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Cover illustration: Butterfly stamps from the Commonwealth of Dominica: Great Southern White, *Ascia monuste* (Pieridae); Polydamas Swallowtail, *Battus polydamas* (Papilionidae); Red Rim, *Biblis hyperia* (Nymphalidae); The Flambeau, *Dryas julia* (Nymphalidae); Cassius Blue, *Leptotes cassius* (Lycaenidae); Monarch, *Danaus plexippus* (Nymphalidae); Godman's Leaf, *Anaea dominicana* (Nymphalidae); Caribbean Buckeye, *Junonia genoveva* (Nymphalidae).

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HESPERIIDAE OF RONDÔNIA, BRAZIL: "*ANTIGONUS*" GENUS GROUP (PYRGINAE), WITH TAXONOMIC COMMENTS AND DESCRIPTIONS OF NEW SPECIES FROM BRAZIL AND GUATEMALA

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ABSTRACT. Some species of the pyrgine (Hesperiidae) "*Antigonus*" group (*sensu* Evans 1953) occurring in central Rondônia, Brazil, are discussed. These are six species of *Mylon* Godman & Salvin, 1894, including two new species ***Mylon simplex*** and ***Mylon argonautarum;*** four species of *Carrhenes* Godman & Salvin, 1895, including the new species ***Carrhenes recurva;*** four species of *Clito* Evans, 1953, including the new combination *Clito clada*, new status; one species of *Xenophanes* Godman & Salvin, 1895; three species of *Antigonus* Hübner [1819]; and one species each of *Timochreon* Godman & Salvin, 1896, and *Anisochoria* Mabille [1877]. Taxonomic comments and illustrations (including male and female genitalia) are provided for these and for some related taxa from elsewhere. The identities of *Leucochitonea jason* Ehrmann, 1907, and *Mylon ozema* var. *exstincta* Mabille & Boullet, 1917, are clarified. A lectotype is designated for *L. jason*. The holotype of *M. o.* var. *exstincta* is identified and *M. exstincta*, new status, is raised from its current synonymy with *M. jason*. ***Mylon cristata***, new species, is described from Guatemala. *Carrhenes chaeremon* (Mabille, 1891), revised status; *Carrhenes leada* (Butler, 1870), revised status; and *Carrhenes lilloi* Hayward, 1947, revised status, are raised to specific level taxa from their current subspecific or synonymic placements.

Additional key words: genitalia, Neotropics, phenology, variation.

Evans (1952, 1953) divided the Pyrginae (Hesperiidae) into several groups of genera. Although these groups may not be monophyletic and may contain misplaced species (e.g., de Jong 1975, Burns 1990), they are convenient for discussions of species richness and taxonomy of local faunas. Near the municipality of Cacaulândia in central Rondônia, Brazil, an area of ongoing studies of the butterfly fauna (Emmel & Austin 1990), seven of the eleven genera of the "*Antigonus*" group have been found: *Mylon* Godman & Salvin, 1894; *Carrhenes* Godman & Salvin, 1895; *Clito* Evans, 1953; *Xenophanes* Godman & Salvin, 1895; *Antigonus* Hübner, [1819]; *Timochreon* Godman & Salvin, 1896; and *Anisochoria* Mabille [1877]. In this paper, sixteen species previously described in these genera are discussed, four new species are described, a new combination is established, and a species considered by Evans (1953) to be a synonym is identified.

STUDY AREA AND METHODS

A detailed description of the study area near Cacaulândia is presented by Emmel and Austin (1990) and Emmel et al. (2000). In the Cacaulândia area, there is a pronounced seasonality of precipitation. A dry season extends from May through September with practically no rainfall in June, July, and August. The wettest months are usually January and February.

Forewing length was measured from the base to the apex. "GTA" numbers associated with specimens refer to genital vial numbers. Structures of the genitalia are those used by Austin and Mielke (1998).

MYLON GODMAN & SALVIN, 1894

Evans (1953) included eleven species and four subspecies in this Neotropical genus which ranges from Mexico to Argentina. Six species, including one considered as a synonym by Evans (1953) and two undescribed, were recorded in central Rondônia. These are present in small numbers throughout the year, but are most prevalent during the early wet season (Figs. 107, 108). I propose that the species of *Mylon* be divided into three species groups based on wing pattern and the morphology of male and female genitalia. I also illustrate the genitalia of taxa from other areas, and describe a new species from Guatemala.

"*lassia*" Group

Three species groups appear within *Mylon*, the first proposed being the "*lassia*" group including, in addition to the species discussed below, *Mylon zephus* (Butler, 1870) and *Mylon salvia* Evans, 1953. This group is characterized by hyaline subapical macules on the forewing, a tibial tuft on the hindleg entering a thoracic pouch , a broadly triangular gnathos in ventral view, no style from the ampulla, one or two prominent spines on the aedeagus, and a membranous sac on the ventral side of the phallobase.

Mylon lassia (Hewitson, 1868)
(Figs. 1, 2, 55, 87)

M. lassia is known from Mexico to northern South America (Evans 1953). Males from Costa Rica have genitalia (Fig. 55) as illustrated by Godman and Salvin (1879–1901) and Evans (1953). The female genitalia (Fig. 87) have a narrow lamella postvaginalis which is shallowly notched centrally on its caudal edge and a lamella antevaginalis with broad lateral plates.

Mylon illineatus illineatus Mabille & Boullet, 1917
(Figs. 3, 56)

The nominotypical subspecies of *M. illineatus* ranges from Ecuador to Peru. The genitalia of a male from Ecuador is illustrated here (Fig. 56) in more detail than by either Hayward (1947, 1948) or Evans (1953).

Mylon orsa Evans, 1953
(Figs. 4, 57)

M. orsa was known from the male and two females of Evans' (1953) original description of this species from Costa Rica. The genitalia of an additional male from Costa Rica is illustrated here (Fig. 57) in more detail than previously.

Mylon mestor Evans, 1953
(Figs. 5, 6, 58, 88)

M. mestor was known only from the unique type from Ecuador (Evans 1953). An additional male and a female from Ecuador are illustrated here. The male genitalia are also shown (Fig. 58) and in more detail than by Evans (1953). The female genitalia (Fig. 88) are similar to those of *M. lassia*, but have a narrower sterigma; the tubular ductus bursae leads to an oblong corpus bursae.

Mylon ander ander Evans, 1953
(Figs. 7, 59)

M. ander is known from Colombia to Bolivia and southern Brazil (Evans 1953). It is rare in the Cacaulândia area with one record in October and three in November (Fig. 108). The male genitalia (Fig. 59) appear as illustrated by Evans (1953).

"*menippus*" Group

The two species of the here proposed "*menippus*" group, discussed below, differ from the "*lassia*" group by the lack of hyaline subapical macules on the forewing, no tibial tuft, a narrower gnathos, a short and blunt style caudad from the ampulla, and no spines and a generally smaller sack-like structure on the aedeagus. They do, however, have a dorsal process from the harpe as does the "*lassia*" group, similarly long arms of the uncus (very long on *M. cajus*), and a very broad vinculum.

Mylon menippus (Fabricius, 1777)
(Figs. 9, 10, 60, 89)

M. menippus is the most common *Mylon* in central Rondônia with records for every month and a peak flight in the early wet season (Fig. 107). The male genitalia (Fig. 60) are as illustrated by Godman and Salvin (1879–1901) and Hayward (1933, 1947, 1948) as *Mylon melander* (Cramer [1780]) and by Evans (1953). There appears to be no variation in the genitalia over the species' broad distribution (Mexico to Argentina), but there is some individual variation in the shape of the harpe. The female genitalia (Fig. 89) have a relatively broad lamella postvaginalis (broader than on *M. lassia* and *M. mestor*), a lamella antevaginalis with broad lateral lobes, a long and thin ductus bursae, and an oblong corpus bursae. There is some individual (but not seasonal) variation in the extent and intensity of markings on the dorsal wings. Some individuals from Rondônia lack the pale-centered dark bar in the mid-discal cell of the forewing, the key character used by Evans (1953) to distinguish *M. menippus* from the following species.

→

FIGS. 1–8. *Mylon* (dorsal surface on left, ventral surface on right). **1.** *M. lassia* male, COSTA RICA: San José Prov.; Finca El Rodeo, 25 Mar. 1989; **2.** *M. lassia* female, COSTA RICA: Alajuela Prov.; 6.8 km W of Atenas, 22 Dec. 1984; **3.** *M. illineatus* male, ECUADOR: Pastaza Prov.; 25 km NE Puyo, 28 June 1980; **4.** *M. orsa* male, COSTA RICA: Alajuela Prov.; 2.8 km S of Cinchona, 27 Sept. 1987; **5.** *M. mestor* male, ECUADOR: Pichincha Prov.; Hotel Tinalandia, 2 July 1980; **6.** *M. mestor* female, ECUADOR: Pichincha Prov.; 47 km E of Santa Domingo de los Colorados, 12 May 1988; **7.** *M. ander* male, BRAZIL: Rondônia; 5 km S of Cacaulândia, 11 Nov. 1995; **8.** *M. cajus hera* male, COSTA RICA: San José Prov.; cerro west of Patarra, 11 Oct. 1987.


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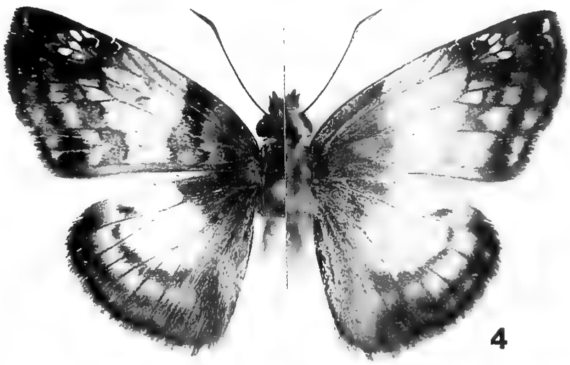
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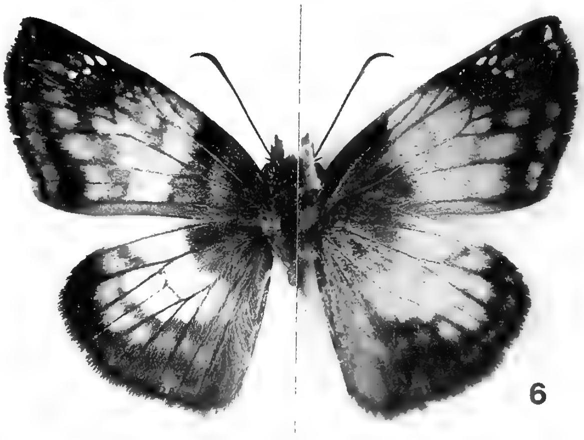
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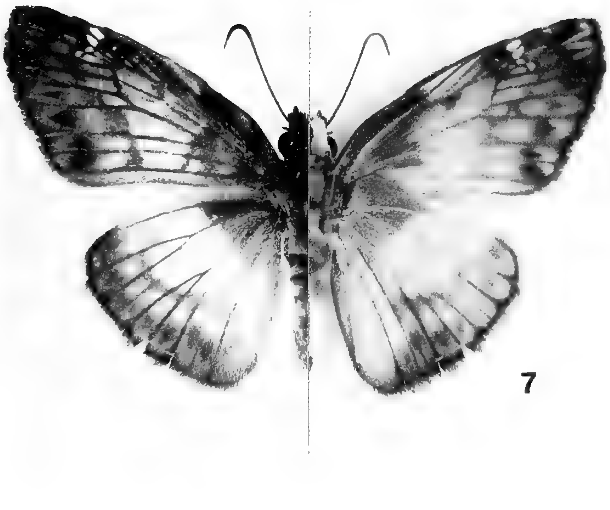
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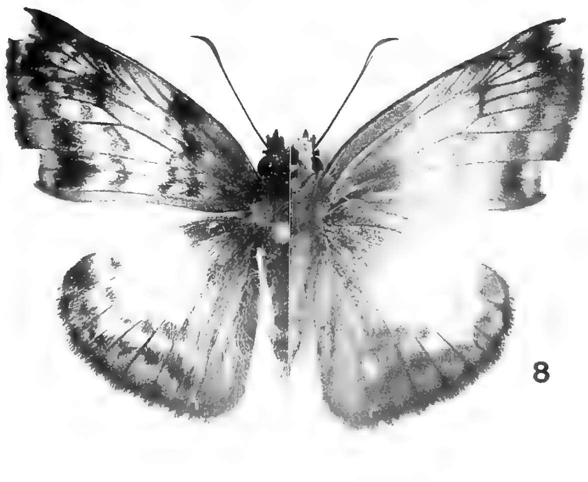
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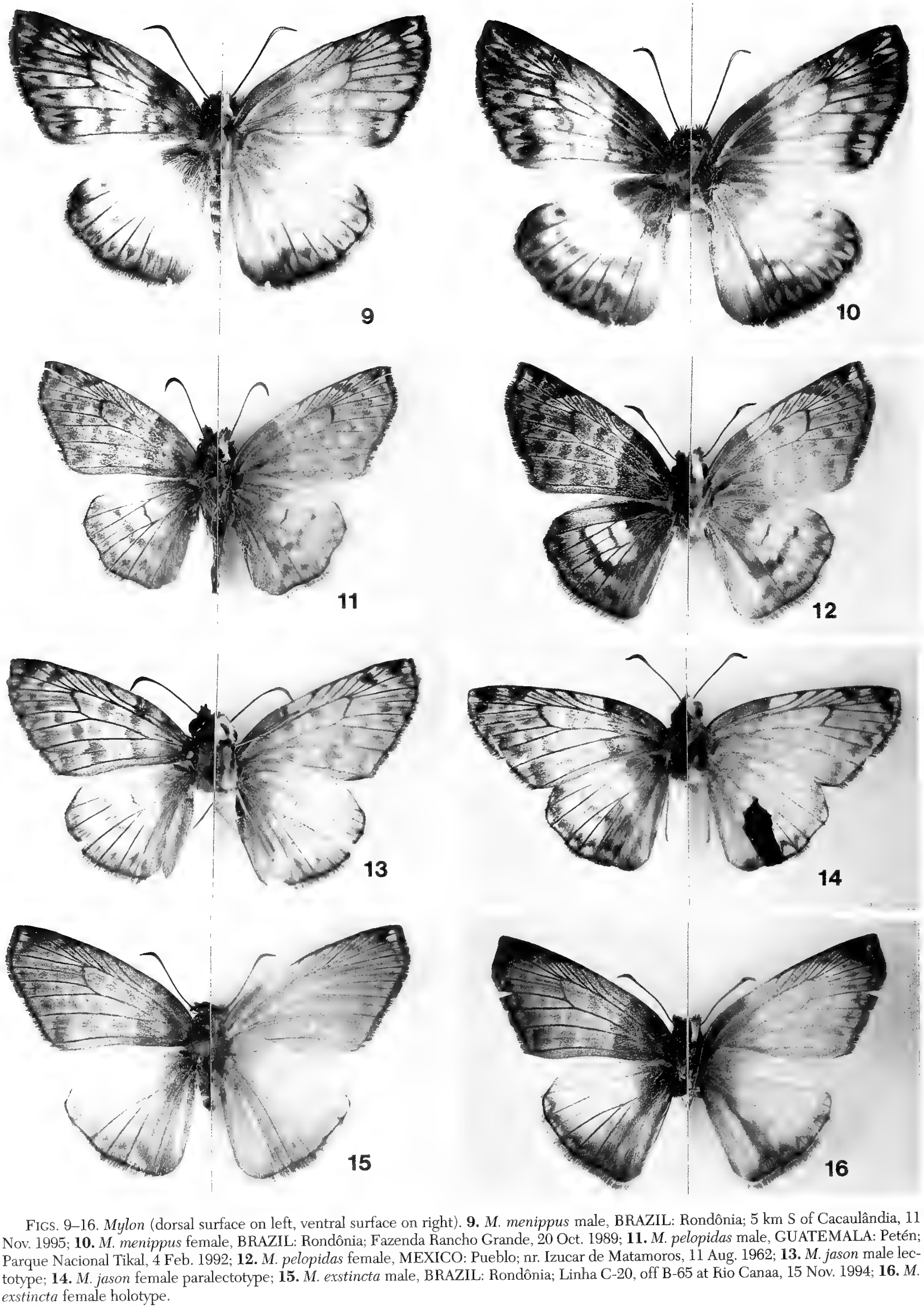
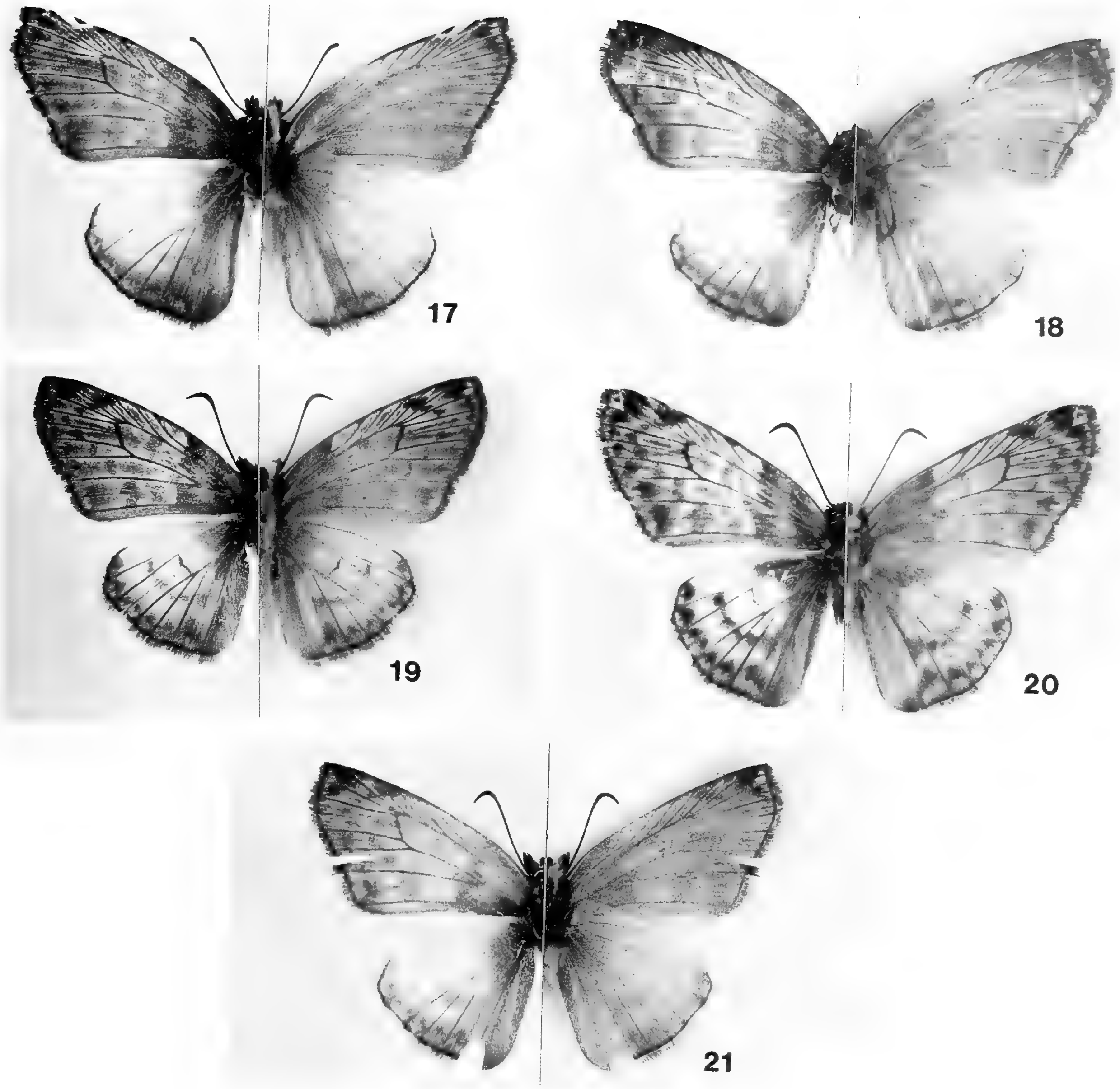


FIGS. 9–16. *Mylon* (dorsal surface on left, ventral surface on right). **9.** *M. menippus* male, BRAZIL: Rondônia; 5 km S of Cacaulândia, 11 Nov. 1995; **10.** *M. menippus* female, BRAZIL: Rondônia; Fazenda Rancho Grande, 20 Oct. 1989; **11.** *M. pelopidas* male, GUATEMALA: Petén; Parque Nacional Tikal, 4 Feb. 1992; **12.** *M. pelopidas* female, MEXICO: Pueblo; nr. Izucar de Matamoros, 11 Aug. 1962; **13.** *M. jason* male lectotype; **14.** *M. jason* female paralectotype; **15.** *M. exstincta* male, BRAZIL: Rondônia; Linha C-20, off B-65 at Rio Canaa, 15 Nov. 1994; **16.** *M. exstincta* female holotype.



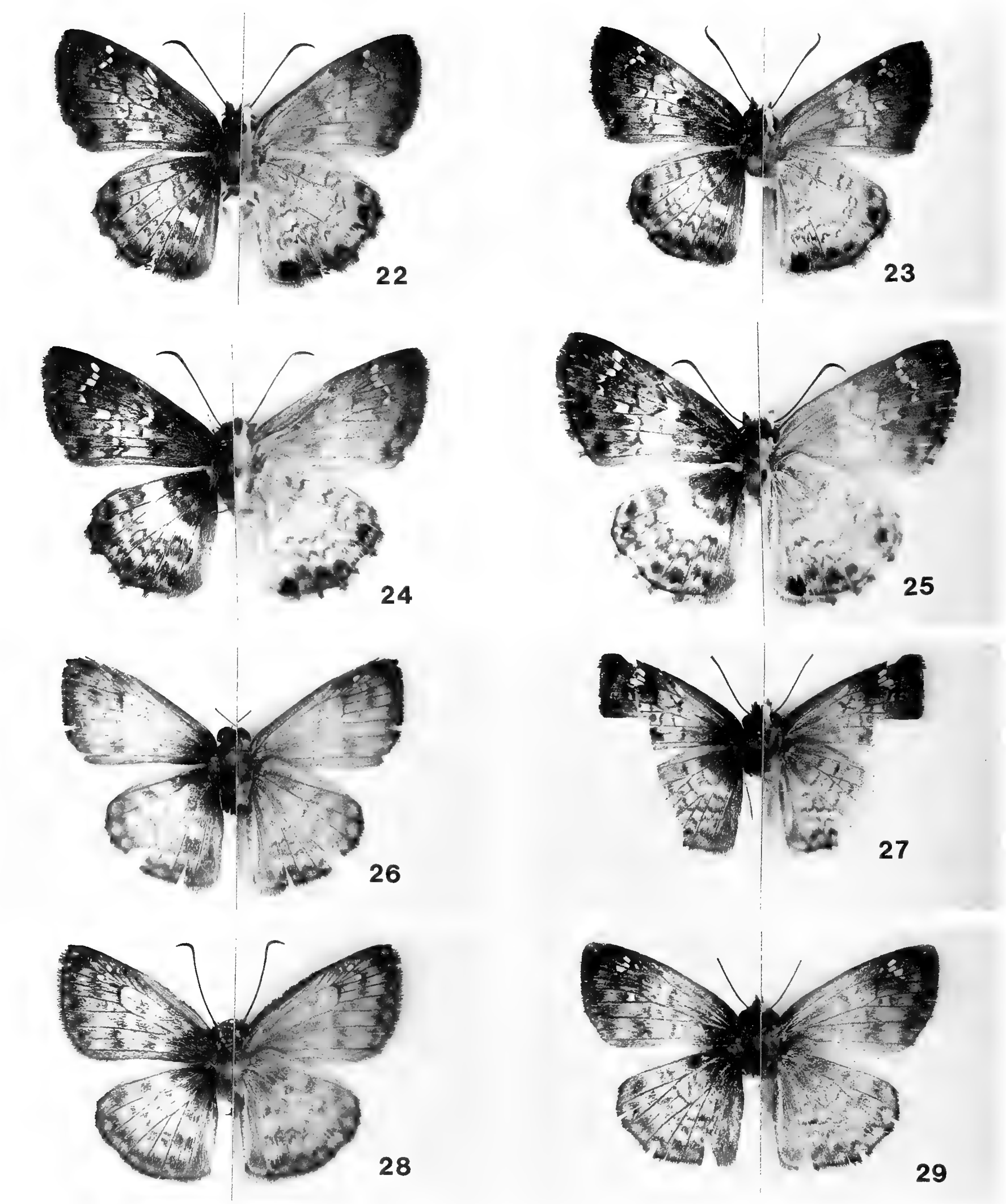
FIGS. 17–21. *Mylon* (dorsal surface on left, ventral surface on right). **17.** *M. argonautarum* male holotype; **18.** *M. argonautarum* female, BRAZIL: Rondônia; 5 km S of Cacaulândia, 18 June 1994; **19.** *M. cristata* male holotype; **20.** *M. cristata* female, GUATEMALA: Petén; Parque Nacional Tikal, 31 May 1993; **21.** *M. simplex* male holotype.

Mylon cajus hera Evans, 1953
(Figs. 8, 61)

This subspecies of *Mylon cajus* (Plötz, 1884) was described from Panama and is known also from Guatemala and Costa Rica (Evans 1953). A male from Costa Rica is illustrated along with its genitalia (Fig. 61) in more detail than by Evans (1953).

"*pelopidas*" Group

The "*pelopidas*" species group, herein designated within *Mylon*, is characterized by the vinculum of the male genitalia extending conspicuously dorsad to envelop most of the tegumen, being supported by a pair of flaps recurving outward from near the caudal end of the tegumen. The group is also distinguished from other *Mylon* by the short arms of the uncus, a comparatively narrow vinculum, an elongate style from the ampulla, the lack of a dorsal process on the harpe (except for *M. pelopidas*), and a dextral hook near the caudal end of the aedeagus in dorsal view. The gnathos of the "*pelopidas*" group is narrow, there are no spines or a sac-like structure on the aedeagus, and, as on the "*menippus*" group, there are no hyaline subapical mac-



FIGS. 22–29. *Carrhenes*; all from BRAZIL: Rondônia (dorsal surface on left, ventral surface on right). **22.** *C. chaeremon* male, 3 km E of Fazenda Rancho Grande, 18 Nov. 1992; **23.** *C. chaeremon* female, 5 km S of Cacaulândia, 10 May 1995; **24.** *C. bamba* male, Fazenda Rancho Grande, 12 Nov. 1994; **25.** *C. bamba* female, 5 km S of Cacaulândia, 7 Apr. 1995; **26.** *C. leada* male, Fazenda Rancho Grande, 7 Nov. 1991; **27.** *C. leada* female, Fazenda Rancho Grande, 13 June 1993; **28.** *C. recurva* male holotype; **29.** *C. recurva* female, B-65, 1 km N of Cacaulândia, 5 Nov. 1990.

ules on the forewing or tibial tuft. The sterigma of the female genitalia is oval in shape and the lamella antevaginalis has a central process extending cephalad which divides a translucent area ("windows") defined caudad and laterad by its lateral lobes. The shape and size of these "windows" and the shape of and the pattern of spiculation on the central process of the lamella antevaginalis are very useful for determining species. The anterior one-half to two-thirds of the sterigma is covered ventrally by a largely transparent membrane. The ductus bursae is long and very slender and leads to a globular corpus bursae. The group includes *M. pelopidas*, *M. jason*, *M. exstincta* (raised from synonymy below), and three new species, all of which are discussed in the following. *M. pelopidas*, *M. exstincta*, and two of the new species were encountered near Cacaulândia.

Mylon pelopidas (Fabricius, 1793)
(Figs. 11, 12, 62, 90)

M. pelopidas is a familar and widespread species (male forewing length = 19.9 mm [19.0–20.3, N = 5]; female forewing length = 21.4 mm [N = 1]; samples from Rondônia) occurring from Mexico south to Paraguay and southern Brazil (Evans 1953). Although there is a certain amount of individual variation in the intensity of dorsal markings (some of this mediated by wear), there appears to be no geographical variation and the male genitalia (Fig. 62) are constant as more or less illustrated by Godman and Salvin (1895), Holland (1927), and Hayward (1933), all as *Mylon ozema* (Butler, 1870), and by Evans (1953). The female genitalia (Fig. 90) have a lamella postvaginalis with a straight caudal end divided by a V-shaped central notch. The lamella antevaginalis is represented by broad lateral lobes extending nearly as far caudad as the caudal edge of the lamella postvaginalis and has a broad central process flared at its cephalad edge and densely spiculose on its lateral edges. The "windows" are broad and rectangular.

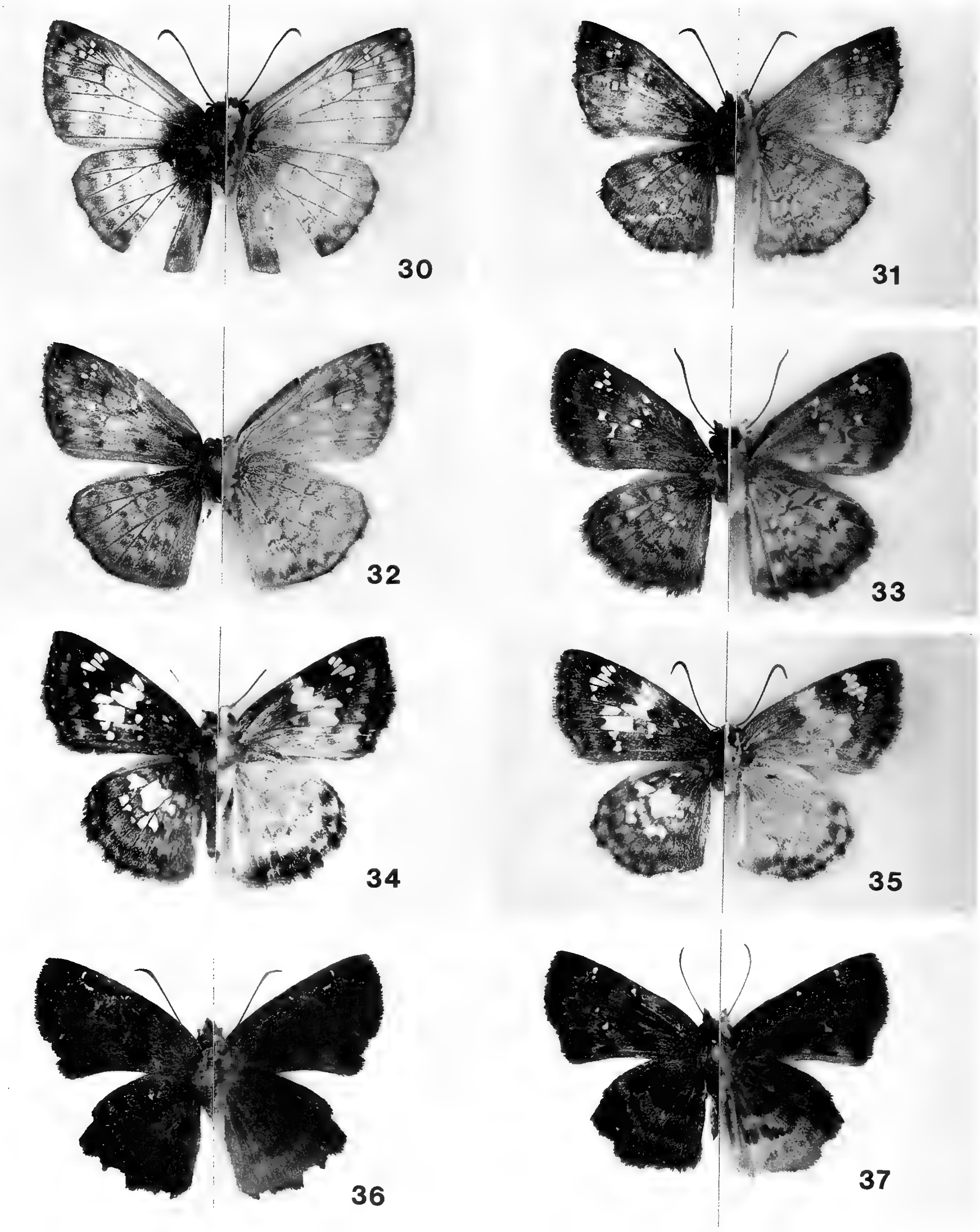
M. pelopidas is uncommon in central Rondônia and is represented by records for January through May, July, and October through December (Fig. 108).

Mylon jason (Ehrmann, 1907)
(Figs. 13, 14, 63, 91)

The concept of *M. jason* has been plagued with problems. The species was described by Ehrmann (1907) as *Leucochitonea jason* from specimens taken in Venezuela. Lindsey (1925) commented on and illustrated the genitalia of a phenotype from South America which resembled *Mylon ozema* (Butler, 1870), a name now synonymized with *Hesperia pelopidas* Fabricius, 1793, but was apparently unaware of Ehrmann's (1907) name. Holland (1927), in correspondence with Lindsey, resolved that two superficially similar taxa with very different genitalia existed and that *M. jason* applied to the unplaced phenotype of Lindsey (1925). Holland (1927) went on to reproduce Lindsey's (1925) illustration of the genitalia of *M. jason*, as well as the Godman and Salvin (1895) figure of *M. ozema*, but took "the liberty of adding the terminal tuft of bristles, which we have found to be highly characteristic and to occur in every one of the numerous specimens which we have microscopically examined . . ." to Lindsey's figure. The "bristles" refer to those at the caudal end of the harpe. Liberty, however, is not always a good thing. The "type" of *L. jason* is a male and, although the genitalia had not been dissected, the harpes were observable beyond the abdominal integument and were clearly without bristles. Apparently, these were not examined by Holland (1927) although Lindsey (1925) may have seen this species as his figure showed no terminal bristles on the harpe. Lindsey, subsequently, also saw specimens with these bristles as noted in correspondence to Holland (Holland 1927), the latter apparently misled Lindsey on the concept of *M. jason*, and thus a confusion concerning the identity of *M. jason* was initiated.

