pp.

FRANKEN, N. A. P. 1984. *Endospermum* Benth., pp. 182–183. *In* Balgooy, M. M. J. van, Pacific plant areas 4. Rijksherbarium, Leiden. 270 pp. + maps.

FREISE, F. W. 1935. Essential oils from Brazilian Euphorbiaceae: *Omphalea diandra* Aubl. Perfum. Essent. Oil Rec. 26:219–220.

FRODEN, D. G. 1984. Guide to standard floras of the world. Press Syndicate of the University of Cambridge. 619 pp.

GAEDE, M. 1926-1930. Unterfamilie Microniinae, pp. 389–394. *In* Seitz, A. (ed.), Macrolepidoptera of the world, Division II: African region 16. Alfred Kernen, Stuttgart. 593 pp.

——— 1933. Unterfamilie Microniinae, pp. 97–103. *In* Seitz, A.(ed.), Macrolepidoptera of the World, Division II: Indo-Australian region 10. Alfred Kernen, Stuttgart. 909 pp.

GILLESPIE, L. J. 1988. A phylogenetic analysis of the genus *Omphalea* L. (Euphorbiaceae); the systematic significance of leaf architecture. Abstr., annual meeting of the Bot. Soc. of Amer., Univ. of Calif. (Davis), 14–18 August 1988. Amer. J. Bot. 75(6), pt. 2.

——— 1990. A revision and phylogenetic analysis of *Omphalea* (Euphorbiaceae). Ph.D. Thesis, University of California, Davis. University Microfilms, Ann Arbor, order no. 8910506.

GOSS, G. J. 1977. The interaction between moths and pyrrolizidine alkaloid-containing plants including nutrient transfer via the spermatophore in *Lymire edwardsii* (Ctenuchiidae). Ph.D. Thesis, University of Miami, Coral Gables. University Microfilms, Ann Arbor, order no. DDJ77 28934.

GOSSE, P. H. 1851. A naturalist's sojourn in Jamaica. Longman, Brown, Green, & Longmans, London. 508 pp., 8 pl.

——— 1880. *Urania sloanus* at home. Entomologist 13:133–135.

——— 1881. *Urania sloanus* at home: II. The larva and pupa. Entomologist 14:241–245.

GOWERS, S. 1976. Some common trees of the New Hebrides and their vernacular names. Report, Forestry Section, Department of Agriculture, Port Vila, New Hebrides. 189 pp.

GRIVEAUD, P. 1959. Sur les deplacements de *Chrysiridia madagascariensis* Less. (Lepidoptera: Uraniidae). Naturaliste Malgache 11:1–2.

GUENÉE, A. 1877. Note sur l'*Urania rhipheus* Drury. Annls Soc. Entomol. Fr. (5)7: 305–308.

GUNDLACH, J. 1881. Contribucion a la entomologia Cubana, 1. Habana. 480 pp.

GUPPY, H. B. 1917. Plants, seeds and currents of the West Indies and Azores. Williams and Norgate, London. 531 pp.

GUPPY, L., JR. 1907. Life history of *Cydimon* (*Urania*) *leilus* L. Trans. Entomol. Soc. London 3:405–410.

HAMPSON, G. F. 1895. Moths, 3, 546 pp. *In* Blanford, W. T. (ed.), 1892–6, The fauna of British India including Ceylon & Burma. Taylor & Francis, London.

HEMSLEY, W. B. 1885. Report of the scientific results of the voyage of H.M.S. Challenger during the years 1873–76. Botany, 1 (3). Reports on the botany of Juan Fernandez, the south-eastern Moluccas, and the Admiralty Islands. Her Majesty's Stationery Office, London. 333 pp.

HOFMANN, E. 1881. Die raupe von *Urania leilus* L. Stettin. Entomol. Ztg 42:487–488.

HOLLOWAY, J. D., J. D. BRADLEY & D. J. CARTER. 1987. CIE guides to insects of importance to man. 1. Lepidoptera. C.A.B. International Institute of Entomology and British Museum (Natural History), London. 262 pp.

HOPFFER, C. H. 1856. *Nyctalemon metaurus* Hopffer. Neue oder weniger bekannte Schmetterlinge der Insekten-Sammlung des Königl. Zoologischen Musei der Universität zu Berlin, 2:2, pl. 2. *In* Klug, J. C. F. & C. H. Hopffer, 1836–1856, Neue Schmetterlinge, Berlin. 16 pp., 10 pl.

HORN, J. M. H., D. C. LEES, N. G. SMITH, R. J. NASH, L. E. FELLOWS & E. A. BELL. 1987. The *Urania-Omphalea* interaction: Hostplant secondary chemistry, p. 394. *In* Labeyrie, V., G. Fabres & D. Lachaise (eds.). Proceedings of the Sixth International Symposium on Insect-Plant Relationships, Pau, France. Dr. W. Junk Pubs., Dordrecht. 464 pp.

JOHNSTON, I. M. 1949. The Botany of San Jose Island. *Omphalea panamensis* (Beurling), comb. nov. Sargentia 8:177–178.

JORDAN, K. 1897. On mimicry. Nature 56:153, 419.

KENNEL, J. VON & F. EGGERS. 1933. Die abdominalen Tympanalorgane der Lepidopteren. Zool. Jb., Abt. Anat. 57:1–104.

KING, P. P. 1826. Narrative of a survey of the intertropical and western coasts of Australia performed between the years 1818 and 1822. Volume 2. John Murray, London. 637 pp.

KITE, G. C., L. E. FELLOWS, G. W. J. FLEET, P. S. LIU, A. M. SCOFIELD & N. G. SMITH. 1988. α-homonojirimycin [2,6-Dideoxy-2,6-Imino-D-Glycero-L-Gulo-Heptitol] from *Omphalea diandra* L.: Isolation and glucosidase inhibition. Tetrahedron Lett. 29(49): 6483–6486.

KITE, G. C., L. E. FELLOWS, D. C. LEES, D. KITCHEN & G. B. MONTEITH. 1991. Alkaloidal glycosidase inhibitors in nocturnal and diurnal uraniine moths and their respective foodplant genera, *Endospermum* and *Omphalea*. Biochem. Syst. Ecol. 19(6):441–445.

KITE, G. C., J. M. HORN, J. T. ROMEO, L. E. FELLOWS, D. C. LEES, A. M. SCOFIELD & N. G. SMITH. 1990. α-homonojirimycin and 5-dihydroxymethyl-3,4-dihydroxypyrrolidine: Alkaloidal glycosidase inhibitors in the moth *Urania fulgens*. Phytochemistry 29(1):103–105.

KÜHN, H. 1887. Zur kenntniss Indischer lepidopterenlarven. Gattung *Nyctalemon* Dalm. KorrespBl. Beil. "Iris" 1:183, taf. VI.

LÉANDRI, J. 1938. Euphorbiacées malgaches nouvelles récoltées par H. Perrier de la Bathie. Geloniae. Bull. Soc. Bot. Fr. 85:525 (pl.); 529–530.

——— 1954. Une mission botanique à Madagascar en 1952-53. Mém. Inst. Sci. Madagascar (B) 5:87–107.

LEON, H. & H. ALAIN. 1953. Flora de Cuba, 3. P. Fernandez, La Habana. 502 pp.

LÉONARD, J. 1958. Notulae systematicae XXIV. Note sur les genres *Suregada* Roxb. ex Rottl. et *Gelonium* Roxb. ex Willd. (Euphorbiacées). Bull. Jard. Bot. État Brux. 28: 443–450.

LEWIS, C. B. 1944. "The Jamaica Emperor". Nat. Hist. Soc. Jamaica 2:133.

——— 1945. *Urania* sp?. Nat. Hist. Soc. Jamaica 2:160.

LIOGIER, A. H. 1971. Novitates Antillanae IV. *Omphalea* in Hispaniola. Mem. New York Bot. Gard. 21:124–131.

——— 1986. La Flora de la Española IV. Universidad Central del Este. San Pedro de Macorís RD, Dominican Republic. 377 pp.

LUCAS, H. 1869. Remarques sur l'*Urania riphaeus*, lépidoptère chalinoptère de la tribu de Uraniens. Annls Soc. Entomol. Fr. (4)9:426.

——— 1876. ["Note relative à une variété de l'*Urania Ripheus*"]. Annls Soc. Entomol. Fr. (5)6, Bull. Entomol.: CXXVI–CXXVII.

LUNDY, W. 1953. The mystery of Panama's migrating moth deepens. Panama Canal Co. Rev. 4:9–25.

MABILLE, P. 1889. [Description of a drawing of the larva of "*Urania ripheus* Drury"]. Annls Soc. Entomol. Fr. (6)9, Bull. Entomol.: XLVI.

MACLEAY, W. S. 1834. A few remarks tending to illustrate the natural history of two annulose genera, viz. *Urania* of Fabricius, and *Mygale* of Walkenaer. Trans. Zool. Soc. Lond. 1:179–195.

MILDBRAED, J. 1936. Euphorbiaceae III. *Omphalea Mansfeldiana* Mildbr. n.spec. Notizbl. Bot. Gart. Mus. Berl. 13:276–277.

MILLER, J. S. 1987. Host-plant relationships in the Papilionidae (Lepidoptera): Parallel cladogenesis or colonization? Cladistics 3:105–120.

MINET, J. 1983. Étude morphologique et phylogénétique des organes tympaniques des Pyraloidea. 1- Généralités et homologies (Lep. Glossata). Annls Soc. Entomol. Fr. 19:175–207.

——— 1986. Ébauche d'une classification moderne de l'ordre des Lepidoptères. Alexanor 14(7):291–313.

——— 1991. Tentative reconstruction of the ditrysian phylogeny (Lepidoptera: Glossata). Entomol. Scand. 22:69–95.

MITTER, C. M. & D. R. BROOKS. 1983. Phylogenetic aspects of coevolution, pp. 65–98. *In* Futuyma, D. J. & M. Slatkin (eds.), Coevolution. Sinauer, Sunderland, Massachusetts. 555 pp.

MONTEITH, G. B. 1986. Presidential address. Some curious insect-plant associations in Queensland. Qd Nat. 26:105–114.

MONTEITH, G. B. & G. A. WOOD. 1987. *Endospermum*, ants and uraniid moths in Australia. Qd Nat. 28:35–41.

MOORE, F. 1884–1887. The Lepidoptera of Ceylon, 3. L. Reeve & Co., London. 578 pp., 215 pl.

MÜLLER, J. 1984. Significance of fossil pollen for angiosperm history. Ann. Mo. Bot. Gdn. 71:419–443.

MÜLLER-ARGOVENSIS, J. 1873–1874. Euphorbiaceae. *In* Martius, C. F. P. de (ed.), Flora Brasiliensis 11(2):513–516. Cramer, Lehre, West Germany. Reprint 1967. 751 pp.

PALGRAVE, K. C. 1977. Trees of Southern Africa. C. Struik, Cape Town. 959 pp.

PAULIAN, R. 1951. Papillons communs de Madagascar. Institut de Recherche Scientifique Tananarive-Tsimbazaza, Antananarivo. 91 pp.

PAX, F. A. & K. HOFFMAN. 1931. Euphorbiaceae. *In* Engler, A. & K. Prantl (eds.), Die Natürlichen Pflanzenfamilien (ed. 2). 19c:11–233. W. Engelmann, Leipzig.

PERKINS, L. 1944. *Urania sloanus*. Nat. Hist. Soc. Jamaica 2:144.

PFEIFFER, L. 1925. Einiges über die Uraniiden und Sematuriden (I p.) der alten und neuen Welt (Fortsetzung). Entomol. Z., Frankf. a. M. 39:127–128; 131–132.

PINHEY, E. C. G. 1975. Moths of Southern Africa. Tafelberg Pubs., Cape Town. 273 pp., 63 pl., 18 figs.

POULTON, E. B. 1931. Two specially significant examples of insect mimicry. Trans. Entomol. Soc. London 79:395–398, 2 pl.

PUNT, W. 1962. Pollen morphology of the Euphorbiaceae, with special reference to taxonomy. Wentia 7:1–116.

QUESNEL, V. C. 1975. The 1973 migration of the day-flying moth *Urania leilus*. J. Trin. Fld Nat. Club [1975]:43–46.

RADCLIFFE-SMITH, A. R. 1987. Flora of East Tropical Africa: Euphorbiaceae (Part 1). A. A. Balkema, Rotterdam & Boston. 407 pp.

——— 1991. Notes on Madagascan Euphorbiaceae IV: The genus *Suregada* in Madagascar and the Comoro Is. Kew Bull. 46:711–726.

ROBINSON, G. S. 1975. Macrolepidoptera of Fiji and Rotuma. A taxonomic and geographic study. E. W. Classey Ltd., Oxford. 362 pp.

ROTHSCHILD, M., R. T. APLIN, P. A. COCKRUM, J. A. EDGAR, P. FAIRWEATHER & R. LEES. 1979. Pyrrolizidine alkaloids in arctiid moths (Lep.) with a discussion on hostplant relationships and the role of these secondary plant substances in the Arctiidae. Biol. J. Linn. Soc., 12:305–326.

RUDALL, P. In press. Laticifers in Crotonoideae (Euphorbiaceae): Homology and evolution. *In* Huft, M. J. & G. L. Webster (eds.), Advances in the Systematics of the Euphorbiaceae. Missouri Botanical Garden Monograph series.

SCHAEFFER, J. 1971. Revision of the genus *Endospermum* Bentham (Euphorbiaceae). Blumea 19:171–192.

SCHODDE, R. 1967. Contributions to Papuasian botany I. A new species of *Endospermum* (Euphorbiaceae). Blumea 15:397–402.

SEITZ, A. 1913. Macrolepidoptera of the world, Division I: Palearctic region 2:275. Alfred Kernen, Stuttgart. 479 pp.

——— 1933. Macrolepidoptera of the world, Division II: Indo-Australian region 10: 93–97. Alfred Kernen, Stuttgart. 909 pp.

——— 1940. Macrolepidoptera of the world, Division II: Neotropical region 6:829–831. Alfred Kernen, Stuttgart. 1452 pp.

SEMPER, C. G. 1896–1902. Die Schmetterlinge der Philippinischen Inseln (2), Die Nachtfalter, Heterocera. Reisen im Archipel der Philippinen, 6. Dr. C. G. Semper, Wiesbaden. 380 pp.

SEVASTOPULO, D. G. 1981. A second list of the foodplants of East African macrolepidoptera. Bull. Amat. Entomol. Soc. 40:96.

——— 1986. Larval foodplant of *Chrysiridia croesus* Gerst—A correction. Bull. Amat. Entomol. Soc. 45:64.

SGANZIN, V. & J. B. A. D. DE BOISDUVAL. 1873. ["Note . . . aux metamorphoses de l'*Urania Ripheus*"]. Annls Soc. Entomol. Fr. (5)3, Bull. Entomol.: CCXX.

SIBREE, J. 1915. A naturalist in Madagascar. Seeley, Service & Co., London. 320 pp.

SICK, H. 1937. Die Tympanalorgane der Uraniden und Epiplemiden. Zool. Jb., Abt. Anat. 63:351–398.

SKUTCH, A. F. 1970. Migrations of the American moth *Urania fulgens*. Entomologist 103:192–197.

SMITH, A. C. 1978. Precursor to flora of Fiji. *Endospermum* Benth. Allertonia 1(6):389–393, figs. 17, 19.

——— 1981. Flora Vitiensis Nova—A new flora of Fiji. Vol. 2. Pacific Tropical Botanical Garden, Lawai, Kauai, Hawaii. 810 pp.

SMITH, N. G. 1972. Migrations of the day-flying moth *Urania* in Central and South America. Caribb. J. Sci. 12:45–58.

——— 1982. Population irruptions and periodic migrations in the day-flying moth *Urania fulgens*, pp. 331–344. *In* Leigh, E. G., A. S. Rand & D. Windsor (eds.), The ecology of a tropical forest: Seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, D.C. 468 pp.

——— 1983. Host plant toxicity and migration in the dayflying moth *Urania*. Fla Entomol. 66:76–85.

——— In press, a. Reproductive behavior and ecology of *Urania* moths and of their larval food plants, *Omphalea* spp. (Euphorbiaceae). *In* Quintero, D. G. & A. Aiello (eds.), Insects of Panama and Mesoamericas. Oxford University Press, Oxford. ca. 700 pp.

SMITHERS, C. N. & J. V. PETERS. 1977. A record of migration and aggregation in *Alcides zodiaca* (Butler) (Lepidoptera: Uraniidae). Aust. Entomol. Mag. 4(3):44.

STEENIS, C. G. G. J. VAN. 1979. Plant-geography of East Malesia. Bot. J. Linn. Soc. 79: 97–178.

SUGI, S. 1987. Larvae of larger moths of Japan. Kodansha Co. Ltd., Tokyo. 433 pp., 120 pl.

SZENT-IVANY, J. J. H. & R. A. CARVER. 1967. Notes on the biology of some Lepidoptera of the territory of Papua and New Guinea with description of the early stages of *Ornithoptera meridionalis* Rothschild. Trans. Papua New Guinea Scient. Soc. 8:1–35.

TOWNSEND, C. H. T. 1893. Swarmings of *Urania sloanus*. J. Inst. Jamaica 1:379.

VIETTE, P. 1972. Contribution à l'étude des lépidoptères Uraniidae Malgaches. Bull. Mens. Soc. Linn. Lyon 41(9):189–193.

VOLLESEN, K. 1980. Annotated check-list of the vascular plants of the Selous Game Reserve, Tanzania. Op. Bot. Soc. Bot. Lund. 59:38–39.

WEBSTER, G. L. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24:593–601.

WESTWOOD, J. O. 1894. Observations on the Uraniidae, a family of lepidopterous insects, with a synopsis of the family and a monograph of *Coronidia,* one of the genera of which it is composed. Trans. Zool. Soc. London 10(7):507–542, 4 pl.

WHITMORE, T. C. 1966. Guide to the forests of the British Solomon Isles. Oxford University Press, London. 208 pp.

YONG, H.-S. 1983. Malaysian butterflies—An introduction. Tropical Press Sdn. Bhd., Kuala Lumpur. 152 pp.

Received for publication 11 December 1989; revised 30 October 1991; accepted 1 December 1991.

Journal of the Lepidopterists' Society
45(4), 1991, 348–355

COURTSHIP AND MATING BEHAVIOR OF *SCYTHRIS FLAVIVENTRELLA* (SCYTHRIDIDAE)

PIETRO PASSERIN D'ENTRÈVES AND CLAUDIO FESSILE

Department of Animal Biology, University of Turin,
Via Accademia Albertina 17 - 10123 Turin, Italy

ABSTRACT. Three larvae of *Scythis flaviventrella* (H.-S.) were found in Italy on *Helianthemum apenninum* (Miller) (Cistaceae) and two on *Astragalus onobrychis* (Linné) (Fabaceae). They were reared in the laboratory so that adult behavior could be studied immediately after eclosion. Courtship and mating are described for the first time; courtship was brief but mating lasted 6–7 hours. Both females remated after 48 hours. Oviposition was not observed. Notes on larval morphology and behavior are included.

Additional key words: *Helianthemum apenninum*, Cistaceae, *Astragalus onobrychis*, Fabaceae, larvae.

Even though much has been published about caterpillars and larval food plants of Scythrididae, numerous discrepancies exist in the observations published by different authors for the same species. These discrepancies throw doubt on the supposed polyphagous habits and intraspecific structural variation of the larvae, or both, of those species.

Recent taxonomic and nomenclatural works (Bengtsson 1984, Jäckh 1977, 1978; Passerin d'Entrèves 1976, 1977, 1979, 1980) based on close examination of adult specimens preserved in museum collections reveal that scythridids frequently have been misidentified. In some cases, the two sexes of the same species have been described under different specific names. Consequently, the previously published data about immatures and food plants of these species are unreliable.

Additionally, there is no published account of the courtship and mating behavior of any scythridid species. Contrary to other groups of Lepidoptera (Grant & Brady 1975, Greenfield & Coffelt 1983, Trematerra 1988, Zagatti 1981, 1985), such behavioral studies are almost non-existent in the Gelechioidea, to which the Scythrididae belong.

Here we describe courtship and mating behavior of adults of the European moth, *Scythris flaviventrella* (Herrich-Schäffer) (Scythrididae), and present some observations of the larvae and food plants. This species belongs to the monophyletic *aerariella* species group as defined by Passerin d'Entrèves (1982). Species of this group mainly use Fabaceae as food plants. Previously, *S. flaviventrella* has been reared only on *Vicia* (Fabaceae) (Hauder 1912, Lhomme 1949, Gozmány 1955).

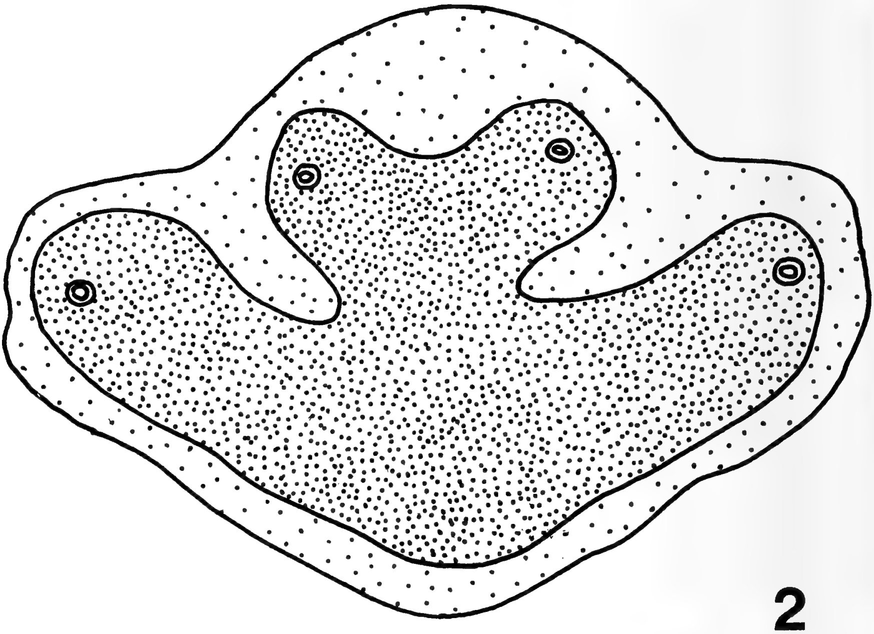
Scythris flaviventrella is known from Spain, France, Italy (newly recorded from specimens mentioned here), Austria, Czechoslovakia, Hungary, Romania, and possibly Yugoslavia and Albania (Passerin d'Entrèves in press).

FIG. 1. Habitat of *Scythris flaviventrella* (H.-S.). on Mt. Rocciamelone, Susa Valley, Piémont, Italy.

MATERIALS AND METHODS

Five last-instar caterpillars were collected on the southern slope of Mt. Rocciamelone, Susa Valley, Piémont, Italy, elev. ca. 1000 m, 11 June 1986. The location was xerothermic and characterized by the phytogeographic association *Trinio-Stipetum* (Braun-Blanquet 1961) (Fig. 1). Three caterpillars were found on *Helianthemum apenninum* (Miller) (Cistaceae) and two were found on *Astragalus onobrychis* (Linné) (Fabaceae). The caterpillars were kept on their respective host plants, brought to the laboratory for study, and kept in cages for observation. The cages were constructed with a framework of light, rectangular timber frames (60 × 35 cm and about 80 cm high) supporting four lateral walls of Plexiglas up to a height of 40 cm and the remaining upper portion with gauze.

The plants, taken with their entire root system and surrounding soil, were placed in the cages and planted in additional soil, taken from the same location as the plants, which covered the floor of the cages. Humidity was regulated by frequent spraying with water. Temperature and lighting were natural, since the cages were kept outside. It did not prove necessary to replace the food plants, which remained in good condition throughout the time period necessary for the maturation of the larvae and the appearance of the adults.



2

FIG. 2. Posterior view of the anal shield of last instar larva of *Scythris flaviventrella* (H.-S.).

RESULTS

Last-instar caterpillars reached 13–14 mm in length and were chestnut-grey and mottled. The anal shield, described here for the first time, was trilobate and shiny black (Fig. 2).

Each caterpillar made a loose web to tie together the apical leaves of the food plant. The web enclosed a more protective and densely woven silken tube that was longitudinally attached to the stem (Fig. 3). Larvae left the silken tube and climbed to the tip of the plant to feed on the apical leaves. If the leaves were touched, the alerted larva first hid motionless alongside the stem; if further disturbed, it swiftly retreated inside the silken tube. If the web was destroyed, the caterpillar immediately built another one.

Pupation occurred inside a thick white cocoon on the host plant (Fig. 4) or elsewhere (e.g., on the cage wall). On Mt. Rocciamelone, adults emerged in late June and early July, during the cooler hours of the day, following a 10–12 day pupal period. The adults flew little, and, during the warmest hours of the day, took refuge at the base of the host plant, near the ground.

Three males and two females were reared from the 5 specimens collected. These specimens are preserved in the Collection Passerin d'Entrèves, Turin, Italy.

FIG. 3. Web of *Scythris flaviventrella* (H.-S.). Larva on food plant *Astragalus onobrychis*.

FIG. 4. Last instar larva of *Scythris flaviventrella* (H.-S.) in silken tube.

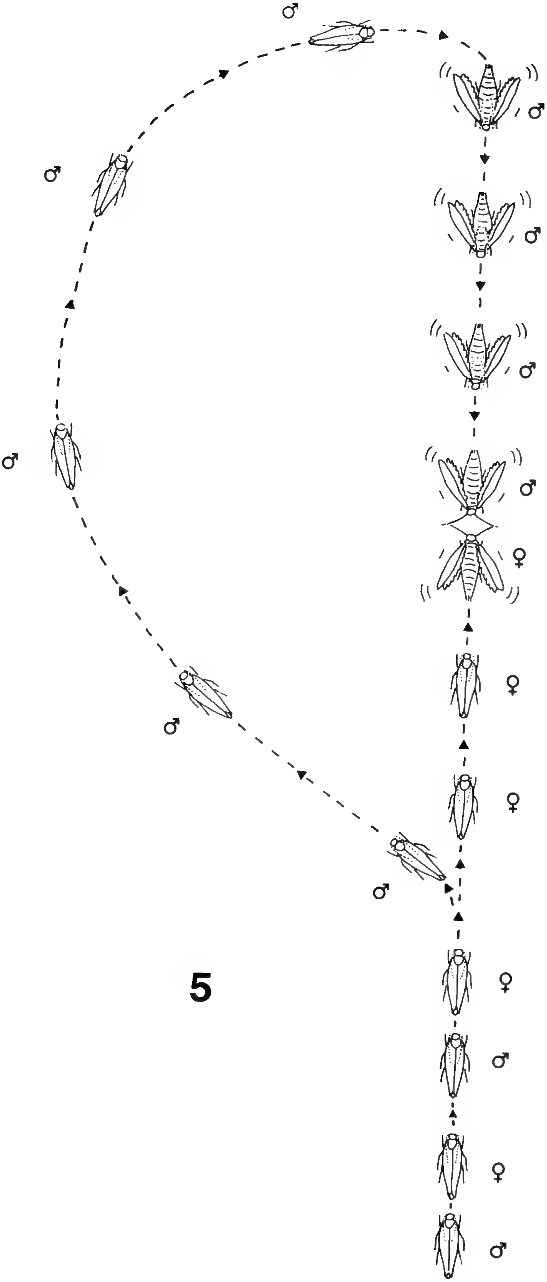


FIG. 5. Preliminary ethogram of courtship behavior of *Scythris flaviventrella* (H.-S.).

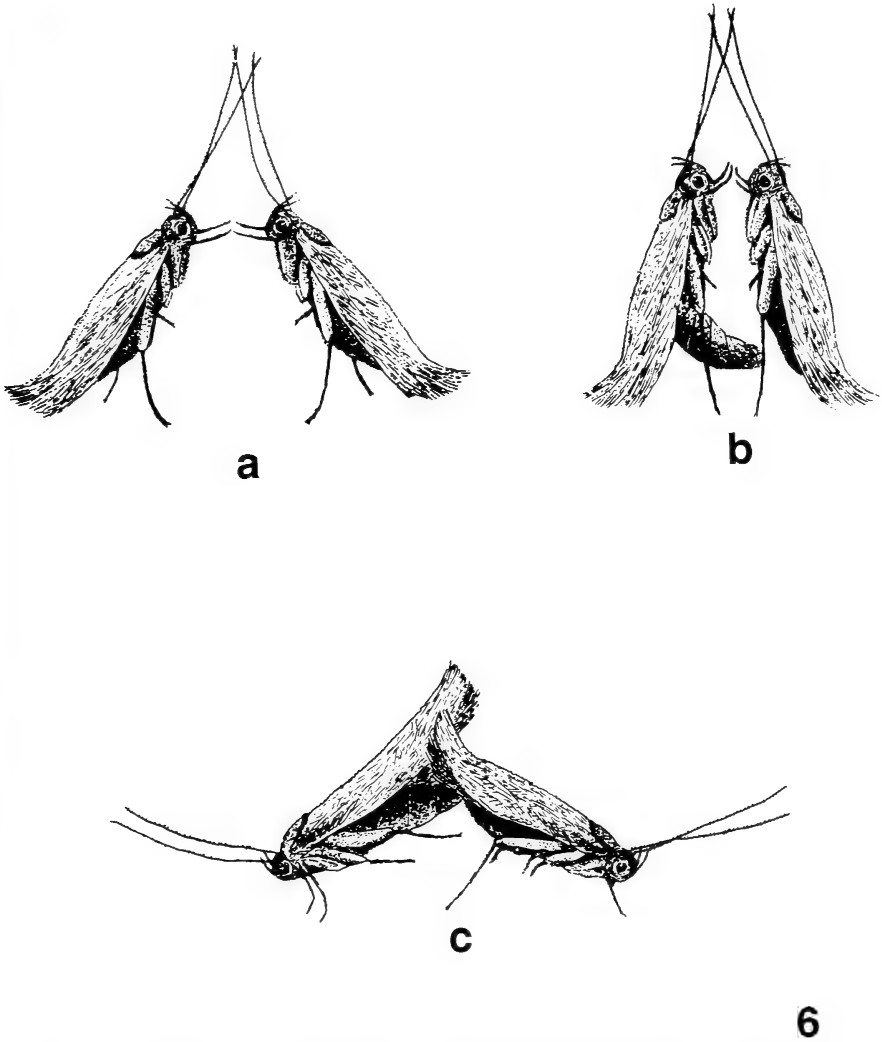


FIG. 6. Courtship and mating behavior of *Scythris flaviventrella* (H.-S.) (see text for explanation).

Courtship and Mating

Four courtships and matings in the rearing cages were observed. Initially, both male and female flew separately to the top of the cage where they landed. A few seconds later, the male located the female, possibly by sensing a pheromone (Zagatti 1985:1257) and began to follow her by walking behind at a distance of about 10 cm. After some time, while the female continued walking in a straight path, the male walked in a broad loop around the female and came to rest 5.6 cm in front of her. There the male began to vibrate his wings and the female stopped. The male walked to within 2–3 cm of the female and vibrated his wings once more, then walked closer again, to within 1 cm, and repeated the wing vibration. Contact then took place, the moths touching the apices of their antennae and simultaneously vibrating their wings very strongly (Fig. 5). They then opposed their forelegs and raised themselves vertically until only their hindlegs and the apices of their wings touched the substrate (Fig. 6a). After a few seconds, the male bent his abdomen toward the female and grasped her genitalia (Fig. 6b). Once coupling had taken place, the moths threw themselves sideways by a rapid rotation of their bodies and finally lay tail to tail, where they remained motionless until mating was completed (Fig. 6c).

During copulation, attempts by another male to displace the mating male were observed, but none was successful. The second male tried to force the mating male away by pushing and hitting him with his head. Three matings began in the middle of the afternoon and lasted about 6–7 hours. Each of the two females remated after an interval of about 48 hours. No oviposition was observed.

DISCUSSION

On the basis of the limited observations reported here, we cannot drawn firm conclusions about the average duration of mating, the significance of the second mating, the possibility of pheromone emission, or the quality and quantity of various stimuli (olfactory, tactile, visual) involved in courtship.

The lengthy and repeated matings we observed could be involved in sperm competition, a phenomenon known in other insects, including Lepidoptera (see Drummond 1984). The long period of copulation may be required for spermatophore transfer, a process known to be lengthy in many Lepidoptera (Drummond 1984). Curiously, we found no evidence of a spermatophore in the *bursa copulatrix* of either of the two mated females. Further rearing is in progress to attempt to answer some of the questions raised by these observations.

ACKNOWLEDGMENTS

We thank Jean-François Landry and E. C. Becker, Biosystematic Research Center, Ottawa, Canada, for kindly reviewing the manuscript and for translating it into English.