Neither Lindsey (1925) nor Holland (1927) seemed aware that in the years between the description of *M. jason* and their studies, Mabille and Boullet (1917) described another taxon, *Mylon ozema* var. *exstincta* which also had direct bearing on the problem in the identification of *M. jason*. That taxon was described from a single female from "Amazone sup." in the Boullet Collection at the Paris Museum. To complete this history, Hayward (1947, 1948) illustrated genitalia of *Mylon "jason"* showing bristles on the harpe and Evans (1953) synonymized *M. exstincta* with *M. jason* and illustrated genitalia without bristles.

As if the complications in the identification and taxonomy of *M. jason* perpetuated through time were not enough, three species of *Mylon* with this general superficial phenotype were found among material from central Rondônia, two without bristles on the harpe and one with. It thus became critical to examine the types of the two applicable taxa for which names are available to establish their identity. As noted, the "type" of *M. jason* has no bristles on the caudal end of the harpe. Dissection of its genitalia revealed that the terminal end of the harpe is very robust, even in dorsal view, and completely unlike any of the three phenotypes from Rondônia. The two female "paratypes" of *M. jason* which exist (Holland 1927) were also dissected and proved to be of two species as thought by



FIGS. 30–37. *Carrhenes*, *Xenophanes*, and *Antigonus* (dorsal surface on left, ventral surface on right). **30.** *C. lilloi* male, ECUADOR: Rio Napo, Limoncocha, 10 July 1983; **31.** *C. canescens* male (gray phenotype), GUATEMALA: Petén; El Remate, Cerro Cahul, 28 Sept. 1994; **32.** *C. canescens* male (brown phenotype), MEXICO: San Luis Potosi; Cd. Valles, 12 July 1972; **33.** *C. canescens* female (brown phenotype), MEXICO: San Luis Potosi; Cd. Valles, 12 July 1972; **34.** *X. tryxus* male, BRAZIL: Rondônia; 5 km S of Cacaulândia, 8 July 1996; **35.** *X. tryxus* female, BRAZIL: Rondonia; 5 km S of Cacaulândia, 14 July 1995; **36.** *A. liborius* male, BRAZIL: Rondonia; 5 km S of Cacaulândia, 15 July 1995; **37.** *A. liborius* female, BRAZIL: Rondônia; 5 km S of Cacaulândia, 28 May 1994.

Holland (1927). That female which he associated with *M. jason* (his Plate 1, fig. 2) matches well in the details of the superficial characters of the "type" male. The second female is a *M. pelopidas*. The "type" of *M. o.* var. *exstincta* likewise had not been dissected. Its genitalia are different from those of both the "paratype" considered above as the female of *M. jason* and those of the associated female of *M. pelopidas*. Similarly, details of the superficial markings of the *M. o.* var. *exstincta* "type" differed from those exhibited by each of those females. These markings, however, were nearly identical to those of males of one of the Rondônia phenotypes, this also without caudal bristles on the harpe (see below).

To firmly establish the identity of *Leucochitonea jason* Ehrmann, 1907, the male "true type" (Holland 1927) is here firmly established as the lectotype, the female with similar superficial markings alluded to above is designated the paralectotype, and the wings and genitalia of both are illustrated herein. The lectotype (forewing length = 21.7 mm) has labels as follows: red, handprinted - TYPE; white, printed - Ehrman [*sic*] Coll. / Carn. Mus. / Acc. 7815; white, handprinted - Ann. Carn. Mus. / vol. [not given] 1927. / Pl. xxviii, fig. 1. ♂; white, handwritten - L. jason Ehrmann / Type No. 555 / E. A. Klages C'oll. / Súapure 10/28. 1899 / Venezuela; white, printed and handprinted - Genitalia Vial / GTA - 7307, with the following label added: red, printed - LECTOTYPE / *Leucochitonea jason* / Ehrmann, 1907 / designated by / G. T. Austin 1997. The paralectotype female (forewing length = 21.8 mm) has labels as follows: red, printed - Paratype; white, printed - Ehrman [*sic*] Coll. / Carn. Mus. / Acc. 7815; white, handprinted - Ann. Carn. Mus. / vol. [not given] 1927. / Pl. xxviii, fig. 2. ♀; white, handwritten - L. jason Ehr. / Type No. 555 / Edw. A. Klages C'ol. / Súapure 1/18/1900 / Venezuela; white, printed and handprinted - Genitalia Vial / GTA - 7309, with the following label added: red, printed - PARALECTOTYPE / *Leucochitonea jason* / Ehrmann, 1907 / designated by / G. T. Austin 1997. As noted above, the second female "paratype" is a *M. pelopidas* with the following labels: red, handprinted - ParaType; white, handwritten - L. jason Ehr. / Type No. 555 / E. A. Klages C'oll. / Súapure 1/9. 1900 / Venezuela; white, printed - Ehrman - [*sic*] Coll. / Carn. Mus. / Acc. 7815; white, handwritten - E. ozema Butl. / ♀. Fixed by Holland, cf. / Ann. C. M., Vol XXII / Art. [not given], p. [not given].; white, handprinted - Ann. Carn. Mus. / vol. [not given] 1927. / Pl. XXVIII, fig. 7.♀ white, printed and handprinted - Genitalia Vial / GTA - 7308.

Superficially, *M. jason* is similar to *M. pelopidas*, but is larger. The mottling of the wings is as on *M. pelopidas*, but the ground color has more sheen, the postmedian line of the hindwing is less prominent than usual on *M. pelopidas*, and there is less gray-brown scaling between this and the margin. The end of the forewing discal cell, represented by darkened cross veins, is more or less parallel to the termen on *M. jason* and thus is directed towards the proximal edge of the postmedian macule in CuA_2–2A whereas the end of the discal cell on *M. pelopidas* is more erect and directed towards the distal edge of this macule; this character was the one superficial character used by Evans (1953) to distinguish the two species.

The genitalia illustrated by Lindsey (1925) are probably of *M. jason*, those illustrated by Holland (1927) represent a mixed drawing of *M. jason* (after the figure by Lindsey 1925) with bristles of an undescribed species added, those represented by Evans (1953) may be of *M. jason*, but appear to be of *M. exstincta* or of an undescribed species. The genitalia represented as *M. jason* by Hayward (1948) have caudal bristles on the harpe and are obviously not of that species. The female genitalia of *M. jason* have a curved caudal edge to the lamella postvaginalis divided by a relatively broad V-shaped central notch and a lamella antevaginalis with wide and lobate lateral lobes and a moderately wide central process with a slightly broadened and convex cephalad end and lateral spicules. The "windows" are narrow and nearly round.

Three additional females of *M. jason* were examined (forewing length = 20.6 mm [20.2–21.3]), all from Guatemala: Petén; Parque Nacional Tikal, 3–4 Feb. 1992 (GTA #7318, 7332, 7337). Thus its distribution extends at least from Guatemala to Venezuela. Records of *M. jason* in the literature must be treated as suspect until the specimens upon which they were based are critically reexamined.

Mylon exstincta Mabille & Boullet, 1917, **new status**
(Figs. 15, 16, 64, 92)

Mylon ozema (Butler, 1870) var. *exstincta* Mabille & Boullet, 1917.
Mylon jason Ehrmann, 1907: Evans, 1953.

The identity and "type" of *M. exstincta* were discussed above. This female type (called a male by Evans 1953, forewing length = 21.8 mm) with the following labels: red, printed - TYPE; white, printed and handprinted - Amazone / Supérieur / 1905 / O. Staudinger / COLL BOULLET (in red letters on left side) / MUSEUM PARIS (in red letters on right side); green, handwritten - M. ozema, / var. Extincta [*sic*] / Mab. & Boull.; white, handwritten - Mylon / ozema var. / Exstincta Mab. Boull. / Bull. Soc. ent. France,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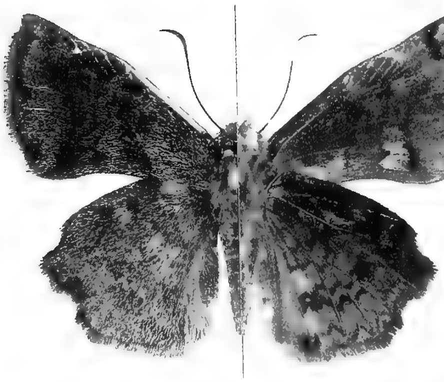
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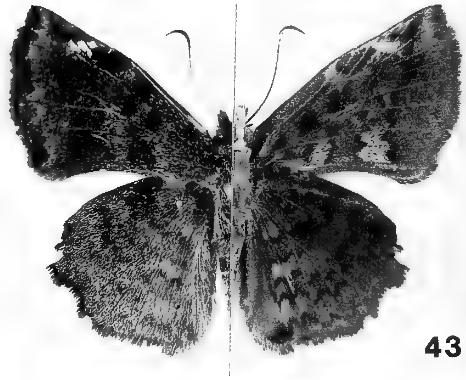
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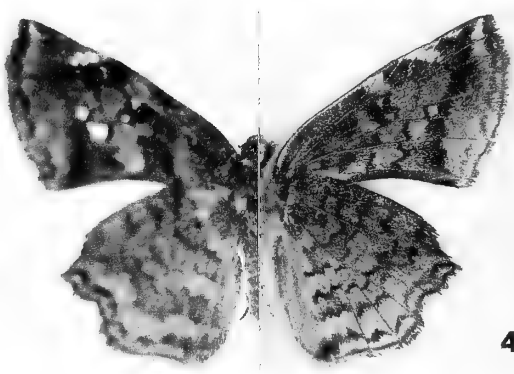
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1917, p. 55; white, printed and handprinted - Genitalia Vial / GTA - 5983, is here identified as the holotype of *Mylon ozema* var. *exstincta* Mabille & Boullet, 1917 and the following label has been added: red, printed - HOLOTYPE / *Mylon ozema* / var. *exstincta* / Mabille & Boullet, 1917 / identified by / G. T. Austin 1997. It and its genitalia are illustrated herein (Figs. 16, 92). A male associated with the holotype is a *Mylon pelopidas* and has the following labels: red, printed - TYPE; white, printed and handprinted - Amazone / Supérieur / 1905 / O. Staudinger / COLL BOULLET (in red letters on left side) / MUSEUM PARIS (in red letters on right side); Genitalia Vial / GTA - 5984; white, printed and handprinted - *Mylon pelopidas* / Fabricius (1793) / det. G. T. Austin 1997.

M. exstincta resembles both *M. pelopidas* and *M. jason* superficially in overall wing shape and color. The species is larger than *M. pelopidas* and about the size of *M. jason*. *M. exstincta* is like *M. jason* in the orientation of the distal end of the forewing discal cell. Although the dark forewing markings are similar on all three species, those of *M. exstincta* are much less contrasting giving a noticably less mottled aspect. The hindwing of *M. exstincta* is largely unmarked with only a gray shade posteriorly and a darker gray submarginal line being apparent. The postmedian line is not traceable anterior to vein M$_3$.

The genitalia of the holotype of *M. exstincta* are generally similar to those of *M. jason*, but differ in detail. The lamella postvaginalis is quadrate with a narrow **U**-shaped notch on the caudal edge (angled with a broad **V**-shaped central indentation on *M. jason*) and the lamella antevaginalis is represented by a pair of rounded lateral lobes (narrower on *M. jason*), a cephalad directed central process which is relatively broadly expanded at and spiculose across its cephalad end (less expanded and with lateral spicules on *M. jason*). The "windows" are more elongate and ovate than they are on *M. jason*. The male from Rondônia, Brazil (Linha C-20, off B-65 at Rio Pardo, 15 Nov. 1990, GTA #830), considered to be *M. exstincta* (forewing length = 21.7 mm), also has genitalia generally similar to those of *M. jason*. The entire genital capsule of *M. exstincta* is less robust than is that of *M. jason*. The structure of the harpe is the key to identity. This is very robust, broad in dorsal view, heavily adorned with thorn-like spines, and recurved to about the level of the style from the ampulla on *M. jason* and much less robust, relatively thin in dorsal view, with fewer and smaller spines, and recurved but slightly on *M. exstincta*.

Because *M. o.* var. *exstincta* differs from *M. jason* in superficial characters and in the genitalia of both sexes, it is here raised from Evans' (1953) synonymy with *M. jason* to specific status.

Mylon simplex Austin, new species

(Figs. 21, 65)

Description. Male - forewing length = 20.6 mm (19.7–21.8, N = 6); ground color of both dorsal wings shining off-white, forewing overscaled with gray and marked with darker gray macules giving mottled appearance, these macules as submarginal, postmedian, postbasal, and basal series in addition to one in discal cell 2/3 distance from wing base to end of cell, submarginal and postmedian macules darkest (nearly black) towards costa; submarginal series sets off relatively distinct pale gray margin; pale ochre-brown between postbasal and basal macules; veins black, those enclosing end of discal cell directed towards proximal edge of postmedian macule in CuA$_1$–2A. Hindwing with extensive gray along anal margin, this broadest at base of wing, extending to vein M$_3$ or M$_1$ as postmedian line; submarginal band of gray-brown decreasing in size and becoming macular (generally chevron-shaped) anteriorly; veins entirely black posteriorly, distally anteriorly. Venter with dorsal pattern very vague to obsolete except at forewing apex where most distinct.

Head black on dorsum with white central patch, white beneath antennae and around eyes, antennae black with white at segments on venter and beneath club, nudum red-brown with 17 (N = 1) or 18 (N = 4) segments, palpi mixed white and dark gray; thorax brown with scattered white scales on dorsum, gray on venter, legs brown with white scales, mid-tibiae with single pair of spurs, hind tibiae with two pairs, no tibial tuft; abdomen gray on dorsum with white at segments, white on venter.

Genitalia - tegumen short, stout, with moderately broad recurved flaps caudad supporting anterior part of broad and enclosing vinculum; vinculum relatively straight; saccus broad, slightly upturned; uncus slightly

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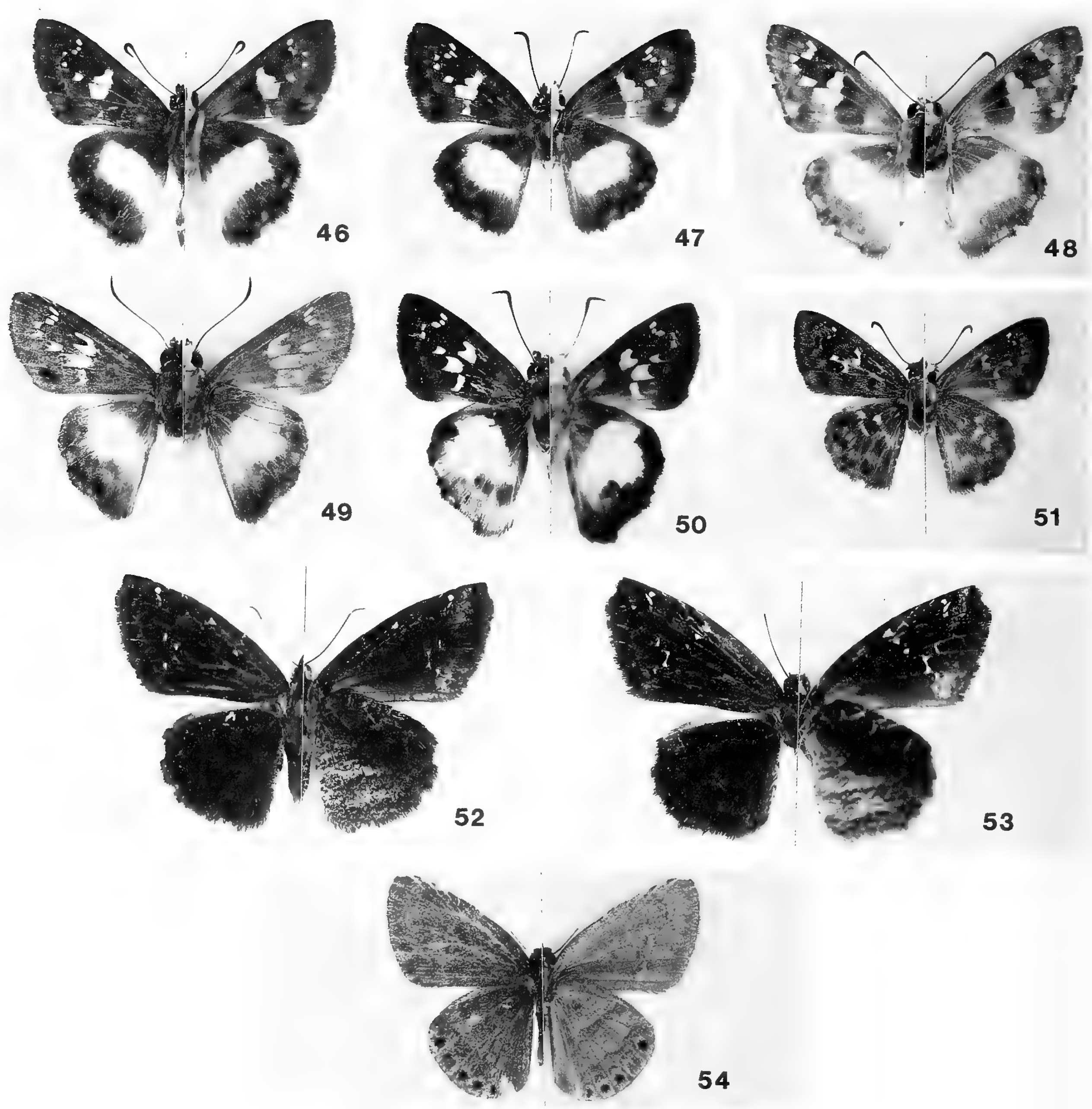
FIGS. 38–45. *Antigonus*; all from BRAZIL: Rondônia (dorsal surface on left, ventral surface on right). **38.** *A. nearchus* male, 5 km S of Cacaulândia, 27 Apr. 1995; **39.** *A. nearchus* male, 5 km S of Cacaulândia, 4 July 1993; **40.** *A. nearchus* male, 5 km S of Cacaulândia, 8 Feb. 1994; **41.** *A. nearchus* female, B-80, between linhas C-10 and C-15, 19 Nov. 1991; **42.** *A. erosus* male, Linha C-20 at Rio Pardo, 10 Dec. 1990; **43.** *A. erosus* male, 5 km S of Cacaulândia, 18 Aug. 1993; **44.** *A. erosus* female, 5 km S of Cacaulândia, 22 July 1995; **45.** *A. erosus* female, 5 km S of Cacaulândia, 2 Oct. 1993.



FIGS. 46–54. *Clito*, *Anisochoria*; and *Timochreon*, all from BRAZIL: Rondônia unless noted (dorsal surface on left, ventral surface on right). **46.** *C. clito* male, Fazenda Rancho Grande, 16 June 1993; **47.** *C. clito* female, 5 km S of Cacaulândia, 30 July 1997; **48.** *C. "aberrans"* male, COSTA RICA: Guanacaste Prov.; La Pacifica, nr. Cañas, 17 Dec. 1984; **49.** *C. littera* male, Fazenda Rancho Grande, 31 Oct. 1993; **50.** *C. zelotes* male, Fazenda Rancho Grande, 20 Nov. 1991; **51.** *C. clada* Fazenda Rancho Grande, 10 Oct. 1993; **52.** *A. pedaliodina pedaliodina* male, Fazenda Rancho Grande, 20 Oct. 1989; **53.** *A. pedaliodina pedaliodina* female, Fazenda Rancho Grande, 3 Nov. 1989; **54.** *T. satyrus* male, Fazenda Rancho Grande, 3 Nov. 1989.

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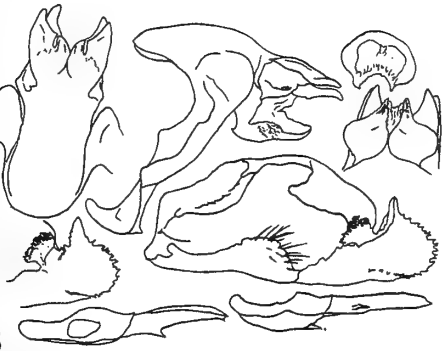
FIGS. 55–62. Male genitalia of *Mylon* (from BRAZIL: Rondônia unless noted otherwise). Structures shown are lateral, dorsal, and ventral views of tegumen, uncus, gnathos, and associated structures; lateral internal view of right valva (second view of partial valva shows the same flattened); lateral and (usually) dorsal views of aedeagus and associated structures; and dorsal view of transtilla and juxta. **55.** *M. lassia*, COSTA RICA (GTA #7354); **56.** *M. illineatus*, ECUADOR (GTA #7355); **57.** *M. orsa*, COSTA RICA (GTA #7359); **58.** *M. mestor*, ECUADOR (GTA #7358); **59.** *M. ander* (GTA #6394); **60.** *M. menippus* (GTA #7349); **61.** *M. cajus hera*, COSTA RICA (GTA #985); **62.** *M. pelopidas* (GTA #2123).



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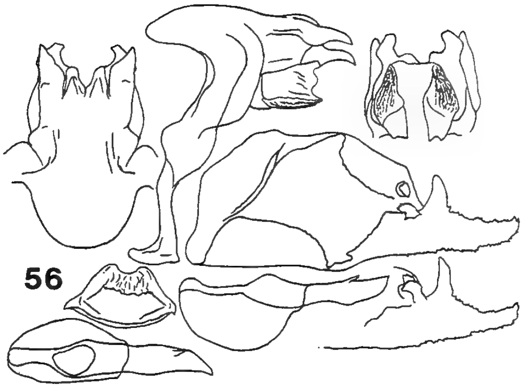

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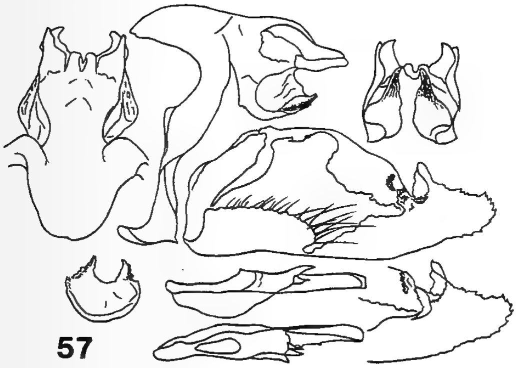

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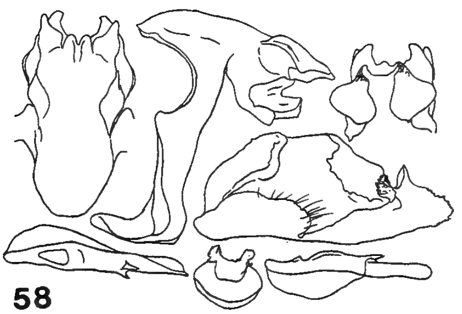

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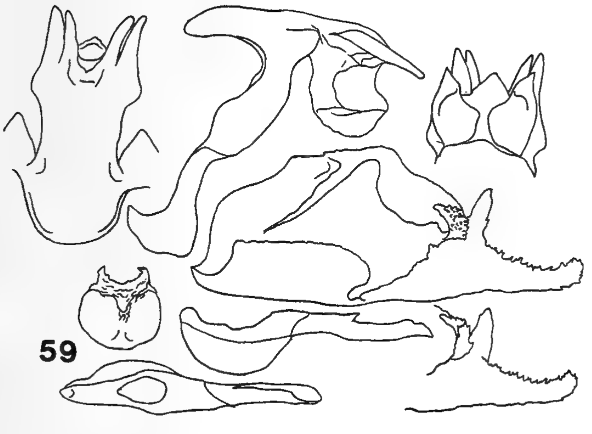

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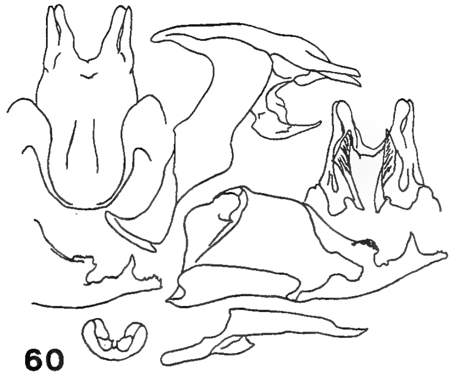

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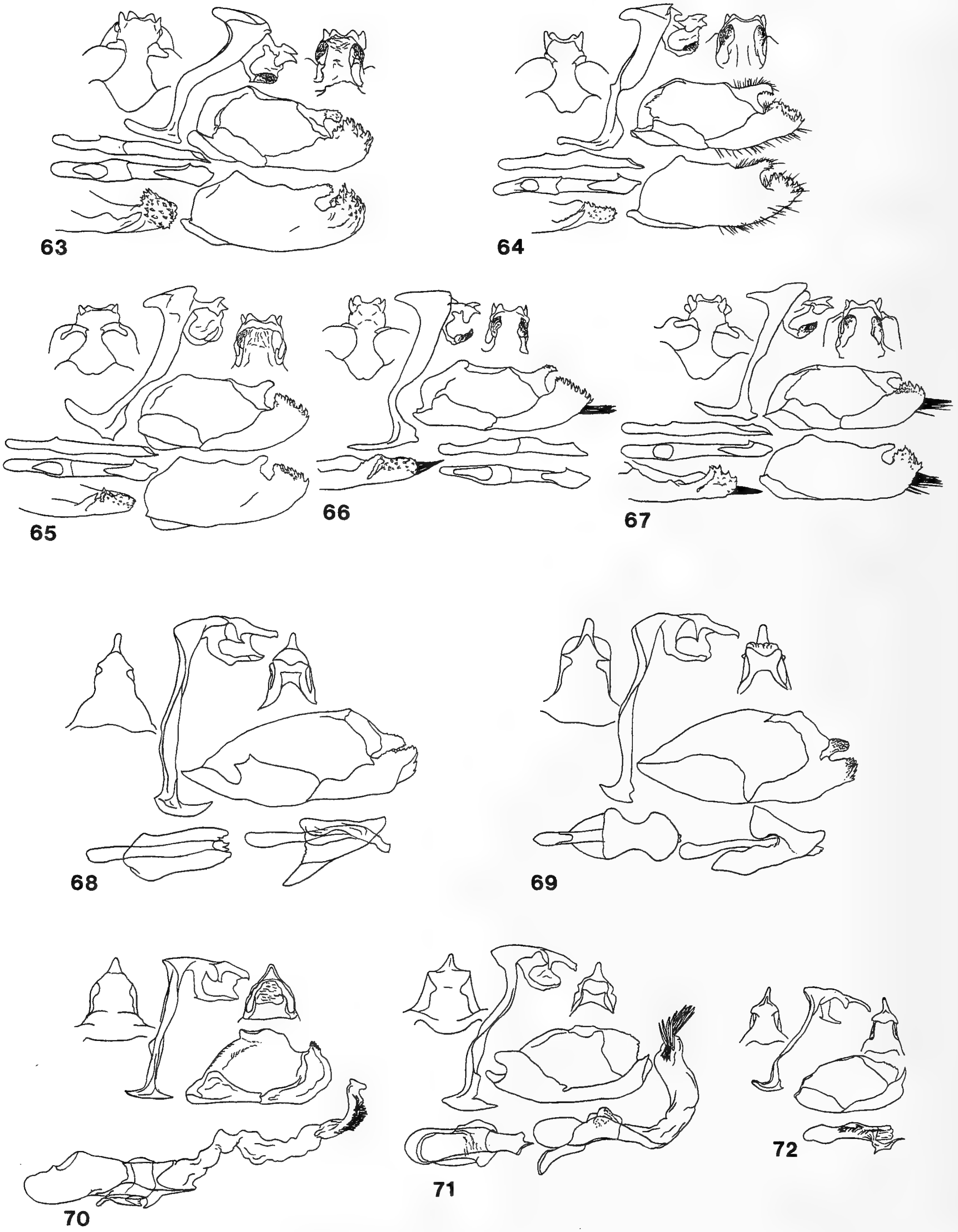


FIGS. 63–72. Male genitalia of *Mylon* and *Clito* (from BRAZIL: Rondônia unless noted otherwise). Structures shown are lateral, dorsal, and ventral views of tegumen, uncus, gnathos, and associated structures; lateral internal view of right valva (for *Mylon*, also shown are lateral external view of left valva and dorsal view of caudal end of valva); and lateral and (usually) dorsal views of aedeagus and associated structures. **63.** *M. jason* holotype, VENEZUELA (GTA #7307); **64.** *M. exstincta* (GTA #830); **65.** *M. simplex* paratype (GTA #808); **66.** *M. argonautarum* paratype (GTA #4251); **67.** *M. cristata* holotype, GUATEMALA (GTA #2639); **68.** *C. clito* (GTA #3146); **69.** *C. "aberrans"*, COSTA RICA (GTA #7312); **70.** *C. littera anda* (GTA #4377); **71.** *C. zelotes* (GTA #5555); **72.** *C. clada* (GTA #3682).

shorter than tegumen, shallowly divided with second pair of lateral processes caudad and ventral triangular lobes; gnathos broadly divided, relatively short, curved in lateral view; valva stout, ampulla with broad, blunt and slightly spiculose style curved inward and oriented dorso-caudad, harpe curved upward, caudal end slightly curved with dorso-caudal orientation and strongly dentate with spine-like hooks, relatively narrow in dorsal view; aedeagus nearly straight, slender, caudal end spatulate, lateral triangular projection on right side near caudal end.

Female - unknown.

Types. Holotype male with the following labels: white, printed - BRASIL: Rondonia / 62 km S Ariquemes / linea C-20, 7 km E / B-65, Fazenda / Rancho Grande / 22 November 1991 / leg. F. West; white, printed and handprinted - Genitalia Vial / GTA - 2122; red, printed - HOLOTYPE / *Mylon simplex* / Austin; to be deposited at the Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil. Paratypes - same location as holotype, 14 July 1994 (1 male, GTA #7319), 20 Oct. 1989 (1 male, GTA #459), 14 Nov. 1990 (1 male, GTA #809), 14 Nov. 1995, at paper lures, 1030–1100 (1 male, GTA #7581), 12 Dec. 1990 (1 male, GTA #808), BRAZIL: Rondônia; Linha 10, off B-65, 5 km S of Cacaulândia, 5 Mar. 1994 (1 male, GTA #7474), 21 Oct. 1989 (1 male, GTA #1410), 8 Nov. 1996 (1 male, GTA #7526). *Type locality.* BRAZIL: Rondônia; 62 km south of Ariquemes, Linha C-20, 7 km (by road) east of route B-65, Fazenda Rancho Grande, 180 meters. This is approximately 5 km northeast of Cacaulândia in typical lowland tropical rainforest.

Etymology. The name means unadorned and refers to the lack of bristles on the caudal end of the harpe and to the relatively plain superficial appearance in comparison to *M. jason*.

Diagnosis and discussion. *M. simplex* is similar to *M. jason* and very similar to the sympatric *M. exstincta*. It is obviously less mottled than *M. jason*. The male genitalia of *M. simplex* are less robust than are those of *M. jason* and differ from that species much as do the genitalia of *M. exstincta*. *M. simplex* may not be separable from *M. exstincta* superficially. The genitalia of all nine males of *M. simplex* are consistent and differ from those of *M. exstincta* by their broader tegumen and uncus in dorsal view, the small and triangular ventral process from the uncus (this broad and lobate on *M. exstincta*), the broader saccus, the more or less erect style from the ampulla (more caudal orientation on *M. exstincta*), and the more robust harpe. It was suggested to me (Steinhauser, *in litt.*) that these were all *M. exstincta*. Because, however, of the consistency of the genitalia of *M. simplex* and their several obvious differences from those of *M. exstincta*, I recognize this phenotype as a species different from *M. exstincta*.

Distribution and phenology. At present, the species is known only from the types taken in March, July, and October through December (Fig. 108).

Mylon argonautarum Austin, new species

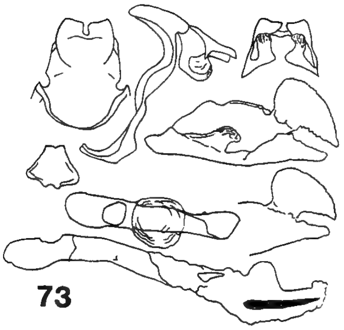
(Figs. 17, 18, 66, 93)

Description. Male - forewing length = 20.6 mm (19.6–21.0, N = 9); ground color of both dorsal wings shining off-white, forewing heavily overscaled with gray and marked with vaguely darker gray macules giving slightly mottled appearance, these macules as submarginal, postmedian, postbasal, and basal series in addition to one in discal cell 2/3 distance from wing base to end of cell, submarginal and postmedian macules darkest (dark gray) towards costa; submarginal series sets off relatively distinct pale gray margin; pale ochre-brown between postbasal and basal macules; veins black, those enclosing end of discal cell directed towards proximal edge of postmedian macule in CuA_1–2A. Hindwing with extensive gray along anal margin, this broadest at base of wing, extending to vein M_3 or M_1 as postmedian line; submarginal band of gray-brown; veins entirely black posteriorly, distally anteriorly. Venter with dorsal pattern nearly obsolete except at forewing apex where more distinct.

Head black on dorsum with white central patch, white beneath antennae and around eyes, antennae black with white at segments on venter and beneath club, nudum red-brown with 17 (N = 4) or 18 (N = 4) segments, palpi mixed white and dark gray; thorax brown with scattered white scales on dorsum, gray on venter, legs brown with white scales, mid-tibiae with single pair of spurs, hind tibiae with two pairs, no tibial tuft; abdomen gray on dorsum with white at segments, white on venter.