This work was carried out under the programs "Fauna delle terre del bacino del Mediterraneo" (Ministero Pubblica Istruzione: 40%) and "Biosistematica dei Lepidotteri Scythrididae" (Ministero dell'Università e della Ricerca Scientifica e Tecnologica: 60%) and presented in part at the 6th Congress of the Societas Europaea Lepidopterologica, in Sanremo, Italy, 5–9 April 1988 (Passerin d'Entrèves & Fessile 1989).

LITERATURE CITED

BENGTSSON, B. Å. 1984. The Scythrididae (Lepidoptera) of Northern Europe. E. J. Brill/Scandinavia Science Press Ltd. Leiden-Copenhagen. 137 pp.

BRAUN-BLANQUET, J. 1961. Die Inneralpine trockenvegetation: von der Province bis zur Steiermark. Ed. Gustav Fisher Verlag, Stuttgart. IX + 273 pp.

DRUMMOND, B. A. 1984. Multiple mating and sperm competition in the Lepidoptera, pp. 291–360. *In* Smith, R. L. (ed.), Sperm competition and the evolution of animal mating systems. Academic Press, Orlando, Florida. 687 pp.

GOZMÁNY, L. A. 1955. Notes on some Hungarian Gelechioidea and Coleophoridae. I. A restriction of the genus *Gelechia* Hbn., concerning the species occurring in Hungary. Annls. Hist.-Nat. Mus. Nat. Hung. VI:307–320.

GRANT, G. G. & U. E. BRADY. 1975. Courtship behavior of phycitid moths. I. Comparison of *Plodia interpunctella* and *Cadra cautella* and role of male scent glands. Can. J. Zool. 53(6):813–826.

GREENFIELD, M. D. & J. A. COFFELT. 1983. Reproductive behaviour of the lesser wax moth, *Achroia grisella* (Pyralidae: Galleriinae): signaling, pair formation, male interactions and mate guarding. Behaviour 84:287–315.

HAUDER, F. 1912. Beitrag zur Mikrolepidopteren-Fauna Oberösterreichs. Mus. Franc. Carol, Linz 1912:208–212.

JÄCKH, E. 1977. Bearbeitung der Gattung Scythris Hübner (Lepidoptera, Scythrididae). 1. Die "grandipennis-Gruppe". Dt. Entomol. Z., N.F. 24(1–3):261–271.

——— 1978. Bearbeitung der Gattung Scythris Hübner (Lepidoptera, Scythrididae) (Forsetzung). 3 Arten mit einer weiβen Längstrieme. Dt. Entomol. Z., N.F. 25(1–3): 71–89.

LHOMME, L. 1949. Catalogue des Lépidoptères de France et de Belgique. 2. Microlépidoptères: 489–1253.

PASSERIN D'ENTRÈVES, P. 1976. Revisione degli Scitrididi paleartici (Lepidoptera, Scythrididae). II. I tipi di *Scythris* del Muséum National d'Histoire Naturelle di Parigi. Boll. Mus. Zool. Univ. Torino, 1976, N. 3:27–70.

——— 1977. Revisione degli Scitrididi paleartici (Lepidoptera, Scythrididae). III. Le specie di *Scythris* descritte da H. G. Amsel. J. Klimesch, J. Müller-Rutz e A. Rössler. Boll. Mus. Zool. Univ. Torino, 1977, N. 5:57–76.

——— 1979. Revisione degli Scitrididi paleartici (Lepidoptera, Scythrididae). IV. I tipi di *Scythris* dell'Instituto Español de Entomología di Madrid. Boll. Mus. Zool. Univ. Torino, 1979, N. 3:83–90.

——— 1980. Revisione degli Scitrididi paleartici (Lepidoptera, Scythrididae). V. I tipi di *Scythris* del Naturhistorisches Museum di Vienna. Boll. Mus. Zool. Univ. Torino, 1980, N. 5:41–60.

——— 1982. Note su alcuni Scitrididi della fauna italiana (Lepidoptera, Scythrididae). Boll. Mus. Zool. Univ. Torino, N. 6:79–86.

——— In press. Scythrididae. *In* Razowski, A (ed.), Check list of European Lepidoptera. Nota Lepid.

PASSERIN, D'ENTREVES, P. & C. FESSILE. 1989. Some biological and behavioral notes on the Scythrididae (Lepidoptera, Gelechioidea). Nota Lepid. 12 Suppl. No. 1:68–69.

TREMATERRA, P. 1988. Studi sul comportamento sessuale di *Corcyra cephalonica* (Staint.) (Lepidoptera, Galleriidae). Atti XV Congr. Naz. Ital. Entomol. L'Aquila 1988:787–793.

ZAGATTI, P. 1981. Comportement sexuel de la pyrale de la canne à sucre *Eldana saccharina* (Walk.) lié à deux phéromones émises par le mâle. Behaviour 78(1–2): 81–98.

——— 1985. Les phéromones aphrodisiaques dans le comportement sexuel des Lépidoptères. Bull. Soc. Entomol. France 90(5–6/7–8):1256–1266.

Received for publication 9 November 1989; revised and accepted 12 September 1991.

Journal of the Lepidopterists' Society
45(4), 1991, 356–365

SYSTEMATIC EVALUATION AND DESCRIPTION OF LIFE STAGES OF "*SESIA*" *ROMANOVI* (LEECH) (SESIIDAE)

Yutaka Arita
Zoological Laboratory, Faculty of Agriculture, Meijo University, Tempaku-ku, Nagoya, 468 Japan

AND

Kazuaki Hirao
Hoshi-cho 219, Hamamatsu-shi, Shizuoka-ken, 431-31 Japan

ABSTRACT. The head, wings, genitalia and the early stages of "*Sesia*" *romanovi* (Leech, [1889]) are described and illustrated. We transfer *romanovi* from the genus *Sesia* Fabricius, 1775 to *Glossosphecia* Hampson, 1919, **new combination**.

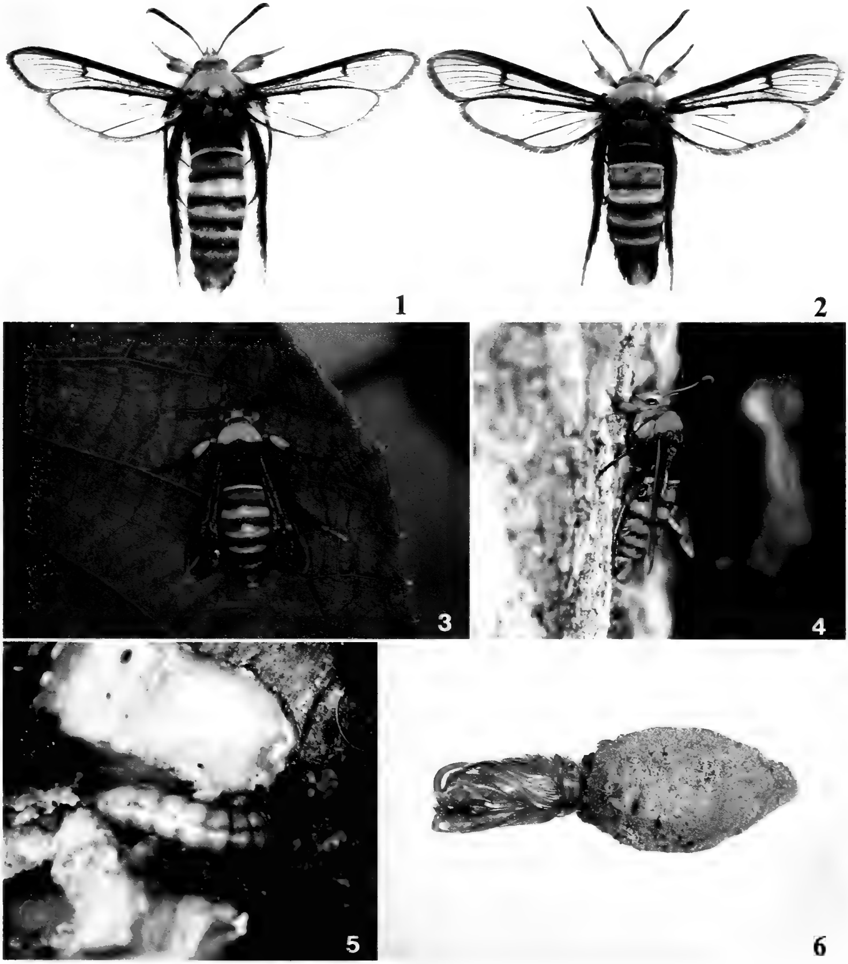
Additional key words: *Glossosphecia romanovi,* early stages, taxonomy, host-plant, Vitaceae.

"*Sesia*" *romanovi* (Leech [1889]) is known as somewhat of a minor pest of cultivated grapevine in a limited and localized area of eastern Kyushu (Nakashima et al. 1978:10–11, 1980:55 & 8029, Nakashima 1984:319). This species was originally described in the genus *Sphecia* Hübner [1819] (a synonym of *Sesia* Fabricius 1775) by Leech ([1889]: 591). Hampson (1919:79) referred it to as *Aegerosphecia* Le Cerf 1916. Afterward, *romanovi* was placed either in *Aegerosphecia* or *Sesia* by most authors, with the exception of its placement in *Synanthedon* Hübner [1819] by Inoue (1982:235).

Having examined the venation and genitalia of *romanovi,* we are convinced that this species should be transferred from *Sesia* to *Glossosphecia* Hampson (1919) (type species *G. contaminata* (Butler 1878)). In addition, *Glossosphecia* is very similar to the North American genus *Cissuvora* Engelhardt (1946) (type species *C. ampelopsis* Engelhardt 1946), by characters of adult and larvae (MacKay 1968, Naumann 1971, Eichlin & Duckworth 1988), *viz.*: antenna long unipectinate in male; labial palpi erect, over the vertex; wing venation of forewing stalk of R_4 plus R_5 stalked with R_3; male genitalia gnathos remarkably long, subscaphium stout, valva with well developed palm-like sensory setae; female genitalia: corpus bursae with many transverse folds throughout; larval anal shield with a pair of stout and remarkable spines in early instar, but scarcely apparent in late instars.

Glossosphecia romanovi (Leech [1889]), new combination
(Figs. 1–17)

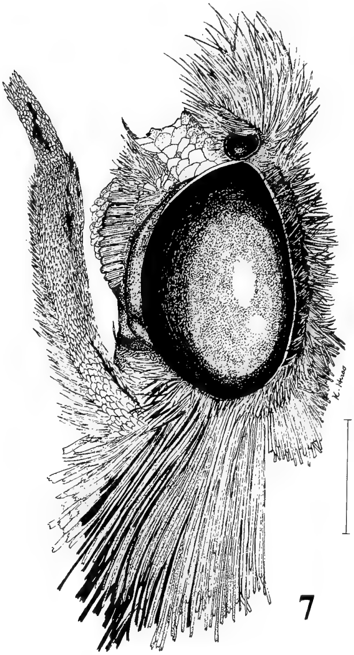
Sphecia romanovi Leech [1889]:591, pl. 30, fig. 1. Bartel 1912:378, pl. 51a. Gaede 1933: 786.



FIGS. 1–6. *Glossosphecia romanovi* (Leech). **1,** Male adult; **2,** Female adult; **3** and **4,** Freshly emerged male adult; **5,** The mature larva in tunnel, exposed; **6,** Earthen cocoon.

Trochilium romanovi; Matsumura 1911:49, pl. 34, fig. 1.
Aegerosphecia romanovi; Hampson 1919:79. Matsumura 1931a:1012, 1931b:9. Inoue 1954:44, 1957:153. Nakashima et al. 1978:10, 1980:55 & 8029. Nakashima 1984:319.
Aegerosphecia romanowi [sic]; Dalla Torre & Strand 1925:173 [misspelling].
Sesia romanovi; Heppner & Duckworth 1981:28.
Synanthedon romanovi; Inoue 1982:235.

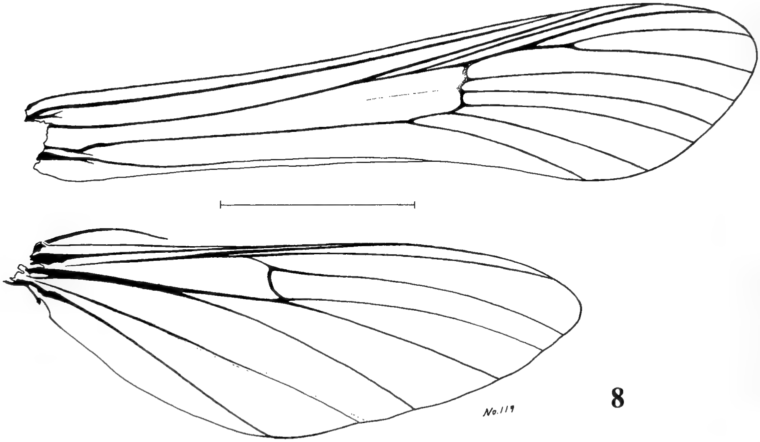
Adult (Figs. 1–4). Wingspan 5–48 mm. Head (Fig. 7): vertex roughened, bright orange; frons dark fuscous, mixed with orange scales. Occipital fringe snow-white. Antenna remarkable long unipectinate in male, black, basal ⅓ and apical part reddish brown; ventral side brownish. Labial palpus bright orange; basal segment reddish orange, slightly



7

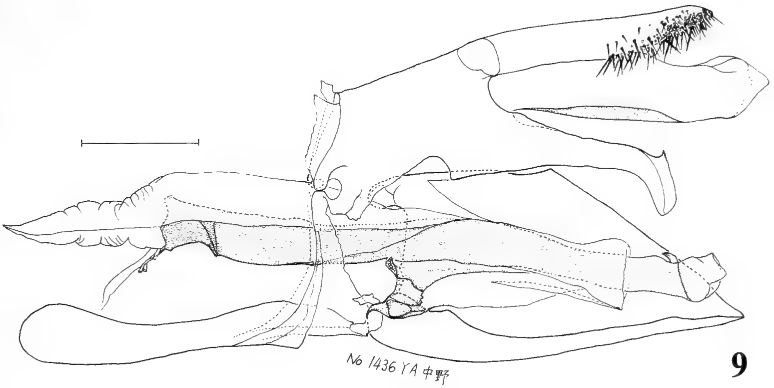
FIG. 7. *Glossosphecia romanovi* (Leech), head profile of male. Scale line = 1.0 mm.

mixed with black scales; terminal segment reddish orange. Thorax black, anterior ⅓ bright orange; patagial collar bright reddish brown, mixed with black scales in male; tegula black, anterior half bright orange. Abdomen dorsally brownish orange; 1st and 2nd segments black, 2nd segment with yellow posterior margin; other segments with blackish

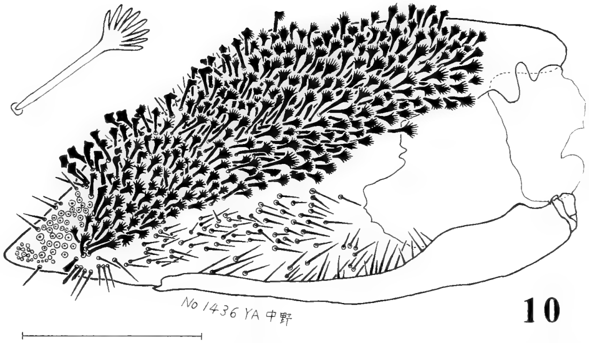


8

FIG. 8. *Glossosphecia romanovi* (Leech), wing venation. Scale line = 5.0 mm.



9

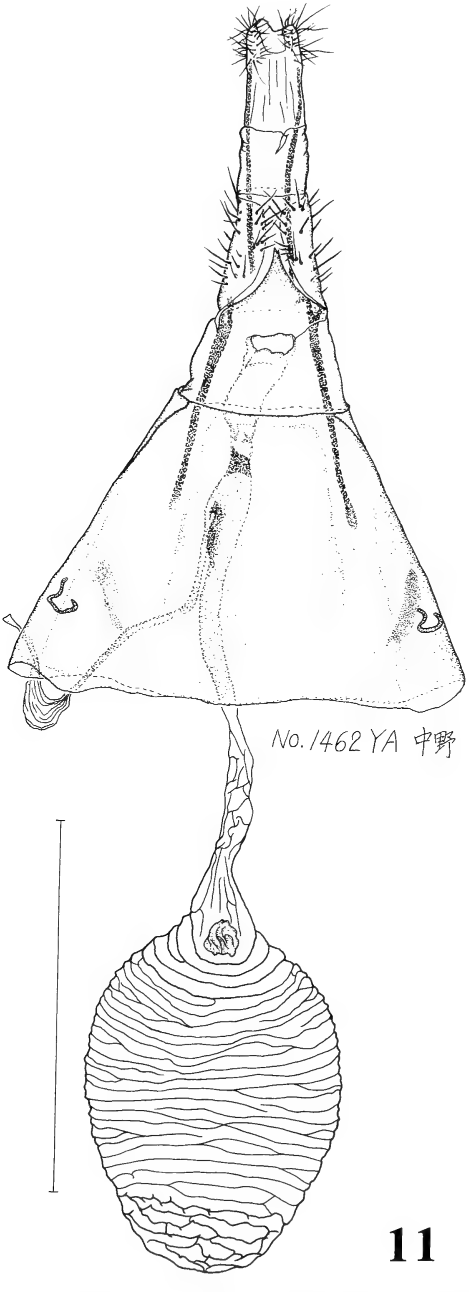


10

FIGS. 9–10. *Glossosphecia romanovi* (Leech), male genitalia, genitalia on slide no. 1436 YA. **9,** Lateral aspect with left valva removed; **10,** Left valva. Scale line = 1.0 mm.

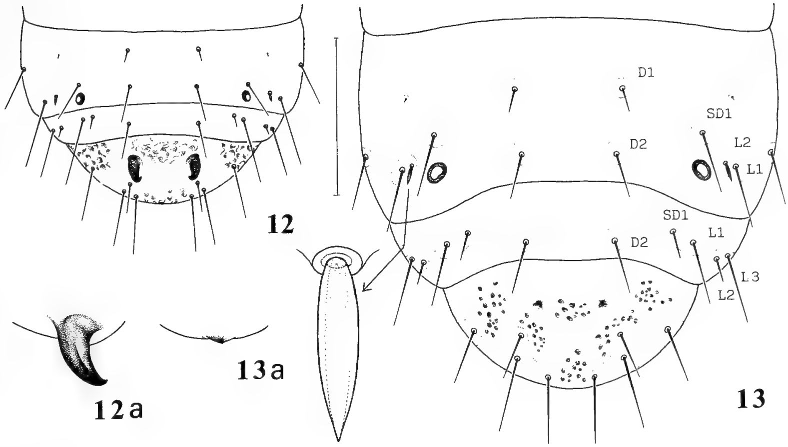
brown posterior bands; terminal segment blackish brown, bright orange on middle; ventral side as on dorsal side. Foreleg: coxa reddish orange, posterior margin black; femur black, posterior tips reddish orange; tibia and tarsus reddish orange. Midleg: coxa black, femur upper half orange, lower half black; tibia basal ⅔ orange, posterior ⅓ dark brown. Hindleg: femur black; tibia black, mixed with dark brown scales, small orange dot on middle outwardly; tarsus black. Forewing (Fig. 8): hyaline, costal and dorsal margin dark brown, mixed with reddish brown scales along subcostal in female; discal spot dark brown; apical area sparsely fuscous, small scales; cilia fuscous. Hindwing (Fig. 8): hyaline, outer half sparsely irrorated with small yellowish scales; cilia fuscous, slightly mixed with yellow scales.

Male genitalia (Figs. 9, 10). Uncus very long, sparsely clothed with hairs on apical half of ventral part. Tegumen broad; with well developed gnathos, apex expanded and minutely hooked upward. Tuba analis long and large, ventral side weakly sclerotized. Gnathos extremely long, apex largely spatulate, acutely pointed dorsally. Saccus very long, almost as long as valva, apex broadly rounded. Anellus long, membranous, basal half of ventral part weakly sclerotized. Valva elongate, broadest near base, tapered to apex, dorsal half with very conspicuous palmate-multifurcate scales, ventral half with setae on apical ⅔. Aedeagus very long, slender, rather straight, with subapical strongly recurved spine.



11

FIG. 11. *Glossosphecia romanovi* (Leech), female genitalia, genitalia on slide no. 1462 YA. Scale line = 5.0 mm.



FIGS. 12–13. *Glossosphecia romanovi* (Leech), dorsal view of eighth to tenth abdominal segments. **a:** enlarged anal shield spine. **12,** Early instar larva; **13,** Mature instar larva. Scale line = 2.5 mm.

Female genitalia (Fig. 11). Papillae anales small and slender, with sparse hairs. Postapophysis and antapophysis long, almost equal in length. Ostium bursae semicircular, opening in intersegmental membrane between 7th and 8th abdominal segments. Antrum very short, on ⅙ of ductus bursae. Ductus bursae long, slender, with ductus seminalis from just beyond antrum. Corpus bursae rather large, obovate, with many transverse folds throughout; signum uneven circular, near entrance of ductus bursae.

Mature larva (Figs. 5, 12, 12a, 13, 13a, 14a–i). Length 38.0–43.0 mm. Head dark brown, mouthpart blackish brown. Body light pinkish purple in late instars; prothoracic shield light brown; thoracic legs light brown. Head broader than long; coronal suture extremely short. Ocelli: six on each side, the relative position as shown in Fig. 14b. Labrum (Fig. 14c) outer margin quite convex. Mandible with four large teeth (Fig. 14d). Spiracle of 8th abdominal segment located in dorsal area and rather near to posterior margin (Figs. 12, 13). Anal shield (Figs. 12, 12a, 13, 13a) close to anterior margin with pair of stout and remarkable spines in early instar (Figs. 12, 12a) but scarcely apparent in late instars (Figs. 13, 13a). Proleg (Fig. 14h) with 38 crochets. Anal proleg (Fig. 14i) with 10 crochets.

Chaetotaxy. Head (Figs. 14a and b) with setae short; AF1 microscopic. A1 and A3 very long; A2 very short, adjacent and posterolateral to A1. P2 microscopic and distant from P1. O1 very short and posteroventral to ocellus III. O2 extremely long and ventral to ocellus I. Prothorax (Fig. 14e) with a L group trisetose and located in almost straight line on large oblong pinaculum. SD1 extremely long and SD2 microscopic on 1st–7th segments. L3 of 1st–9th segments very long. L2 of 8th segment scale-shaped.

Material examined. Japan: Kyushu—11 specimens, feeding within trunk of cultivated grape, Ohita-ken, Usa-gun, Ajimu-cho, 18.IX.1985, K. Hirao leg.

Pupa (Figs. 6, 15a and b, 16a–c, 17a–c). Length 20.0–21.0 mm. Width 6.0 mm. Brown, very stout. Frontal process (Figs. 15a and b) broad, depressed orbicular, slightly concave at middle of posterior margin in dorsal view; low pointed in lateral view. Clypeus large, squared; maxillae longer than prothoracic legs. Metathoracic legs reaching to posterior margin of 5th abdominal segment. Wing tips nearly reaching to posterior margin of 4th abdominal segment. Dorsum of mesothorax with strong enlarged and ridged alar furrows. Dorsal spines of abdominal segments as follows: one row on segments 1, 8 and 9 in male (also on 7 in female), two rows on segments 2–7 in male and 2–6 in female. Tenth abdominal segment (Figs. 17a–c) with five pairs of spines; one pair of spines on dorsal side and four pairs of spines on lateral side.

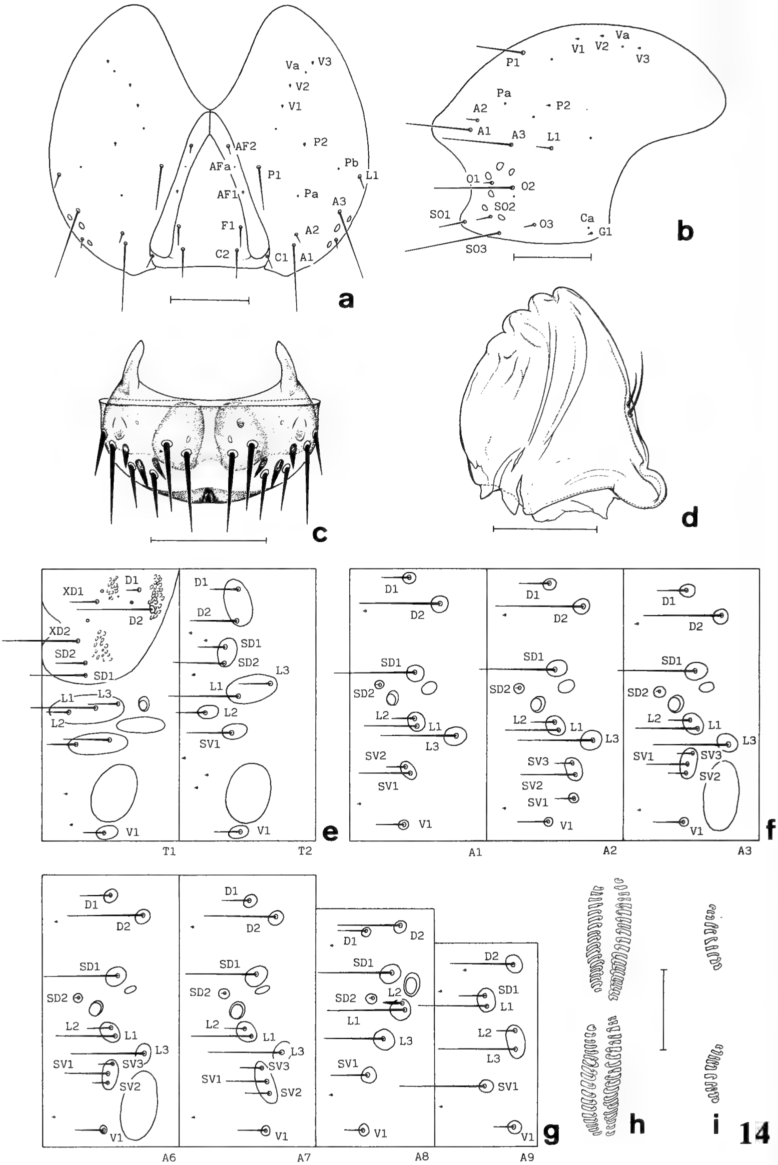
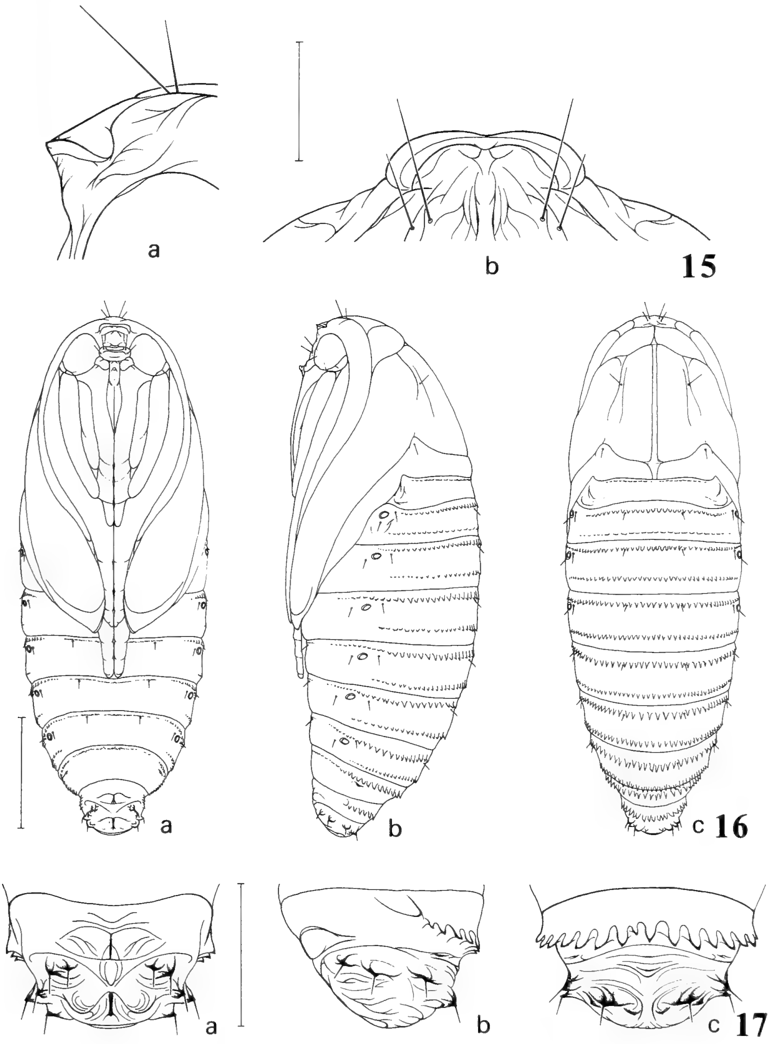


FIG. 14. *Glossosphecia romanovi* (Leech), mature larva. **a.** head, dorsal view; **b.** ocellar region, left side; **c.** labrum, dorsal view; **d.** mandible, ventral view; **e.** pro- and mesothorax; **f.** first to third abdominal segments; **g.** six to ninth abdominal segments; **h.** third abdominal proleg, ventral view; **i.** anal proleg, ventral view. Scale line: a, b, h and i = 1.0 mm, c and d = 0.5 mm.



FIGS. 15-17. *Glossosphecia romanovi* (Leech), pupa, male. **15,** Pupal frontal process (**a:** lateral view; **b:** dorsal view); **16,** Total aspect (**a:** ventral view; **b:** lateral view; **c:** dorsal view); **17,** Spines of tenth abdominal segments (**a:** ventral view; **b:** lateral view; **c:** dorsal view. Scale line: 15a–b = 1.0 mm; 16a–c = 5.0 mm; 17a–c = 2.0 mm.

Material examined. Japan: Kyushu—1 ♂, pupa from earthen cocoon in soil close to cultivated grape, Ohita-ken, Usa-gun, Ajimu-cho, 30.IV.1985, K. Hirao leg., fixed on 30.V.1985; 1 ♂ with same locality, 22.V.1986, Y. Arita leg.

Bionomics. Univoltine. The egg is laid singly in bark crevices during August. The larva constructs a linear horizontal ringed tunnel around the trunk, between bark and wood in the lower part from ground level to near one meter high on the trunk of host-plant (Fig. 5). The brown frass and reddish violet sap are extruded or oozed from the larval tunnel through bark from middle July through early September. The larva may cause heavy injury to grapevines. The full-grown larva drops out its burrow and forms a tough and irregular earthen cocoon which is closely lined with silk. The rough oblong cocoon measures 28 mm in length and 14 mm in width (Fig. 6). Formation of the cocoon takes place in autumn at a depth of up to about 5 cm in the soil, and the larva overwinters within the earthen cocoon. Pupation occurs near the end of May. Adults fly from the end of June through August.

Host-plant. Cultivated grapevine, *Vitis* species (Vitaceae).

Distribution. Japan (Hokkaido, Honshu, Shikoku, Kyushu).

ACKNOWLEDGMENTS

We wish to express our thanks to Mr. M. Nakashima, Oita Prefectural Agricultural Research Center, Oita, for his valuable information on the habitats and bionomics of this rare species.

LITERATURE CITED

BARTEL, M. 1912. Family: Aegeriidae (Sesiidae). *In* Seitz, A. (ed), Macrolepidoptera of the world. Vol. 2:375–416, pls. 50–52. A. Kernen, Stuttgart.

DALLA TORRE, K. W. VON & E. STRAND. 1925. Aegeriidae. *In* Strand, E. (ed.), Lepidopterorum Catalogus 31:202 pp. W. Junk, Berlin.

EICHLIN, T. D., & W. D. DUCKWORTH. 1988. Sesioidea: Sesiidae. *In* Dominick, R. B. *et al.*, The moths of America north of Mexico, fasc. 5.1. Wedge Entomological Research Foundation, Washington, D.C. 176 pp.

ENGELHARDT, G. P. 1946. The North American clear-winged moths of the family Aegeriidae. Bull. U.S. Nat. Mus. 190:vi + 222 pp., 32 pls.

GAEDE, M. 1933. Family Aegeriidae. *In* Seitz, A. (ed), Macrolepidoptera of the World. Vol. 10:777–802, pls. 94–95. A. Kernen, Stuttgart.

HAMPSON, G. F. 1919. A classification of the Aegeriadae [*sic*] of the Oriental and Ethiopian regions. Novit. Zool. 26:46–119.

HEPPNER, J. B. & W. D. DUCKWORTH. 1981. Classification of the superfamily Sesioidea (Lepidoptera: Ditrysia). Smithson. Contr. Zool. 314:1–144.