Genitalia - tegumen short with narrow recurved flaps caudad supporting anterior part of broad and enclosing vinculum; ventral one-third of vinculum curved; saccus slender, straight; uncus shorter than tegumen, shallowly divided with second pair of lateral processes caudad and ventral rounded lobes; gnathos broadly divided, relatively short, curved in lateral view; valva stout, ampulla with broad, blunt, and slightly dentate style curved inward and oriented mostly caudad, harpe curved upward, caudal end triangular with dorso-caudal orientation and moderately dentate with long spine-like hooks, narrow in dorsal view, tuft of long bristles originating from ventral edge just before caudal dentate portion; aedeagus nearly straight, slender, caudal end spatulate, lateral triangular projection on right side near caudal end.

Female - forewing length = 21.2 mm (N = 1); nearly identical to male, antennal nudum with 18 segments (N = 1).



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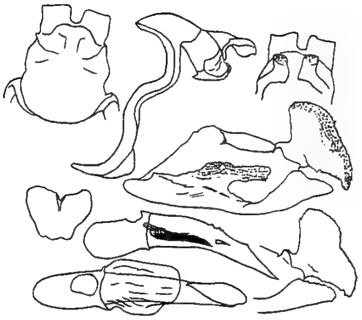

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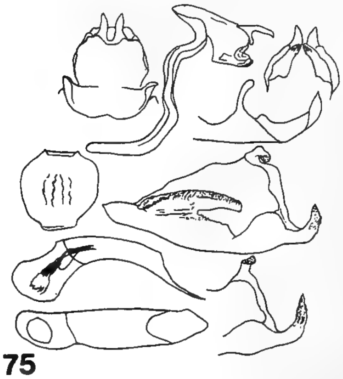

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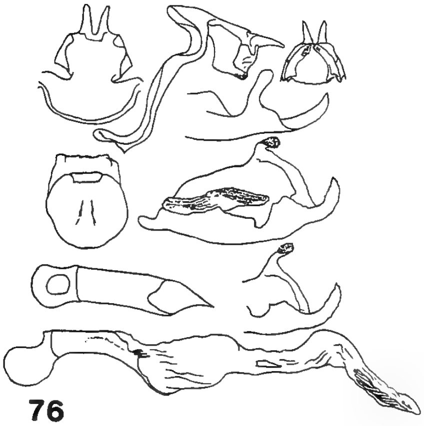

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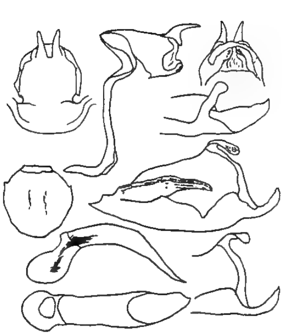

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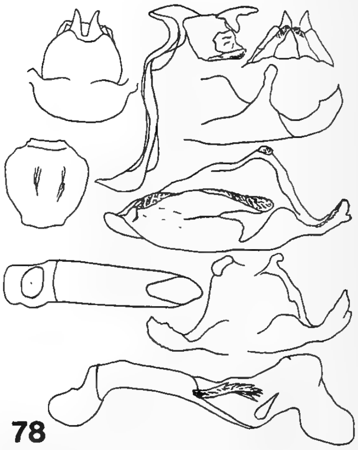

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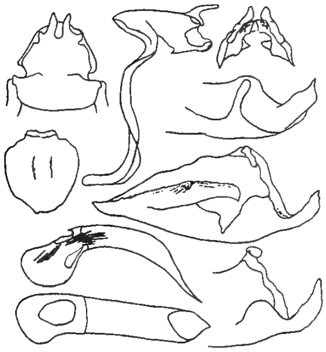

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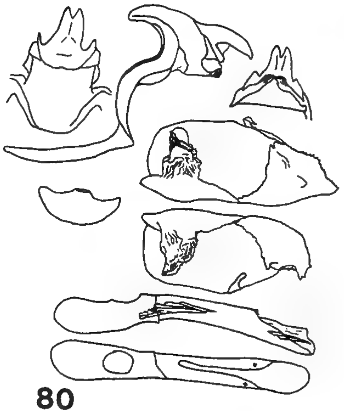

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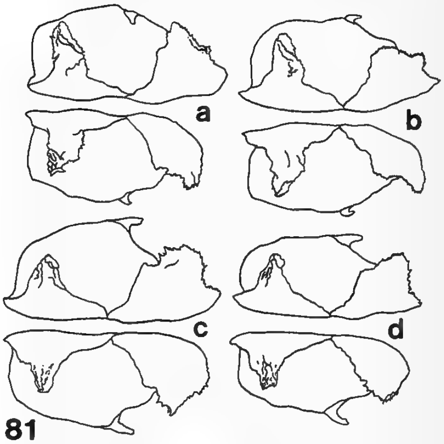

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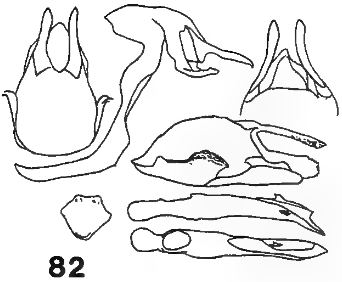

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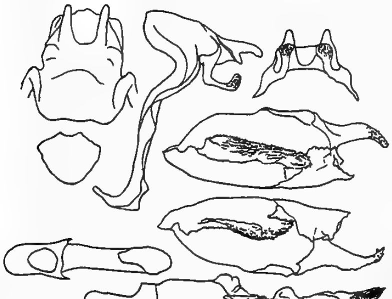

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Genitalia - lamella postvaginalis narrow, caudal end quadrate with narrow U-shaped central notch; lamella antevaginalis with narrow lateral lobes and central process expanding gradually cephalad to pair of lateral lobes just caudad of convex cephalad end, this process spiculose only laterad, "windows" broadly ovate; posterior 1/2 of sterigma covered by transparent membrane; ductus bursae gradually expanded caudad, very narrow cephalad; corpus bursae globular with net-like mass of signa.

Types. Holotype male with the following labels: white, printed - BRASIL: Rondonia / 62 km S Ariquemes / linea C-20, 7 km E / B-65, Fazenda / Rancho Grande / 21 April 1992 / leg. G. T. Austin; white, printed and handprinted - Genitalia Vial / GTA - 7320; red, printed - HOLOTYPE / *Mylon argonautarum* / Austin; to be deposited with the paratype female at the Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil. Paratypes - same location as holotype, 15 Apr. 1992 (1 male, GTA #2237), 16 Apr. 1997 (1 male, GTA #7644), 13 Aug. 1997 (1 male, GTA #8284), 6 Sept. 1992 (1 male, GTA #3522), 25 Oct. 1993 (1 male, GTA #4390), 16 Nov. 1991 (1 male, GTA #2404), BRAZIL: Rondônia; Linha 15, lot 36, W of Cacaulândia, 9 Oct. 1993 (1 male, GTA #4251), BRAZIL: Rondônia; Linha 10, 5 km S of Cacaulândia, 25 Jan. 1997 (2 males, GTA #7651, 7670), 6 Feb. 1994 (1 male, GTA #7328), 4 Mar. 1996 (1 male, GTA #7477), 5 June 1994 (1 male, GTA #7321), 18 June 1994 (1 female, GTA #7323), 22 July 1995 (1 male, GTA #7329), 9 Aug. 1996 (1 male, GTA #7473), 12 Oct. 1996 (1 male, GTA #8469), 10 Nov. 1996 (1 male, GTA #7527), 16 Nov. 1995 (1 male, GTA #7322), 29 Nov. 1996 (1 male, GTA #8316). *Type locality.* BRAZIL: Rondônia; 62 km south of Ariquemes, Linha C-20, 7 km (by road) east of route B-65, Fazenda Rancho Grande, 180 meters. This is approximately 5 km northeast of Cacaulândia in typical lowland tropical rainforest.

Etymology. The name, meaning "of the argonauts," indicates the apparent relationship of this species to *M. jason*, Jason being the best known argonaut in Greek legend.

Diagnosis and discussion. The examination of the lectotype of *M. jason* and a male of *M. exstincta* showed that neither represented the phenotype with bristles on the caudal end of the harpe as illustrated by the figures in Holland (1927) and Hayward (1947, 1948). It is obvious that a "bristled" species is common in collections as Holland (1927) found bristles on all specimens of *M. "jason"* that he examined (see above). It is unknown if these individuals represent *M. argonautarum*, the species to be described next, or an as yet unrecognized species; all need to be carefully reexamined by some future researcher of *Mylon*.

M. argonautarum, with its weakly mottled dorsum, does not appear to be superficially separable from *M. exstincta* or *M. simplex*. *M. jason* is noticeably more mottled. The male genitalia of *M. argonautarum* are similar in overall form to those of *M. jason*, *M. exstincta*, and *M. simplex*, but are immediately distinguished by the tuft of bristles from near the caudal end of the harpe. Otherwise, the tegumen and uncus are less robust (in dorsal view) than on those three species and the teeth on the caudal end of the harpe are longer and appear more orderly; the overall shape of the harpe most closely resembles that of *M. simplex*. The female genitalia have a narrower sterigma than do either *M. jason* or *M. exstincta*, have the lamella postvaginalis shaped as on *M. exstincta*, and have a uniquely shaped central process of the lamella antevaginalis with its lateral lobes.

Distribution and phenology. The species is known only from the types taken in January through April and June through November (Fig. 108).

Mylon cristata Austin, new species

(Figs. 19, 20, 67, 94)

Description. Male - forewing length = 19.2, 21.0 mm (N = 2); ground color of both dorsal wings shining gray-white, forewing marked with darker gray macules giving strongly mottled appearance, these macules as submarginal, postmedian, postbasal, and basal series in addition to one in discal cell 2/3 distance from wing base to end of cell, macules darkest (nearly black) towards costa; ochre-brown between postbasal and basal

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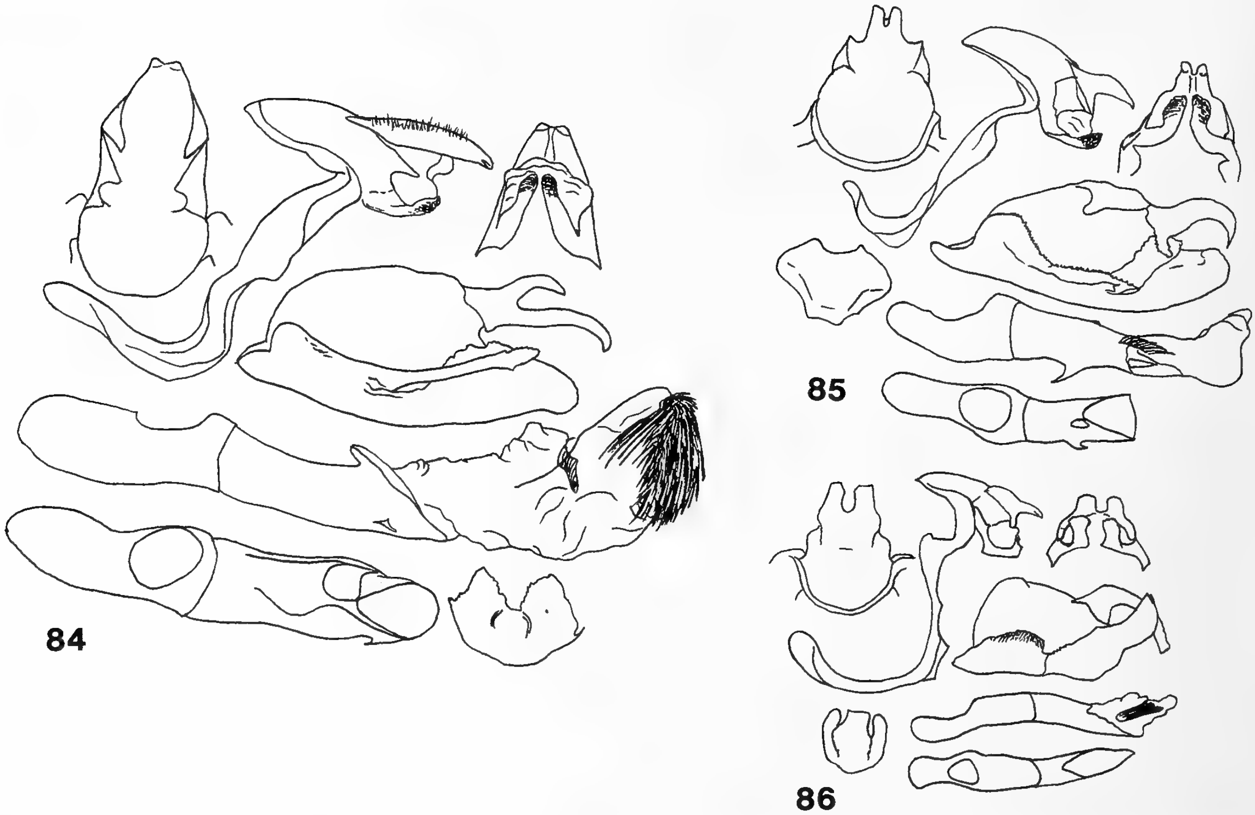
FIGS. 73–83. Male genitalia of *Carrhenes*, *Xenophanes*, *Timochreon*, and *Anisochoria* (from BRAZIL: Rondônia unless noted otherwise). Structures shown are lateral, dorsal, and ventral views of tegumen, uncus, gnathos, and associated structures; lateral internal view of right valva (second view of partial valva shows the same flattened); lateral and dorsal views of aedeagus and associated structures; and dorsal view of transtilla and juxta. **73.** *C. chaeremon* (GTA #7313); **74.** *C. bamba* (GTA #374); **75.** *C. leada* (GTA #2033); **76.** *C. canescens*, MEXICO (GTA #7368), also shown is dorsal view of caudal end of valva; **77.** *C. canescens*, GUATEMALA (GTA #5189), also shown is dorsal view of caudal end of valva; **78.** *C. lilloi*, ECUADOR (GTA #7367), also shown is dorsal view of caudal end of valva and lateral internal view of caudal end of left valva; **79.** *C. recurva* holotype (GTA #1170), also shown is dorsal view of caudal end of valva; **80.** *X. tryxus* (GTA #7390), also shown is lateral internal view of left valva; **81.** *X. tryxus*, variation of valvae (shown are lateral internal views of right and left valvae), **a.** (GTA #7461), **b.** (GTA #7389), **c.** COSTA RICA (GTA #7467), **d.** COSTA RICA (GTA #7464); **82.** *T. satyrus tampa* (GTA #959); **83.** *A. pedaliodina pedaliodina* (GTA #2125), also shown is lateral internal view of left valva.



FIGS. 84–86. Male genitalia of *Antigonus* (all from BRAZIL: Rondônia). Structures shown are lateral, dorsal, and ventral views of tegumen, uncus, gnathos, and associated structures; lateral internal view of right valva; lateral and dorsal views of aedeagus and associated structures; and dorsal view of transtilla and juxta. **84.** *A. nearchus* (GTA #7470); **85.** *A. erosus* (GTA #3968); **86.** *A. liborius* (GTA #7311).

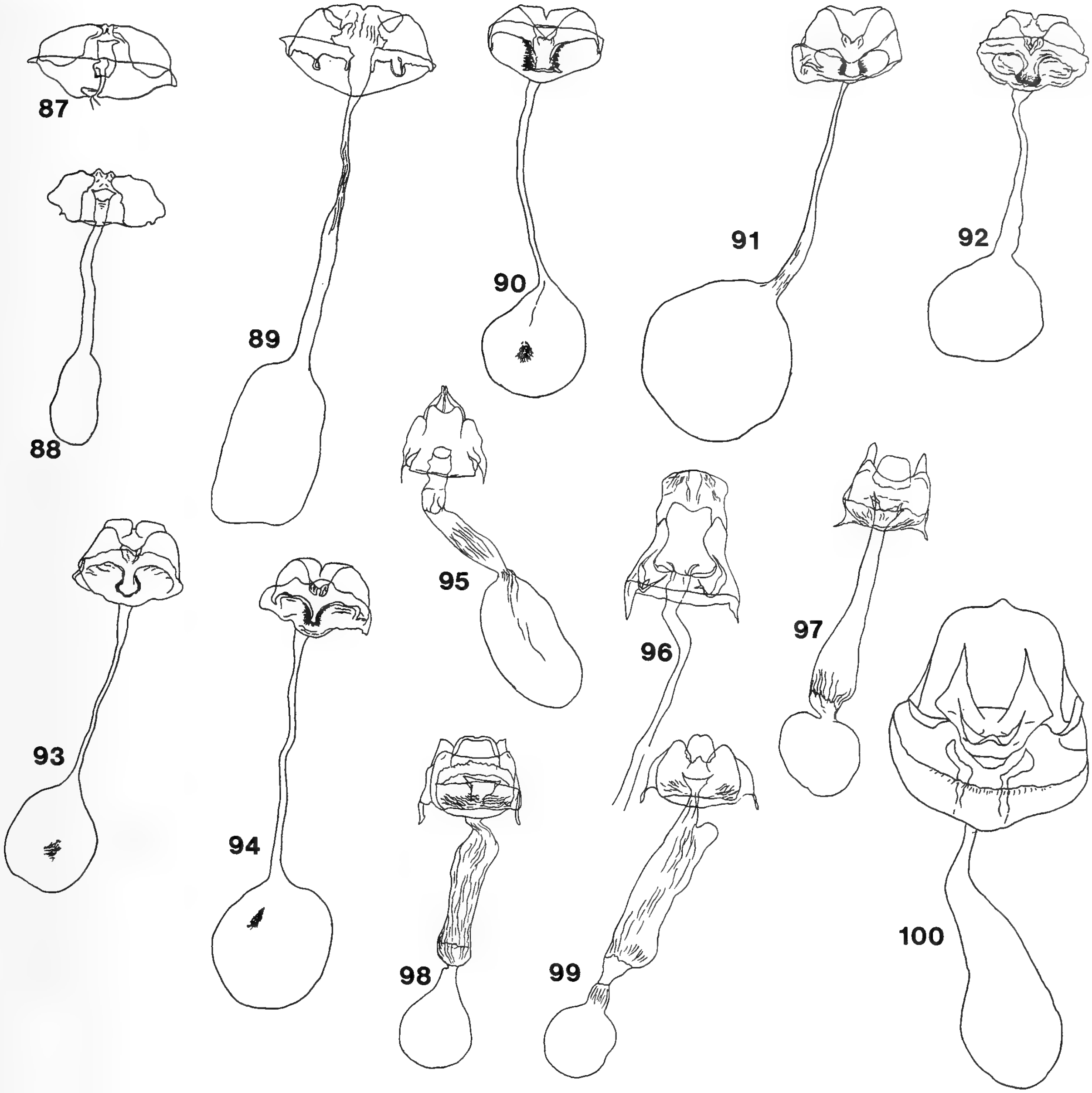
macules; veins black, those enclosing end of discal cell directed towards proximal edge of postmedian macule in CuA_1–2A. Hindwing with extensive gray along anal margin and basad where broadest, extending to vein Rs as usually distinct postmedian line; submarginal series of chevron-shaped gray-brown macules; veins entirely black. Venter with dorsal pattern less distinct especially centrally on forewing.

Head black on dorsum with white central patch, white beneath antennae and around eyes, antennae black with white at segments, pale yellow beneath club, nudum red-brown with 18 (N = 1) segments, palpi mixed white and dark gray on dorsum, white ventrally; thorax brown with scattered white scales on dorsum, gray on venter, legs brown with white scales, mid-tibiae with single pair of spurs, hind tibiae with two pairs, no tibial tuft; abdomen gray on dorsum with white at segments, white on venter.

Genitalia - tegumen short with relatively narrow recurved flaps caudad supporting anterior part of broad and enclosing vinculum; vinculum relatively straight; saccus slender, slightly upturned; uncus shorter than tegumen, shallowly divided with second pair of lateral processes caudad and rounded ventral lobes; gnathos broadly divided, relatively short, abruptly curved in lateral view; valva stout, ampulla with broad, pointed and slightly spiculose style curved inward and oriented predominently caudad, harpe curved upward, caudal end rounded with nearly dorsad orientation and dentate with spine-like hooks, robust in dorsal view, tuft of long bristles originating from ventral edge just before caudal dentate portion; aedeagus nearly straight, slender, caudal end narrowly spatulate, lateral hook-like projection on right side near caudal end.

Female - forewing length = 21.1 mm (20.4–21.8, N = 3); similar to male, antennal nudum with 18 (N = 1) or 19 (N = 3) segments.

Genitalia - lamella postvaginalis moderately broad, caudal end curved gradually to narrow V-shaped central notch; lamella antevaginalis with relatively broad lateral lobes and a narrow central process flared slightly at cephalad edge, this process heavily spiculose laterad and cephalad, "windows" narrowly ovate; posterior 1/2 of sterigma covered by transparent mem-



FIGS. 87–100. Female genitalia (ventral view) of *Mylon*, *Carrhenes*, and *Clito* (from BRAZIL: Rondônia unless noted otherwise). **87.** *M. lassia*, COSTA RICA (GTA #7357); **88.** *M. mestor*, ECUADOR (GTA #7384); **89.** *M. menippus* (GTA #7350); **90.** *M. pelopidas*, MEXICO (GTA #7339); **91.** *M. jason* paralectotype, VENEZUELA (GTA #7309); **92.** *M. exstincta* holotype, "Amazone Supérieur" (GTA #5983); **93.** *M. argonautarum* paratype (GTA #7323); **94.** *M. cristata* paratype, GUATEMALA (GTA #7333); **95.** *Carrhenes chaeremon* (GTA #7456); **96.** *C. bamba* (GTA #7361); **97.** *C. leada* (GTA #3601); **98.** *C. recurva* paratype (GTA #7460); **99.** *C. canescens*, MEXICO (GTA #7369); **100.** *Clito clito* (GTA #8278).

brane; ductus bursae gradually expanded caudad, very long and very narrow cephalad; corpus bursae globular with net-like mass of signum.

Types. Holotype male with the following labels: white, printed and handprinted - GUATEMALA / Petén; Parque / Nacional Tikal / 16 April 1992 / leg. N. M. Haddad / piste; white, printed and handprinted - Genitalia Vial / GTA - 2639; red, printed - HOLOTYPE / *Mylon cristata* / Austin. Paratypes - same location as holotype, 2 Feb. 1992 (1 female, GTA #7344), 3 Feb. 1992 (1 female, GTA #7335), 5 Feb. 1992 (1 male, GTA #7330), 31 May 1993 (1 female, GTA

#7316), 15 July 1993 (1 female, GTA #7333). The holotype male and a paratype female will be deposited in the Entomological Collections at the Universidad del Valle, Guatemala City, Guatemala. *Type locality.* GUATEMALA: Petén; Parque Nacional Tikal. The types were taken at flowers in disturbed areas near the edge of forest and along roads.

Etymology. The name means tufted and refers to the bristles on the caudal end of the harpe.

Diagnosis and discussion. Superficially, *M. cristata* appears distinctly mottled and, as such, resembles *M. pelopidas* and *M. jason*. It is at once distinguished from *M. pelopidas* by the orientation of the end of the forewing discal cell towards the proximal edge of the dark macule in CuA$_2$–2A. *M. jason* is very similar, perhaps averaging less heavily marked, but the genitalia will need to be examined for determination of most individuals. The dorsa of *M. exstincta*, *M. simplex*, and *M. argonautarum* are less mottled. The male genitalia of *M. cristata* are generally like the preceding four species, are most similar in overall form to those of *M. jason*, but have the less robust aspect of the tegumen and uncus and the caudal tuft of bristles on the harpe as do the genitalia of *M. argonautarum*. The female genitalia generally resemble those of *M. jason*, but the central process of the lamella antevaginalis is much narrower and more heavily spiculose to include the cephalad edge.

The types of *M. cristata* were encountered while examining comparative material for the Rondônia study and were originally identified as *M. jason* (Austin et al. 1996) and included in series with the females of that species also from the same area of Guatemala. The material listed by Holland (1927), Evans (1953), and others as *M. jason* needs to be reexamined and correctly identified and undoubtedly mixed series determined as *M. jason* exist in many collections. The *M. "jason"* illustrated by Hayward (1947, 1948) resemble *M. cristata* more than they do *M. argonautarum* or may represent yet another undescribed species of this group.

Distribution and phenology. At present, *M. cristata* is known only from the types taken in February, May, and July and a male examined from Colombia (Cesar, La Jaque, 15 km S Becerril, 20 July 1969, AME). This species is undoubtedly more widespread judging by the discussion in Holland (1927, see also above under *M. jason*).

Key to the males of the "*pelopidas*" group species of *Mylon*

1. End of forewing discal cell erect, not parallel to termen, oriented towards distal edge of dark macule in cell CuA$_2$–2A; harpe elongate, slender, not upurned or prominently toothed . . . . *pelopidas*
   End of forewing discal cell angled, parallel to termen, oriented towards proximal edge of dark macule in cell CuA$_2$–2A; harpe short, broad, blunt, upturned and prominently toothed 2
2. Harpe without caudal bristles 3
   Harpe with caudal bristles 5
3. Harpe robust (especially in dorsal view) with robust teeth; tegumen elongate; dorsal wings mottled . . . . *jason*
   Harpe less robust, relatively thin in dorsal view, teeth smaller; tegumen shorter; dorsal wings less distinctly mottled 4
4. Harpe triangular in lateral view, style with prominent dorsal orientation . . . . *simplex*
   Harpe not triangular in lateral view, style with orientation more caudal . . . . *exstincta*
5. Harpe triangular in lateral view, style more erect; dorsal wings not prominently mottled, southern Neotropics . . . . *argonautarum*
   Harpe not triangular in lateral view, style more caudad in orientation; dorsal wings mottled, northern Neotropics . . . . *cristata*

Key to the known females of the "*pelopidas*" group species of *Mylon* (female of *M. simplex* unknown)

1. End of forewing discal cell erect, not parallel to termen, oriented towards distal edge of dark macule in cell CuA$_2$–2A; central process of lamella antevaginalis broad, flared cephalad, spiculose on lateral edges; "windows" broad and rectangular . . . . *pelopidas*
   End of forewing discal cell angled, parallel to termen, oriented towards proximal edge of dark macule in cell CuA$_2$–2A; genitalia without above combination of characters 2
2. Central process of lamella antevaginalis narrow, densely spiculose on lateral and cephalad edges; wings distinctly mottled . . . . *cristata*
   Central process of lamella antevaginalis broad, not densely spiculose on cephalad and/or lateral edges; wings distinctly mottled or not 3
3. Central process of lamella antevaginalis gradually expanded cephalad where lobate, spiculose laterad, "windows" ovate; wings weakly mottled . . . . *argonautarum*
   Central process of lamella antevaginalis expanded only at cephalad end, not lobate, spiculose on cephalad and/or lateral edges; "windows" ovate or round; wings distinctly mottled or not 4
4. Wings distinctly mottled; central process of lamella antevaginalis spiculose only on lateral edges; "windows" round . . . . *jason*
   Wings weakly mottled; central process of lamella antevaginalis spiculose on lateral and cephalad edges; "windows" ovate . . . . *exstincta*

CARRHENES GODMAN & SALVIN, 1895

Four species of *Carrhenes* were recognized by Evans (1953). Steinhauser (1974) raised one species from synonymy and (1989) described two additional species and raised one of Evans' (1953) subspecies to the specific level. The genus occurs from Mexico (one species straying into southern Texas) to Argentina. Four species have been encountered in central Rondônia, of which one is undescribed. These are present mainly in the early wet season and are virtually absent during the dry season (Figs. 109, 110). Female genitalia are illustrated for the first time.

"fuscescens" group

The *"fuscescens"* group of *Carrhenes* (proposed by Steinhauser 1989) is readily recognized by the prominent expansion of the ampulla of the male valva. All species, except *Carrhenes infuscescens* Steinhauser, 1989, appear to have prominent mid-costal hyaline macules on the forewing. The group includes *Carrhenes fuscescens* (Mabille 1891), *Carrhenes calidius* Godman & Salvin, 1895, *Carrhenes bamba* Evans, 1953, *Carrhenes sinesinus* Steinhauser, 1989, and *C. infuscescens*. Two species, including one raised from subspecific status below, were found in central Rondônia.

Carrhenes chaeremon (Mabille 1891), **revised status**
(Figs. 22, 23, 73, 95)

Leucochitonia chaeremon Mabille, 1891.
Carrhenes fuscescens chaeremon (Mabille 1891): Evans, 1953.

A *"fuscescens"* group species of *Carrhenes* from central Rondônia similar to, but smaller than, the sympatric *C. bamba* and with different genitalia appears to be *C. chaeremon*. Evans (1953) included this as a subspecies of *C. fuscescens*. Its male genitalia, however, are more similar to those of *C. calidius* than to *C. fuscescens*, especially in the configuration of the ampulla process and the tooth on the right side of the aedeagus. *C. chaeremon* has an additional smaller tooth on the left side of the aedeagus and lacks the row of small teeth on the left side of the vesica opening seen on *C. calidius* (and *C. fuscescens*). The female genitalia have a narrow and pointed lamella postvaginalis and an elongate lamella antevaginalis with a broad central process and resemble those of *C. bamba*. Because of the genital differences, *L. chaeremon* is here returned to specific status.

C. chaeremon is rare in central Rondônia with records for February, March, May, and November (Fig. 110).

Carrhenes bamba Evans, 1953
(Figs. 24, 25, 74, 96)

C. bamba was described as a subspecies of *C. fuscescens* by Evans (1953). Based on differences in genitalia and sympatry with *C. calidius*, Steinhauser (1989) raised this taxon to specific status (see also Steinhauser 1974). Further reinforcing its specific distinctness from other *"fuscescens"* group taxa, *C. bamba* is sympatric with *C. chaeremon* in central Rondônia. There, it is the most abundant of the *Carrhenes* with records in January through May and July through December (Fig. 109). The genitalia of males from Rondônia are as illustrated by Steinhauser (1989). The female genitalia are particularly distinctive with their elongate sterigma, quite different from those of *C. fuscescens*.

"canescens" Group

The *"canescens"* group includes the remaining species of *Carrhenes*, *Carrhenes canescens* (R. Felder, 1869), *Carrhenes callipetes* Godman & Salvin, 1895, and *Carrhenes santes* Bell, 1940 plus, as follows here, two taxa raised to specific status and one new species. Males do not have the produced ampulla on the valva as seen on *"fuscescens"* group species and the forewing is without mid-costal hyaline macules.

Carrhenes leada (Butler, 1870), **revised status**
(Figs. 26, 27, 75, 97)

Achlyodes leada Butler, 1870.
Carrhenes canescens leada (Butler, 1870): Evans, 1953.

The taxa of *C. canescens* (*sensu* Evans 1953) are in need of more study. Subtle differences in genitalia and superficial markings and potential sympatry indicate that more than one species is involved, but their combinations will not be clear until the group is revised. Evans (1953) noted that the taxa "seem to have 2 seasonal forms" ("dark" and "whitened"). In Mexico and Central America, for example, the two "forms" included in *C. c. canescens* (Figs. 31–33) have different male genitalia (Figs. 76, "dark" form; 77, "whitened" form).

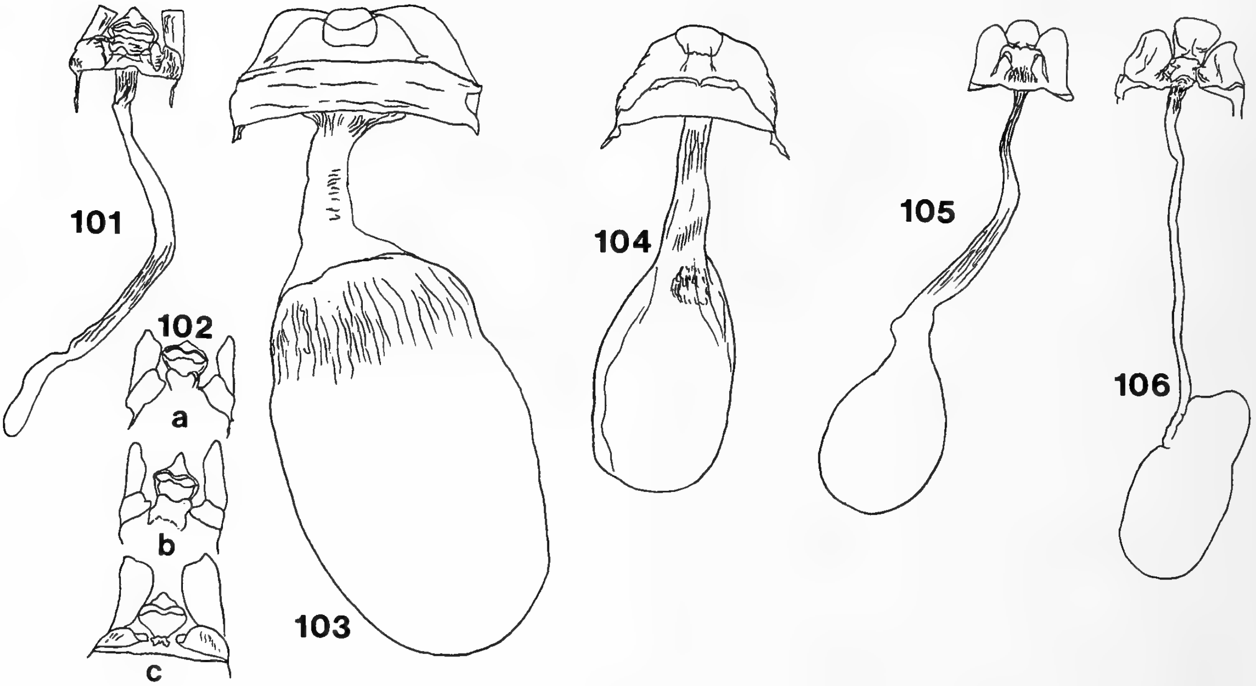
In central Rondônia, the *"canescens"* group is represented by two species. One of these is of the *Achlyodes leada* Butler, 1870, concept. It differs from both apparent taxa of the *"canescens"* group from Mexico and Central America by its shortened and less flaring uncus, the configuration of the valva (ampulla process, harpe, sacculus), and in the shape of the aedeagus. In this latter character, the butterfly from Rondônia resembles Hayward's (1939) figure of *Carrhenes leada* although the valva appears different (less curved harpe, different shape to ampulla), but this may be individual variation. Because of its genitalic differences from *C. canescens* (Figs. 75–77, 97, 99), *C. leada* is here considered as a species.

C. leada is rare in the Cacaulândia area with single records for June and August and three for November (Fig. 110).

Carrhenes lilloi Hayward, 1947, **revised status**
(Figs. 30, 78)

Carrhenes lilloi Hayward, 1947.
Carrhenes canescens pallida Röber, 1925: Evans, 1953.

Hayward (1947) described *C. lilloi* from the holotype from Macas, Rio Upano, Ecuador, and included



FIGS. 101–106. Female genitalia (ventral view) of *Xenophanes*, *Antigonus*, and *Anisochoria* (from BRAZIL: Rondônia unless noted otherwise). **101.** *X. tryxus* (GTA #7388); **102.** *Xenophanes tryxus*, variation of lamellae, **a.** (GTA #7465), **b.** (GTA #7387), **c.** MEXICO (GTA #7466); **103.** *Antigonus nearchus* (GTA #7472); **104.** *A. erosus* (GTA #3958); **105.** *A. liborius* (GTA #7385); **106.** *Anisochoria pedaliodina pedaliodina* (GTA #7469).

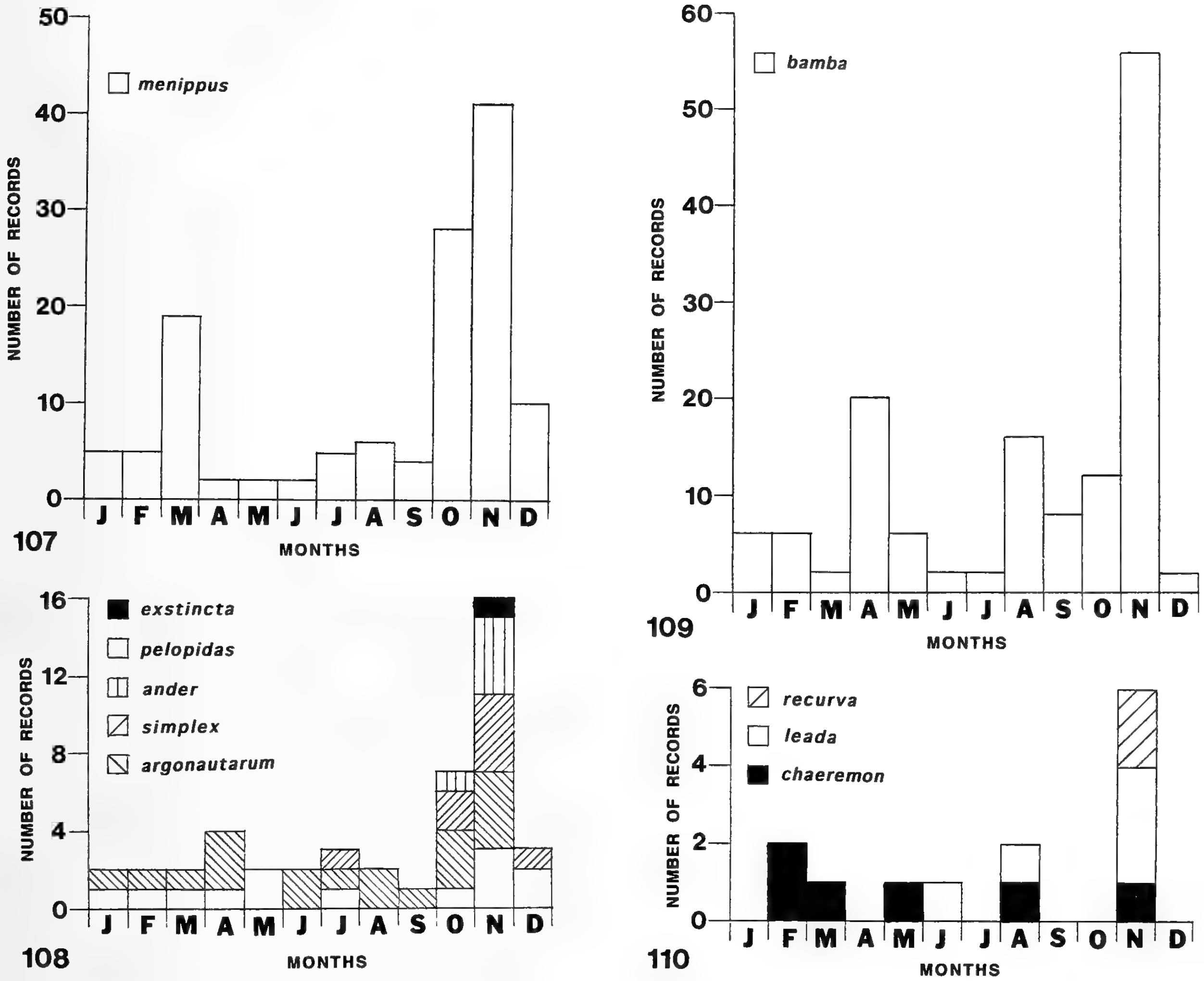
eight specimens from Argentina as paratypes. He noted that the markings on the paratypes were very faint in comparison with the holotype. This taxon was synonymized with *Carrhenes canescens pallida* Röber, 1925, by Evans (1953) with his usual lack of justification. Mielke (1989) examined the holotype of *Carrhenes pallida* and commented that *C. c. pallida* was a subspecies known from southern Brazil, Paraguay, and Argentina. The paratypes of *C. lilloi* actually are *C. c. pallida* (*fide* Mielke). A more recently taken male from Ecuador (Rio Napo, Limoncocha, 10 July 1983) is here illustrated, shows superficial and genitalic characters more or less like those in the figures by Hayward (1947, 1948, one or both of these may be of specimens from Argentina and thus *C. c. pallida*), and is obviously different from other taxa of *C. canescens* (*sensu* Evans 1953). This specimen from Ecuador is taken to represent *C. lilloi* and, as such, the taxon deserves specific status. It is superficially similar to *C. leada* from Rondônia, but is paler. The genitalia also differ (Figs. 75, 78). On *C. lilloi*, the uncus is narrower than on *C. leada*, the process from the ampulla is longer, broader and not twisted at its distal end, the harpe is broader and bifurcate, and the aedeagus is more abruptly curved cephalad in lateral view.

Carrhenes recurva **Austin, new species**

(Figs. 28, 29, 79, 98)

Description. Male - forewing length = 16.2 mm (holotype); forewing with costal fold; dorsum pale gray-brown, outer one-third of both wings darker; forewing marked with darker gray-brown as submarginal band from costa to anal margin leaving margin of paler ground color, incomplete postmedian band most prominent towards costa and in CuA$_2$–2A, indistinct postbasal band, and dark wing base; three white hyaline subapical macules in R$_3$–R$_4$, R$_4$–R$_5$, and R$_5$–M$_1$, central one smallest and set just proximad of other two; small white hyaline macule near base of Sc–R$_1$; additional small white hyaline macule near base of M$_3$–CuA$_1$. Hindwing also with dark markings; submarginal band as on forewing, postmedian band of quadrate macules posteriad becoming smaller and nearly lineal anteriad; vague postbasal macules, wing base dark. Venter much paler than dorsum and with glossy sheen; markings, especially on forewing, reduced.

Dorsal head and thorax dark brown with scattered white scales, white around eyes, palpi missing, antennae black with white at segments on inner side becoming most prominent distad, pale yelow beneath club,



FIGS. 107–110. Phenology of some Hesperiidae in the vicinity of Cacaulândia, Rondônia, Brazil. **107.** *Mylon menippus*; **108.** several *Mylon* species; **109.** *Carrhenes bamba*; **110.** *Carrhenes chaeremon*, *C. leada*, and *C. recurva*.

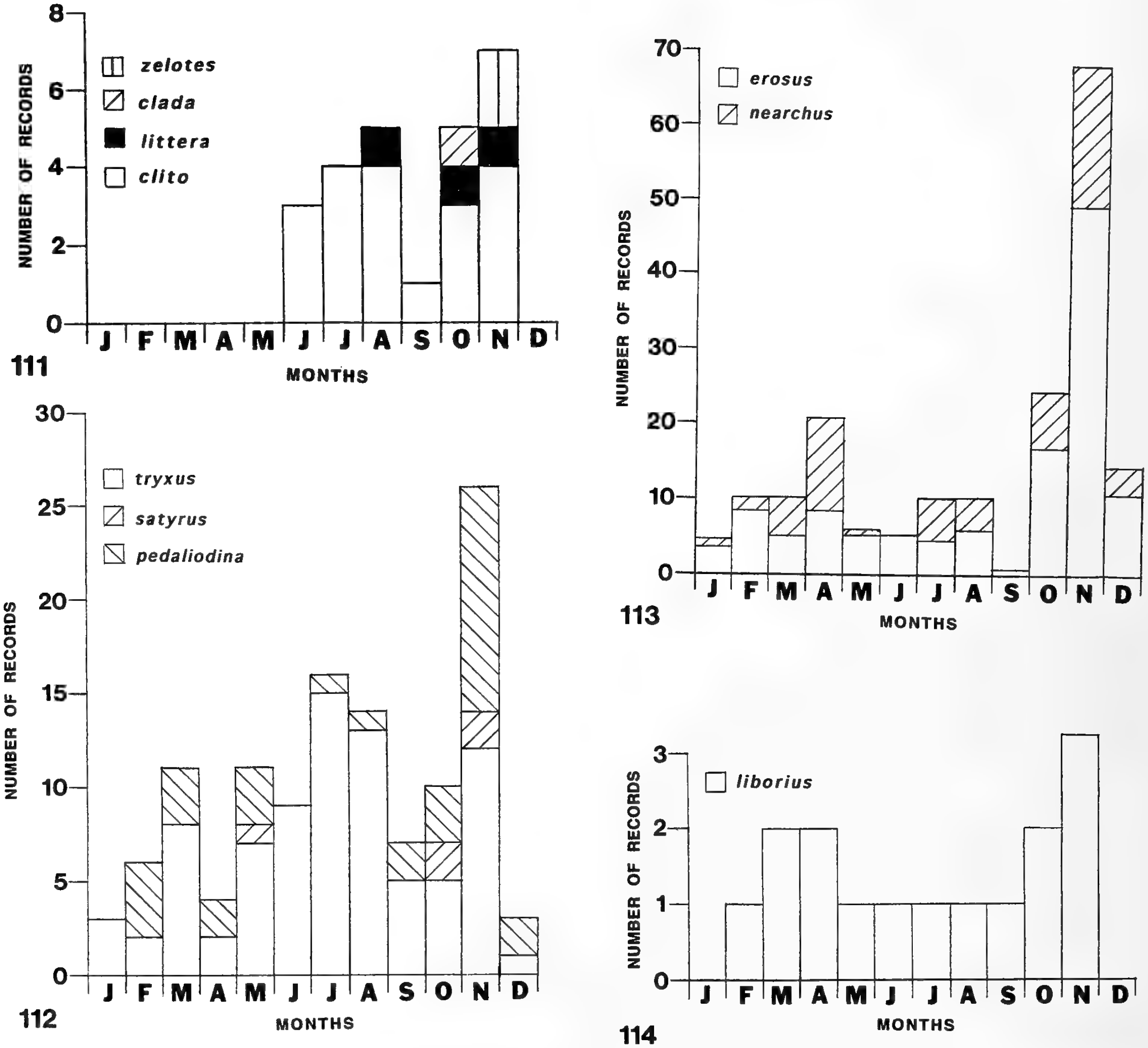
nudum black, 16 segments; ventral thorax white, legs pale ochre and black with white hairs, mid-tibia with single pair of spurs, hind tibia with two pairs and long dark gray hair-tuft fitting into thoracic pouch.

Genitalia - tegumen short and broad, narrowed caudad; uncus divided, arms narrow and slightly divergent; gnathos divided; valvae symmetrical, ampulla with thin lobe having slight caudal orientation extending inward from its highest point, harpe blade-like, curving upward and slightly inward, edges weakly toothed; sacculus with spiculose process extending caudad from upper edge, this curved very slightly downward; aedeagus short, strongly recurved, phallobase bulbous.

Female - forewing length = 16.6 mm (paratype); similar to male; no costal fold or tibial tuft; dark markings more distinct; forewing subapical macules larger than on male with additional macule in M_1–M_2 under outer edge of macule in R_5–M_1; macule in M_3–CuA_1 larger than on male; additional small triangular macules anteriorly and posteriorly in CuA_1–CuA_2 under end of discal cell; large divided hyaline macule in discal cell 2/3 distance from base; palpi black above, white below; nudum red-brown, 15 segments.

Genitalia - sterigma more or less quadrate, lamella postvaginalis represented by short lateral lobes extending caudad about same distance as broad central lobe of lamella antevaginalis, antrum flared caudad, ductus bursae broad, constricted cephalad where joining narrow and elongate corpus bursae.

Types. Holotype male with the following labels: white, printed - BRASIL: Rondonia / B-65, 3 km N



FIGS. 111–114. Phenology of some Hesperiidae in the vicinity of Cacaulândia, Rondônia, Brazil. **111.** several *Clito* species; **112.** *Xenophanes tryxus*, *Timochreon satyrus*, and *Anisochoria pedaliodina*; **113.** *Antigonus nearchus* and *A. erosus*; **114.** *Antigonus liborius*.

C-20 / 8 km N Cacaulandia / 1 Nov. 1990 / leg. G. T. Austin; white, printed and handprinted - Genitalia Vial / GTA - 1170; yellow, printed - photographed / G. T. Austin & / J. P. Brock / March 1992; red, printed - HOLOTYPE / *Carrhenes recurva* / Austin. Paratype - BRAZIL: Rondônia; "Fernandes Trail" off B-65, 1 km N of Cacaulândia, 5 Nov. 1990 (1 female, GTA #7460). Both will be deposited at the Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil. *Type locality.* BRAZIL: Rondônia; road B-65, 8 kilometers north of Cacaulândia, 170 m elevation in disturbed, but otherwise typical, lowland tropical rainforest.

Etymology. The species is named after the strongly recurved aedeagus.

Diagnosis and discussion. *C. recurva* closely resembles other "*canescens*" group species, but especially the "whitened" phenotype of *C. "canescens"* from Central America. It differs from the sympatric *C. leada* by the apparent larger size, the more rounded wings, the more heavily marked dorsum (note that on *C. leada*, the forewing markings are prominent only in the apical area), the broader and less upcurved harpe, and the more recurved and slender aedeagus. The male genitalia of *C. recurva* differ from those of *C. canescens* by their shorter processes from the uncus, more triangular valva, broader sacculus, more inwardly directed process from the ampulla, and broader harpe. The female genitalia differ from those of *C. leada* by the broader sterigma, the relatively broad ductus bursae, and the more elongate corpus bursae.

Distribution and phenology. At present, the species is known only from the types taken in November (Fig. 110).

CLITO EVANS, 1953

Clito includes seven Neotropical species recognized by Evans (1953); an additional species was described by de Jong (1983). The genus occurs from Mexico to Bolivia and Brazil, but most species appear to be rare and not widely distributed. Four species are known from the Cacaulândia area of which one was included in another genus. These have been recorded in the dry and early wet seasons (Fig. 111).

Clito clito (Fabricius, 1787)

(Figs. 46, 47, 68, 100)

C. clito is the most frequently encountered member of the genus in central Rondônia and is represented by records in June to August, October, and November (Fig. 111). Its male genitalia are as illustrated by Evans (1953). Female genitalia have a spiked lamella antevaginalis, a short and thin ductus bursae, and an elongate and bulbous corpus bursae.

Students of *Clito* should be aware that *Hydraenomia aberrans* Draudt, 1924, described from Tefe (Amazonas, Brazil), may represent a recognizable taxon. A single male of *C. "clito"* examined from Costa Rica is pale (Fig. 48) and has genitalia different (Fig. 69) from those of *C. clito* from Rondônia and appears to be of that concept. *H. aberrans* was considered a synonym of *C. clito* by Evans (1953) and Mielke (1993); more material needs to be examined to determine its status.

Clito littera anda Evans, 1953

(Figs. 49, 70)

C. littera is apparently a very rare species. Evans (1953) saw only the type of *Clito littera littera* (Mabille, 1977), saw no specimens of *Clito littera nebulosa* (Draudt, 1924), and the type and an additional male of *C. l. anda*. Mielke and Casagrande (1991) obtained the first example of this species from Brazil in Roraima. Four males, taken in August, October, and November (Fig. 111), are known from the Cacaulândia area and extend the distribution far southward. The genitalia resemble those illustrated by Evans (1953).

Clito zelotes (Hewitson [1873])

(Figs. 50, 71)

Two males of *C. zelotes* are known from central Rondônia, both taken in November. Their genitalia are as shown by Evans (1953).

Clito clada Evans, 1953, **new combination, new status**

(Figs. 51, 72)

Eracon menmon clada Evans, 1953.

Description. Male - forewing length = 12.2 mm (N = 1); forewing with costal fold, termen evenly convex except slightly concave in CuA$_2$–2A; hindwing termen weakly undulate, concave in M$_1$–M$_3$ and M$_3$–CuA$_2$; dorsum brown; forewing overscaled with gray except in submarginal, median, and postbasal areas which remain ground color and appear as dark macular bands; white hyaline macules as follows: discal cell, proximal edge straight, distal edge excavate in V-shape; CuA$_1$–CuA$_2$, curvate bar, more distad than discal cell macule, proximal edge at origin of vein CuA$_1$; M$_3$–CuA$_1$, near base of cell; series of small subapical in R$_3$–R$_4$, R$_4$–R$_5$ (smallest, offset proximad), and R$_5$–M$_1$, continued as similarly-sized submarginal macules offset distad in M$_1$–M$_2$ and M$_2$–M$_3$; fringe dark gray; hindwing overscaled with gray distad, proximad with many long hair-like gray scales in discal cell and along vein 2A; narrow, irregular whitish bands in submarginal and median areas and whitish postbasal bar in discal cell; fringe gray, paler than on forewing.

Venter similar to dorsum; brown ground color paler; forewing with much less (only submargin and along costa) and hindwing with much more (covering nearly entire wing) gray overscaling; forewing with opaque white macule in upper portion of CuA$_2$–2A, more proximad than macule in CuA$_1$–CuA$_2$; anal margin broadly gray; hindwing with whitish bands more prominent.

Head dark brown with many gray scales; palpi black above with a few white scales, white beneath; antennae black with white at segments distad and entirely white proximad beneath, nudum gray, 19 segments; thorax dark brown above and heavily overscaled with gray, white beneath; middle and hind legs missing; dorsal abdomen dark brown with gray at segments and heavily overscaled with gray, ventral abdomen white.

Genitalia - tegumen long, thin, with lateral lobes sloping ventrad; uncus undivided, slightly shorter than tegumen, narrow in both lateral and ventral views; gnathos undivided, shorter than uncus; vinculum thin, slightly sinuate; saccus short, stout, blunt; valva with broad costa and narrower ampulla, ampulla with dorsal margin serrate, harpe curved dorsad to fine and sharply pointed tooth; aedeagus short, stout; cornutus as series of short spikes; juxta and transtilla fused into prominent sheath enclosing aedeagus.

Discussion. This species was described as a subspecies of *Eracon mnemon* (Schaus, 1913). *C. clada* is obviously different from that species in being smaller, having more rounded forewings, having hindwings not produced at the tornus, and having a more well-developed hindwing pattern (see figure of *E. mnemon* in Schaus 1913). Further, although this taxon was included in *Eracon* Godman & Salvin, 1894, by Evans (1953), the generic placement of *C. clada* was initially unclear because of its wing shape, markings, and small size. The pattern of its markings and, especially, its genitalia, with the thin and undivided uncus, the form of the gnathos, the aspect of the valva, and the sheathed aedeagus indicated that it was a member of the genus *Clito*.

A single male of *C. clada*, taken in October, was seen from central Rondônia.

XENOPHANES GODMAN & SALVIN, 1895

The single species of *Xenophanes* occurs from Mexico to Argentina with strays occurring north into southern Texas.

Xenophanes tryxus (Stoll [1780])
(Figs. 34, 35, 80, 81, 101, 102)

X. tryxus is not uncommon in the Cacaulândia area with records in all months, but is most common in the dry and early wet seasons (Fig. 112). The species varies superficially in color (gray to dark gray-brown) and in the size of the hyaline macules. This does not seem to be seasonal variation, at least in Rondônia; the only seasonal variation is an apparently larger size among early wet season individuals.

The previously illustrated male genitalia of *X. tryxus* (Godman & Salvin 1895, Lindsey et al. 1931, Hayward 1933, 1948, Bell 1942, Evans 1953) exhibit a variety of valval configurations and three (Bell 1942, Hayward 1948, Evans 1953) show asymmetry. This latter, prominent in material from Rondônia, involves the ventral portion of the right harpe generally extending caudad of its dorsal lobe while the left harpe curves dorsad (Figs. 80, 81). The shape and size of the harpes vary not only locally, but also geographically. For example, the left harpe of Central American *X. tryxus* is more massive than it is in Rondônia. There is also variation, local as well as apparent geographic, in the female genitalia (Figs. 101, 102). These differences need to be examined in collections with a broad geographic scope.

ANTIGONUS HÜBNER, [1819]

Antigonus, distributed from Mexico to Argentina, includes nine species recognized by Evans (1953) and another described by Mielke (1980). Three species have been seen at the Rondônia study area. These occur throughout the year, but are most prevalent during the early wet season (Figs. 113, 114).

Antigonus nearchus (Latreille [1817])
(Figs. 38–41, 84, 103)

A. nearchus is relatively common in the Cacaulândia area and is often found at mud. Records are for January through May, July, August, and October through December (Fig. 113).

The most common form of male *A. nearchus* is very dark blackish brown with vaguely darker black bands. This predominates in the wet season, when there also occurs a rare brown form. During the dry season, the dorsum of most individuals is grayer on which the black bands are more conspicuous. The venter is palest on the gray form and darker on the brown form, but not as dark as on the black form. A single female seen from July (dry season) is paler than one from November (wet season).

The male genitalia of *A. nearchus* were previously illustrated by Godman and Salvin (1879–1901), Hayward (1933, 1948), and Evans (1953). Those of Rondônia material are typical. The female genitalia have a broad and short sterigma, a short and stout ductus bursae, and a large and oblong corpus bursae.

Antigonus erosus (Hübner [1812])
(Figs. 42–45, 85, 104)

A. erosus is the most abundant *Antigonus* in central Rondônia with records from all months (Fig. 113). Like *A. nearchus*, the species is frequently encountered at mud.

A. erosus exhibits seasonal forms as does *A. nearchus*. Throughout the year, males are heavily overscaled with gray and vaguely marked with darker bands. Dry season males are paler gray than they are in the wet season. Individuals from the dry season and early wet season have three prominent subapical macules; these are vague or absent at other times of the year. The venter is palest during the dry season. Females are very variable and too few were seen from the dry season to examine the seasonal distribution of their variation. The ground color of females varies from tan with prominent dark brown bands to dark brown and overscaled with gray and they have 2–4 subapical macules. Some have additional hyaline macules including one or two in the discal cell, a large one in CuA_2–2A, and a smaller one in CuA_1–CuA_2.

The male genitalia have been illustrated several times (Godman & Salvin 1895, Hayward 1933, 1948, Evans 1953). The female genitalia are similar to those of *A. nearchus*, but have a narrower sterigma and a less robust corpus bursae.

Antigonus liborius liborius Plötz, 1884
(Figs. 36, 37, 86, 105)

A. liborius is rare in central Rondônia, but records occur throughout much of the year from February through November (Fig. 114).

Apparent seasonal variation is shown by *A. liborius* in Rondônia. Five males from the wet season are dark brownish black on the dorsum with vaguely darker bands. All five have a single subapical macule. One has a minute mid-costal macule and a lower one in the discal cell; the others are without these and all lack discal macules. The two dry season males seen are paler brown with more contrasting bands. One has single subapical and mid-costal macules. The other has three subapical macules, a mid-costal macule, a minute macule near the base of M_3–CuA_1, and a large one in the middle of cell CuA_1–CuA_2. Six females from the late dry and early wet seasons are brown with conspicously contrasting black bands, have 1 to 3 subapical macules, have a usually prominent mid-costal macule (absent on one), usually have a macule in CuA_1–CuA_2 (this entire, divided, or only with the lower portion hyaline; absent on one), and two have a hyaline macule in M_3–CuA_1. A single female from the early wet season is darker with less contrasting bands and a single subapical, but no other, hyaline macule. The ventral hindwing of males is contrasting medium gray-brown distad on the posterior 1/2 of the wing. Females are much paler here. Evans (1953) did not mention seasonal variation in this species. Additionally, care should be taken in using Evans' (1953) key to superficial characters since the mid-costal macule may be absent on some *A. liborius*.

The male genitalia of *A. liborius* from Rondônia appear as those previously illustrated (Hayward 1948, Evans 1953). The sterigma of the female genitalia has an overall form similar to those of *A. nearchus* and *A. erosus*, but is much narrower. The ductus bursae is long and relatively thin and the corpus bursae is bulbous.

TIMOCHREON GODMAN & SALVIN, 1896

Two species of *Timochreon*, distributed from Panama to Brazil, were recognized by Evans (1953). One species occurs in central Rondônia.

Timochreon satyrus tampa Evans, 1953
(Figs. 54, 82)

T. satyrus is rarely seen in the Cacaulândia area with records for May, October, and November (Fig. 112). The valva of *T. s. tampa* was illustrated by Evans (1953); the aedeagus has a prominent thorn-like structure on the right side of its dorsum.

ANISOCHORIA MABILLE, [1877]

Eight species were included by Evans (1953) in *Anisochoria* and Nicolay (1980) described another. These range from Mexico to Argentina; one is known from central Rondônia.

Anisochoria pedaliodina pedaliodina (Butler, 1870)
(Figs. 52, 53, 83, 106)

A. pedaliodina is relatively common in the Cacaulândia area with records for February through May and July through December, mostly in the early wet season (Fig. 112). There is no apparent seasonal and little individual variation among this material.

The male genitalia of Rondônia material are as illustrated by Evans (1953) with asymmetrical valvae. Female genitalia have a relatively narrow lobate lamella postvaginalis, broad lateral lobes to the lamella antevaginalis, and a long and thin ductus bursae entering the side of a bulbous corpus bursae.

SUMMARY

This paper adds to the knowledge of the fauna of Hesperiidae in Rondônia, Brazil, and the Neotropics in general. Many of the species of seven genera of the "*Antigonus*" group are discussed and their genitalia are illustrated in more detail than before; for most, the female genitalia have never been illustrated. In all, three new species are described from Rondônia and one from Guatemala, a revised status is established for three taxa, a new status is proposed for two taxa, and a new combination is suggested for one species. The adds to the growing body of information on the taxonomy of this family of butterflies.

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DECLINE IN THE FREQUENCY OF THE WHITE MORPH OF THE MONARCH BUTTERFLY (*DANAUS PLEXIPPUS PLEXIPPUS* L., NYMPHALIDAE) ON OAHU, HAWAII

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ABSTRACT. The frequency of a white morph of the monarch butterfly *Danaus plexippus plexippus* on Oahu, Hawaii was observed to increase from less than 1% in 1965 to approximately 8% in 1988–1989, and then to decrease in the nine year period from 1988–1989 to 1997–1998 to about 1.7%. The increase was attributed to the accidental release in 1965 and 1966 of two species of predatory birds, selective predation of these birds on the orange morph and the supposedly greater crypsis of the white morph. It is proposed that the decrease in the proportion of the white morph has been caused by a change in the predatory behavior of these birds, a switch from predation on adults to predation on larvae. The larvae of the two morphs are indistinguishable.

Keywords: *Danaus plexippus,* polymorphism, white morph.

There are many examples of balanced and transient polymorphism in Lepidoptera. In most cases, the polymorphism involves a difference in wing colors or pattern. Polymorphism has also been observed in the larvae and pupae of some species (Clarke et al. 1963, Smith et al. 1988). Although many of these polymorphisms are thought to be the result of Batesian or Müllerian mimicry (Ford, 1953, Smith et al. 1993), the most famous example of polymorphism in Lepidoptera, that in *Biston betularia,* involves cryptic coloration. The frequency of the melanic phenotype of these moths increased dramatically in England, Netherlands, and the U.S. (Clarke et al. 1985, Brakefield 1990, Grant et al. 1996), but has declined since the 1950's. In Manchester, the melanic morph increased from 0% to 98% in 100 years (Kettlewell 1973); in Merseyside the melanic form decreased by 50% as pollution decreased and tree surfaces became lighter (Clarke et al. 1985). Polymorphism has also been observed in the butterfly *Danaus chrysippus* L. (Smith et al. 1993). Among four forms of *D. chrysippus* in Kampala, Uganda, the form *alcippus* increased from 16% to 71% and the form *aegyptius* decreased from 66% to 24% in approximately 80 years Hybridization, Batesian mimicry and Müllerian mimicry are thought to be involved in the origin of this polymorphism. The changes in frequency are thought to be due to recent habitat alteration; allopatric populations previously isolated by forest barriers are now hybridizing. Both these examples involved rapid change in morph frequency.

The monarch butterfly, *Danaus plexippus*, which appeared in Hawaii in the mid 1800's (Zimmerman 1958), is dimorphic for wing color on Oahu, Hawaii. In addition to the normal orange morph, there is a white morph which has white scales in place of orange on all wings (Riotte & Uchida 1978). The pattern of black scales is the same in both morphs. Genetic crosses have shown that the white morph is homozygous for an autosomal recessive allele (Stimson & Meyers 1984).

The history of the white monarch in Hawaii goes back to the 1890's. A white monarch from Hawaii was received in the mid 1890's by the Walter Rothschild collection (now in the Natural History Museum, London: Vane-Wright 1986). In Zimmerman's (1958) monograph of Hawaiian insects, there was no mention of a white morph in Hawaii, but in a collection of 600 monarch pupae made on Oahu by Mitchell (1966) in 1965, a small percentage, less than 1% of eclosing adults, were white individuals. In the early 1970's, the frequency of the white morph increased and reached approximately 5% by the mid 1980's (Stimson & Berman 1990).

Both morphs of the butterfly oviposit, feed and bask on the same host plant, the introduced milkweed *Calotropis gigantea*. These plants have large white inflorescences, and their leaves have a white pubescence, particularly on the underside. Stands of these plants occur in residential areas and attract large numbers of butterflies from November to February or March. When the butterflies are common at these stands, the introduced, insect-eating, red-whiskered bulbul (*Pycnonotus jacosus*) and red-vented bulbul (*Pycnonotus cafer)* can be seen searching inside the canopy for larvae and flying off with them to neighboring trees (pers. obs.).

Stimson and Berman (1990) suggested that the reason for the increase in frequency of the white morph

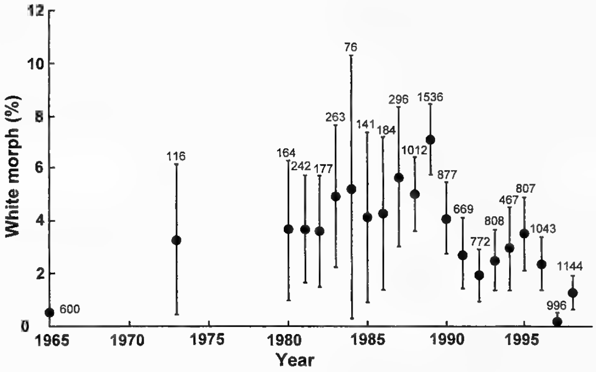

FIG 1. Proportion of white monarch adults emerging from pupae collected on the campus of the Univ. of Hawaii, Manoa, Oahu. The figure for 1965 is for a collection of 600 pupae made by Mitchell (1966). Vertical bars are 95% binomial confidence intervals for the proportions. The period of peak monarch abundance occurs in the winter spring and straddles the change in year; the annual proportion of whites has been plotted at the year of the spring of the peak. Values in association with each point are the numbers of monarch which eclosed and were scored each year.

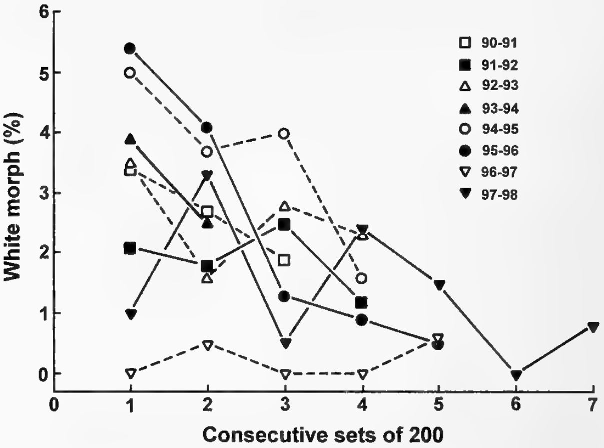

FIG. 2. Decrease in the proportion of white morph through each season during the years of decline of the proportion of the white morph in the University of Hawaii population on Oahu. All points are based on a minimum of 200 butterflies.

was predation by these birds. These birds escaped from captivity on Oahu in 1965 and 1966 (Williams 1983) and have spread to most areas of Oahu (Williams & Giddings 1984, R. Pyle, Bishop Musuem, pers. comm). Red-vented bulbuls occur at most lower elevations (<200 m) of Oahu. Red-whiskered bulbuls have a more restricted distribution and are more common in higher elevations and in the central parts of Oahu (Williams & Giddings 1984). The abundance of these two species of birds has increased about a thousand fold in Honolulu between the mid 1960's and the early 1980's according to the Audubon Christmas censuses (Williams & Giddings 1984). These birds are not deterred by the cardiac glycosides in the monarch's tissues and are documented to feed on monarch larvae and adults (Stimson & Berman 1990). The date of escape of these birds and the subsequent rise in frequency of the white morph coincide.