INOUE, H. 1954. Check list of the Lepidoptera of Japan, Part 1: Micropterigidae—Phalonidae. Rikusuisha, Tokyo. xiii + 112 pp.

——— 1957. Aegeriidae. *In* Esaki, T. et al., Icons Heterocerorum Japonicorum Coloribus Naturalibus: 152–154, pl. 27. Hoikusha, Osaka. [In Japanese.]

——— 1982. Sesiidae. *In* Inoue, H. et al., Moths of Japan 1:234–238, 2:201–202, pls. 4, 228, 296–297. Kodansha, Tokyo. [In Japanese.]

LE CERF, F. 1916. [Contribution.] *In* Oberthür, C., Explication des planches. Étud. Lép. Comp. 12(1):14 pages of legends, plates 373–381.

LEECH, J. H. [1889]. On the Lepidoptera of Japan and Corea.—Part II. Heterocera, Sect. I. Proc. Zool. Soc. London 1888:580–655.

MACKAY, M. 1968. The larva of *Cissuvora ampelopsis* Eng. and the generic position of *phoradendri* Eng. (Lepidoptera: Aegeriidae). Can. Entomol. 100:1328–1330.

MATSUMURA, S. 1911. Thousand insects of Japan. Supplement 3:1–147 pp., pls. 30–41. Keiseisha, Tokyo. [In Japanese with English description for new species.]

——— 1931a. 6000 Illustrated Insects of Japan-Empire. Toko Shoin, Tokyo. 1497 + 191 pp. [In Japanese.]

——— 1931b. A list and new species of Aegeridae [*sic*] from Japan. Ins. Mats. 6:4–12, pl. 1.

NAKASHIMA, M. 1980. Kubiakasukashiba. *In* Genshoku Atarashii Byôgaichû: 55 & 8029. Zenkoku Byôgaichû Senmon Gijyutsuin Kyôgikai. Tokyo. [In Japanese.]

NAKASHIMA, M. 1984. Ohita-ken ni okeru Kubiakasukashiba no hassei to seitai ni tsuite [On the occurrence and bionomics of *Aegerosphecia romanovi* in Ohita-ken] Pulex 70:319. [In Japanese.]

NAKASHIMA, M., T. YAMASHITA & A. ONO. 1978. Budou no gaichu, Kubiakasukashiba ni tsuite [On the grapevine insect pest, *Aegerosphecia romanovi*]. 67:10–11. [In Japanese.]

NAUMANN, C. M. 1971. Untersuchungen zur Systematik und Phylogenese der holarktischen Sesiiden (Insecta, Lepidoptera). Bonner Zool. Monogr. 1:1–190. [English translation: 1977, Studies on the systematics and phylogeny of Holarctic Sesiidae (Insecta, Lepidoptera). 208 pp. Amerind Publish., New Delhi.]

Received for publication 3 August 1991; revised and accepted 26 September 1991.

GENERAL NOTES

Journal of the Lepidopterists' Society
45(4), 1991, 366–371

NOTES ON THE NATURAL HISTORY OF *QUADRUS* (*PYTHONIDES*) *CONTUBERNALIS* (HESPERIIDAE) IN COSTA RICA

Additional key words: skipper butterflies, larval behavior, pupae, parasitism, Piperaceae.

Skipper butterflies of the genus *Quadrus* (Hesperiidae) exploit various species of *Piper* (Piperaceae) in the Amazon Basin (Moss, A. M. 1949, Acta Zool. Lilloana 7:27–79). *Quadrus contubernalis* Mabille is widely distributed from Mexico to Colombia and Brazil (Draudt, M. 1922, pp. 886–887 [text] *in* Seitz, A. (ed.), Macro-Lepidoptera of the world. Vol. 5. Div. 2. The American Rhopalocera. Stuttgart: A. Kernan Verlag). Adults of this small skipper are chocolate brown with two transverse light-blue stripes on the uppersides of the hindwings. Nothing has been reported previously on the life cycle and other aspects of its natural history. Here I report for the first time the caterpillar food plant, the unusual larval shelter, notes on the abundance of caterpillars and pupae, and other aspects of the natural history of this species at one locality in Costa Rica.

The study site consisted of a border strip of abandoned cacao (1400 m^2) mixed with lowland tropical wet forest (Holdridge, L. R. 1964, Life zone ecology [rev. ed.]. San Jose, Costa Rica: Tropical Science Center) at "Finca Experimental La Lola," near Siquirres (10°06'N, 83°30'W; 50 m elev.), Limon Province, Costa Rica. This forest was composed of densely-shaped Matina cacao (*Theobroma cacao* L.) trees with an overstory chiefly of *Hura crepitans* L. (Euphorbiaceae) and many woody-to-herbaceous understory species (Young, A. M. 1986, J. Trop. Ecol. 2:163–168), including a dense patch of the larval food plant of *Q. contubernalis* (Fig. 1). Observations at this site were made on five dates between 1986 and 1990 (see Table 1).

Following initial discovery of an unidentified hesperiid caterpillar enclosed in a perforated leaf shelter (Fig. 2) during March 1986 at the study site, I subsequently collected, reared, and examined caterpillars of this species. Periodic censuses were taken of caterpillars, pupae (which I also discovered to be inside the folded-leaf structure), and shelters in this stand of food plant that encompassed an area of approximately 40 × 30 m. For time to time, partly-grown caterpillars (n = 8) collected in the wild were confined, with food plant cuttings or transplants, in jars or plastic bags for rearing. I did not count eggs, but only checked plants that had one or more of the distinctive and conspicuous larval shelters. I scored these tent shelters for the presence of a caterpillar, pupa or pupal shell, or as being unoccupied (empty). Voucher specimens of the food plant were taken for identification and deposited in the National Museum of Costa Rica, and adult butterfly specimens reared were deposited in the Milwaukee Public Museum. Parasitic flies obtained from rearings (Diptera: Tachinidae) were saved for identification (U.S. National Museum).

Larval food plant and shelter. The caterpillar food plant at La Lola is *Piper pseudolindenii* C. DC., identified from non-flowering material. In the study plot this semi-woody, shrub-like forest understory plant (Fig. 1) ranged in height from about 0.5 to 1.5 m. Individual plants occurred closely together, forming large patches. They were easy to distinguish from other plants in the area by their leaves and growth profile (Fig. 1). Folded leaf shelters of various sizes and shapes (Fig. 2) were easy to spot, because the caterpillar partially excises a portion of tissue from the edge of the leaf and folds it back over the top of the leaf, securing it with silk. In this manner the pale underside of the leaf becomes exposed against the dark green upper surface, and the unusual holes made by the caterpillar in the shelter top made the shelters easy to locate in the shaded understory (Fig. 2). Smaller shelters, made by folding over a piece of leaf near its edge, were occupied by smaller caterpillars (up to 14 mm long). Larger shelters, involving a whole leaf being folded over and perforated (Fig. 2), were made by larger caterpillars (20–35 mm long).

FIG. 1. Top: Abandoned cacao habitat at La Lola. Below, left: *Piper pseudo-lindenii* at study site (8 stems showing plant life-form or profile); below, right: *P. pseudo-lindenii*, close-up of leaves.

FIG. 2. Folded leaf shelter construction by *Quadrus contubernalis* larvae. Clockwise, from upper left: shelters made by progressively larger caterpillars. Note the unusual perforations in the folded-over portion of the partly-excised (top photos) or entirely-folded over (bottom photos) leaves. Scale in mm.

No preference for young meristem leaves, as opposed to older leaves, was observed for either feeding or constructing shelters. Caterpillar feeding, which occurred at either end of the shelter and distally on portions of the leaf not part of the shelter, is presumably nocturnal, since none was observed during the day.

Holes in the larval shelter were made by a larva chewing all the way through the leaf (although this behavior was not examined for very small larvae). The holes were covered with a thin webbing of silk. Larger shelters had more holes than smaller ones, although

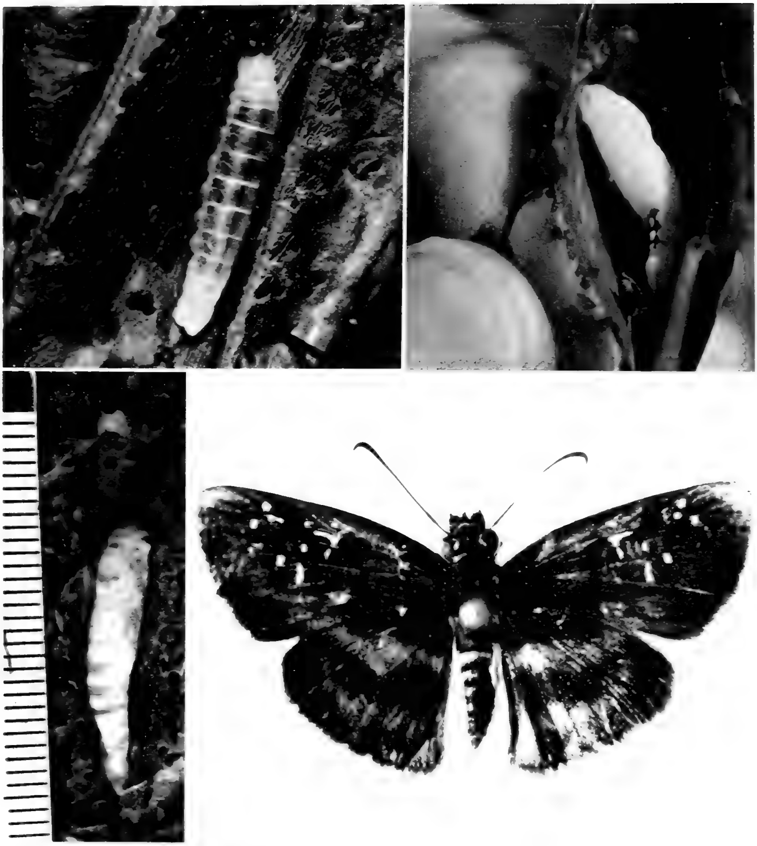


FIG. 3. Life stages of *Q. contubernalis*. Clockwise from upper left: final instar larva; lateral aspect of pupa; adult male (forewing length 14 mm); dorsal aspect of pupa. Scale in mm.

a correlation between shelter size and the number of holes was not investigated. Shelters with pupae did not necessarily have more holes than those with larvae. Mandibles of larvae were not examined to determine if they were modified in any way for cutting holes.

Life stages (Fig. 3). Material examined in the field and laboratory provided descriptions of some early stages and behavior as follows:

Small larva (10 mm long) (n = 6): Head capsule 1.00 mm (range 0.90–1.10), black. Body ground color translucent greenish-yellow; lateral thin white line running lengthwise beginning on first abdominal segment. This line more yellowish on last 3 segments; overall less pronounced in larger larvae. Prolegs blackish. Prothoracic shield not pronounced but edged in yellow or white. Anal plate yellow or white.

Large larva (20–35 mm long) (n = 7): Head capsule 3.00 mm (range 2.90–3.00), now more heart-shaped and reddish brown with small patch of darker brown on lower lateral area. Body ground color greenish-blue, owing to gut contents; lateral markings as before but less pronounced. Prolegs black. Prothoracic shield prominently ridged in white or

TABLE 1. Distribution and abundance of larvae and pupae of *Quadrus contubernalis* Mabille in a stand of its larval food plant, *Pipe pseudo-lindenii* C.DC., in a cacao forest, near Siquirres, Limon Province, Costa Rica.*

Census dates	No. of food plants searched	Total no. of larvae	Total no. of pupae	No. of immatures per plant	No. of pupal exuviae	No. of empty shelters	Total no. of immatures, exuviae, and shelters per plant
30-VI-86	201	8	1	0.045	5	12	0.13
28-II-87	198	4	1	0.025	2	25	0.16
15-II-88	208	5**	3	0.038	11	34	0.25
20-II-89	270	0	1	0.004	2	30	0.12
2-III-90	235	0	0	0.000	2	24	0.11

* Censuses taken within a rectangular plot of understory vegetation approximately 40 × 30 m.
** Two individuals of *Siphosturmia* sp. near *rafaeli* (Townsend) (Tachinidae) were obtained from one of these larvae.

yellow. Anal plate yellow or white. Intersegmental rings pronounced and yellow or white (Fig. 3). A 10 mm long larva required about 3 weeks to reach pupation (n = 4).

Pupa (n = 7): 18.00 mm long (range 17.50–18.25), slender, white (Fig. 3), with cluster of small black dots ventrally near distal end of abdomen; cremaster (2.0–3.0 mm long) black and attached to shelter with yellow silk. Within a few days after formation, pupae developed a yellowish-white waxy bloom; day before eclosion, pupa darkens. Duration of pupa (n = 3): 12–13 days. Both larvae and pupae wriggled vigorously when the shelter was opened. Eclosion occurred quickly, with adult (Fig. 3) ready for flight within 30 min. Adults very wary and difficult to capture in the wild.

Parasites. Three dipteran parasitoids (Tachinidae), all *Siphosturmia* sp. near *rafaeli* (Townsend), were obtained from wild-collected caterpillars. Two of these emerged as full grown maggots from one caterpillar (February 1988). A second caterpillar was successfully transferred from *P. pseudo-lindenii* at La Lola to *Piper nigrum* L. (black pepper) from another locality and produced a tachinid pupa (on 18 Feb. 1988) and an adult fly two weeks later.

Abundance. The number of immatures per plant at the La Lola study site for the five census dates ranged from 0 to 0.045 (Table 1) and showed little variation between drier (February–March) and wetter times of the year. Adult *Q. contubernalis* were either absent or very scarce at the study site; usually only one individual was encountered per visit.

The unusual shelter construction by larvae in the genus *Quadrus* (also documented by Moss *op. cit.*; Kendall, R. O. & W. W. McGuire. 1975, Bull. Allyn Mus. Entomol. No. 27), may function as a line of defense against parasites and other natural enemies. Heavy parasitism of *Quadrus* by tachinids and hymenopterans has been observed in Mexico (R. O. Kendall pers. comm.). Perforated shelters, such as those described here, may enhance air circulation inside the shelter, preventing buildup of pathogenic bacteria and fungi which thrive in the wet, shaded forest understory of the larval food plant. The vigorous body-flicking movements of the caterpillar and pupa also may be a defense against parasites, as noted in other lepidopterans (e.g., Young, A. M. 1985, J. Lepid. Soc. 39:225–227).

All food plants reported *Quadrus* are in the genus *Piper* (also R. O. Kendall pers. comm.). Moss (*op. cit.*) reported the caterpillar food plants of *Quadrus cerealis* Stoll and *Quadrus deyrollei* Mabille as *Piper* sp. Unpublished records of Roy O. Kendall (pers. comm.) from Mexico indicate *Piper* food plants for *Q. cerealis Stoll* and *Q. lugubris Felder*.

This research is a by-product of grants from the American Cocoa Research Institute of the United States of America. I thank Jorge Gomez Laurito (Museo Nacional de Costa Rica and INBIO) for identifying the caterpillar food plant and Dr. N. E. Woodley, Systematic Entomology Laboratory, U.S. National Museum, for identifying the tachinids.

Roy O. Kendall generously shared his unpublished records, provided pertinent literature references, and reviewed the manuscript.

ALLEN M. YOUNG, *Zoology Section, Milwaukee Public Museum, Milwaukee, Wisconsin 53233.*

Received for publication 14 June 1991; revised and accepted 29 August 1991.

Journal of the Lepidopterists' Society
45(4), 1991, 371–373

OBSERVATIONS OF *AMORPHA*-FEEDING *CATOCALA* (NOCTUIDAE) IN WISCONSIN

Additional key words: Catocalinae, *abbreviatella, whitneyi, amestris,* Fabaceae, prairie.

Although recent efforts to preserve and restore Wisconsin prairies have focused attention on prairie *Catocala* whose larvae feed on lead plant (Fabaceae: *Amorpha*), little has been published recently on the early stages of these moths (see Dodge, E. A. 1925. Entomol. News 36:267–268 for larval notes). Here we report our observations in Wisconsin on three of the largely sympatric *Amorpha*-feeding *Catocala*: *C. abbreviatella* Grt., which occurs from Manitoba to Texas and east to central Wisconsin and Illinois; *C. whitneyi* Dodge, which ranges slightly farther southeastward to northern Kentucky; and *C. amestris* Stkr. which ranges further to Florida.

We first encountered *C. whitneyi* on 16 July 1978 when RJB flushed an adult out of the grass while observing *Hesperia ottoe* Edw. (Hesperiidae) on Muralt Bluff Prairie (Green Co., Wisconsin), a 62-acre dry prairie on a curved ridgetop of sandstone thinly capped with limestone. Over 100 species of prairie plants have been identified on this ridge, where managed fires have halted the invasion of encroaching woody plants (Department of Natural Resources, Wisconsin Scientific Areas. 1977. 52 pp.). Xeric conditions have fostered abundant growth of *Amorpha canescens* Pursh.

Subsequently, having obtained the necessary permits from the Wisconsin Department of Natural Resources, we attempted to attract adult *Catocala* at Muralt Bluff with artificial bait, fluorescent blacklights, and a 175-watt mercury vapor lamp. Although the open prairie was not conducive to baiting, short baitlines at the edges of the prairies attracted one *C. whitneyi* and three *C. abbreviatella* adults. Initially, *C. whitneyi* was thought to be uncommon; at least we seldom collected this species during the period between 2130 and 0030 h. Although never as common as *C. abbreviatella* during fifteen nights of observations over a six-year period (1986–91), *C. whitneyi* was, however, later found to be more common at its peak flight time between 0130 and 0300 h (*C. abbreviatella* numbers peaked between 2300 and 0200 h). Our earliest Wisconsin collection dates for *C. abbreviatella* and *C. whitneyi* were 27 June and 2 July, respectively.

We began our search for larvae on Muralt Bluff and neighboring prairies on 18 May 1990 between 1900 and 0100 h as larvae were thought to be crepuscular or nocturnal. Leaf buds of *Amorpha* were barely opening and no larvae were found on 18 May. The sites were revisited on 26 May, 1 June, and 19 June 1990. By 26 May the leaves had begun to unfurl and we found 36 *Catocala* larvae ranging in length from 13–47 mm ($\bar{x} = 30$, SD = 8 mm). Most larvae rested at the uppermost tips of old growth, with no more than one or two individuals per plant. The striped larvae appeared cryptic against the *Amorpha* stems and were capable of jumping when disturbed. On 1 June another search yielded 46 more *Catocala* larvae ranging in length from 15–53 mm ($\bar{x} = 42 \pm 9$ mm).

Larvae found on nearby north-facing slopes were significantly less advanced in their growth. By 19 June no more larvae could be found on mature leaves.

Captured larvae were reared individually on *A. canescens*. None of the field-collected larvae were parasitized. All adults reared from these larvae in 1990 proved to be *C. abbreviatella*. Its larval ground color was generally pale whitish brown, tinted with olive, orange, and yellow in the third, fourth, and fifth instars, respectively. Final instar larvae were marked with longitudinal double lines. Bands were separated by a stripe of the body color having a row of brown dots through the middle. A brown dorsal line was followed by a brown subdorsal band outlined in dark brown with a dotted brown line through the middle. The next band was much lighter. A distinctive dark brown spiracular band, which was outlined in black, had dark blue spiracles on the lower line. Below this was a broad pale yellow band and another subspiracular light brown band. Brown stripes extended onto the white head. The underside was greenish-white with a black spot on each body segment. Larvae were semi-loopers with prolegs retained and bodies tapered at both ends.

Larvae grew about 1.7 mm per day and upon reaching just over 50 mm wrapped themselves in leaves with silk, became quiescent, and assumed a curled prepupal position between 31 May and 18 June ($\bar{x}$ = 7 June). Each larva remained as a prepupa for about five days prior to becoming a deep reddish-brown pupa measuring 20–25 mm long. The pupal stage lasted 15 to 25 days ($\bar{x} = 20 \pm 2$ days; $n = 28$), but those larvae pupating earliest spent five days longer in the pupal stage compared to the latest. Eclosion occurred only at night between 28 June to 11 July ($\bar{x}$ = 1 July ± 2 days; $n = 28$).

In 1991 we resumed our larval search in a season that was over a week advanced from normal due to continued warm temperatures. A daytime search by TSB between 1400 and 1700 h on 24 May 1991 produced only an old pupal shell at the base of *A. canescens*. The first larva was found at 1800 h resting on dead plant growth from a previous year. Between 2045 and 2130 h another ten larvae were found on nearby prairies and between 2230 and 2330 h 25 more larvae were noted on Muralt. Larvae generally were between 30 mm and 40 mm in length; nine of the largest were collected for rearing. Eight of nine larvae pupated between 26 and 31 May; three died in the pupal stage, but the remaining five eclosed as adult *C. abbreviatella* between 15 and 19 June 1991.

Returning to Muralt on 31 May 1991, RJB found no larvae before dark but between 2300 h on 31 May and 0200 h on 1 June 1991, he noted 19 larvae scattered over Muralt prairie resting above dew soaked vegetation on old *A. canescens* growth. Despite profuse new *A. canescens* growth on a recently burned section of the prairie no larvae were found on the burned area. Ten hours were then spent watching 3 individual larvae which were found resting on two *A. canescens* plants between 0200 and 1200 h. At 0425 h one 40 mm larva began feeding. It finished feeding at 0450 h whereupon it moved to the base of the plant where it continued to remain motionless. The other two larvae also had moved to the base of the plant as darkness faded at about 0445 h but each went up to feed for about 20 minutes, one at 0730 h and one at 1000 h, before returning to the base. No more larvae were found on subsequent trips to this prairie on 6 June 1991 when the temperature dropped to 9°C or on 14 June 1991.

Of ten larvae collected on 31 May and reared on *A. canescens*, seven pupated between 5 and 12 June 1991. On a hot 29 June night between 2230 and 2300 h three of the pupae eclosed, producing two *C. whitneyi* and one *C. abbreviatella*. When collected, we thought that all ten larvae were *C. abbreviatella*, but our later examination of larval photographs revealed that the creamy white *C. whitneyi* larvae with longitudinal bands matched the *C. whitneyi* description given by Dodge (*op. cit.*). Our photographs showed that *C. whitneyi* larvae had bands that were more irregular, more grey, and less clearly defined; and that those *C. whitneyi* larvae with reddish spiracles above a white stripe of body color lacked the pale yellow band found beneath the dark blue spiracles in *C. abbreviatella*. Three more *C. whitneyi* eclosed between 3 and 5 July 1991.

Also on 31 May 1991, at another dry prairie about 80 km east of Muralt in the southern Kettle Moraine, TSB found seven *C. amestris* larvae resting on *A. canescens* between 2200 and 2300 h. An additional five larvae were noted there on 1 June 1991 by RJB.

The seven larvae collected on 31 May were reared on *A. canescens*; they pupated between 2 and 5 June and eclosed between 22 and 25 June 1991.

These observations show that *C. abbreviatella, C. whitneyi,* and *C. amestris* all feed on *A. canescens* in Wisconsin. *Catacola whitneyi* and *C. abbreviatella* were found to be sympatric whereas *C. amestris* was found separately (except for one worn *C. amestris* adults taken at Muralt on 2 July 1988). We provided several eggs from adult female *C. abbreviatella* and *C. whitneyi* captured in 1990 to Wayne Miller who successfully reared them to adults. The two *C. whitneyi* he reared took about a week longer to develop than *C. abbreviatella*.

Six adults and two preserved larvae have been deposited at the Peabody Museum of Natural History at Yale University and at the Milwaukee Public Museum. We thank Larry Gall, Allen Young, and Mogens Nielsen for helpful suggestions on the manuscript.

ROBERT J. BORTH & THOMAS S. BARINA, *Wisconsin Gas Company, 626 E. Wisconsin Avenue, Milwaukee, Wisconsin 53202.*

Received for publication 18 December 1990; revised and accepted 30 September 1991.

Journal of the Lepidopterists' Society
45(4), 1991, 373–374

OBSERVATIONS ON *CATOCALA MARMORATA* (NOCTUIDAE)

Additional key words: underwing moths, behavior, Virginia, West Virginia, collecting techniques.

During the past decade I have been studying *Catocala marmorata* (Edwards) in Virginia and West Virginia. This moth is not as rare as sometimes implied (e.g., Sargent, T. D. 1976, Legion of night, Univ. Massachusetts Press, Amherst, 222 pp.; Covell, C. V. 1984, a field guide to the moths of eastern North America, Houghton Mifflin Co., Boston, 496 pp.), but rather has a somewhat localized distribution. Collecting methodology also greatly influences capture success. My field collection records for *C. marmorata* in Virginia and West Virginia span 68 days, from 28 June (1991) to 3 September (1981) and indicate that the moth is most common in mid to late August. Females retained for oviposition have lived as long as 81 days after capture, and as late as 30 October (1989), suggesting an unusually long flight period for this species, probably late June through October.

My introduction to *Catocala marmorata* was in Pendelton Co., West Virginia, between 26 and 30 August 1981, when I collected three specimens at the same location. On 3 September 1981, I collected seven *C. marmorata* in Montgomery Co., Virginia. All ten specimens were resting on tree trunks 0–3 m above ground, with ambient temperatures of 30–33°C. By contrast, *C. marmorata* was not seen during trips to the same two areas through the period 1982–85 (collecting between 14 August and 3 September), when ambient temperatures ranged between 21 and 28°C. (Collecting above 3 m on tree trunks was not attempted between 1981 and 1985.)

Between 21 and 23 August 1986 in Montgomery Co., Virginia, I collected six *C. marmorata* as they rested on tree trunks 3–5 m above ground, with ambient temperatures between 23 and 28°C. On return to the same locality on 17 August 1987, I collected 14 specimens on trunks within 1 m of the ground, when the temperature was about 35°C, but saw no moths on 16 August 1987 at the same locality when the temperature was about 28°C.

A total of 100 adults has been collected in Giles and Montgomery counties, Virginia, and Pendelton County, West Virginia, between 22 July 1988 and 24 August 1991. All of the collecting localities were in deciduous woods between 730 and 1130 m elevation and in the vicinity of a stream or pond. Daytime maximum temperatures during these collecting periods ranged from a low of 21°C on 7 August 1989 to a high of 35°C on 8 July 1991. On warmer days (30–35°C) adults often were collected 0–2 m above ground. On cooler days (21–29°C), adults were seldom encountered, and were usually resting 3–8 m above ground when flushed from trees. Often, moths were not found on tree trunks in the mornings, whereas many were found there in the warmer afternoons of the same day. Such behavior may be an attempt by moths to regulate body temperature by roosting higher in trees when the ambient temperature is cool and moving lower on the trees as the temperature rises. Such movements also may minimize desiccation as temperatures rise during the day.

My best collecting for *C. marmorata* was achieved by tapping large diameter white oak (*Quercus alba* L.: Fagaceae), maple (*Acer* sp.: Aceraceae), and hickory (*Carya* sp.: Juglandaceae) trunks during warm afternoons. Trees with diameters greater than 0.5 m were the most productive. I have also collected *C. marmorata* on white pine (*Pinus strobus* L.: Pinaceae), red oak (*Quercus rubrum* L.), tulip tree (*Lirodendron tulipifera* L.: Magnoliaceae), and other large trees with light-colored bark.

Unlike most underwings, *C. marmorata* rests head-up on the trunks of trees. When the moth alights on a tree, the dark forewing bands are carefully aligned with bark furrows before settling into a resting position. In this manner, adults become extremely cryptic and are almost invisible. The species is sluggish and, unless vigorously disturbed, seldom flies very far. The slow, fluttering flight is distinctive when compared to the flight of species of similar size found in the same area (*C. subnata, C. cerogama, C. ilia, C. vidua,* and *C. cara*).

I dissected 40 females that died in captivity. A female that survived for 81 days (collected 10 August 1989) had about 50% of the ova mature (mature ova are dark; immature ova are yellow). Dissections of other females show that the ova begin to enlarge and darken 4–6 weeks after capture, which suggests that these moths do not oviposit until the females have lived for 6–8 weeks. Thus, oviposition probably occurs mostly during September and October depending on the emergence date of the female. Of the 40 females dissected, only 4 (10%) had mature ova. Only two of these females had oviposited in captivity and their eggs did not hatch. Thus, to obtain viable eggs from *C. marmorata,* it appears that one must either be fortunate enough to collect an aged female or else keep a collected female alive for 6–8 weeks and induce it to oviposit.

Most of my collecting sites were distant (1.5–8 km) from suspected foodplants: willow (*Salix* sp.) and poplar (*Populus* sp.) (Salicaceae). Suspected foodplants (*Salix*) were in the immediate vicinity at only two of my six collecting sites. Thus, presence of large trees with light bark seems to be a better predictor for finding adult *Catocala marmorata* than presence of foodplants. Perhaps females move closer to foodplant sites later in the season when oviposition occurs. This could explain why worn females were seldom collected and why dissection of collected females usually resulted in finding only immature ova.

I thank Richard Gillmore, David Baggett, and Lawrence Gall for encouragement, and for sharing their *Catocala* experiences. My sons, Mark, Christopher, and Andrew Willis supplied some of the collected specimens. Lawrence Gall, Ted Sargeant, and Grant Gaumer gave invaluable help in reviewing and editing this manuscript.

G. DARRYL WILLIS, *145 Westfield Drive, Holliston, Massachusetts 01746.*

Received for publication 19 July 1989; revised 11 September 1989; revised and accepted 28 September 1991.

Journal of the Lepidopterists' Society
45(4), 1991, 375–376

BOOK REVIEWS

BUTTERFLIES AND DAY-FLYING MOTHS OF BRITAIN AND EUROPE, by Michael Chinery (Foreword by Sir David Attenborough). 1989. A New Generation Guide. University of Texas Press, Box 7819, Austin, Texas 78713-7819, USA. 319 pp. + endpaper notes, numerous color figures. Hard cover, 13 × 20 cm, ISBN-0-292-75539-2, $22.95.

With the exception of British birds, perhaps no other subject in natural history has seen as many field guides devoted to it as British butterflies. In recent years alone, fine new handbooks have appeared from Robert Goodden, Jeremy Thomas and others, as well as the definitive monograph in the *Moths and Butterflies of Great Britain and Ireland* series (John Heath, general editor). How, you might ask, can a butterfly fauna about the size of Alaska's justify so many treatments—let alone this new one?

From the cover alone one can tell that the latest entry by Michael Chinery—first published in William Collins Sons' New Generation Guide series—is different from its predecessors. First, the area covered, while stressing Great Britain, includes all of Europe. Second, the cover illustration shows both a swallowtail and a noctuid (likewise, the frontispiece, a downland scene, shows emperor and burnet moths as well as copper, heaths, graylings, and blues). With the inclusion of an array of diurnal moths, the book makes a striking departure from most of its predecessors. A brief foreword by Sir David Attenborough, the doyen of British public naturalists and General Editor of the series, shows the regard with which these insects are held across the Atlantic. It was Sir David's idea, by the way, to include the day-flying moths.

In his preface, Michael Chinery says that the book is "aimed at the naturalist who wants to do more than just put names on things." In this, it succeeds. The front- and back-matter are far more extensive than in most field guides, and are extensively illustrated. The 1500-plus color drawings were provided by four artists: Brian Hargreaves did most of the butterfly species portraits, Denys Ovenden the moths, while Sophie Allington and John Wilkinson carried out the many striking text illustrations.

The book is organized into three main sections. "The Evolution of Butterflies and Moths" covers general characteristics of the order, evolutionary origins and development, anatomy, voltinism, metamorphosis, and classification. "The Directory of Species" constitutes the field guide proper. "From Egg to Adult" traces the biology of the Lepidoptera in each stage, including phenology, predation, and defenses; ecology of habitats and populations; senses in the adult; courtship, flight, resting, and feeding behavior; discussions of migration, hibernation, variation, monitoring, gardening, and conservation. Given the breadth of subjects covered, the treatment, though succinct, is admirably clear, full, and up-to-date. The book thus serves as a beginning text-book on the Lepidoptera as well as a field guide, in the same way that the 1951 Peterson *Field Guide to the Butterflies of North America, East of The Great Plains*, by A. B. Klots, had done. Chinery's use of current research literature (though not crediting individual sources) is impressive, and his style entirely readable.

The heart of the book, of course, is the "Directory of Species." The species accounts treat 360 species of butterflies from 9 recognized families, and 260 diurnal moths representing 20 families. With so many species covered, the accounts are necessarily brief. They typically include English name (other European vernaculars omitted, unfortunately), scientific name (author omitted), chief field marks, habitat, altitude, flight months, number of generations, hostplants, immature descriptions and phenology, overwintering stage, and variation (naming and describing some subspecies). Terse notes on recognition and natural history sometimes follow. The range is indicated first by a symbol denoting occurrence in Britain; second, by a status notation by country (endangered, vulnerable, rare, legally protected); and third, by a small, red-shaded map for each species. Nicely, the species accounts conclude with cross-references to further information on the species' biology in other sections of the book.