The white morphs were thought to be more cryptic than the orange form when associated with the milkweeds, because their white wings do not contrast with the whiteness of the inflorescences and the whiteness of the leaves caused by pubesence. Because of this presumed crypsis, it was proposed that white morphs had a lower risk of predation (Stimson & Berman 1990). The decrease in the proportion of white individuals since the 1988–1989 season requires a reexamination of this hypothesis. This study examines the change in frequency of white *D. plexippus* at one collection site on Oahu for the last 25 years and offers a possible explanation for the increase and decrease in frequency of the white morph.

MATERIAL AND METHODS

The frequency of the two morphs was determined at eclosion by collecting pupae from the field and scoring adults daily as they emerged in captivity. Pupae were collected from two stands of milkweed, *Calotropis gigantea*, at Edmondson Hall on the University of Hawaii campus, Honolulu, Oahu, Hawaii. The two stands are 60 meters apart on opposite sides of a building. Each stand consisted of 9 plants and each plant was approximately 1–2 m in diameter and 3 m tall. Other stands of plants occur on campus and in nearby residential neighborhoods. After the sex and morph of each adult was determined, the individuals were released. Since the 1987–1988 season, searches have been exhaustive, thus the numbers of adults in each morph are almost a complete collection of pupae produced at the Edmondson stands.

Bulbuls were observed to prey on larvae and adults at the stands of milkweed. After capturing adults the birds frequently took the prey to the ground, broke off their wings, and then flew off with the body. Birds were not seen consuming the bodies. During each of our searches for pupae, a search was also made for wings lying on the ground near the bushes.

RESULTS

Adult monarch butterflies are present the year-around on Oahu, but the peak of the breeding lasts for only 2–3 months, generally between December and February. During this period, individual milkweed plants can have hundreds of eggs and larvae, and in some years the bushes are stripped of leaves. As many as ten adults can be seen at any time at each of the two milkweed stands during the peak of abundance.

The proportion of white adults which emerged from pupae collected at each of the Edmondson stands increased during the 1970's and 1980's, and reached a peak of 7.3% in the 1988–1989 season (Fig 1). Since that season, there has in general been a decrease in the proportion of white individuals. In the latest season (1997–1998), only 1.7% of the collection were white individuals. A polynomial regression (binomial) was fitted to the data from 1980 on, i.e., when the sampling intervals were constant, 1 year apart. This regression shows that fitting the polynomial results in a significant reduction in unexplained sums of squares ($F = 12.85$, $df = 2,19$, $p < 0.0004$), and that there is a significant quadratic term. The signs of the terms of the polynomial indicate that the shape of the fitted curve is a hyperbola

$$(Y = -0.945 + 0.024X - 0.0001X^2).$$

To test whether the proportion of the white morph changed within each annual monarch season, the record of daily emergences within a peak season was divided in half, the first 50% of emergences, second 50% of emergences, and the proportion of white individuals in each half of the collection was calculated. Only peak seasons with collections of 200 or more pupae were used in this analysis. The proportion of the white morph was significantly higher in emergences from the first half of the peak season by a non-parametric Wilcoxon's sign rank test (16 peak seasons, $p < 0.05$). The proportion of white morph over the course of each season was also computed by dividing each season's emergences into consecutive groups of 200 emergences, and then calculating the proportion of white morph in each of these consecutive groups. The proportions calculated in each season were then plotted against date; the proportion of white individuals starts relatively high at the beginning of most seasons and then declines as the season progresses (Fig. 2).

During the 1980's, bulbuls could frequently be seen attacking flying adults. Many wings could be collected from the ground near or under the milkweed bushes during the annual peak season of monarch abundance. Since 1989–1990 season, fewer wings have been found (less than 10 per season), fewer attack on adult monarchs have been seen and bulbuls have been seen to prey more heavily on larvae than on adults. All these observations suggest that there is less opportunity for differential mortality of adults as a result of predation.

DISCUSSION

The proportion of white monarchs increased from 1966 to 1988–1989 and then decreased in the last nine years. An explanation for the increase in the proportion of white individuals, proposed in Stimson and Berman (1990), was that the white butterflies are less conspicuous against the whitishness of the pubesence of the leaves and the white of the flowers of *Calotropis gigangtea*, particularly when large numbers of butterflies frequented the milkweeds. As a result of this reduced conspicuousness if was proposed that the white individuals had a higher fitness than orange individuals. In support of this hypothesis is the fact that the increase in the proportion of white individuals in Honolulu appears to coincide with the date of escape of the two alien bulbul species on Oahu in 1965 and 1966 (Williams 1983). Following their escape these birds increased rapidly in the Honolulu area (Williams & Giddings 1984), and in the subsequent 15 years have spread into all the low elevation sites on Oahu where milkweeds are common (R. Pyle, Bishop Museum, pers. comm.). In the previous approximately 100 year history of the monarch in Hawaii the white individuals were evidently never very common. The differential predation exerted by these birds during the 1980's was detectable in the collections of wings; a higher proportion of orange wings were found in collections made from the ground around the bushes than the proportion of orange butterflies in the contemporaneous flying population (Stimson & Berman 1990). The role of these birds in causing the increase in frequency of the white morph is also supported by the fact that in collections of at least 100 butterflies made on Maui, Hawaii and Kauai in the late 1980's, the peak of abundance of the white morph on Oahu, no white butterflies were found. The lack of white individuals on these islands is consistent with the fact that bulbuls have not yet established breeding populations on islands other than Oahu, and thus the selective pressure for the increase in whites has not existed on these other islands.

The decline in the proportion of white individuals since 1988–1989 may be the result of a change in the predatory behavior of bulbuls. This change is evident in the decrease in the number of wings of either color collected at the milkweed bushes since the beginning of the decline; over 100 wings could be collected from the ground beneath and around the milkweed stands at Edmondson Hall during a monarch season (Stimson & Berman 1990). Now, very few wings are collected during a season. The bulbuls now seem to prey more heavily on larvae than on adults, especially at the peak of abundance. Because we cannot distinguish which larvae will turn into white or orange adults, we assume that there is no differential predation on larvae which will turn into white or orange individuals. With this proposed shift to predation on larvae, white adults are presumably no longer at a selective advantage. Selection coefficients have not been calculated for the periods of increase and decrease in the frequency of the white morph because: there are many generations of this butterfly per year, generations overlap, abundances differ greatly among generations, and because there is evidence (Fig. 2) that during the decline of the white morph since 1989, the direction of selection is reversed within the course of a year. Since 1988–1989, the proportion of the white morph has tended to be higher at the start of each season than at the end of the last season. Unfortunately no data is available to directly test the idea that a switch in predation behavior, a switch from preying primarily on adults to preying primarily on larvae, took place in the late 1980's.

While white individuals seem to have been at a disadvantage in the last 9 years, they have not disappeared from this population. The fact that white individuals constitute a higher proportion at the beginning of the annual peak of abundance (Fig. 2) suggests they may be at a selective advantage outside the period of peak abundance. When monarchs are at lower density, larval monarchs may not be a conspicuous resource drawing predators to the milkweeds. At such times, the adults may be the more conspicuous resource, and among the adults the white individuals may be less conspicuous than the orange, giving rise to an increase in the proportion of white adults in the non-peak part of the year. When the density of larvae and adults becomes very high, hunting and predation become very concentrated at the residential stands of milkweeds because of the conspicuousness of the resource. Several bulbuls can be feeding at a stand of milkweeds and sometimes both species of bulbuls are in the area of the milkweed stands. At such times mortality caused by predation evidently falls most heavily on larvae, and therefore indiscriminately with regard to the color of the adults. The proportion of white individuals in the population possibly declines during the peak season because white butterflies are at a disadvantage due to some process such as mate selection. Since the white morph seems to enjoy a selective advantage outside the peak season, this polymorphism could persist for some time.

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RANGE EXTENSION OF *DOLESCHALLIA TONGANA* (NYMPHALIDAE) TO THE SAMOAN ARCHIPELAGO, WITH NOTES ON ITS LIFE HISTORY AND ECOLOGY

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ABSTRACT. Adults and larvae of the nymphalid butterfly *Doleschallia tongana vomana* Fruhst. were recently documented for the first time in the Samoan archipelago, on the island of Tutuila, American Samoa. Distributed from Melanesia to western Polynesia, this species consists of several sub-species, with *D. t. vomana* endemic to Fiji. The establishment of this species on Tutuila is likely the result of natural dispersal by adult(s) blown from Fiji, though the success of this colonization was made possible only as the result of human introduction of the host plants *Graptophyllum pictum* and *Pseuderanthemum carruthersii* (Acanthaceae).

The nymphalid butterfly *Doleschallia tongana* Hopkins is distributed through Melanesia eastward to western Polynesia. Formerly considered a subspecies of *D. bisaltide*, *D. tongana* was elevated to full species status by Parsons (1999). Based on a review of *Doleschallia* specimens, Parsons (1999) determined that *D. bisaltide* extended from India eastward to New Guinea, and that further eastward, specimens considered to be subspecies of *D. bisaltide* were in fact, *D. tongana*. *D. tongana* consists of about six sub-species, and is reported from the Bismarck Archipelago; the Solomons; New Caledonia; the New Hebrides; Tonga; Fiji; and Samoa (Parsons 1999). At the eastern end of the species' range, *D. t. vomana* Fruhst. is endemic to a number of islands in Fiji (Robinson 1975) and *D. t. tongana* Hopkins is endemic to a number of islands in the Tongan group (Hopkins 1927, Miller & Miller 1993).

The inclusion of Samoa in this species' range by Parsons (1999) appears to be based on a misreading of Hopkins (1927). In his account of *Doleschallia*, Parsons (1999) makes reference to a Samoan specimen of *D. bisaltide*, citing Hopkins (1927). However, while the principal focus of Hopkins (1927) was Samoa, he only reported *Doleschallia* from Tonga. Thus, prior to the observations reported here, there have been no records of *Doleschallia* from the Samoan Archipelago (Swezy 1921, Hopkins 1927, Comstock 1966, Kami & Miller 1998).

On 9 April 1997, an unidentified caterpillar was collected by RPC moving across a broad expanse of sidewalk in an urbanized section of the village of Pago Pago, island of Tutuila, American Samoa. It pupated on 11 April and emerged on 18 April. Just prior to pupation, the caterpillar measured ca. 50 mm in length. It possessed a black ground color with light speckling dorsally and prominent cream colored stripes running longitudinally, located dorso-laterally and ventro-laterally. Each body segment had seven prominent black spines, with numerous smaller secondary spines. The base of each primary spine was pale metallic blue. From a distance, the most prominent features of the caterpillar are the black ground color with metallic blue spots, and the pair of light parallel stripes running longitudinally on each side.

On October 6, 1997, several unidentified caterpillars (Fig. 1) were independently observed by DV feeding on a *Pseuderathemum carruthersii* (Seem.) Guillaumin (Acanthaceae) on the campus of American Samoa Community College located in the Malaeimi Valley. Several were collected and adults reared. These specimens were compared with that from April 1997, and all were tentatively identified as *Doleschallia bisaltide*. Assignment to the sub-species *vomana* was subsequently made by Dr. Jacqueline Miller, Allyn Museum of Entomology, Florida Museum of Natural History. Based on the revised taxonomy (Parsons 1999) these specimens would now be assigned to *D. tongana vomana.*

Since these initial records, the occurrence of larvae on the host plants or observations of adults in flight has become more frequent. Two additional adult specimens were collected in the Tafuna section of Tutuila (12 February 1998, 23 May 1998; Fig. 2) and *Doleschallia* larvae can now be found throughout the inhabited areas of Tutuila. Three adults have been deposited at the Allyn Museum of Entomology, Florida Museum of Natural History (Accession Number 1998-12). Considering that the records are distributed temporally and spatially (from Tula on the east end to Fagamalo on the west end, a distance of 30 km) and include both adult and larval forms, it appears that a breeding population has become established on Tutu-

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FIG. 1. Mature larvae of *Doleschallia tongana vomana* Fruhst. feeding on *Pseuderanthemum carruthersii*, Mapusaga, Tutuila, American Samoa. Photo by Don Vargo.

FIG. 2. Dorsal and ventral view of female *Doleschallia tongana vomana* Fruhst, collected 23 May 1998, Tafuna, Tutuila, American Samoa. Allyn Museum of Entomology, Florida Museum of Natural History Accession 1998–12. Photos by Jacqueline Miller.

ila. This seems to be a recent occurrence, as this is a large, conspicuous species, readily observed and identified on the wing (once initially identified in hand).

Prior to the observations reported here, neither one of us had observed the species on Tutuila. While one of us (RPC) had only been making observations on Tutuila since 1996, the other (DV) has been observing and collecting butterflies on Tutuila since 1988. Hopkins (1927) spent two years in Samoa and Comstock (1966) spent four months (June to October) collecting on Tutuila without encountering this species. In the Samoan Archipelago, *Doleschallia* presently is only known from Tutuila. We have spent many days afield in the Manu'a islands of American Samoa without observing it. We have not observed it on Upolu or Savaii either, but time spent afield on these islands has been very limited.

Existing data on the host plants of *Doleschallia* indicate the genus feeds primarily on members of the Family Acanthaceae, with Moraceae of minor importance to some species (Parsons 1999). *Doleschallia* in New Guinea feed principally on *Graptophyllum pictum* T. (Parsons 1991), and *Pseuderanthemum variable* is the principal host plant of *D. bisaltide* in Australia (McCubbin 1971, D'Abrera 1978, Common & Waterhouse 1972). Host plants recorded for *D. tongana* include *Graptophyllum pictum* on Manus and New Britain (Parsons 1999), *Pseuderanthemum* sp. on New Caledonia (Holloway & Peters 1976), and, in Fiji, *Graptophyllum insularum* (A. Gray) A.C. Smith, *G. pictum*, *Pseuderanthemum laxifolium* A. Gray, *Artocarpus altilis* Parkinson, *A. integra* Thunb., and *Erythrina* sp. (Robinson 1975). While there are no accounts of host plants of *D. tongana* from Tonga, *G. insularum* is a native species of Acanthacaeae there (as well as in Fiji) (Whistler pers. comm.), and presumably serves as the host plant. On Tutuila, larvae of *D. t. vomana* have been observed feeding on *Pseuderanthemum carruthersii* (syn. *P. reticulatum*) and *Graptophyllum pictum*. These two plant species are native to Melanesia and Asia-Malaysia respectively.

With the exception of *Dicliptera samoensis* Seem, endemic to Upolu and Savaii (in the independent nation of Samoa) there are no native Acanthaceae in the Samoan archipelago. All are European introductions (primarily in the 20th century) and arrived either as weeds (7 species) or ornamentals (21 species) (Whistler 1992, 1994, 1995, pers. comm.). On Tutuila, *P. carruthersii* and *G. pictum* are widespread ornamental plantings.

Doleschallia occurs in primary and secondary forest, although accounts suggest it prefers forest edge or clearings rather than deep forest. *D. bisaltide* is reported from rain forest (Common and Waterhouse 1972) and "open spaces on the outskirts of jungle patches" (McCubbin 1971). In New Guinea, *D. tongana* occurs in marginal secondary forest, especially along creeks (Parsons 1999) and in New Caledonia it prefers rich primary forest but is often seen on low vegetation in the sun (Holloway & Peters 1976). However, its occurrence on ornamental hedges of *G. pic-*

tum (Parsons 1999), suggest an ability to utilize human-modified habitats as well. On Tutuila, observations have been in areas characterized by a mosaic of residences, plantations, secondary growth and urban/commercial development. Occurrence of *D. b. vomana* on Tutuila appears linked to the distribution of the ornamental plantings that serve as their larval host, though the extent of plantation and forest on Tutuila provide a habitat structure that is probably not unlike that in which it occurs elsewhere.

While it is impossible to be certain of the mechanism by which *D. t. vomana* has reached Samoa, there are at least two scenarios. First, it may have arrived as larvae, in a shipment of *Pseuderanthemum* or *Graptophyllum*. However, importation of these plant species to Samoa occurred early in the 20th century. Our report of the first occurrence of *D. t. vomana* in Samoa, decades after the importation of its host plants suggests it did not arrive in association with that activity.

A second and more likely scenario is one of colonization from Fiji. Though not without exception for some species, there is consensus that most of the Samoan macro-lepidoptera arrived via Fiji (Hopkins 1927, Swezey 1948, Robinson 1975, Holloway 1979, 1983). Given this species' vagility, and the fact that tropical storms and cyclones in this region often pass from west to east, it seems inevitable that individuals of *D. t. vomana* would arrive in Samoa from time to time. However, until fairly recently (the 20th century), its ability to successfully colonize Samoa would have been limited by a lack of host plants. The modern introduction of several species of Acanthaceae, which serve as larval hosts on Tutuila, has apparently allowed a more recent colonization event to meet with some success. Whether this will result in a more permanent establishment is unknown, as is the extent of this species' present distribution among the other islands of the Samoan Archipelago.

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BOOK REVIEWS

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THE BUTTERFLIES OF COSTA RICA AND THEIR NATURAL HISTORY, VOLUME II, RIODINIDAE, by P. J. DeVries. 1997. Princeton University Press, 41 William Street, Princeton, New Jersey 08540. vi–xxv + 288 pp., including 25 color plates, 59 figures, 11 tables, ISBN: 0-691-02890-7. Available from BioQuip Products for $90.00 U.S. ($29.95 paperbound).

This is the second in a series of field guides to the diurnal lepidoptera of Costa Rica, and an excellent introduction to this poorly known family of butterflies. Like volume one, this book contains not only admirable coverage of the species from this area, but also an amazing wealth of natural history information. Illustrations of the early stages of many species are included, as well as scanning electron micrographs of a selection of eggs and larval morphological features. This work now stands as the most useful tool for identifying and studying riodinids in Costa Rica and the neotropics in general.

This book is much more than a simple field guide. As it allows the reader to accurately identify riodinid species from Costa Rica (and genera from most of Central and South America), it is undeniably useful as a field guide; however, it is also the most complete work covering all aspects of riodinid biology. Its usefulness as a guide to the biology, systematics and identification is surpassed only by its utility as a springboard towards further research and fieldwork on this poorly known group of butterflies. Some problems with the printing notwithstanding (See corrections in Swinethrottle 1997), any student of butterflies can use this book in the field to quickly identify a specimen, assess the current state of knowledge concerning its biology, and act accordingly in gathering important data. It is indeed, far more than a guide to labeling specimens, and is instead an important tool to be used by all students of butterfly biology and natural history.

Following in the tradition of D'Abrera, the plates included in this volume are of superior quality and useful for identifying pinned specimens. While each species is also described in detail in the text, including mention of similar species, I found myself wishing the author had included more information on identifying butterflies in the field and while on the wing. For example comparisons or notes on the prominent color patterns visible in flight would be extremely useful for use of this work in the field. The section on *Calephelis*, written by G. T. Austin, is especially useful for identification purposes, as it includes a table of characters useful in separating species of this confusing genus. This type of a table might have also been useful for other confusing genera such as *Theope* or *Euselasia*.

In addition to the color plates, this volume includes a small selection of electron micrographs of riodinid eggs. While I realize the limitations imposed by printing costs, it is a shame that more of these wonderful pictures could not have been included. These detailed views of such an important stage in the butterflies' life are wonderful not only for identifying and comparing eggs, but also for stimulating thought on the functional morphology and biology of these structures.

As in Volume I, the artist Jennifer Clark has provided beautiful and informative drawings of the larvae and pupae of many species. The drawings in this volume surpass those from the previous work in quality as well as clarity. However, the location of these drawings, dispersed throughout the text, is unfortunate. As this book is obviously more than a guide to the adults, it was disappointing to have to search through the text in order to locate illustrations of larvae. It would have been more helpful to have a consolidated grouping of these drawings that would allow easier larval identification.

Included in the text of this book is a reanalysis of a previously published morphological phylogeny. While others may feel this is inappropriate for a field guide, I maintain that its inclusion is not only interesting, but accomplishes its mission by stimulating critical thought and pointing out our lack of knowledge about riodinid butterflies. I did find that Table 3, which is a matrix of those characters used in the reanalysis, was of minimal utility since the reader must look up the original publication for a full description of the characters analyzed. Overall, the sections covering riodinid systematics, mimicry, enemies and defenses, and life cycles and morphology are extremely useful as an introduction to the study of these organisms.

While I was disappointed to find my personal hero, the Rev. Miles Moss, was not mentioned in the section covering butterfly biologists, I was nevertheless delighted to find this section included. As with all aspects of biology, our understanding of butterfly biology and our ideas for further study rest upon the shoulders of those who came before us. Any serious student of butterflies will be fascinated by this section and be pleasantly surprised to find it included in this book.

As with the previous volume covering the papilionids, pierids, and nymphalids, Volume II includes an astounding amount of natural history and behavioral data for most of the species included. Observations are taken from the literature as well as the extensive fieldwork of the author, and serve to whet the appetite of anyone aspiring to study butterflies. The formatting of the species descriptions is as detailed as possible, yet concise and easy to read, with an occasional humorous anecdote illustrating a particular point. One additional section included in the species descriptions, which was left out of the earlier volume, is the listing of localities for each species with associated dates. I did not find these data particularly useful and feel that they take up space that could be better used for more illustrations or more extensive comments on field identification.

This book is far more than a field guide, but rather an invaluable collection of data on a group of organisms that are not only poorly known, but also are facing possible extinction from the pressures of industrialization and expanding human civilizations. The natural history data, along with the pictures for species identification, make this a useful book in the field as well as in the library. This book belongs not only on the shelf of all tropical lepidopterists, but in the hands of every biologist attempting to unravel the mysteries of our dwindling tropical ecosystems.

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MICROLEPIDOPTERA OF EUROPE, VOLUME 1, PTEROPHORIDAE, by Cees Gielis. 1996. P. Huemer, O. Karsholt, and L. Lyneborg, editors. Published by Apollo Books, Kirkeby Sand 19, DK-5771 Stenstrup, Denmark. 222 pages, 16 color plates. Hardcover, 17.5 × 25 cm, ISBN 87-88757-36-6. Recently listed at DDK 400 by publisher.

Delicate spindly moths, most with the wings elegantly divided into feather-like lobes or plumes, the Pterophoridae have historically been a popular group with European lepidopterists. The palearctic fauna has been documented with an abundance of scattered publications in several languages, but this recent book, with its beautiful illustrations and concise English text, is a welcome, up to date, identification guide.

The main text consists of introductory material (7 pages), a key to the European genera (3 pages), checklist (10 pages), and the systematic treatment of the 32 genera and 139 species (89 pages). The male and female genitalia illustrations are included in a section near the end of the book (49 pages) and followed by a distribution table, an extensive list of references, index to hostplants, and index to entomological names. The 16 color plates are bound near the middle of the book. Color photos of adults of all but 2 species are included as well as the larvae and/or pupae of 12 species. The photographs are, with little exception, of excellent quality. Text and line illustrations are attractively printed on glossy paper, color plates on a slightly thicker matte stock. Together with an apparently good quality binding, these features result in an altogether handsome book.

The introduction begins with "Historical notes", with attentive citations of authors and years of significant contributions to the European fauna from Linnaeus, up to the first two decades of the twentieth century with Tutt, and Meyrick. The section ends somewhat abruptly with mention of names of more recent authors from Europe and other regions, but without citing any specific significant publications.

The next section, "General remarks", gives an overview of adult external morphology, emphasizing wing shapes, maculation, venation, and head characters. Included is a labeled dorsal habitus drawing of an adult, venation figures representing six genera, a lateral view of an adult head, and 3 figures showing scaling on labial palpi. The rows of specialized scales which arise from the median and cubital vein on the hind wing undersurface of both sexes are mentioned. As a defining characteristic of the family, it is unfortunate that the arrangement of these scales is not depicted on an enlargement of one of the venation figures. The reader is referred to labeled figures appearing in the illustration section for terminology of the male and female genitalia. A discussion of these terms, patterns and peculiarities within the family would have been appropriate.

Four subfamilies are defined: Agdistinae, Pterophorinae, Ochyroticinae, and Deuterocopinae, the first two occurring in Europe. Gielis refers to his 1993 revision of the superfamily Pterophoroidea (Zool. Verhand., Leiden 290: 1–139) as the basis for the arrangement of genera and the subfamily groupings. The "General remarks" section ends in an interesting discussion of the variety of habitats, larval hosts, and habits, and simplified descriptions of the variety features found in the immature stages.

Under the heading "How to collect plume-moths" the author makes some general comments about responsible collecting practices. Techniques for collecting adults with nets and lights are outlined. Although applicable to other moth groups, specific points are made about pterophorid flight habits, attraction to different types of light, and the tendency to rest at the periphery of an attracting light source. The author stresses the importance of labels and the advantages of field processing material but does not recommend specific techniques for killing and setting, pin types or sizes, or offer any tips on collecting or rearing larvae.

The introductory section entitled "The preparation of genital slides" includes a detailed protocol for preparing slides and comments on alternative mounting media. The techniques generally apply to most microlepidoptera. As the first volume in this series, this is certainly valuable information, but prone to repetition in subsequent volumes. There might have been some comments specific to pterophorid genital preparations such as whether or not to completely remove particular scale-hair tufts in males of *Hellinsia*, *Oidaematophorus*, and *Stenoptilia*, and noting the fragility of valvular lobes in the *Oxyptilus* group.

The key to the European genera uses external characters, male and female genitalia characters, and forewing venation. The user may need specimens of both sexes and a forewing venation slide. The last couplet refers to the point of origin of the ductus seminalis. This structure is unfortunately not labeled in any drawings. Most of the couplets do, however, refer to figures. As completely illustrated as the book is, the key is more a formality, and along with the diagnoses and illustrations, most genera can be suitably recognized.

The checklist includes 139 species and their synonyms. Each valid species is assigned a number which is also used in the systematic treatment and the indices. One species, *Stenoptilia brigantiensis* Nel & Gibeaux, 1992, is assigned the number "50a" as it was apparently only recently regarded as distinct by the author. Perusing the checklist, one notices a number of recent synonyms, 3 of which are newly established with this book (noted in the "Abstract" and species accounts). The genus *Stenoptilia* is particularly troublesome, with 13 synonyms preceded by a question mark to indicate their uncertain status and need for future verification. In the systematic treatment of *Stenoptilia* and *Crombrugghia*, Gielis makes some comments regarding the work of certain authors in France. Indeed, looking at the European checklist, since 1960 (most from the 80's) there have been 38 European pterophorid species described by French authors. Of these, only 5 are now treated as valid species. The "Editorial foreward" notes Gielis' conservative view and the potential controversy over some of his decisions. There is little doubt that the taxonomy of the family will continue to fluctuate. It is important to note, however, that Gielis has worked on this family with a worldwide scope for over 20 years and is keenly aware of the range of variation exhibited by certain species.

The systematic treatment of species includes accounts of each genus and species. Each begins with an annotated synonymy followed by text under the headings: diagnosis, male genitalia, female genitalia, variation (where applicable), distribution, biology, and remarks. Some of the diagnoses are very short depending on the complexity of the species. Repetition is avoided in genitalia descriptions of several species by referring to the genus account or related species. The distribution statements are very general and include the distribution outside of Europe. These are supplemented with a table near the end of the book which indicates the European distribution in greater detail. The table lists the species with 38 country/political regions denoted by two letter codes across the top. Presence in a region is marked by an "x", doubtful records with a "?". Traditional distribution maps would have been more aesthetically pleasing and informative, especially for countries covering larger areas, but the chart does allow the reader to quickly determine the fauna recorded for a particular region. The biological information is nicely summarized for each species and includes flight season, broods, hosts, larval habits, habitats, and pupation sites where known. This information is not always complete given what is available in earlier literature but essential references are cited which lead the reader to further information. Larval hosts are cross-referenced in the index by species number. Additional, non-European hosts mentioned in the genus accounts are not indexed.

One can't help but notice the incongruous backgrounds of the adult photographs assembled together to form each plate. Still, the photographs are impressive and of great value for identifications. All are printed to 2.5× the natural size. The specimen data for each is given in the captions. Some specimens are damaged or lack abdomens but these evidently belong to species of limited availability. The host and locality data is lacking from the larva and pupa photographs. These excellent photographs, however, result from years of dedicated work on the family. It is curious that no photographs showing the natural (and very characteristic) resting positions of adults were included in this book.

The genitalia illustrations are generally of consistent quality with significant structures emphasized by stippling and arrows. Like the adult photos, they include corresponding specimen data and slide numbers in the captions, thus adding to the lasting scientific value of the publication. Males and females for nearly all species are illustrated, the females of many species, though, with only the ostium and ductus bursae depicted. While 31 pages are devoted to male illustrations, only 18 pages illustrate females. It seems it would have been worthwhile to include a complete female genital drawings of at least one species per genus. Certain characters mentioned in the diagnoses are missed in these partial illustrations, such as the distinctive "blotches" on the lamina postvaginalis of *Platyptilia* species, three-tipped apophyses anteriores in *P. farfarellus*, or "long" apophyses anteriores of *P. nemoralis*. The partial drawings appear to be on a larger scale but unfortunately no scale lines are indicated for any of the drawings.

This is an excellent book despite a few shortcomings in content and overlooking typographical errors. The author has done a remarkable job of condensing essential characters and biological data into a useful reference. The book is also the result of years of examining specimens, type material, and literature to untangle the taxonomic webs created by two centuries of lepidopterists. The European fauna is by no means completely known, there are still species groups to closely examine along with life histories to describe, unknown hosts and biological information, and species with sketchy distributional data. This book is a steppingstone for enthusiasts and a practical guide for any lepidopterist encountering these moths.

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Journal of the Lepidopterists' Society
54(1), 2000, 38

MELANISM: EVOLUTION IN ACTION, by Michael E.N. Majerus. 1998. Published by Oxford University Press, Oxford, U.K. xiii + 388 pp. Available from the publisher. Hardcover, ISBN: 0-19-854983-0. $105.00; Paper, ISBN: 0-19-854982-2. $45.00.

I once served briefly as Book Review Editor of Evolution. That journal publishes more frequently than Journal of the Lepidopterists' Society (JLS), but also faces a much broader range of potential reviewables—from textbooks and semi-popular works to systematic monographs covering all the kingdoms. I found the job uncomfortable. Most of the "major" works of interest to most readers of Evolution had long since been reviewed in the weekly journals Science and Nature, and were old news. Even the Quarterly Review of Biology often "beat" us, and Trends in Evolution and Ecology routinely did. We had to ourselves the specialty monographs that eleven of our readers would care about. What was the point of reviewing at all?

I raise the issue because *Melanism: Evolution in Action* has been out for two years, and it seems rather late to review it. But if ever a late review was justified, this is the one. Aside from the fact that the book may still be news to many readers of JLS, a late review cannot help but profit from the excesses of some of the early reviewers and the controversy they engendered. This is a book best viewed with 20-20 hindsight.

One of the first reviews appeared in Nature. It was by the brilliant population geneticist Jerry Coyne (1998, *Not black and white*, Nature 396: 35–36), who concluded that the classic tale of industrial melanism in the peppered moth, *Biston betularia*, was so tainted that it should be expunged from the textbooks. This review inspired a long, densely-argued counter-review by Bruce Grant (1999, *Fine-tuning the peppered moth paradigm*, Evolution 53: 980–984). Meanwhile, both the book and its notices had been picked up by creationists, who predictably used them as proof of the bankruptcy of neo-Darwinism. What Coyne treated as sloppiness on the part of H. B. D. Kettlewell, they denounced as fraud. Clearly, a close reading of the peppered moth part of this book is in order. [Plenty of people knew about problems with the Kettlewell story well before the book appeared. In the United States, Ted Sargent has been a consistent critic (see Sargent et al. 1998, *The 'classical' explanation of industrial melanism*, Evolutionary Biology 30: 299–322). In Europe, Kauri Mikkola had sounded the alarm in print as early as 1984; he and I had a conversation about this at the "Biology of Butterflies" meeting at the The Natural History Museum (London) in September 1981. For the creationists, the continued appearance of the story in texts after questions had been raised constitutes fraud.]

I should be "up front" with my own involvement in all this, since I work on butterflies and my bona fides to review the book are not obvious. In my salad days I collected moths too, and in 1964 published a paper on industrial melanism in eastern Pennsylvania (J. Res. Lepid. 3 (1): 19–24). In 35-year retrospect this is a piece of rank juvenilia, but, as it happened, so astonishingly little on the phenomenon had been published in the United States that it was actually important. History moves in strange ways. There was to be a meeting on "Mathematical Challenges to the Neo-Darwinian Interpretation of Evolution" at the Wistar Institute in Philadelphia in April 1966. Kettlewell was coming and wanted to know about the local melanics. Charles Remington steered him to me. One of my professors got me a false credential to get me into the symposium—my first, and in many ways a turning point in my academic career. Kettlewell and I hit it off, and he invited me to come work for/with him at Oxford, which I did in the summer of 1969. The first half of the visit I was posted to the Orkney Islands to trap non-industrial melanic Oak Eggars (*Lasiocampa quercus*). There weren't any. The second half I spent in Kettlewell's lab at Parks Road, except for time censusing the famous Cothill population of the Scarlet Tiger (*Panaxia dominula*—part of the 1969 data on p. 87 of Majerus' book are mine). So I got to know him, his methods and operation well. I have plenty of Kettlewell stories, some E.B. Ford stories, and a fond remembrance of Bernard Kettlewell as a friend, a mentor, and a fine specimen of an English type rapidly approaching extinction. He was an enthusiast, but not a fraud. His experimental designs were flawed—to the extent they were largely due to, or at least vetted by Ford, he must share any blame, but he was not a bungler. He did about as well as anyone could be expected to do in those days, and the important thing is that he did it. Nobody else did. And to our shame, no one did anything at all similar in America, despite ample opportunities.

If there is to be breast-beating, it should be by those of our profession who were content to coast on his work. The story was so pretty that there was little temptation to dig deeper. It could be understood easily by the layman, by school kids—what more was there to do or say? Creationists are sometimes outright intellectually dishonest, but perhaps their belief that natural selection rises or falls on the tale of the peppered moth is at least a little justified by how proud most of us were of that tale.

That said, I will not review the flaws in Kettlewell's work here; read the book. (By and large, I agree with Grant's review.) Most of the reviews have talked about the peppered moth and little or nothing else. But there is more to this book. It was explicitly intended as an update of Kettlewell's 1973 book *The Evolution of Melanism: A Recurring Necessity* (Clarendon Press, Oxford). This book, HBDK's magnum opus, is described on Majerus' book jacket as a "classic," but it wasn't. It was not a success because it ranged far beyond HBDK's competence: "melanism" covered altogether too many very different phenomena—it was, if you will, a polyphyletic concept. Majerus tries to cover this very broad field (both taxonomically and phenomenologically) and is at least marginally better at it. The effect of both books is to impress the reader that there is no overarching single explanation for "melanism," and that the industrial case, despite all its ambiguities, is probably the best-defined one. Perhaps that, after all, is the intended message. Understand that we know much more about industrial melanism than we know about the function of "melanism" in our own species, where it is charged with historical baggage and racial mythology and is so much more important. The human case is the one conspicuous case that Majerus explicitly declines to analyze in any depth.

Specialists will find minor errors in the book (e.g., the reference to "*Pieris protodice* ssp. *occidentalis*" on p. 161, when Kingsolver and Wiernasz, who are referenced, gave the name correctly as *P. occidentalis*—it's generally *Pontia* now). These things are no big deal. The quality of the photographs is variable, and both the decision to have color plates at all and the selection of photographs to use in them are debatable—without them, the book might have been appreciably cheaper. Nonetheless, the book is absolutely required reading for evolutionary biologists, laypeople interested in evolution, melanism, or moths (and, in the tradition of E. B. Ford's books, Majerus gives a basic course in transmission genetics early on) and, interestingly, historians, philosophers and sociologists of science who study how science is actually done. Its bibliography alone is worth the price (at least of the paperback), even if it does omit my 1964 juvenilia. And Majerus does not libel Kettlewell, and I thank him for that.

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Journal of the Lepidopterists' Society
54(1), 2000, 39

GELECHIIDAE I (GELECHIINAE: TELEIODINI, GELECHIINI), by P. Huemer and O. Karsholt. 1999. In P. Huemer, O. Karsholt, and L. Lyneborg (eds.): Microlepidoptera of Europe 3: 1–356. Available from Apollo Books, Kirkeby Sand 19, DK-5771, Stenstrup, Denmark. ISBN 87-88757-25-0. 500 Danish Kroner, excluding postage.

Hurrah! For the first time, a significant segment of the European gelechiid fauna is presented in a comprehensive manner that permits workers to see genital and abdominal characters as well as good colored photographs of imagines. Lack of this kind of treatment has seriously hampered study of the group because knowledge of the genera ultimately is based on correct identification of each type species. Many of them have remained in question because the type specimens had/have not been examined and the species name correlated with a morphologic entity. Thanks to the long-term program to locate and study the type material of each gelechiid described for the Palearctic Region of Klaus Sattler (The Natural History Museum, London), followed by Linda Pitkin (The Natural History Museum, London), and concluded by the authors, the user can feel relatively confident that each species is correctly associated with a name. Sixteen new specific synonymies are recognized, and one genus and one species are resurrected from synonymy in this work.

This volume is the first of four that will treat the European Gelechiidae. The tribes Teleiodini and Gelechiini of the subfamily Gelechiinae have 18 genera and 60 species and nine genera and 91 species respectively. Eight genera of teleiodines (*Recurvaria, Coleotechnites, Exoteleia, Evippe, Pseudotelphusa, Teleiopsis,* and *Xenolechia*) are shared with North America. However, *Recurvaria* is introduced into North America, and *Coleotechnites* is introduced into Europe. *Lita cistiflora* Constant is treated as questionably belonging to *Telphusa* (a North American genus); however, it is not congeneric with *Telphusa longifasciella* (Clemens), the type species. Likely, a new generic name will have to be proposed for it. Seven genera of Gelechiini (*Gelechia, Mirificarma, Chionodes, Aroga, Filatima, Prolita,* and *Athrips*) are shared, but *Mirificarma* and *Athrips* are represented by introduced species in North America. That the European fauna is relatively well known is evidenced by the fact that the 10 new species (6.6% of the fauna) all occur in the circum-Mediterranean area. In contrast for North America 94 species of teleiodines (of an estimated 200) and 352 species of gelechiines (of an estimated 500) are present. The estimated undescribed species for North America is 61% of the fauna. The latter percentage would be higher if the 115 species of Chionodes described in 1999 were not included with the described taxa.

Following the introduction, which includes definition of higher taxa, illustration of pertinent character systems, key to subfamilies of Gelechiidae, key to genera of Teleiodini and Gelechiini (based on genital characters), and check-list, is the systematic treatment. Full synonymies for all taxa, a diagnosis, description of male and female genitalia, geographic distribution (summary for described taxa, full data for newly described species), biology (recorded hosts and general phenology), and remarks (indication of inaccuracies in the literature to permit association with the current concept of the name) provide the textual substance of the volume. In addition, the male and female genitalia and adult of each species are illustrated by very good photographs. Adults are represented by one to four photographs of each species on 14 colored plates. As an aside, photographs of genitalia and adults are identified by the number assigned to the species name in the check-list and text.

Identification of the species and genera is a major achievement and will provide the basis for all future study by European workers. For workers elsewhere this work will permit recognition of introductions and provide clarification of generic and specific concepts, visual documentation of highly important character systems, and good access to the extended literature.

One puzzling error is the duplication of the eighth abdominal segment to represent *Schistophila laurocristella* Chrétien (text figure 22) [likely] and *Teleiodes huemeri* Nel (text figure 25) [unlikely].

The only suggestion I have for the future parts is to develop identification keys for the species of each genus. I do not know what the editorial policy is on this point, but I feel it makes authors define how they recognize the species.

Again, congratulations on a fine and much needed work.

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Journal of the Lepidopterists' Society
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MANUSCRIPT REVIEWERS, 1999

The merit of a scientific journal depends on the quality of its reviewers as well as its authors, but the former are usually unknown to the readers of the published articles. The *Journal* relied on the expertise of 62 reviewers last year to provide 83 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 1999. Those who reviewed two or more manuscripts are denoted by asterisks.

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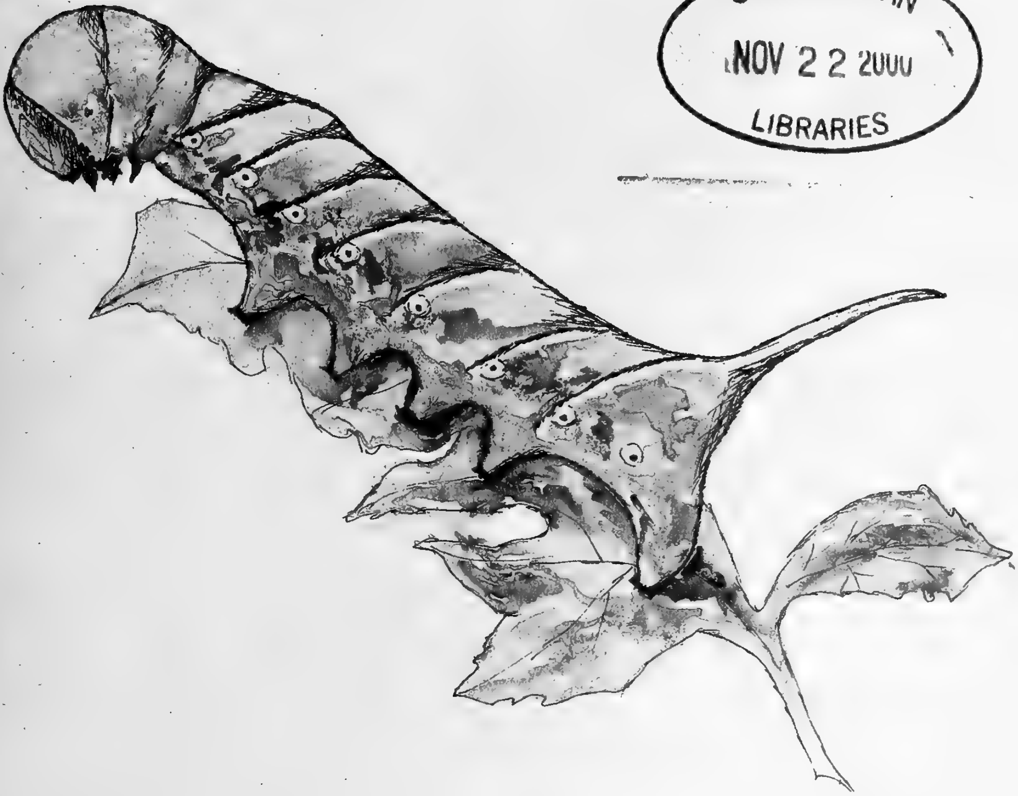

15 November 2000

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54(2), 2000, 41–46

TWO NEW GENERA IN THE NEOTROPICAL RIODINID TRIBE NYMPHIDIINI (RIODINIDAE)

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ABSTRACT. Two new monotypic Neotropical riodinid genera, *Behemothia*, new genus, and *Protonymphidia*, new genus, are described in the myrmecophilous tribe Nymphidiini, to respectively contain the taxa *godmanii* Dewitz, 1877, formerly treated in *Pandemos* Hübner, [1819], and *senta* (Hewitson, 1853), formerly treated in *Adelotypa* Warren, 1895. These genera are characterized and their systematic position discussed.

Additional key words: cladistics, morphology, Theopeiti.

The butterfly family Riodinidae is almost entirely confined to the Neotropics, where approximately 1300 species or 95 percent of the familial diversity occurs (Heppner 1991). Despite constituting a significant proportion of the Neotropical butterfly fauna in low and middle elevation forest habitats (Robbins 1982, 1993), and containing numerous genera that exhibit fascinating adult and early stage biology (Callaghan 1983, DeVries 1990, 1991, 1997, Hall 1999b), the Riodinidae has received relatively little systematic attention, and the first cladistically derived phylogenies for the group were only very recently generated (Hall 1998, 1999a, Penz & DeVries 1999).

This paper forms part of a broader study to create a natural generic classification for the largest and probably systematically least well understood of the riodinid tribes, the Nymphidiini Bates, 1859 (*sensu* Hall 1999a [=Lemoniini + Nymphidiini of Harvey 1987]) (Harvey 1987, Hall 1999a, b). A recent comprehensive cladistic analysis of the nymphidiine subtribe Theopeiti (*sensu* Hall 1999a), based on the inclusion of all known species (75) and over 100 characters of male and female morphology and wing pattern, indicated the existence of five monophyletic clades worthy of generic status (Hall 1999a, b) (see Fig. 1), however only the single generic name *Theope* Doubleday, 1847, was available for them. One genus, *Archaeonympha* Hall, 1998, has subsequently been described (Hall & Harvey 1998), another is soon to be described (Hall & Harvey in prep.), and the remaining two are described here to contain the taxa *godmanii* Dewitz, 1877, and *senta* Hewitson, 1853, currently treated in the genera *Pandemos* Hübner, [1819], and *Adelotypa* Warren, 1895, respectively (Bridges 1994). The terminology for male and female genital and abdominal structures follows Klots (1956) and Eliot (1973), while nomenclature for venation follows Comstock and Needham (1918).

Behemothia Hall, new genus

Figs. 2A–D; 4A–F; 6A–D

Type species. *Behemothia godmanii* (Dewitz 1877)

Description. MALE: typical forewing length 32–33 mm. *Wing shape:* forewing costa smoothly convex, distal margin rounded, apex markedly falcate; hindwing rounded and slightly elongate. *Venation* (Fig. 4A): four forewing radial veins. *Dorsal surface:* forewing ground color russet-brown, dark brown mark at discal cell end; a narrow postdiscal white band curves from costa to vein Cu2 then becomes lilac as far as anal margin, basal half of wing lilac except for costal, basal and discal russet-brown areas; distal fringe black. Hindwing entirely blue except for russet-brown anal margin and small area of black scaling at base of costal margin; fringe black. *Ventral surface:* forewing ground color brown; white postdiscal band as on dorsal surface but broader and entirely white; basal area of wing black except for brown at costal margin and very base of wing in cell Cu2, and blue in basal half of discal cell and upper portion of cell Cu2; a black spot discernible at proximal edge of basal black in cell Cu2, typically with some lilac scaling distally, another smaller one within brown scaling further towards wing base and a variably prominent one within blue scaling of discal cell. Hindwing ground color brown; dark brown line marks discal cell end, a dark brown spot towards base of cell Sc+R1 above discal cell; a dark brown postdiscal band extends from costa to vein Cu2 then curves inwards in cell Cu2, band displaced proximally in cell Sc+R1 and enlarged into large square surrounded by whitish scaling. *Head:* ventral surface of labial palpi a mixture of pale and dark brown scaling on segments one and two, pale brown on very short third segment, dorsal surface entirely dark brown (Fig. 4B). Eyes bare and brown (in dried specimens), pale brown scaling at margins. Frons dark brown, paler brown at margins and ventrally. Antennae brown with whitish scaling at base of each segment becoming more prominent towards clubs dorsally, narrow nudum region devoid of scaling along inner edge of shaft; flattened clubs brown dorsally and orange-brown ventrally. *Body:* dorsal surface of thorax and abdomen, including patagia, russet-brown, ventral surface pale gray-brown. All legs pale gray-brown; tarsus of foreleg unimerous and elongate, coxa elongate (Fig. 4D); midleg and hindleg with a tibial spur and a group of spines at inner distal tip of tarsal segments one to four, numerous further spines along entire inner distal margin of first tarsal segment (Fig. 4F). *Genitalia* (Fig. 6A, B): uncus more elongate dorsally, separated from triangular tegumen by triangular lateral fenestration; falci of average size and shape; vinculum broad, especially ventrally, and incomplete dorsally (i.e., not extending around entire anterior margin of tegumen) where it is folded over; valvae rectangular with a prominent angular dorsal projection and a smaller ventral one; aedeagus gradually tapers to a very narrow and slightly undulating tip with a ventral bulge before tip, a single large cornutus is teardrop-shaped in lateral view and crescent-shaped in dorsal view; pedicel short, heavily sclerotized, and broad, especially ventrally. Last tergite a plain rectangle; last sternite rounded anteriorly, produced into two triangular points posteriorly, distal third heavily sclerotized and dorsally invaginated (Fig. 6C).

FEMALE: differs from male in following ways: *Dorsal surface:* white postdiscal forewing band broader at costa, lilac present on forewing only in tornus as extension of white postdiscal band; fringe dark brown. Hindwing entirely russet-brown except for dark brown scaling at base of costal margin, marking cell end and forming a faint postdiscal band; fringe dark brown. *Ventral surface*: blue scaling at base of forewing absent, basal half of wing a paler dark brown, highlighting two basal dark brown spots in cell Cu2 and three spots in discal cell, one marking cell end, and a postdiscal line of dark brown spots proximal to postdiscal white band. Hindwing an even plain brown color, typically with slightly fainter dark brown markings. *Head:* second palpal segment slightly more elongate (Fig. 4C), ventral surface of third segment a mixture of dark and pale brown scaling. White scaling at base of antennal segments reduced, especially on dorsal surface, considerably broader nudum region along inner edge of shaft. *Body:* foreleg with one or two spines at inner distal tip of tarsal segments one to four (Fig. 4E). *Genitalia* (Figs. 6D): corpus bursae narrow and elongate, signae triangular, tooth-shaped sclerotized invaginations with jagged basal margin; ductus bursae and ductus seminalis unsclerotized; ostium bursae consists of a broad sclerotized band ventrally which narrows laterally and dorsally.

Diagnosis. The single species of *Behemothia*, *B. godmanii,* bears little resemblance to any other riodinid. The combination of its large size, markedly falcate forewing apex, black scaling at the base of the dorsal hindwing and ventral forewing, and russet-brown dorsal ground color covered with lilac and blue scaling in the male is unique.

Etymology. The name is derived from the Hebrew word "behemoth", meaning "enormous animal," in reference to the huge size of this species, one of the largest in the Riodinidae.

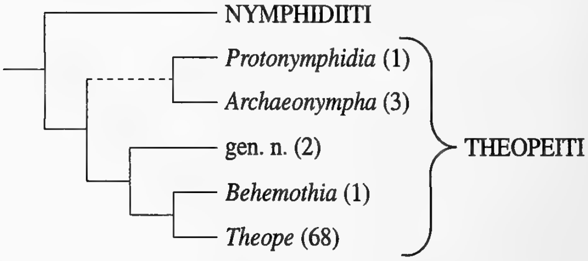
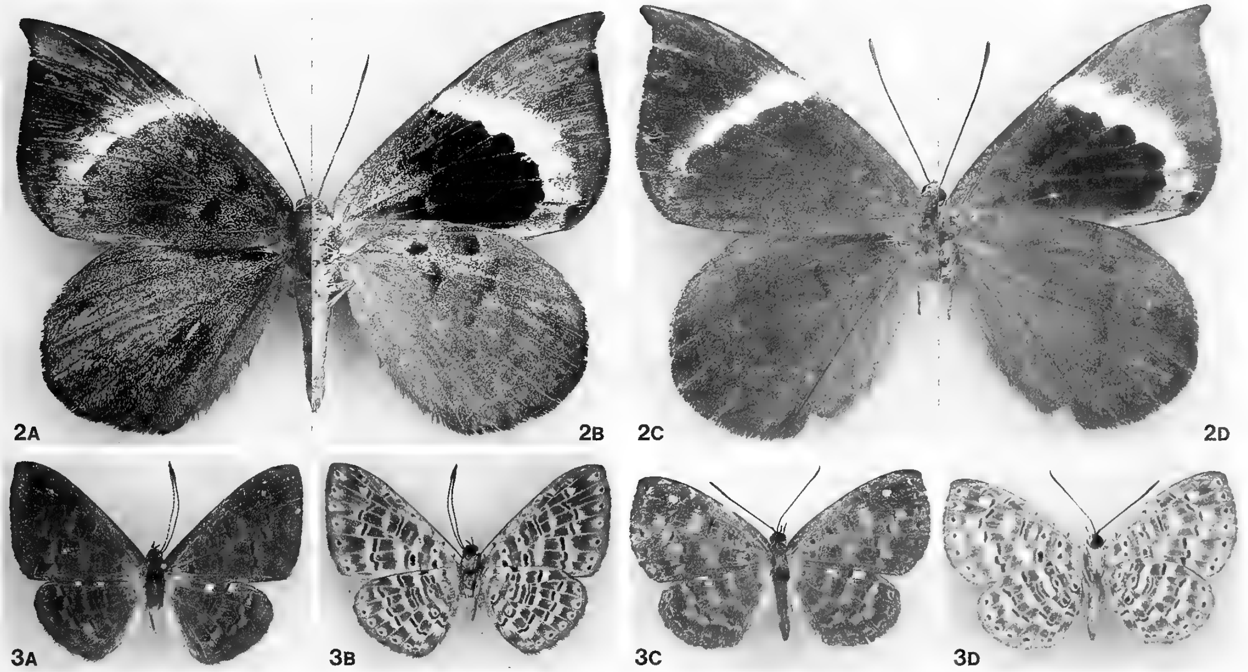


FIG. 1. A generic-level phylogeny for the nymphidiine riodinid subtribe Theopeiti (*sensu* Hall 1999a), the putative sister clade to the subtribe Nymphidiiti (*sensu* Hall 1999a), adapted from the species-level phylogeny of Hall (1999a). Numbers in parentheses represent the number of species in each genus. The dashed line indicates uncertainty regarding the sister group relationship of *Protonymphidia* and *Archaeonympha*; *Protonymphidia* may form a distinct lineage at the very base of the Theopeiti.

Systematic position: The genus *Pandemos* was erected by Hübner ([1819]) to include the single new species *arcassa* (a synonym of *pasiphae* Cramer 1775), and Hewitson (1870) and Dewitz (1877) subsequently added *palaeste* and *godmanii* respectively (Stichel 1930–31, Bridges 1988, 1994). However, the only unifying characteristic of these three species is their huge size, and Harvey (1987), D'Abrera (1994) and DeVries (1997) all raised doubts as to the monophyly of *Pandemos*. In fact, each *Pandemos* species belongs in a different subtribe of the Nymphidiini (*sensu* Hall 1999a). Harvey (1987), and subsequently DeVries (1997), noted that *palaeste* actually belonged in the genus *Synargis* Hübner, [1819] (subtribe Lemoniaditi (*sensu* Hall 1999a) =Lemoniini Auctt—see Hall & Heppner 1999, Hall 1999a, b), after the early stages and genitalic structures had been examined. Harvey (1987) was also the first to note that *godmanii* was not closely related to *pasiphae*, but its true systematic affinities have remained unknown. However, recent cladistic studies of the tribe Nymphidiini indicate that by virtue of possessing a ventrally positioned spiracle on male abdominal segment three (the character proposed by Harvey (1987) as a synapomorphy for his Nymphidiini) and lacking sclerotized tissue joining the male genitalic valve tips, *godmanii* belongs in the subtribe Theopeiti (Hall 1999a, b). A morphological cladistic analysis of the subtribe Theopeiti (see introduction) indicates that *godmanii* represents the sister clade to the large genus *Theope* (Hall 1999a, b) (see Fig. 1), although the only universal synapomorphy that unites these two clades is the resting posture of their members; all species rest with their wings closed over the body instead of outspread (DeVries 1997, Hall 1999a, b), as is typical for the Riodinidae. However, *godmanii* lacks the wing pattern and male abdominal synapomorphies that support the monophyly of the recently revised genus *Theope* (Hall 1999b). The large morphological differences separating *godmanii* from its nearest relatives necessitate the description of a new genus for it. *Pandemos* should be regarded as a monotypic genus of the subtribe Nymphidiiti (*sensu* Hall 1999a).



FIGS. 2–3. **2.** *Behemothia godmanii* (Dewitz, 1877), Mexican male: **A,** dorsal surface; **B,** ventral surface. Mexican female: **C,** dorsal surface; **D,** ventral surface. **3.** *Protonymphidia senta* (Hewitson, 1853), Brazilian male: **A,** dorsal surface; **B,** ventral surface. Brazilian female: **C,** dorsal surface; **D,** ventral surface.

Biology: Very little is known about the biology of the single *Behemothia* species, *godmanii*. Museum label data indicate that this uncommon species occurs primarily in relatively dry semi-deciduous woodlands, and de la Maza and de la Maza (1993) report it as occurring from 100 to 700 m in Chiapas, Mexico. DeVries (1997) reports finding a female in Belize perched beneath a branch with its wings folded over the body and the forewings dropped back into the hindwings. The foodplants and early stages remain undiscovered, but the position of *Behemothia godmanii* in the Nymphidiini indicates that the larvae will be myrmecophilous (Harvey 1987).

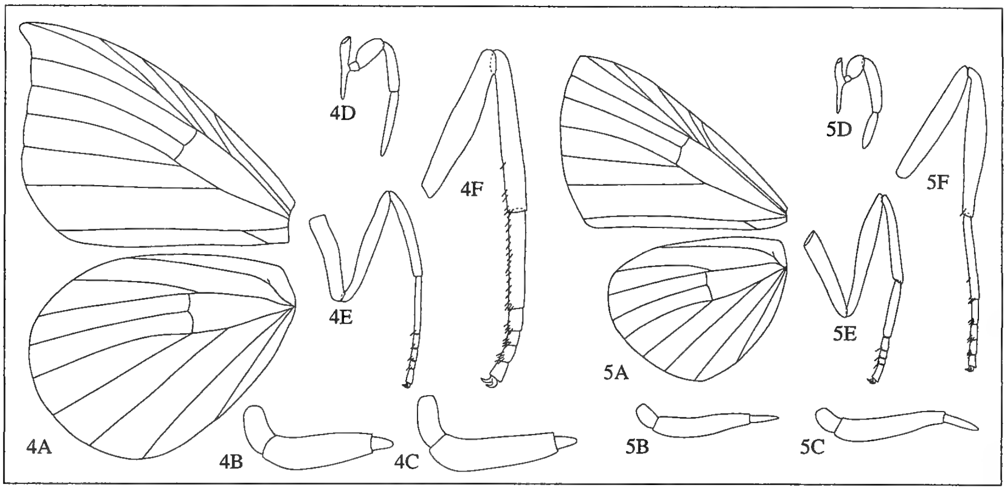
Distribution: *Behemothia godmanii* is known to range from central Mexico to Costa Rica.

Protonymphidia Hall, **new genus**

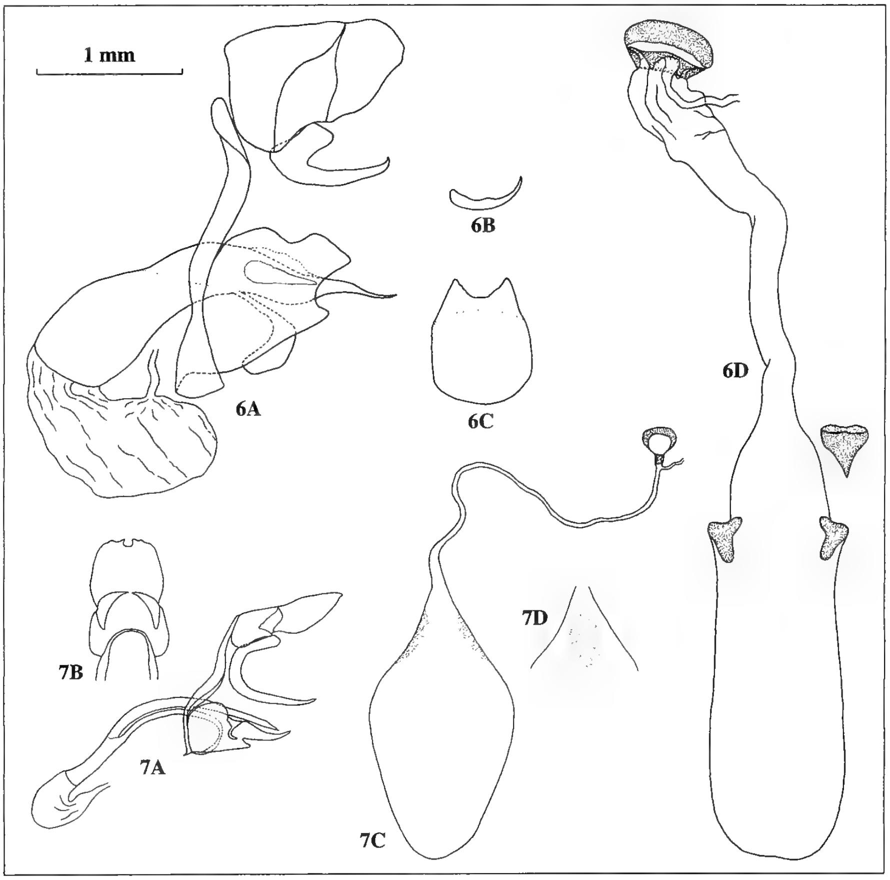
Figs. 3A–D; 5A–F; 7A–D

Type species. *Protonymphidia senta* (Hewitson 1853).

Description. MALE: typical forewing length 14.5–15.5 mm. *Wing shape:* both wings somewhat elongate; forewing costa straight, distal margin relatively straight; hindwing elliptical, rounded at tornus and apex. *Venation* (Fig. 5A): four forewing radial veins. *Dorsal surface:* forewing ground color dark orange; paler orange at very wing base, one dark brown spot at base of discal cell ringed by pale orange, another at middle of cell, a similar elongate line marking cell end with an additional line of paler orange proximally, two similar spots towards base of cell Cu2 below those in discal cell; a pale orange postdiscal band kinks proximally at vein M3, a disjointed line of postmedial dark brown lines surrounded by paler orange extends from costa to vein 2A, small patch of white scaling distal to mark in cell R4+5; a column of dark brown spots at submargin faintly ringed by slightly paler orange extends from cell Cu2 to cell R3, two spots in former and one in remainder, few white scales at proximal edge of apical spots; distal fringe dark orange. Hindwing similar to forewing except anal margin cream, two prominent white marks present in cell R4+5 at costa, one postdiscal and one discal, and basal brown spots less prominent with additional one towards base of cell R4+5; white scaling present at middle of distal margin of cells Cu2 to R4+5. *Ventral surface:* forewing ground color orange-brown; pattern elements same as on dorsal surface except paler orange areas very pale orange-cream and more extensive, five additional evenly spaced small dark brown spots present along costa, and veins outlined in pale orange-brown. Hindwing ground color orange-brown; pattern elements same as on dorsal surface except paler orange areas very pale orange-cream and more extensive, two additional dark brown spots visible at base of costa, and veins outlined in pale orange-brown. *Head:* ventral surface of labial palpi cream, distal third of elongate second segment and entire elongate third segment brown dorsally, remainder orange (Fig. 5B). Eyes bare and brown (in dried specimens), dark orange scaling at margins. Frons dark orange. Antennae brown with whitish scaling at base of each segment ventrally, narrow nudum region devoid of scaling along inner edge of shaft; tubular clubs brown, tips orange-brown. *Body:* dorsal surface of thorax and abdomen, including patagia, dark orange, ventral surface pale orange-cream. Forelegs pale orange-cream, femurs of mid and hindlegs pale orange, remainder dark orange; tarsus of foreleg unimerous and short, coxa elongate (Fig. 5D); midleg and hindleg with a tibial spur and a group of spines at inner distal tip of tarsal segments one to four, tibia broader at middle (Fig. 5F). *Genitalia* (Figs. 7A, B): uncus very elongate, especially dorsally, with rounded notch and two small points at middle of distal dorsal edge, separated from rec-



FIGS. 4–5. Morphology. **4.** *Behemothia godmanii* (Dewitz, 1877): **A,** male venation; **B,** male palpus; **C,** female palpus; **D,** male foreleg; **E,** female foreleg; **F,** male hindleg. **5.** *Protonymphidia senta* (Hewitson, 1853): **A,** male venation; **B,** male palpus; **C,** female palpus; **D,** male foreleg; **E,** female foreleg; **F,** male hindleg.



FIGS. 6–7. Genitalia (setae of male genitalic unci and valvae are omitted for clarity). **6.** *Behemothia godmanii* (Dewitz, 1877): **A,** male genitalia in lateral view; **B,** dorsal view of aedeagal cornutus; **C,** ventral view of last (eighth) abdominal sternite; **D,** female genitalia in dorsal view with lateral view of signa. **7.** *Protonymphidia senta* (Hewitson, 1853): **A,** male genitalia in lateral view; **B,** dorsal view of uncus; **C,** female genitalia in dorsal view; **D,** lateral view of corpus bursa.

tangular tegumen by rectangular lateral fenestration; falci very elongate; vinculum broader at middle, forms tiny saccus ventrally, narrows considerably around anterior margin of tegumen; valvae consist of large basal bulge with downwardly pointed remainder divided by weakly sclerotized tissue dorsally, triangular point at middle of ventral margin; aedeagus long and very narrow with triangular tip; pedicel very elongate, evenly narrow and rounded. Last tergite and sternite plain rectangles, middle of distal margin of last sternite weakly sclerotized.

FEMALE: differs from male in following ways: both wings with more convex distal margins. *Dorsal surface:* paler orange areas broader, white scaling proximal to submarginal brown spots more extensive and present around entire submargin, white scaling in forewing cell R4+5 and at hindwing costa more prominent and also present distal to tiny dark brown marks in forewing cells R3 and R2, and at base and middle of hindwing cell R4+5. *Ventral surface:* ground color slightly paler, especially distally, pale orange-cream areas more extensive. *Head:* second palpal segment slightly more elongate, third segment markedly more elongate (Fig. 5C). Nudum region along inner edge of shaft considerably broader. *Body:* foreleg with single long spine at inner distal tip of tarsal segments two to four (Fig. 5E). *Genitalia* (Figs. 7C, D): corpus bursae round, signae consist of a small ovoid sclerotized band either side of ductus bursae opening; ductus bursae and ductus seminalis unsclerotized and very narrow; ostium bursae small with broad sclerotized band dorsally and only soft tissue ventrally.

Diagnosis. The single species of *Protonymphidia*, *P. senta*, presents a unique phenotype in the Riodinidae. The slightly elongate wing shape, entirely pale and dark orange dorsal surface and orange-brown and cream banded ventral surface are quite distinctive. The ventral patterning closely resembles that of *Archaeonympha* species, but they all have black and blue dorsal surfaces and distinct morphology (see below).