The illustrations are uniformly fine. Happily, they include good color representations of the eggs, larvae, and pupae of many species. Butterflies, in all cases, are drawn half dorsal, half ventral, and females and major subspecies are shown if warranted. Of course, not every variant appears. Only two races each, for example, demonstrate the range of variation in *Parnassius apollo* and *P. phoebus*. For the moths, a different pattern is followed, showing the left side with the wings drawn down in a natural pose, the right side with the forewing raised to expose the hindwing. Moth coverage ranges from minute micropterigids to the largest saturniines, and includes many larvae but not eggs or pupae.

Drawings situated elsewhere in the text illustrate a wide and welcome array of lepidopteran biology, from a blue in a skink's maw to a purple emperor visiting a rotting rabbit, and many stations in between. The selection shows great imagination and a keen sense of suitability. I was impressed, and I know I will use the book to demonstrate principles to students.

I found few drawbacks with this book. Outright errors are rare to absent and the editing is good. Infraspecific names are used with variable consistency: the illustrations of the ochre ringlets, or the heaths (*Coenonympha*) include English vernacular names for species, scientific trinomials for subspecies, forms in italics rather than the correct use of roman with quotation marks, and something called "the Italian race" of the *C. rhodopensis*. This may prove confusing to less experienced users. There is a definite bias against collecting, without recognizing that the knowledge on which the book is based came about due to collectors' efforts over many decades. The concern about overcollecting might be more warranted in Europe than North America, although European conservation legislation has concentrated ineffectually on collecting instead of on meaningful habitat protection and management. In any case, the attempt to bring butterflies to the attention of watchers and other naturalists is welcome.

The worst part of the book is the jacket and promotional copy, which advances unmet claims ("a complete guide to the eggs, caterpillars, pupa [*sic*] and adults" it is not) and descends to ungrammatical nonsense on the back cover. This is not the author's fault. The most serious flaw is the omission of a list of published sources drawn upon or any bibliography for further reference by readers. Nor does the author indicate which taxonomical authority, system, or standard source he used for names. That the index includes only names, and no informational headings, is most unfortunate. These lacunae should be corrected in future editions.

Finally, one must ask why William Collins Sons saw fit to replace their standard *A Field Guide to the Butterflies of Britain and Europe* by Lionel Higgins and Norman Riley. A comparison shows that the older guide (1970, revised in 1980 and condensed in 1983 by Higgins alone) was the more authoritative, providing greater detail on variation and subspecies, and better maps. The Chinery book is more telegraphic, omitting significant details such as the enormous disjuncture in the range of *Pseudochazara hippolyte*. The illustrations of butterfly species, though newly drawn, are by the same artist (Brian Hargreaves) and of similar quality. So is the new book merely redundant, or perhaps inferior?

It is not. First, by integrating the drawings and maps with the text, and adding immatures, Chinery's book becomes instantly more useable than Higgins and Riley's field guide. Second, the addition of diurnal moths greatly expands the application of Chinery's book in the field. And wrapping the field guide portion between copious biological information means that one can use this book to become truly acquainted with the subject, not merely to identify specimens.

In this, the *New Generation Guide* series typifies a whole new trend in natural history handbooks. Naturalists today, most of them not collectors, want to see their plants and animals in three dimensions—not simply as dorsals and ventrals on the stalk of a pin. Serious collectors will still want Higgins and Riley in their library; but they would do well to buy Chinery too. For anyone else remotely interested in adding butterflies and moths to their outdoor repertory, on either side of the Atlantic, I highly recommend this innovative, appealing, and satisfying entry in the long and crowded derby of British butterfly books.

ROBERT MICHAEL PYLE, *Swede Park, 369 Loop Road, Gray's River, Washington 98621.*

Journal of the Lepidopterists' Society
45(4), 1991, 377–379

DIE GEOGRAPHISCH-SUBSPEZIFISCHE GLIEDERUNG VON *COLIAS ALFACARIENSIS* RIBBE, 1905 UNTER BERÜCKSICHTIGUNG DER MIGRATIONSVERHÄLTNISSE (LEPIDOPTERA, PIERIDAE), by Eduard Reissinger. 1989. Neue Entomologische Nachrichten aus dem Entomologischen Museum "Dr. Ulf Eitschberger," #26. Distributed by Dr. Ulf Eitschberger, Humboldtstrasse 13a, D-8688, Marktleuthen, Germany. 351 pp., 82 pls. Soft cover, 17 × 24 cm, ISSN 0722-3773, DM 145 (about $81 US).

The title of this monograph translates as "The Geographic-Subspecific Arrangement of *Colias alfacariensis* Ribbe, 1905 in the Light of its Pattern of Migration." *Colias alfacariensis* is the correct name for the species listed in most older Palearctic literature as *C. australis* Verity 1911. It has always been confused with the partly sympatric *C. hyale* Linnaeus 1758; L. Higgins and N. D. Riley (1970, *A Field Guide to the Butterflies of Britain and Europe*, Houghton Mifflin, Boston, p. 63) say of this pair: "Both species are variable and there is no reliable single external character for identification. . . . females may be very difficult." The complex also includes *C. erate* Esper 1804, extending from eastern Europe to the Far East. It has been known for decades that *C. alfacariensis* is dispersive or perhaps migratory, and an occasional visitor (and breeder) in southern Britain, for example. In its taxonomic career it had accumulated a fairly typical (for Europe, whose fauna is chronically overworked, mostly by amateurs) backlog of subspecies, varietal, and form names. That was before Reissinger got ahold of it.

Reissinger has been working on this project since the mid-1950's. He examined some 17,000 specimens for this revision (and provides full data for all of them). There are so many plates (14 color, 68 black-and-white) that one gets the feeling he wanted to illustrate every one of the 17,000. Map 44 in Higgins and Riley's book suggests that *C. alfacariensis* is very nearly continuously distributed over southern Europe, but Reissinger's Fig. 1 (p. 17) says otherwise. He uses phenotypes and sex-ratio data to infer that there are about thirteen permanent populations, from which temporary expansions and colonizations take place (creating an illusion of continuous distribution). (Sex-ratio is important, according to Reissinger, because it is primarily the females that emigrate. His sex-ratio method was first published in 1962, and this hard-to-find paper is reproduced in part on pp. 180–183 of the present work.) Given the close proximity of some of these populations and the dispersiveness of the animals, it is difficult to imagine how the genetic distinctness of the permanent populations could be maintained against gene flow. ("Wenn zudem ♂♂ mitwandern, so ist das ein weiterer Faktor zur subspecifischen Stabilisierung," p. 16.) But of course, there is no documentation of their genetic distinctness anyway—only a claim of *phenotypic* distinctness. And all of Reissinger's claims are deeply suspect.

The sex-ratio data confound multiple sources of variation and are thus ambiguous and unreliable (despite Reissinger's attempt to define various kinds of sex ratios and thereby define away the problem). Sex ratios may indeed be indicative of dispersal phenomena (I have published on this myself: Shapiro, A. M. 1970, Amer. Nat. 104:367–372), but the determinants thereof are complex and subtle. And the phenotypic differentiation he claims is supported only by vague, qualitative statements. The "subspecies" are much less well-defined than the phenotypes of the species *alfacariensis* and *hyale*, which are, as noted before, extremely similar. That is only to be expected, but it translates into the generalization that the way to identify *alfacariensis* to subspecies is by its locality label, not its wing markings! (Mammalogists traditionally had a "75% rule" for subspecies—75% of the specimens had to be correctly assignable by eyeball, or the subspecies wasn't accepted. It was totally arbitrary, but one wishes Reissinger subscribed to it.) Reissinger seems to think he can convince readers of the validity of the subspecies by printing huge numbers of photographs of specimens. Not so! While this is a way of dealing with variation and is thus an improvement over primitive typology, it is no substitute for quantitation. In the age of multivariate morphometrics, it is astonishing to see a 17,000-specimen study with *no statistical analysis whatsoever*. Indeed, the only quantitative phenotypic data reported here are wing-lengths for the successive seasonal generations of three taxa. These are presented in tabular form with sample sizes, means, and ranges *only*. Reissinger was trained as a medical doctor, not a biometrician—but I know practicing physicians who have heard of standard deviations.

All of this might still be marginally palatable had Reissinger not succumbed to *Haarspalterseuche*—Splitter's Disease. Having decided there are discrete populations, he could not possibly let them go unnamed. Thus this paper erects 12 new "subspecies" of *alfacariensis*, plus one of *hyale* for good measure. (One of the *alfacariensis*, named *kantaraica*, is from Algeria, where it is not even certain that the species is a permanent resident. Its distinctness, to judge by the plates, is underwhelming.) This sort of work draws inspiration from Bryk and Eisner's infamous studies of *Parnassius*, advanced through a special series called *Parnassiana Nova*. (The naive American reader might look up a copy of Capdeville, P., 1978, *Les Races Géographiques de Parnassius apollo*, Editions Sciences Nat, Compiègne, France, 190 pp., to see where this lunacy leads.) Such work greatly amplifies the nomenclature but somehow fails to generate biological insight. (It may be compared with the rigorous population biology done on *Parnassius mnemosyne* L. by Descimon, H., and Napolitano, M., 1990, Alexanor 16:413–426, which makes serious conceptual and empirical scientific contributions.) Yet even the multiplication of names might be bearable were it not for the impetus they give to anal-retentive amateurs to persecute endangered local populations in the name of synoptic completeness. Such behavior in turn led to the enactment of very restrictive legislation in much of western Europe, where butterfly collecting is now on a legal par with dope trafficking. Reissinger did his collecting before all this happened. In an Afterword, he laments the restrictions—complaining that to restrict collecting while failing to protect habitats is "throwing the baby out with the bath-water." True enough. This Afterword has the air of an *Apologia pro vita sua*, and is rather sad reading.

Nor, alas, does the multiplication of names end with "subspecies." Bryk and Eisner and Roger Verity on the Continent developed complex systems of polynomials to characterize all kinds of variation (and Jeane Gunder did somewhat the same thing in the United States.) Reissinger preserves this tradition where seasonal "forms" are concerned. Thus the three annual generations of the new Bavarian subspecies *alfacariensis orthocalida* are to be called *anteorthocalida*, typical *orthocalida*, and *postorthocalida*. In warmer Hungary the new subspecies *alfacariensis magyarica* has four generations: *antemagyarica*, *magyarica*, *postmagyarica* and *ultimamagyrica*! One hesitates to think what he would do with *Colias eurytheme* Bdv. in the Imperial Valley of California, which may have ten generations a year. Reissinger knows these names have no standing under the Code, and tells the reader that no one is obligated to use them. Dare any collector *not* get the complete "set" if he possibly can? Would a philatelist settle in the long term for a "short set" of stamps?

The study of geographic variation is an important component of population and evolutionary biology. Historically, it contributed to an understanding of the role of geographic isolation in the speciation process. But historically, phenotype was all we had to go on. Today we have various techniques for getting into the genome and quantifying genetic differentiation—and we have learned that phenotypic differentiation is not an especially reliable indicator of genetic relationships. The phenetic subspecies of the taxonomist may or may not reflect important genomic differences; they certainly cannot be assumed to be incipient species. Reproductive barriers, on the other hand, can exist in the complete absence of phenotypic differentiation. The lack of a biological subspecies concept, already evident to the perceptive and the subject of intense polemics by the 1950's, has only become all the more apparent with the passage of time.

The study of migration and dispersal is important ecologically and evolutionarily. There have been major advances in technique for such studies, mainly in the United States. Recent years have, moreover, seen a veritable explosion of interest in and techniques for the study of gene flow among populations, and the concept of the "metapopulation" has begun to clarify a lot of fuzzy thinking about populations as discrete entities, although it itself is bogged down in definitional problems (Gilpin, M. & I. Hanski, 1991, *Metapopulation Dynamics: Empirical and Theoretical Investigations*, Academic Press, New York, 336 pp.). The conflict between phenotypic and genomic evidence has been explored creatively in butterflies (e.g., Porter, A. H. & H. J. Geiger, 1988, Can. J. Zool. 66:2751–2765), using a gene-flow approach. All of this is relevant to *Colias alfacariensis*, but not to a worker with Reissinger's mind-set.

What is the point of a study like Reissinger's today? To ask this question is to miss the point. Publication of this study in a sense marks the end of an era, the era when a dedicated amateur like Reissinger could expect to rival the "pros" in sophisticated studies of variation, evolution or systematics. Work like this was already largely out of date several decades ago; now it is virtually a curiosity—both theory and technique have long ago passed it by. This is sad. It does not mean the amateur can no longer make valuable contributions to science, but it does force a redefinition of what those might be. Superb morphological and life-history work is still being done by amateurs, for example. The early stages of much of the world's lepidopteran fauna remain undescribed at a technical level. This kind of work requires a degree of sophistication, but no expensive equipment or statistical arcana. Perhaps the future of amateur contributions lies in the collaboration of amateurs and "pros" in addressing questions of mutual interest.

Eduard Reissinger died on 16 July 1991 at the age of 71. His close collaborator Ulf Eitschberger has written a moving obituary (Atalanta 22:ii–ix, 1991) which is equally the obituary of an era. I wish that Reissinger had published his *magnum opus* much earlier, but it will stand as a monument to one man's dedication to one bug. *Ave atque vae.*

ARTHUR M. SHAPIRO, *Department of Zoology and Center for Population Biology, University of California, Davis, California 95616.*

Journal of the Lepidopterists' Society
45(4), 1991, 379–380

BUTTERFLIES OF SOUTHEASTERN ARIZONA, by Richard A. Bailowitz and James P. Brock; photographs by Charles A. Hedgcock (Foreword by Gale Monson). 1991. Sonoran Arthropod Studies, Inc., P.O. Box 5624, Tucson, Arizona 85703. ix + 342 pp., with 4 color plates, 3 figures (including two regional maps), and 624 black-and-white photographs covering all species. Soft cover, 15.2 × 22.9 cm, ISBN 0-9626629-0-9. $29.95 (+$3.00 shipping).

REVIEW BY CLIFFORD D. FERRIS

Arizona boasts a broad diversity of life zones and habitats spread over its 15 counties. Much of its area is relatively arid, but lush meadows occur in coniferous forest in the White Mountains and Mogollon Rim country of the central and northeastern portions of the state. The southeastern portion of the state, the region covered by this book, is generally Sonoran desert interspersed with a variety of mountain ranges generally aligned with north-south orientation. Coniferous forest is found at the higher elevations in many of these ranges, whereas riparian canyons with unique flora and fauna exist at their bases. In some localities, one may pass through five ecological life zones when climbing from the desert floor to a mountain summit. Consequently, more than 240 butterfly species have been recorded from the six counties represented in this book. Many of these species are endemic, while others are Mexican migrants that occur with some regularity, and some species are single-specimen records.

Sonoran Arthropod Studies, Inc. (SASI) was founded in 1986 as a non-profit organization devoted exclusively to educating the public about arthropods and their interrelations with other animals, plants, and humans. Located in Tucson, Arizona, SASI operates the Arthropod Discovery Center in Tucson Mountain Park. A newsletter and quarterly magazine are published for SASI members, but *Butterflies of Southeastern Arizona* is the organization's first publication for a wide audience.

This book is divided into three parts following the prefatory matter. The Forward, by Gale Monson, is followed by an authors' Preface. Part 1 provides information on observing butterflies in southeastern Arizona, the topography of the region, and the systematics/nomenclature used in the book. The nomenclature used generally follows that recommended in *Memoirs 2* and *3* of the Lepidopterists' Society (one deviation is the use of *Limenitis* in place of *Basilarchia*). A list of abbreviations used in the book concludes Part 1. Part 2 contains the species accounts, in the order of the 1981 Miller and Brown check list (*Memoir No. 2*), starting with the Hesperiidae and ending with the Nymphalidae, which is broadly interpreted to include the satyrids, danaids, and heliconiids. Each species is represented by life-size black-and-white photographs; in most cases, both the dorsal and ventral surfaces are shown. In some instances, both sexes are illustrated when sexual dimorphism occurs. Generally speaking, the black-and-white photographs are good. The exception is in the Pieridae section, in which the species with indistinct wing borders (many of the Coliadinae in particular) are poorly reproduced. The wing borders tend to blend into the background. In my copy of the book, certain photographs (in the skippers especially) appear to be slightly out of focus, but it is not clear if this is a problem with the original photographs or an artifact of printing. On the plus side, it is nice to have a book that clearly illustrates some of the problem *Amblyscirtes* (such as *elissa, prenda, eos,* and *nereus*) and the enigmatic *Cogia mysie* (also figured in color). Generally, specimens in good condition are illustrated, with damaged examples portraying only casual species and rare strays. The species descriptions are limited to general comments but include information on larval foodplants, flight period, and distribution. Part 3 consists of a series of appendices, which include the four color plates (illustrating 90 specimens), explanation of the black-and-white photographs (listed in order by Miller and Brown check list number), the collecting policy of the Lepidopterists' Society, resource organizations, references, an index to larval foodplants, and an index to butterflies. The four color plates are quite good and depict 90 species at less than life size.