Etymology. The name is derived from the Greek words for "first" or "primitive", and "nymph", in reference to the basal position of the genus in the subtribe Theopeiti.

Systematic position: The taxon *senta* was described by Hewitson (1853) in the genus *Lemonias* Hübner, 1807, then subsequently transferred to *Echenais* Hübner, [1819], by Kirby (1871), and *Adelotypa* by Bridges (1988, 1994) for nomenclatural reasons (see Hemming 1967). However, cladistic studies involving the tribe Nymphidiini indicate that *Adelotypa* is a polyphyletic genus, and the taxon *senta* is not closely related to the type species of *Adelotypa*, *bolena* Butler, 1876 (Hall & Harvey 1998, Hall 1999a, unpubl. data). In fact, whilst *bolena* is a relatively derived member of the subtribe Nymphidiiti (Hall unpubl. data), *senta* is a plesiomorphic member of the subtribe Theopeiti, and a comprehensive morphological cladistic analysis of that subtribe (see introduction) indicates that *senta* is most closely related to the genus *Archaeonympha* (see Fig. 1) (Hall & Harvey 1998, Hall 1999a). Characters that place *senta* at the base of the Theopeiti include the plain rectangular shape of the last male abdominal sternite and the complete (albeit very narrow) vinculum dorsally, which is complete in the majority of members of the subtribes Lemoniaditi and Nymphidiiti, and incomplete (totally absent dorsally) in the remaining species of the Theopeiti. The fact that *senta* lacks the synapomorphies of *Archaeonympha*, especially the unique synapomorphy of the ductus bursae of the female genitalia (see Hall & Harvey 1998), and every other genus in the Theopeiti, and possesses an unusually high number of autapomorphies, such as the sclerotized signal bands on the corpus bursae of the female genitalia and the very elongate falci and dorsally notched uncus of the male genitalia, amply justify the description of a new genus for it.

Biology: The single species of *Protonymphidia*, *senta*, is locally common along forest edges, streamsides, and in secondary growth habitats, where it is typically encountered in association with its foodplant *Bauhinia* (Leguminosae). Several individuals of both sexes may be found feeding simultaneously from the extrafloral nectaries of this plant where they remain unmolested by the resident ants, identified by DeVries et al. (1994) as *Pheidole* nr. *biconstricta* (Myrmicinae). Oviposition appears to be dependent on the presence of these ants, and the larvae are tended by them. The myrmecophilous larvae, which are yellow-brown to pale green, covered with tiny granulations, and possess a fringe of ventro-lateral setae that are especially long on the first thoracic segment, feed on leaf tissue between the main veins and also on the extrafloral nectaries; the pupa is brown with a slight dorsal keel (DeVries 1997, J. Turner pers. comm.).

Distribution: *Protonymphidia senta* occurs throughout the western Amazon basin from Colombia to Bolivia and in the western half of Amazonian Brazil.

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BOREAL OLETHREUTINI 2. (TORTRICIDAE): WING AND GENITALIA ILLUSTRATIONS, A NEW SYNONYMY, AND A NEW HOLARCTIC ADDITION

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ABSTRACT. We provide photographs of wings and genitalia of the Holarctic *Tia enervana* (Erschoff), *Olethreutes aquilonanus* (Karvonen), *O. heinrichanus* (McDunnough), *O. concretanus* (Wocke), *O. nordegganus* (McDunnough), and the Nearctic *O. mengelanus* (Fernald), *O. costimaculanus* (Fernald), and *O. bowmananus* (McDunnough). We report *O. kennethanus* McDunnough to be a junior synonym of *O. nordegganus* (McDunnough). We present new Nearctic distribution records for *O. heinrichanus* and *O. bowmananus*, and the first Palaearctic records for *O. nordegganus*, which establish it as Holarctic. Recent discoveries change to 63% the Beringian tortricids that are also Holarctic.

Additional key words: Holarctic, Nearctic, Palaearctic.

We previously reported 11 boreal species of Tortricidae newly confirmed or discovered to be Holarctic (Jalava & Miller 1998, Miller 1995). Here we revisit eight of these species, all poorly known. The wings of four have not been illustrated before, and sexes of four have not previously been associated or their female genitalia illustrated. Larval foodplants of all but one are still unknown. The scant knowledge of boreal tortricids results from lack of collecting and rearing, and from inadequate handbook treatment. The latter fault is meant to be at least partially redressed here. The new findings presented result from collecting sponsored by the Finnish Lepidopterological Society and the Finnish Academy of Science (Proj. No. 20), and from closer scrutiny of existing collections.

References to body size derive from forewing lengths, which were measured to the nearest 0.5 mm with a ruler.

Depository abbreviations are as follows: ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania; CNC, Canadian National Collection, Ottawa, Ontario; UCB, Essig Museum of Entomology, University of California, Berkeley, California; INHS, Illinois Natural History Survey, Champaign, Illinois; MZH, Finnish Museum of Natural History, Helsinki, Finland; BMNH, Hatural History Museum, London, England; UMSP, University of Minnesota Entomology Museum, St. Paul, Minnesota; USNM, U. S. National Museum of Natural History, Washington, DC; ZIN, Zoological Institute, St. Petersburg, Russia.

Tia enervana (Erschoff)
(Figs. 1–3)

Forewing length 6.0–8.0 mm (n = 13). We previously confirmed that this taxon is Holarctic (Jalava & Miller 1998). Genitalia of one or both sexes have been line illustrated by Dang (1990), Kuznetsov (1987), Heinrich (1926), and McDunnough (1922). The wings were illustrated in color by Kuznetsov et al. (1998). Here, we reillustrate in one place the wings and genitalia (Figs. 1–3).

Material examined is in CNC, MZH, UCB, USNM, ZIN, as enumerated by Jalava and Miller (1998).

Olethreutes aquilonanus (Karvonen)
(Figs. 4–6)

Forewing length 6.5–7.0 mm (n = 3). We previously reported this species as new to the Nearctic, which established it as Holarctic (Jalava & Miller 1998). The wings were photo illustrated by Karvonen (1932) and Kuznetsov and Mikkola (1991) (as *O. kononenkoi*), and the male genitalia line illustrated by Kuznetsov and Mikkola (1991) (as *O. kononenkoi*). The female genitalia (Fig. 6) are illustrated here for the first time. The sexes were associated by simultaneous capture, similarity in forewing scale pattern and body size, and equally unique male and female genitalia (Figs. 5, 6).

Material examined is in MZH, as enumerated by Jalava and Miller (1998).

O. heinrichanus (McDunnough)
(Figs. 7–9)

Forewing length 7.0–9.0 mm (n = 14). We previously reported this species to be Holarctic by synonymy (Jalava & Miller 1998). The wings were photo illustrated by Karvonen (1932) (as *Argyroploce hyperboreana)*, and the male genitalia line illustrated by Heinrich (1926). Newly examined Canadian specimens fill a previous gap in Nearctic records between Labrador and Yukon Territory, and also provide the first female genitalia illustration (Fig. 9). Distribution records are now essentially circumpolar. The sexes were associated by simultaneous capture, and similarity in forewing scale pattern and body size.


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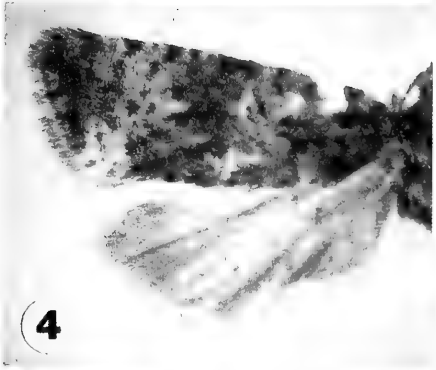
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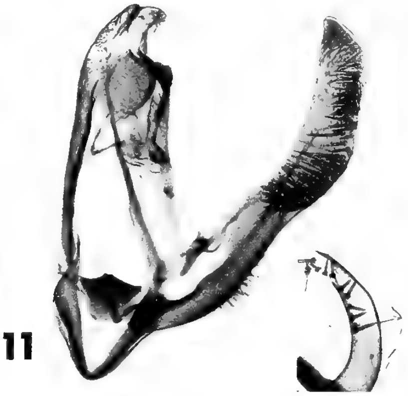
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Material examined is in MZH and UCB, as enumerated by Jalava and Miller (1998), plus 8 males, 1 female, Knob Lake, Quebec, 11-24-VII-48, E. G. Munroe, genit. slides WEM 36971-3, and 1 genit. in vial on pin; l male, Bathhurst Inlet, Northwest Territories, 30-VII-51, W. I. Campbell; 1 male, Kuusamo, Finland, 6-VII-83, K. Saloranta, genit. in vial on pin (CNC).

O. concretanus (Wocke)
(Figs. 10–12)

Forewing length 5.0–5.5 mm (n = 3). We previously reported this species as new for the Nearctic, and thus Holarctic (Jalava & Miller 1998). Kuznetsov (1987) line illustrated the male genitalia. As far as we know, the wings and female genitalia are illustrated here for the first time (Figs. 10, 12). The sexes were associated by simultaneous capture and similarity in forewing scale pattern and body size. This species appears to have the smallest body size among boreal *Olethreutes*.

Material examined is in MZH and UCB, as enumerated by Jalava and Miller (1998).

O. nordegganus (McDunnough)
(Figs. 13–15)

Argyroploce nordeggana McDunnough (1922).

Olethreutes nordeggana; Heinrich (1926).

O. kennethana McDunnough (1941); Jalava and Miller (1998). **New Synonymy**.

O. obsoletana (not Zetterstedt 1840); Miller (1985), Kuznetsov and Mikkola (1991).

Forewing length 7.0–10.0 mm (n = 43). McDunnough (1941) expressed uncertainty whether *nordegganus* and *kennethanus* were separate entities. In light of our study, the differences he cited between them appear to be individual rather than specific. For example, McDunnough's (1941) comparative illustrations of male valvae show that the extent of spining between sacculus and cucullus is minimal in *nordegganus* and maximal in *kennethanus*. Our sample encompasses these illustrated extremes and all gradations between them (n = 14). Dark areas of the forewing also vary from rust to blackish–brown among individuals.

We report *O. nordegganus* here as new for the Palaearctic, which makes it Holarctic. It appears that records of *O. obsoletanus* from northeast Siberia (Kuznetsov & Mikkola 1991) are misidentified *O. nordegganus*. The easternmost *O. obsoletanus* we have seen are from Buryatia (east of Lake Baikal), ~3000 km from the Pacific Ocean. Genitalia of these two species are superficially similar, but diagnostic differences lie in the number, size, and arrangement of vesical cornuti (Jalava & Miller 1998). Our most recently examined material confirms that the *O. obsoletanus* vesica has two to three plates each bearing a cluster of short cornuti, whereas the *O. nordegganus* vesica lacks such plates, but has from one to eight long, separate cornuti.

In addition to McDunnough's (1922, 1941) line illustrations of the male genitalia, Heinrich (1926) photo illustrated them, and line illustrated the female genitalia. The wings (Fig. 13) are illustrated here for the first time.

Material examined is in CNC, MZH, UCB, USNM, as enumerated by Jalava and Miller (1998), plus the following: *nordegganaus* holotype male, Nordegg, Alberta, 14-VII-21, J. McDunnough, genit. slide Arg. 13 m (CNC); 1 *nordegganus* paratype male, same data as holotype except 18-VII-21; 1 male, Mt. McKinley Pk., Alaska, 3-VII-38, G. P. Engelhardt; 16 males, Peters Lk., Alaska, 14-VII-73, J. F. G. Clarke, genit. slides USNM 24173–6, 9; 3 males, McKinley Park, Alaska, 5-VIII-31, F. W. Morand, genit. slide WEM 154971; 1 female, Umiat, Alaska, 1950, N. A. Weber No. 2686, genit. slide WEM 154975 (USNM); 1 male, nr. Anderson, Alaska, 26-VI-79, P. Opler and J. Powell; 16 males nr. Cantwell, Alaska, 26–28-VI-79, P. Opler and J. Powell, genit. slides JAP 4463, 4476 (UCB); 1 male, 40 km NE Mistassini, Quebec, 22-VII-92, K. Mikkola; 1 male, 97 km post Dempster Hwy., Yukon Territory, 6-VII-94, L. Kaila; 11 males, nr. Kulu village, Magadan oblast, Russia, 10–15-VII-97, Jalava and Tammaru, genit. slides JJ 4, 5, 7–12, 15–17/10-29-97; 1 male, Upper Kolyma River, Magadan oblast, Russia, 26-VII-87, K. Mikkola, genit. slide WEM 215961 (MZH).

O. mengelanus (Fernald)
(Figs. 16–18)

Forewing length 7.5 mm (n=3). This species is thus far known only from the Nearctic. Heinrich (1926) photo illustrated the male genitalia, and line illustrated the female genitalia; he also photo illustrated the wings (Heinrich 1935). Because these illustrations are scattered, and the wing pattern variable, we reillustrate wings and genitalia here (Figs. 16–18). In addition to the published distribution records mentioned by Jalava and Miller (1998) and Danks (1981), MacKay and Downes (1969) noted that adults of this species from Ellesmere Island, Northwest Territories, had been misidentified as *Aphania* sp. in the report of Oliver (1963). MacKay and Downes also stated that on Ellesmere Island the larvae feed among leaves of *Dryas integrifolia* Vahl (Rosaceae), but this record needs confirmation as larvae from this plant were not reared to the adult stage for positive identification.

Material examined is in MZH, UMSP, and USNM, as enumerated by Jalava and Miller (1998).

O. costimaculanus (Fernald)
(Figs. 19–21)

Forewing length 6.5–7.0 mm (n = 6). This species, thus far known only from the Nearctic, is superficially similar to the Holarctic *O. dalecarlianus* (Guenée) and the Palaearctic *O. ledianus* (L.) (Jalava & Miller 1998). Heinrich (1926) line illustrated the female genitalia, and photo illustrated the male genitalia. The wings (Fig. 19) are illustrated here for the first time. The lectotype female illustrated here was designated by Miller (1970).

Material examined is in INHS, MZH, USNM, as enumerated by Jalava and Miller (1998).

O. bowmananus (McDunnough)
(Figs. 22–24)

Forewing length 7.5–8.0 mm (n = 12). No illustrations of this Nearctic species accompanied its description (McDunnough 1923),

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FIGS. 1–12. Wings and genitalia of Olethreutini. Unless otherwise shown or stated, signa are absent. **1–3,** *Tia enervana*. **1,** Wings of male from Nordegg, Alberta (*vulgana* holotype). **2,** Genitalia of male from Peters Lake, Alaska (USNM slide 24168). **3,** Sterigma and associated structures of female from Schrader Lake, Alaska (slide WEM 154972). Signum slight or nonexistent. FIGS. 4–6. *Olethreutes aquilonanus*. **4,** Wings of male from Ogilvie Mts., Yukon Territory. **5,** Genitalia of male from Ogilvie Mts., Yukon Territory (slide WEM 151972). **6,** Sterigma and associated structures of female from Kilpisjärvi, Finland (slide WEM 1512954). Inset shows signum at same scale. FIGS. 7–9. *O. heinrichanus*. **7,** Wings of male from Knob Lake, Quebec. **8,** Genitalia of male from Knob Lake, Quebec (slide WEM 36971). **9,** Sterigma and associated structures of female from Knob Lake, Quebec (slide WEM 36973). FIGS. 10–12. *O. concretanus*. **10,** Wings of female from Murphy's Dome, 32 km NW of Fairbanks, Alaska. **11,** Genitalia of male from Eagle Pass, 105 km SW of Circle, Alaska (slide JAP 4564). Inset shows aedeagus at same scale. **12,** Sterigma and associated structures of female from Upper Kolyma River, Magadan oblast, Russia (slide WEM 151973).


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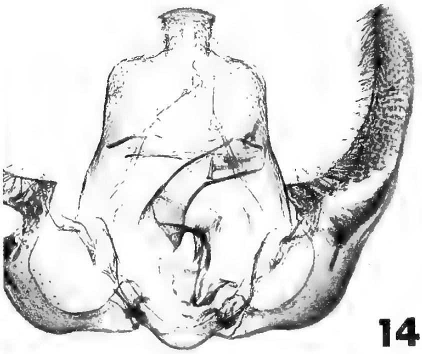
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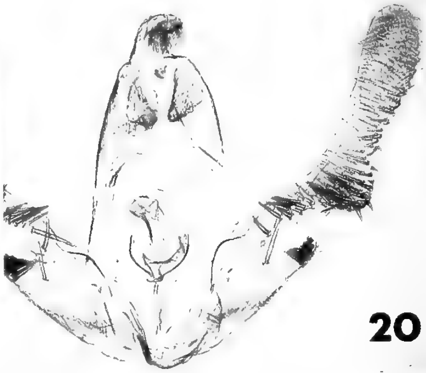
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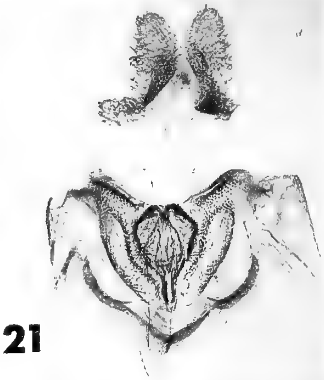
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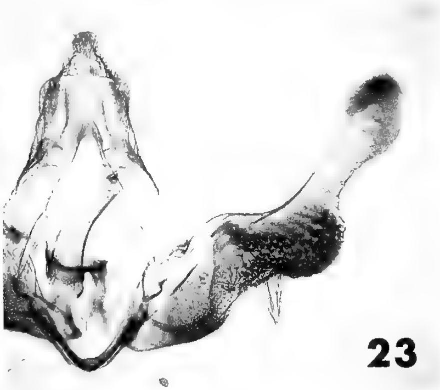
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but the whole male genitalia were photo illustrated by Heinrich (1926). The wings (Fig. 22) and female genitalia (Fig. 24) are illustrated here for the first time. The sexes were associated by simultaneous capture and similarity in forewing scale pattern and body size.

We earlier differentiated this species from *O. exaridanus* Kuznetsov (Jalava & Miller 1998). It also superficially resembles *O. magadanus* (Falkovitsh), but differs in structural details. The structural differences chiefly concern the mid-valval spined area, which is flatter and more rounded in outline than in *O. magadanus*.

Material examined is in MZH and USNM, as enumerated by Jalava and Miller (1998) for *O. bowmananus*, plus the following: 7 males, 1 female, Schrader Lk., Alaska, 2–13-VII-73, J. F. G. Clarke, genit. slides USNM 24165-6, WEM 94974 (USNM); and *O. magadanus*, 1 male, 21-VII-89, Upper Anadyr River, Chukchi Peninsula, Russia, K. Mikkola, genit. slide WEM 94972; 2 males, 15-VII-87, Upper Kolyma River, Magadan oblast, Russia, K. Mikkola, genit. slides JJ 2/5.10.1994, WEM 285962 (MZH).

DISCUSSION

Two forewing pattern groups are evident in Olethreutini treated here: (i) the simple bifasciate type in *Tia enervana, Olethreutes aquilonanus, O. heinrichanus, O. concretanus*, and (ii) the white-marked-costa type in *O. mengelanus, O. costimaculanus*, and *O. bowmananus*. Whether such groups reflect convergence or inheritance remains to be determined.

The number of Beringian tortricid species that are Holarctic previously stood at 61% (42/69) (Jalava & Miller 1998). Some adjustments to these tallies are now necessary: (i) Removing *O. obsoletanus*, which does not appear to be Beringian, (ii) Adding *O. nordegganus*, which is reported here to be both Beringian and Holarctic, and (iii) Adding *Clepsis danilevskyi* Kostjuk, which was recently reported elsewhere to be Beringian and Holarctic (Kuznetsov et al. 1998). These adjustments increase the percentage of Beringian tortricids which are also Holarctic to 63 (44/70). The rapid rate at which boreal Tortricidae have recently been discovered to be Holarctic suggests that the numbers will climb still higher with further investigation.

ACKNOWLEDGMENTS

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FIGS. 13–24. Wings and genitalia of Olethreutini. Unless otherwise shown or stated, signa are absent. FIGS. 13–15, *Olethreutes nordegganus*. **13,** Wings of male from Peters Lake, Alaska. **14,** Genitalia of male from Peters Lake, Alaska (USNM slide 24169). **15,** Genitalia of female from Peters Lake, Alaska (USNM slide 24174). Signum a tiny scobinate patch, not shown. FIGS. 16–18. *O. mengelanus*. **16,** Wings of male from "Greenland". **17,** Genitalia of male from Ogilvie Mts., Yukon Territory (slide JJ 42/9-12-94). **18,** Genitalia of female from "Greenland" (USNM slide 72157). Corpus bursae missing from slide, so the signum, a scobinate patch (Heinrich 1926), is not shown. FIGS. 19–21. *O. costimaculanus*. **19,** Wings of lectotype female. **20,** Genitalia of male from Ogilvie Mts., Yukon Territory (slide JJ 1/4-15-95). **21,** Genitalia of lectotype female (slide WEM 1512951). FIGS. 22–24. *O. bowmananus*. **22,** Wings of paratype male from Nordegg, Alberta. **23,** Genitalia of male from Schrader Lake, Alaska (USNM slide 24165). **24,** Genitalia of female from Schrader Lake, Alaska (USNM slide 24166). Inset shows signum at same scale.

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PYRGUS COMMUNIS AND *PYRGUS ALBESCENS* (HESPERIIDAE: PYRGINAE) ARE SEPARATE TRANSCONTINENTAL SPECIES WITH VARIABLE BUT DIAGNOSTIC VALVES

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ABSTRACT. Since 1906, the question of whether *Pyrgus albescens* Plötz is a species distinct from *Pyrgus communis* (Grote) or only a subspecies (or mere form) of it, has arisen repeatedly with no real resolution. Although these differentiates are superficially inseparable, highly variable features of the valves (claspers) of the male genitalia distinguish them—provided the valval variation is properly analyzed. Most workers erroneously have seen this excessive variation as more or less continuous, taken the supposed intergrades as evidence of interbreeding, and so considered the differentiates subspecies.

Since 1963, I have critically compared the genitalia of 3060 males (1910 *P. communis* and 1150 *P. albescens*) to determine not only their taxonomic rank but also their geographic distribution: *P. communis* ranges from southern Canada through most of the United States to southern Mexico; *P. albescens*, from the southern United States to southern Mexico. Long considered a southwestern differentiate (in the USA) ranging no farther east than the Corpus Christi area of Texas, *P. albescens* actually extends eastward along the Gulf Coast to the Atlantic Coast of Florida and currently is expanding its eastern range. Narrowly sympatric in the eastern and far western USA, these species are broadly sympatric in the southwestern USA and montane Mexico. Though more austral than *P. communis*, *P. albescens* flouts conventional wisdom by occurring high in various southwestern mountains. In Mexico, it extends from coast to coast and through the entire Baja California peninsula.

The rampant, ostensibly continuous genitalic variation in mixed samples of these species is clearly bimodal. Comparison of genitalia throughout each species' range shows fully as much intraspecific genitalic variation in areas removed from interspecific contact as in areas of overlap. The variation is inherent in each species, not a result of hybridization. I develop these points with comparative figures of the genitalia of 484 males (253 *P. communis* and 231 *P. albescens*) from diverse situations.

Pyrgus communis is slightly larger than *P. albescens* in average size.

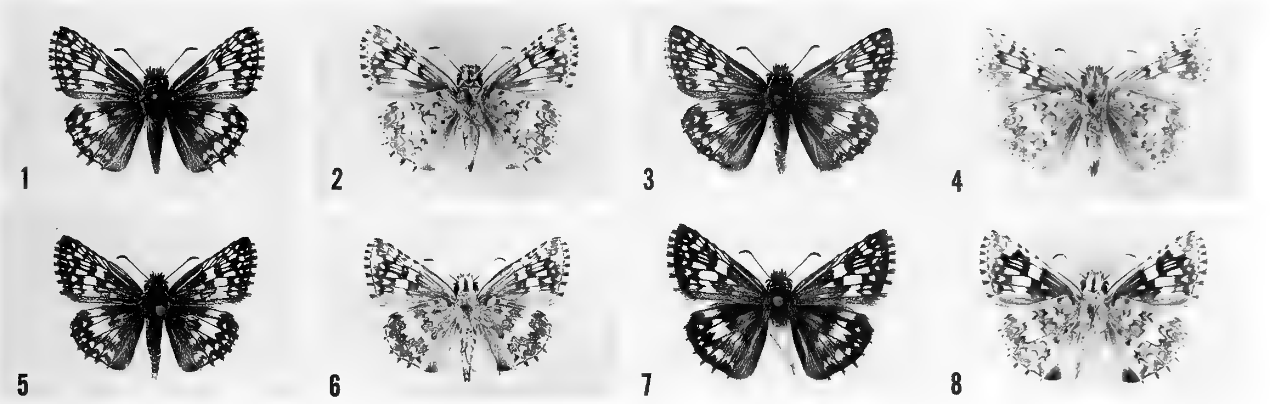
Additional key words: genitalia, geographic distribution, speciation, systematics, variation.

Pyrgus communis (Grote 1872) and *P. albescens* Plötz (1884) have a checkered history. These black-and-white skipper species (Figs. 1–8) were originally described more than once; they were variously referred to different genera (*Hesperia*, *Pyrgus*, *Syrichtus*, *Urbanus*); and names applied to related, similar-appearing species were misapplied to them. Nevertheless, by the time Lindsey et al. (1931) was published, most nomenclatural problems—which involved homonymy as well as synonymy, specific identity, and proper generic usage—had been solved; and these skippers were designated by the names we continue to use today. Current synonymy may be found in Evans (1953), dos Passos (1964), and Miller and Brown (1981, 1983).

On the other hand, biological problems involving the mutual status of *Pyrgus communis* and *albescens*—i.e., whether they are completely separate species, variably hybridizing species, freely interbreeding subspecies, or one and the same taxon—surfaced early in this century and persist to its end. Knowledge of the geographic distributions of these skippers—which, early on, was unavoidably sketchy and partly erroneous—is still notably deficient.

Just seven months after Skinner (1906a:96) briefly described what he called "*Pyrgus occidentalis* n. sp." (=*P. albescens*) from "the Northwest territory [an invalid source for this skipper] and . . . the southwest generally" (specifically "San Bernardino Ranch, Cochise Co., Arizona, . . . and Brownsville, Texas"), he (Skinner 1906b:278) backtracked by declaring, "This is not a species, but only a form or geographical race of *tessellata*" (Scudder) (=*P. communis*). But eleven years later, on 27 September 1917, "Williams made some interesting remarks on the genus [*Pyrgus*], especially regarding characters possessed by the genitalia and illustrated them by drawings. He stated that, based on the genitalic characters, *occidentalis* seems to be distinct from *tessellata*" (Cresson 1918:38). Lindsey (1921:41) treated *occidentalis* as a race of *tessellata* with the comments "California, Arizona and Texas. This form is scarcely worthy of a name, but may be regarded as a pale southwestern geographical race. I have not looked for differences in the genitalia." However, the observation by "Williams . . . regarding the apparent specific distinctness of *H. occidentalis* Skin. and *tessellata* Scud. on the basis of genital structure led [Barnes & Lindsey 1921:79] to examine a long series of these races. . . . The genitalia do undoubtedly show two very easily separable forms of valves, but these are connected by a great variety of intermediate forms. . . . It is impossible to draw a definite line between the extreme forms, so we prefer to retain the old conception of *occidentalis* as a pale western race of *tessellata*."

Independently investigating the relationship of these two entities from a greater distance, Swiss lepidopterist Reverdin (1921) took what, for that time, was the remarkable step of comparing 90 dissections of their male genitalia. He recognized, thoroughly de-



FIGS. 1–8. *Pyrgus* males in dorsal (odd-numbered) and ventral (even-numbered) views; collected by J. M. Burns (and deposited in USNM). **1, 2, 5, 6,** *P. albescens*. **3, 4, 7, 8,** *P. communis*. **1–4,** Southwestern Research Station of the American Museum of Natural History, Cave Creek Canyon, Chiricahua Mountains, 5400 ft [1645 m], Cochise County, Arizona, USA, 7 September 1959. **5, 6,** Cantonment, Escambia County, Florida, USA, 7 September 1984. **7, 8,** Skippers, Greensville County, Virginia, USA, 25 September 1980.

scribed, and carefully illustrated two divergent genitalic extremes (which he even found coexisting in Chihuahua City, Mexico); and, at first, he thought that they characterized the two differentiates in question. But he encountered so much genitalic variation and so many transitional forms between the extremes—as well as specimens from the American specialists Williams and Lindsey that had *occidentalis* labels but the "wrong" kind of genitalia—that he rejected this idea, concluding (while admitting that the evidence was still imperfect) that *tessellata* (=*communis*) is a distinct and well-defined species whose male genitalia display a wide range of variation and that *occidentalis* (=*albescens*) is only a variety of it, occurring in a southwestern portion of its range and far to the south of that. (For far southern *occidentalis*, Reverdin listed Panama and even Surinam—areas which, in reality, greatly exceed the southern limits of both *P. albescens* and *P. communis*. Reverdin's [1921:pl. 7, figs. 1, 2, and 6] excellent photographs of male genitalic extremes—all of which he ascribed to *tessellata*—depict, respectively, a typical example of *P. communis*, a typical example of *P. albescens*, and a mildly atypical *P. communis*.)

Given the studies of Barnes and Lindsey (1921) and particularly Reverdin (1921), it is not surprising that Skinner and Williams (1923:289)—while clearly illustrating the basic valval difference between *tessellata* (fig. 7) and *occidentalis* (fig. 8)—called the latter nothing but a variety of the former. They noted that "The [varietal] name should be restricted to apply only to the smaller, paler form of the species inhabiting the low arid regions along the Rio Grande to the north and south, and thence to and up the Californian coast." Using revised nomenclature that is still current, Lindsey et al. (1931:pl. 10, figs. 7, 8) reprinted the diagnostic Skinner and Williams (1923) genitalic figures but reiterated the Lindsey (1921) view of *albescens* as a weak race of *P. communis* ranging from California to Texas and Mexico.

Later, with no intention of probing the *communis*/*albescens* relationship but, rather, in an effort to gain some appreciation of levels of individual variation in the male genitalia of skippers, Lindsey (1939:174) turned to *P. communis* (in the strictest sense) "solely because of the availability of a long series of reared specimens, most of them closely related. The genitalia of 100 males were mounted on microscope slides, projected at the same magnification, and measured from the magnified image in millimeters to provide data for statistical study." Four of the five measurements taken (Lindsey 1939:fig. 1) involved the distal end of the valve (which happens to be that part of the valve where *P. communis* and *P. albescens* differ most); and the individual variation there (in what had to be pure *communis*) was enormous: coefficients of variation for the four valval measurements were 10.48, 25.44, 29.14, and 59.42.

In his field guide, Klots (1951:216) wrote, "Opinions differ as to whether *albescens* should be considered a color variety or subspecies of *communis*, or a separate species. Despite its name it varies through the same range from dark to light forms as *communis*. But it appears to be constantly genitalically distinct from *communis*, with which its range overlaps. So I treat it as a distinct species." At about the same time, Evans (1953)—with his post-Mayr (1942) proclivity for lumping related species that seemed at least partly allopatric into a single polytypic species (see Burns &

Kendall 1969 for fuller discussion)—treated *albescens* as a subspecies of *communis*. On the basis of British Museum (Natural History) material, he recorded *P. communis communis* from Canada through the United States to southern Mexico (Guerrero, Puebla, and Veracruz) and *P. communis albescens* from the southwestern United States (southern California, Arizona, Colorado [just one male], and Brownsville, Texas) to southern Mexico (Colima, Michoacán, and Veracruz).

After recording *P. communis albescens* from 20 mi. east of Descanso and from San Quintin, Powell (1958:31) observed, "While previously known in Baja California only as far north as Angeles Bay, *albescens* is a typical arid-country form and is to be expected throughout the peninsula. The Descanso specimen, a male, is intermediate between *albescens* and *communis communis* in genitalic structure, as is characteristic of populations in the San Diego [California] area."

Tilden (1965:91) opened his questioning note with "The status of *Pyrgus communis* Grote and *Pyrgus albescens* Ploetz is one of the unsettled problems in the study of American Hesperiidae. *P. albescens* has been considered a form or a subspecies of *P. communis*, or a distinct species"; and he (Tilden 1965:93) closed it with "*P. communis* and *P. albescens*, while perceptibly different, do not seem to exhibit the degree of differences usually associated with either specific or subspecific status. Since each occupies a range, with intergradation along the lines of meeting and in some instances over considerable areas as well, they do not seem to be forms of one another in the usual sense of the term. There seems to be no taxonomic category that expresses their relationship precisely." In the body of his short paper, Tilden provided some new distributional and ecological information, some of which he used to justify his taxonomic equivocation. For example, "In Arizona, specimens from north of the Mogollon Rim were *P. communis*, as were those from higher elevations in the isolated ranges to the south. The higher elevations of such ranges as the Santa Catalina Mountains and the Santa Rita Mountains yield *P. communis*, while the open desert usually is inhabited by *P. albescens*. At Sycamore Canyon, Santa Cruz County, Arizona, specimens with genitalia of both types were taken. This is a locality of intermediate elevation. . . . On the basis of available data, it appears that *P. communis* occupies cool and temperate regions, even when such areas occur as islands surrounded by deserts. *P. albescens* seems to be adapted to low-elevational warm areas, which may be either dry (Arizona, southern California) or humid (Gulf Region of Texas) [this was a novel and, as it turns out, significant observation]. . . . [Some workers] regard each as a valid species that replaces the other in the proper environment. . . . The genitalic differences suggest this view. Yet it seems unlikely that this treatment would have been proposed by these workers had they been aware of the degree of intergradation that takes place along some of the interfaces. . . . [Some workers] regard each as a subspecies that replaces the other in the proper environment. . . . This interpretation also presents some problems. If the ranges are mapped in southern Arizona, we find the interesting condition of one subspecies (*P. communis communis*) existing as small islands surrounded by populations of the other (*P. communis albescens*)." Two decades later, in his field guide, Tilden treated *albescens* as a subspecies but remarked, "Status remains unsettled; some experts consider it a separate species" (Tilden & Smith 1986:256).