This book is an invaluable field guide for any collector who has visited or plans to visit southeastern Arizona and contiguous regions. Although the geographic area covered by the book is restricted, many of the species discussed and illustrated are found in neighboring northern Mexico, southern New Mexico, and west Texas. Consequently, this book can be used effectively as a field guide over a much wider geographic area than the title implies.

Butterflies of Southeastern Arizona is attractively produced on acid free coated white paper with sewn signatures. The cover (with a superb color photograph of *Thessalia theona thekla* in the field) is plastic coated heavy paper, and should prove reasonably durable. This book should be on the shelf of any lepidopterist who has a serious interest in the butterflies of the southwestern United States. I recommend it highly.

CLIFFORD D. FERRIS, *Bioengineering Program, University of Wyoming, P.O. Box 3295 University Station, Laramie, Wyoming 82071-3295.*

Journal of the Lepidopterists' Society
45(4), 1991, 380–381

BUTTERFLIES OF SOUTHEASTERN ARIZONA, by Richard A. Bailowitz and James P. Brock; photographs by Charles A. Hedgcock (Foreword by Gale Monson). 1991. Sonoran Arthropod Studies, Inc., P.O. Box 5624, Tucson, Arizona 85703. ix + 342 pp., with 4 color plates, 3 figures (including two regional maps), and 624 black-and-white photographs covering all species. Soft cover, 15.2 × 22.9 cm, ISBN 0-9626629-0-9. $29.95 (+$3.00 shipping).

ADDITIONAL COMMENTS BY RAY E. STANFORD

I feel qualified to comment on this important publication because I have known and corresponded with the authors for many years, have been in the field with them on several occasions, and knew a few of their predecessors including F. X. Williams, J. A. Comstock, L. M. Martin, D. L. Bauer, K. C. Hughes, and others acknowledged in this work. I have made observations myself in all 15 counties, even before there were 15 counties!

The book's Preface gives some historical perspective and lays the groundwork for the remainder. The Introduction is outstanding, giving documented background for the region, comments on the mountain ranges, nomenclatural issues, and statistics for each county and mountain range. The nomenclature used is conservative, which most readers will appreciate. The species accounts are very well written, concise but precise when needed. The photographs are good, many showing species seldom before illustrated well (especially skippers). Biological and distribution information is presented very well in a somewhat telegraphic format.

I have only a few constructive comments. The illustration of *Apodemia mormo mormo* on page 204 is not that subspecies, but probably *cythera* or *mejicana*. The discussion of *Poladryas minuta* on page 220 is terribly wrong! The typical insect may be extinct at the type locality in Kendall Co., Texas, but is very much alive and well northward in Texas and in eastern New Mexico; S. Cary, P. Opler, R. Holland, and I have taken good *minuta* in the following counties in the last decade: Colfax, Union, Mora, Harding, San Miguel, Guadalupe, Quay, Curry counties, New Mexico; Randall, Briscoe, Floyd, Lubbock, Crosby, Dickens, Baylor, Garza, Kent, Borden, Howard, Culberson, Jeff Davis, Presidio, and Brewster counties, Texas. It is NOT extinct!

My final point concerns *Phyciodes campestris* (*camillus*), which was excluded despite vigorous correspondence between me and the authors over the last 20 years. The book treats several "dubious" species in some detail, but omits this one with 4 believable records over the last 120 years. The first was by Professor Francis Henry Snow, M.D., Ph.D., Sc.D., Professor and Chancellor of the University of Kansas, who collected in the 1880's and published in 1907 (Trans. Kans. Acad. Sci. 22:141–164). His material is surely extant at the KU collection in Lawrence, Kansas, and the authors should have examined it. There is a second specimen, in the National Museum of Natural History in Washington, D.C., determined by Paul Opler in 1989. Keith C. Hughes collected one near Portal, 8 October 1963, which could be a misdetermination, and the specimen was discarded. I caught one myself at Turkey Creek Road, just W of Onion Saddle, Chiricahua Mountains, 30 August 1967, but KCH apparently threw it away. No proof, it would seem, and academic degrees probably do not count heavily in butterfly records, but the above four records include two M.D.'s, three Ph.D.'s, one Sc.D., and one J.D. Play the Academic Festival Overture, please, and go on to the next paragraph.

The book ends with four beautiful color plates, references, and index. It belongs on the shelf of every western lepidopterist, especially those with interest in Arizona, New Mexico, and Mexico. I look forward to an expanded book covering the entire state of Arizona.

RAY EDMUND STANFORD, M.D., *University of Colorado, Denver and Denver Museum of Natural History; 720 Fairfax Street, Denver, Colorado 80220.*

Journal of the Lepidopterists' Society
45(4), 1991, 381–383

THE MOTHS OF AMERICA NORTH OF MEXICO, FASCICLE 15.3, PYRALOIDEA, PYRALIDAE (PART), PHYCITINAE (PART), by H. H. Neunzig. 1990. The Wedge Entomological Research Foundation, Washington, D.C. 165 pp., 70 text figures, 5 color plates, 2 black and white plates. Soft cover, 8.5 × 11 in. (21.6 × 27.9 cm), ISBN-0-933003-06-6, $55.

About a half dozen years ago I purchased a secondhand copy of C. Heinrich's 1956 *American Moths of the Subfamily Phycitinae* (Bull. U.S. Nat. Mus. 207, 581 pp.), in which 640 species of phycitines in 194 genera are categorized into four groups on the basis of wing venation. It was probably not a "used" copy, because as an introduction to the Phycitinae the book is confoundedly difficult to use. After several futile attempts to navigate the keys, with their antiquated system of numbering vein branches, I soon learned to bypass them and follow Heinrich's advice in the introduction (p. vi): "Anyone wishing to identify phycitids must resign himself to the tedium of dissection and slide making." By comparing my slide with the detailed genitalic illustrations in the back of the text, then reading Heinrich's meticulous descriptions and diagnoses, I could put a name on most phycitines with confidence.

At first glance, H. H. Neunzig's second contribution to *The Moths of America North of Mexico,* Fascicle 15.3, seems to be a weird conglomeration of what previously were considered to be some of the most primitive and the most derived phycitine species. However, in the Preface, Neunzig explains that the arrangement, suggested by a table (p. vii) in Heinrich's 1956 monograph, is our first glimpse of an alternative to Heinrich's venation-based categorization. The revised treatment combines all but four of the first 16 and last 23 genera in the 1983 check list of the Phycitinae by E. G. Munroe in R. W. Hodges et al. (*Check List of the Lepidoptera of America North of Mexico,* E. W. Classey Ltd. and Wedge Entomological Foundation, London, 284 pp.) into what Neunzig purports to be a natural group. The entire group is covered in Neunzig's Fascicles 15.2 and 15.3. (There was no hint of revision in the first of these two parts.) All species in this first new group have simple genitalia and, apparently, common larval characteristics unique to the group. Presumably, Fascicle 15.1 will contain generic keys to all the phycitines and a fuller explanation of Neunzig's revised categorization.

A classification based upon genitalia, the touchstone of phycitine identification, is definitely a convenience and seemingly would be an improvement over Heinrich's categorization based upon wing venation. However, in the Preface to Fascicle 15.2, Neunzig noted that there is insufficient information upon which to establish tribes of phycitines. In the absence of that information, it seems imprudent to toss out over 30 years of stability in favor of an alternative classification that may be no more capable of withstanding the challenge of a broad-based cladistic analysis than Heinrich's categories.

It is even more dismaying to find that the utility of genitalic dissections for identifications is seriously undermined by Neunzig's concept of species. Geographic differences in wing pattern or coloration among populations that cannot be separated on the basis of genitalia are regarded as indicative of species, often without any substantive biological information. Can there really be so many new species of *Ephestiodes* and *Euzophera,* for example, when a long series of our local populations taken over the duration of the flight season reveals a tremendous range of variation? Should *Vitula serratilineella* of the west be considered a species rather than a subspecies of *V. edmandsii* of the east, from which it differs only by hindwing coloration? Again, I would have preferred opting in favor of stability until compelling reasons for change are discovered.

On the positive side, Neunzig's decisions give us two fewer genera than were previously recognized. With their great variety of secondary sexual characteristics, the Phycitinae at slightly over three species per genus approach the apparent ideal of generic and specific parity held by some butterfly taxonomists. It is hoped that continued synonymization will enable generic identification by genitalia alone, including those of females, rather than by a combination of genitalic and some secondary sexual characteristics of the male. I still do not understand why differences in male antennal structure are considered to be indicative of genera whereas equally profound differences in maxillary palpi are not.

Included in Fascicle 15.3 is *Pseudocabima arizonensis,* which was omitted from the 1983 check list, whereas another species, *Ectomyelois decolor,* is excluded without explanation. Also missing from the sequences of species at the beginning and end of the check list are *Myelois grossipunctella* and *Barberia affinitella.* Presumedly the latter and the four species in *Anerastia* and *Coenochroa,* which follow in the check list, have been relegated to the Peoriinae. The misspelling of *Eurythmia fumella* in the check list is corrected to *E. furnella,* and the gender of several species names in *Ephestiodes* is emended from feminine to masculine. Added to the U.S. fauna are three tropical species, recently recorded from Florida, and a few new genera and several new species, most of which cannot be discounted as possible regional forms.

Other additions and improvements over Heinrich's work are some larval keys, which despite incompleteness are a desirable inclusion as many of the species are pests of stored products and nobody knows these larvae better than Neunzig. There are excellent SEM photographs of a few of the important antennal characters, and some may find the photographs of the adults helpful in identifying species. There are some new biological data, but because many of the larvae are general scavengers, the specific identifications of some host plants are not meaningful.

In general, the species descriptions and the genitalic illustrations are no improvement and often inferior to those in Heinrich's revision. Particularly annoying are the squiggly lines in the aedeagus, presumably the vesica, which obscure the sometimes diagnostic cornuti. The overall quality would have been better had Neunzig abandoned the *MONA* structure and used the format of his 1988 revision of the genus *Salebriaria* (N.C. Agric. Res. Serv. Tech. Bull. 287) with its well-presented descriptions and diagnoses of adults, larvae, and larval biologies; its excellent line drawings of genitalia, larvae, and pupae; and its black and white photographs of the adults—all for a mere $6.00 a copy.

Fascicle 15.3 is neither the worst nor the best of the *MONA* series, which, with its apparent lack of editorial guidelines over the last 20 years, seems to cater to the whims of the contributors, cannot seem to decide what constitutes a fascicle or a part of a fascicle, and continues to be plagued by inconsistency. About the only constants are the flimsy beige soft cover, the verbosity and superfluous white space in the text, and the "anything-worth-doing-is-worth-overdoing" series of little color photographs of mostly grey and white moths. Black and white close-ups would be more helpful in identifying species and might reverse the rapidly escalating *MONA* prices, now approaching the dollar-a-species-level. (Have mercy! There are more than 10,000 species of North American Lepidoptera!)

This is definitely a volume for the specialist and the "completist," but at $55 for 81 species the cost-conscious lepidopterist would be better served to seek out a copy of Heinrich's 1956 revision with its broader coverage and superior descriptions and genitalic illustrations bound in a hard cover. The editorial board of *MONA* might look to that same volume with its concisely written descriptions, diagnoses, distributions, and larval hosts as a model for drawing up guidelines for future contributors.

JOHN DE BENEDICTIS, *Department of Entomology, University of California, Davis, California 95616.*

Journal of the Lepidopterists' Society
45(4), 1991, 383–384

FOODPLANTS OF WORLD SATURNIIDAE, by Stephen E. Stone. Forward by Claude Lemaire. 1991. The Lepidopterists' Society, Memoir Number 4. xv + 186 pp. 1 color plate. Soft cover, 16 × 23 cm, ISBN 0-930282-05-1, $7.20 (members of the Society), $12.00 (non-members), plus $2 (postage and handling).

Foodplants of World Saturniidae is an important source book that far exceeds the quality and usefulness of older publications. Attractively produced, its cover is illustrated with a painting by John Cody of a mature larva of the Hickory Horned Devil (*Citheronia regalis*). The forward by Claude Lamaire points out that knowledge of larval morphology, behavior, and foodplant preferences is often gained only by rearing the immature stages. He correctly implies that moth rearers often do not keep detailed records of successes and failures, so that their observations are not as useful to others as they could be. The single color plate illustrates five seldom seen larvae, but more importantly, illustrates the range of larval diversity found in this large family.

The two-part organization of the book is easy to use, and helpful for searching out prospective larval foodplants for the 503 species (139 genera) of Saturniidae covered. Part I is alphabetized by moth genera and species. Under each species, the foodplant records are provided with a reference identifying the source of that information. The reference is important as it will often lead the user to additional biological information that may be critical for successful rearing. This section also includes foodplant records for hybrids. Part II is an alphabetical listing of foodplant genera and species, which also identifies the plant family as well as which Saturniidae have been reported from each. Helpful additions are the two indexes, one for moths and one for plants, and an appendix of vernacular and Latin plant names.

It is difficult to evaluate the completeness of the literature search when one considers that saturniids occur in almost all countries and continents not covered by ice. The greater than two hundred references appear to span the globe, with no obviously significant omissions. In general, there appear to be far fewer errors than might be expected in a work of this kind.

This publication was not intended to discuss Saturniidae biology or rearing techniques, nor does it identify which hosts are most commonly accepted. Instead, the book does well what it set out to do, that is, to help you identify alternative foodplants for the larvae you want to rear, with information arranged in an easy-to-use format. *Foodplants of World Saturniidae* is ideal for anyone interested in rearing Saturniidae.

PAUL M. TUSKES, *3808 Sioux Avenue, San Diego, California 92117.*

Journal of the Lepidopterists' Society
45(4), 1991, 385–390

INDEX TO VOLUME 45

(New names in **Boldface**)

NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of Lepidoptera study. Categories are Articles, Profiles, 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 111 in Volume 44(2). *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 submit manuscripts in *triplicate*, typewritten, *entirely double-spaced*, with wide margins, on one side only of white, letter-sized paper. Prepare manuscripts according to the following instructions, and submit them flat, not folded.

Abstract: An informative abstract should precede the text of Articles and Profiles.

Key Words: Up to five key words or terms not in the title should accompany Articles, Profiles, General Notes, and Technical Comments.

Text: Contributors should write with precision, clarity, and economy, and should use the active voice and first person whenever appropriate. Titles should be explicit, descriptive, and as short as possible. The first mention of a plant or animal in the text should include the *full scientific name* with *author*, and *family*. Measurements should be given in metric units; times in terms of the 24-hour clock (0930 h, not 9:30 AM). Underline only where *italics* are intended.

Literature Cited: References in the text of Articles and Profiles should be given as Sheppard (1959) or (Sheppard 1959, 1961a, 1961b) and listed alphabetically under the heading LITERATURE CITED, in the following format without underlining:

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

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

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

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.

Tables: Tables should be numbered consecutively in Arabic numerals. Headings for tables should not be capitalized. Tabular material must be typed *on separate sheets*, and placed following the main text, with the approximate desired position indicated in the text. Vertical lines as well as vertical writing should be avoided.

Voucher specimens: When appropriate, manuscripts must name a public repository where specimens documenting identity of organisms can be found. Kinds of reports that require vouchering include life histories, host associations, immature morphology, and experimental enquiries.

Proofs: The edited manuscript and galley proofs will be mailed to the author for correction of printer's errors. Excessive author's changes at this time will be charged to authors at the rate of $2 per line. A purchase order for reprints will accompany proofs.

Page charges: For authors affiliated with institutions, page charges are $20 per *Journal* page. For unaffiliated authors, page charges are $10 per *Journal* page with a $50 maximum. Authors of Book Reviews and Obituaries are exempt from page charges. Authors unable to pay page charges for reasons such as difficulties with foreign exchange should apply to the editor for free publication.

Correspondence: Address all matters relating to the *Journal* to the editor.

PRINTED BY THE ALLEN PRESS, INC., LAWRENCE, KANSAS 66044 U.S.A.

CONTENTS

General Notes

Book Reviews

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.