At that point in time, Austin (1986:55) introduced his analysis of the situation in Nevada with "The status of *Pyrgus communis* (Grote) and *Pyrgus albescens* Plötz . . . has been in question up to the present. They have been treated as separate species, as subspecies, or neither (Tilden 1965). Even the most recent regional and taxonomic treatments vary"; and he (Austin 1986:57) concluded with "Intermediacy, at least in southern Nevada, is greater than previously reported. This indicates that the two phenotypes are closely related, and are probably no more than allopatric subspecies of *Pyrgus communis*." He examined the left valves of more than 500 Nevadan males; classified them as *communis*, *albescens*, or intermediate; and mapped their distribution, with the following results: "Individuals of the *P. communis* phenotype occur throughout Nevada (Fig. 2); those of the *P. albescens* and intermediate phenotypes occur in southern Nevada except for one *P. albescens* from Carson City (Fig. 2). At most stations where *P. albescens* were taken, intermediates and *P. communis* were taken also. Individuals with intermediate valvae occur only within the range of *P. albescens*. There is no strict ecological or elevational segregation in southern Nevada, but phenotype proportions do vary. The *P. albescens* phenotype dominates at lower elevations and latitudes. Intermediates and *P. communis* become more prominent with increase in elevation and latitude. . . . The Nevada distribution is compatible with that previously noted (Tilden 1965) for *Pyrgus communis*; the latter is a more northern and higher elevation phenotype, *P. albescens*, a lower-elevation and more southerly phenotype."

For southeastern Arizona, Bailowitz and Brock (1991:59) treated these skippers as sibling species and repeated the Tilden (1965) view of the more cool-adapted *communis* occupying mountain islands in a sea of the more warm-adapted *albescens* but conceded that "the situation is not quite so clear cut as genitalic intergrades occur regularly in areas of overlap." Specifically they noted that, in contrast to the widespread *albescens*, "*communis* is restricted to the higher mountain ranges. Tilden (1965) cited the taxon from the Sta Catalinas, Sta Ritas, and even Sycamore Cyn but all specimens examined genitalically from these areas have proved to be *albescens*. To date, confirmed records exist only for the Pinaleños, Chiricahuas, and the Dragoons with several intermediate specimens from around Safford."

Differences of opinion endure. They are reflected most recently in *Systematics of Western North American Butterflies* where the checklist of California butterflies (Emmel et al. 1998:836) calls *communis* and *albescens* separate species while, on the facing page, the checklist of Nevada butterflies (Austin 1998:837) calls them subspecies.

The subspecific interpretation hinges on the perception of genitalic intergrades between *communis* and *albescens* (presumably stemming from interbreeding between the differentiates). As indicated above, such intermediacy has repeatedly been seen and cited over the years. I started looking into the *communis/albescens* relationship in 1963; and, for far more than a decade, I, too, saw continuous valval intergradation. But I finally realized that it does not exist—that, instead, males of each species (Figs. 1–8) vary greatly in valval expression around readily separable modes (Figs. 9–20) and that even the seemingly continuous variation actually forms two discrete clusters. There are no intergrades. There are two reproductively isolated species.

MATERIALS AND METHODS AND RELEVANT BACKGROUND

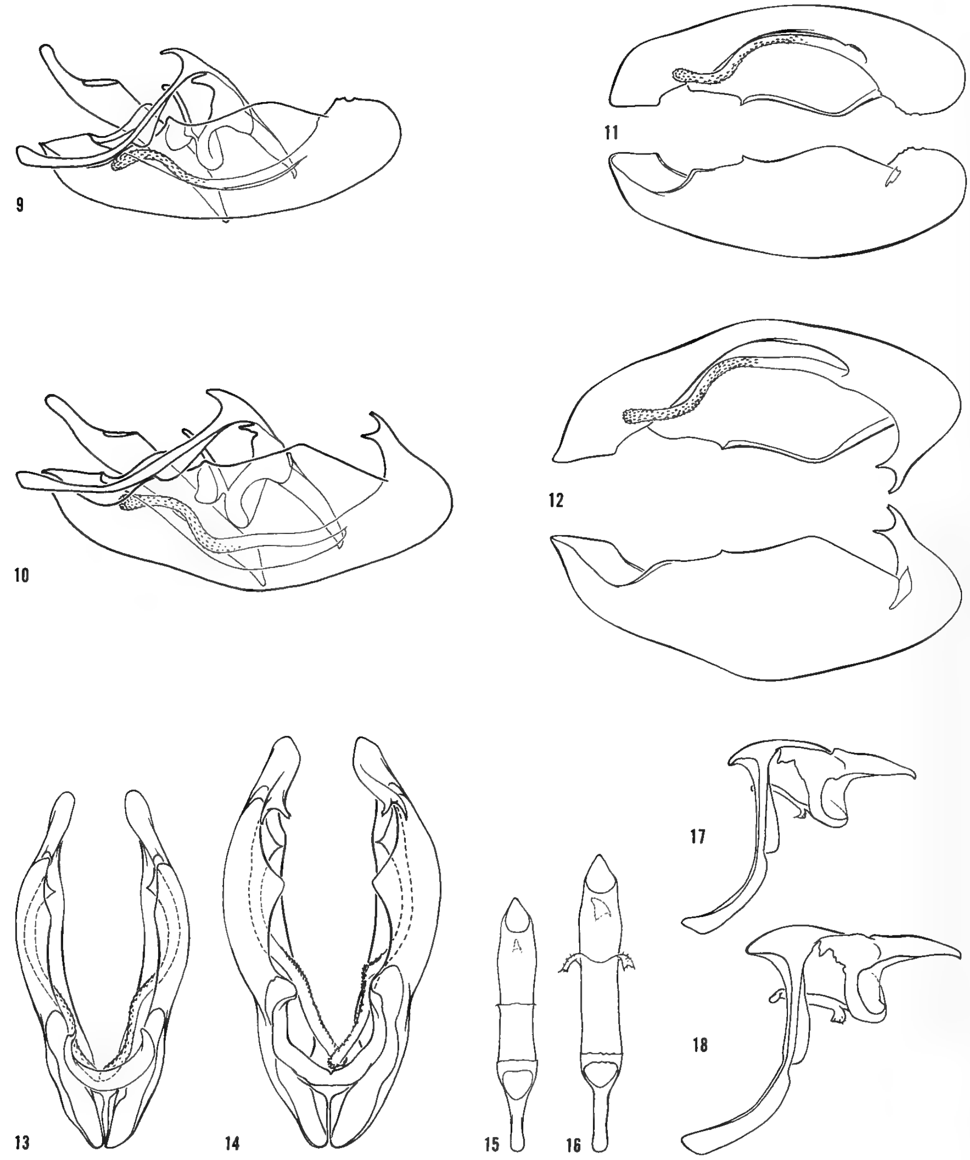
Over the course of this prolonged project I critically compared the genitalia of 3060 males (I still cannot distinguish females of *P. communis* from those of *P. albescens*) and pinned my sex-and-determination label on each. Genitalia were fully dissected (after brief boiling of detached abdomens in 10% KOH) and stored free in one-dram vials of glycerol (Burns 1997) or, more often, were partly dissected—or simply dusted—dry, *in situ*, to expose the valves. From 1978 to 1981 a detached observer prepared a 4″ × 6″ file card for each male that he dissected (his dry-dissected males were individually coded P-1 to P-975) as well as for each previously KOH-dissected male, with a drawing of the distal end of its left valve on one side and all other information, including field data, on the reverse. I gradually came to recognize two discrete clusters within ostensibly continuous valval variation by repeatedly playing a sort of genitalic solitaire—i.e., by thoroughly mixing and shuffling the cards and trying to sort the genitalia to kind without knowing their geographic origin in advance.

Material accumulated from many sources (see Acknowledgments) was augmented both by my own opportunistic collecting in various situations and, more importantly, by field trips expressly for *P. communis* and *P. albescens* with my wife, Sarah: to southeastern Arizona in 1974, to southcentral California in 1987, to northern New Mexico in 1989, to eastern Arizona in 1991, and to southeastern Arizona in 1999. Where these skippers fly together, we sampled them randomly because they are superficially inseparable.

While collecting material for my evolutionary study of *Erynnis* (Burns 1964), Sarah and I incidentally had taken males of *albescens* (but not of *communis*) at high elevations in mountains of southeastern Arizona, as follows:

Chiricahua Mountains: Rustler Park, 8500 ft [2590 m], 21 June 1958, 1 ♂.
Pinaleño Mountains: Treasure Park, 8900 ft [2715 m], 19 June 1958, 1 ♂;
  Soldier Creek Campground, 9400 ft [2865 m], 26 June 1958, 1 ♂;
  Swift Trail, twixt Ladybug Saddle & Shannon Park, 8600–9000 ft [2620–2745 m], 27 June 1958, 1 ♂.
Blue Range of White Mountains: twixt Grey Peak & Rose Peak, 6000–7000 ft [1830-2135 m], 6 June 1959, 4 ♂.
White Mountains: K.P. Cienega, 5 mi [8 km] S Hannagan Meadows, 9000 ft [2745 m], 6 June 1959, 1 ♂.

Somewhat conversely, on 25 April 1959, we—and on 3 and 6 September 1959, I—had taken males of both *communis* and *albescens* together at relatively low elevations of 4600 to 4100 ft (1400 to 1250 m) on the bahada at the foot of the Chiricahua Mountains and much farther out in the desert, a little north of Rodeo, New Mexico. Because these data did not support Tilden's (1965) Arizonan pattern of highland *communis* and lowland *albescens*, we made the Southwestern Research Station (in the Chiricahua Mountains) of the American Museum of Natural History our base of operations during the summer of 1974, with the intention of sampling *Pyrgus* in numbers from the desert floor to the tops of several of the mountain islands to see whether *communis* and *albescens* really do show average differences in their elevational preference and remain partially segregated for that reason. Unfortunately, Arizona had just been through a long, record-



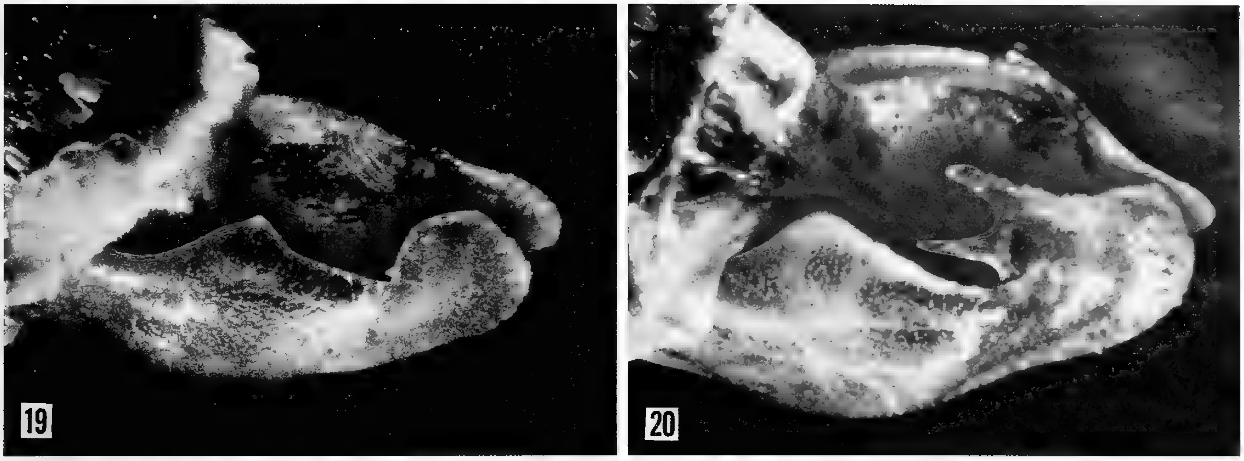
FIGS. 9–18. Genitalia of 2 ♂ *Pyrgus* from Portal, Chiricahua Mountains, 4800 ft [1465 m], Cochise County, Arizona, USA, 21 & 30 July 1974, J. M. & S. N. Burns (USNM). **9, 11, 13, 15, 17,** *P. albescens* (odd-numbered) (genitalia dissection no. X-1016). **10, 12, 14, 16, 18,** *P. communis* (even-numbered) (X-1013). **9, 10,** complete genitalia (minus right valva) in left lateral view. **11, 12,** left valva in medial (upper) and lateral (lower) views. **13, 14,** both valvae in dorsal view. **15, 16,** aedeagus in dorsal view. **17, 18,** tegumen, uncus, gnathos, vinculum, and saccus in left lateral view.

breaking drought so severe that most rhopaloceran populations were extremely depressed. The only place we could find these normally common and widespread skippers in any numbers was at Portal, at the base of the Chiricahuas, in an irrigated alfalfa field (complete with weedy, malvaceous larval foodplants, including the introduced *Malva parviflora* L.), whose owners graciously allowed us to work its perimeter again and again. During the early seventies, I had been preparing to publish on a complex, transcontinental hybrid zone between *communis* and *albescens*. Our hard-won 1974 Portal sample of 119 *Pyrgus* males, plus a lot of subsequent genitalic solitaire, changed all that.

In the end I examined the genitalia of 1910 males of *P. communis* (Canada 100, USA 1700, Mexico 110) and 1150 males of *P. albescens* (USA 930, Mexico 220).

GENITALIC DIFFERENCES

Differences between *P. communis* (Figs. 10, 12, 14, 16, 18, 20) and *P. albescens* (Figs. 9, 11, 13, 15, 17, 19)



FIGS. 19, 20. Genitalia *in situ* of 2 ♂ *Pyrgus*; left dorsolateral view. **19,** *P. albescens*, Cantonment, Escambia County, Florida, USA, 7 September 1984, J. M. Burns (USNM). **20,** *P. communis*, Skippers, Greensville County, Virginia, USA, 9 October 1982, J. M. Burns (USNM).

appear in the valves (or claspers) of the male genitalia—primarily at the distal end. Here, in *communis*, a major process sweeps anterodorsally, typically terminating in a pair of prominent prongs (Figs. 10, 12, 20). By contrast, in *albescens*, the distal end of the valve presents a relatively low profile, either with or without (Figs. 9, 11, 19) one or two incipient prongs which are usually so undeveloped as to look more like teeth. Secondarily, the body of the valve is higher and more massive in *communis* (Figs. 10, 12, 20) than it is in *albescens* (Figs. 9, 11, 19), where it is typically lower and leaner (a difference not previously reported).

Because some arguments in my analysis of genitalic variation depend on knowing how these skippers are geographically distributed with respect to each other, I consider that next.

GEOGRAPHIC DISTRIBUTION

Pyrgus communis ranges from southern Canada through most of the United States to southern Mexico. In Canada (see Layberry et al. 1998:45 [map]) it occurs primarily in southern portions of the Prairie Provinces (Manitoba, Saskatchewan, and Alberta) plus southeastern British Columbia; eastward, it edges into far southern Ontario. Although in the USA (Fig. 21) it extends from coast to coast and from sea level to over 10,000 ft (3050 m), in the East it shuns northern New England (Maine, New Hampshire, and Vermont) and adjacent eastern New York—and, at the other extreme, the southern tip of Florida—while in the West it essentially avoids southern California and adjacent southwestern Arizona. In Mexico (Fig. 22) it extends south at least to Oaxaca, apparently through interior, more or less montane, country (however, the spotty data [Fig. 22] may be somewhat misleading, especially in view of this skipper's low-level, coastal-plain occurrence in Cameron County at the southmost tip of Texas just across the Mexican border [Fig. 21]).

Pyrgus albescens ranges from the southern United States to southern Mexico. In the western USA (Fig. 21) it extends from southern California through southern Nevada, the southwestern corner of Utah, all or almost all of Arizona, and southern and central New Mexico (with one male straying northward in California [Calaveras County], Nevada [Carson City according to Austin 1986], Utah [Tooele County], and Colorado [Alamosa County]), and on through western Texas to southern Texas (as far east as the Corpus Christi area of the Gulf Coast according to Tilden 1965). This has long been considered its eastern limit. But, in reality, *P. albescens* continues eastward along the Gulf coastal plain through eastern Texas, southern Louisiana, southern Mississippi, southern Alabama, southern Georgia, and the Florida panhandle to a point on the Atlantic Coast nearly halfway down the Florida peninsula (Fig. 21). Repeatedly characterized as an arid-country differentiate, *albescens* clearly thrives in very humid climates, too (as noted before by Tilden [1965]). In mainland Mexico (Fig. 22) it occurs from coast to coast and extends south at least as far as Veracruz and Guerrero; moreover, it extends the entire length of the Baja California peninsula (Fig. 22 and Brown et al. 1992:35 [map]).

Despite their similar southern limit in mainland Mexico—which may be attributable, at least in part, to replacement by a near relative, *P. adepta* (Plötz)—*P. communis* and *P. albescens* differ sharply in total distribution, with *albescens* much the more austral of the

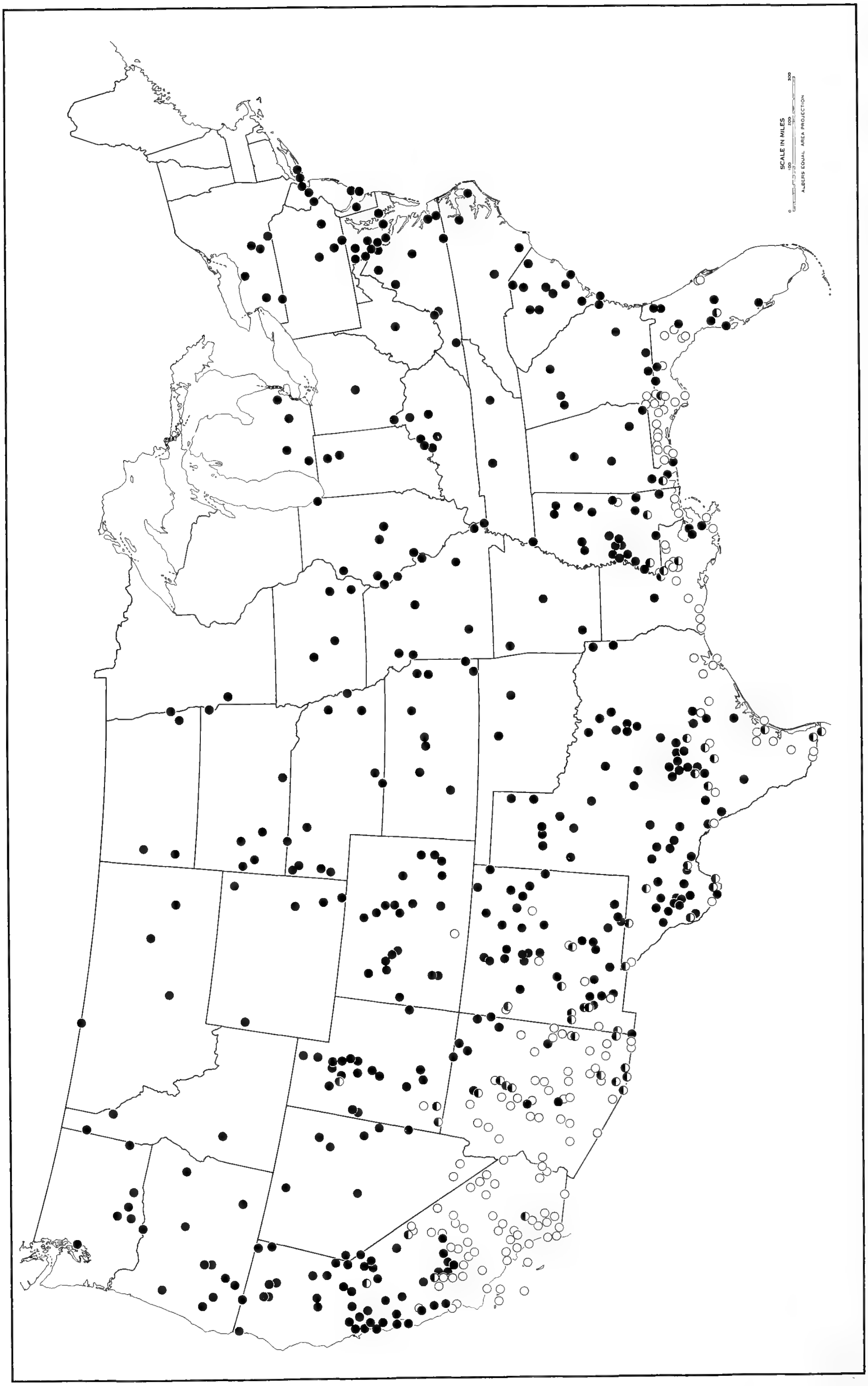


FIG. 21. Geographic distribution of *Pyrgus communis* and *P. albescens* in the United States of America (based on males whose genitalia I have examined). Dots, *P. communis*; circles, *P. albescens*; half-dots, both species at the same spot.

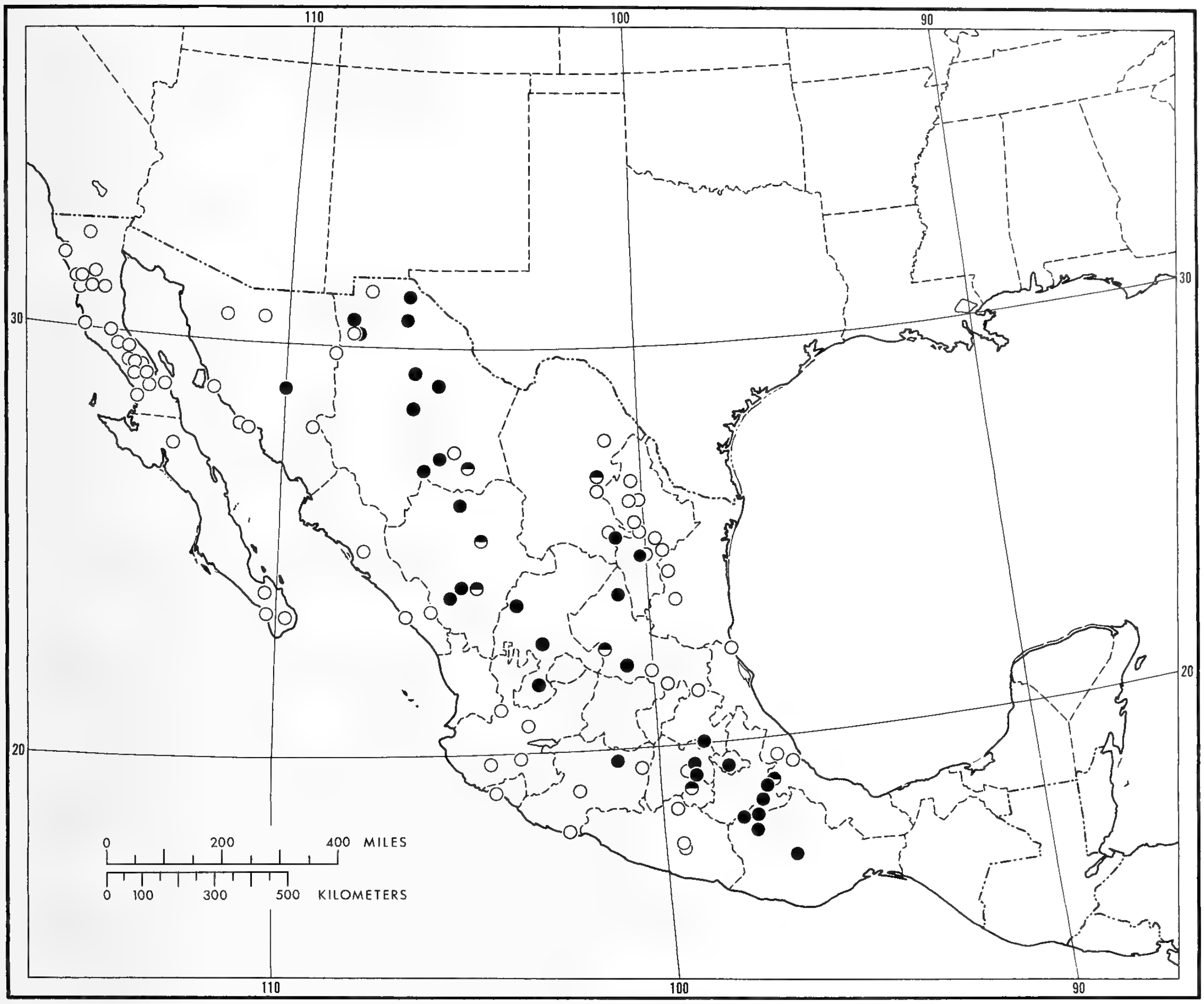
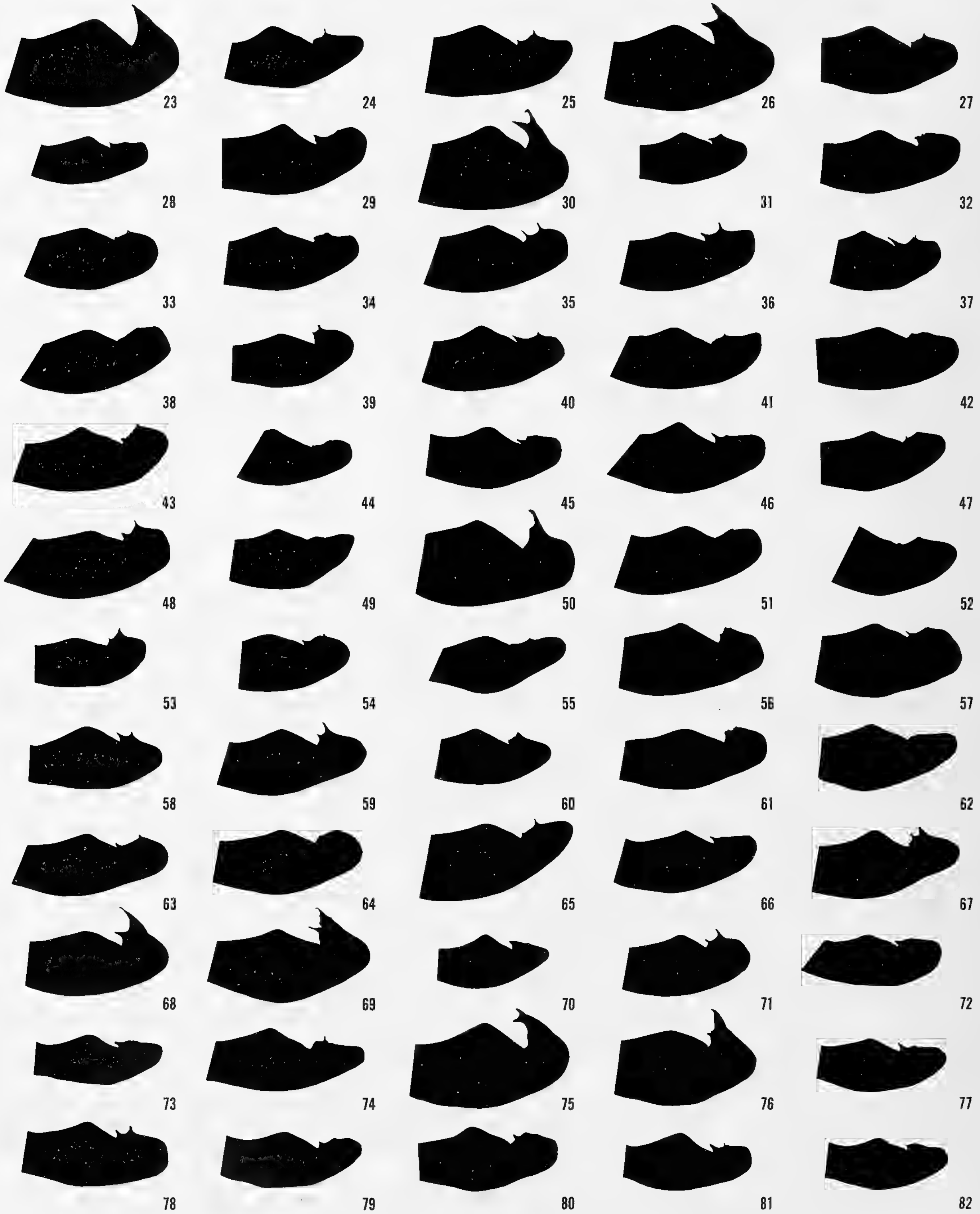


FIG. 22. Geographic distribution of *Pyrgus communis* and *P. albescens* in Mexico (based on males whose genitalia I have examined). Dots, *P. communis*; circles, *P. albescens*; half-dots, both species at the same spot.

two. But their spatial interaction is not simple. Except for one male *albescens* from western Calaveras County (Mokelumne Hill, F. E. Blaisdell [CAS]) and one male *communis* from the San Jacinto Mountains (Tahquitz Canyon, Riverside County, 21 October 1939, F. H. Rindge [AMNH]), *communis* and *albescens* closely replace each other across southcentral California with little or no regard for elevation (Fig. 21). Each species seems to inhibit the other's expansion. Again, they appear to be only narrowly sympatric along the Gulf Coast from eastern Texas to Florida (Fig. 21). On the other hand, these species are broadly sympatric through the southwestern USA and montane Mexico (Figs. 21, 22)—areas in which they may have been in contact for the longest time.

How recent is the range of *P. albescens* in the eastern USA? My earliest record is 1 ♂ from 3 mi (4.8 km) east of Liberty, Liberty County, Texas (this is northeast of Houston), which was reared out on 24 July 1923 from a larva on *Sida rhombifolia* L. (Malvaceae) (USNM). The next *albescens* come from Houston itself on 4 July 1949 (1 ♂, J. J. Winston [LACM]) and 11 & 12 August 1957 (3 ♂, J. M. & S. N. Burns [USNM]). Specimens from Louisiana (49 ♂, G. Strickland [USNM]) and Mississippi (18 ♂, B. Mather, M. & E. Roshore, R. Kergosien, C. Bryson [MEM, USNM]) date from the sixties and early seventies—one from 1960, the rest from 1967–72 (for an exact plot of most localities in these two states, see Fig. 375). Specimens from the western tip of Florida (Escambia County)



FIGS. 23–141. Genitalia of 119 ♂ *Pyrgus*—in order of capture—from a single field at Portal, Chiricahua Mountains, 4800 ft [1465 m], Cochise County, Arizona, USA, summer of 1974, J. M. & S. N. Burns (USNM); distal end of left valva in lateral view. **23–27,** 11 July; **28, 29,** 13 July; **30–43,** 17 July; **44–46,** 18 July; **47–49,** 20 July; **50–52,** 21 July; **53–67,** 23 July; **68–87,** 27 July; **88–111,** 30 July; **112–141,** 5 August. **23, 26, 30, 50, 68, 69, 75, 76, 83, 86–90, 93, 95–102, 105, 106, 108, 112–141,** *P. communis* (N = 56). **24, 25, 27–29, 31–49, 51–67, 70–74, 77–82, 84, 85, 91, 92, 94, 103, 104, 107, 109–111,** *P. albescens* (N = 63).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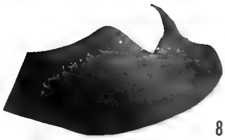
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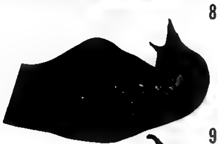
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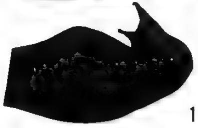
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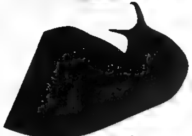
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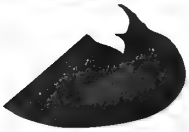
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date from 22 May 1976 (Pensacola Beach, 1 ♂ [USNM]) and 7 September 1984 (Cantonment, 12 ♂, J. M. Burns [USNM]). Those from farther east in Florida as well as directly to the north in Alabama and Georgia (34 ♂, J. V. Calhoun) date from 1989–95. An eastward progression of *albescens* suggested by these dates could be an artifact because the dates largely reflect times when I begged sympathetic, suitably situated, local collectors to sample *Pyrgus*. (Most collectors find these ubiquitous skippers trashy and do not stoop to collecting them, especially not in series). If the presence of *albescens* along the Gulf Coast is none too recent, then consider this: Grote (1872:69) described *P. communis* from "central Alabama"—presumably the vicinity of Demopolis, which was his home—so he may have come within a hundred miles (160 km) of catching its look-alike, *P. albescens*, instead (or besides).

However, it is clear that *P. albescens* is currently increasing in numbers and spreading eastward and southward in Florida at a rapid rate. In September and October 1999, J. V. Calhoun caught a total of 70 male *albescens* not only in most counties of the panhandle but also at the top of the peninsula—in Alachua, Gilchrist, and Levy counties—and nearly halfway down the peninsula in Pasco County on the Gulf side and in Volusia and Brevard counties on the Atlantic side (Fig. 21). At the same time, he caught no *P. communis* whatsoever. In Pasco County, he took 12 male *albescens* in the very area (southeast of Dade City) in which, 9 and 10 years earlier, at similar times of year, he got only *communis*. In examining the *Pyrgus* material of the Florida State Collection of Arthropods, I found 33 male *P. communis*—taken between 1942 and 1977 in Alachua, Clay, Duval, and Liberty counties—but no Florida examples of *P. albescens*. At least at this evolutionary moment, *albescens* seems to be expanding at the expense of *communis* and even displacing it—a potentially instructive situation that should be closely followed.

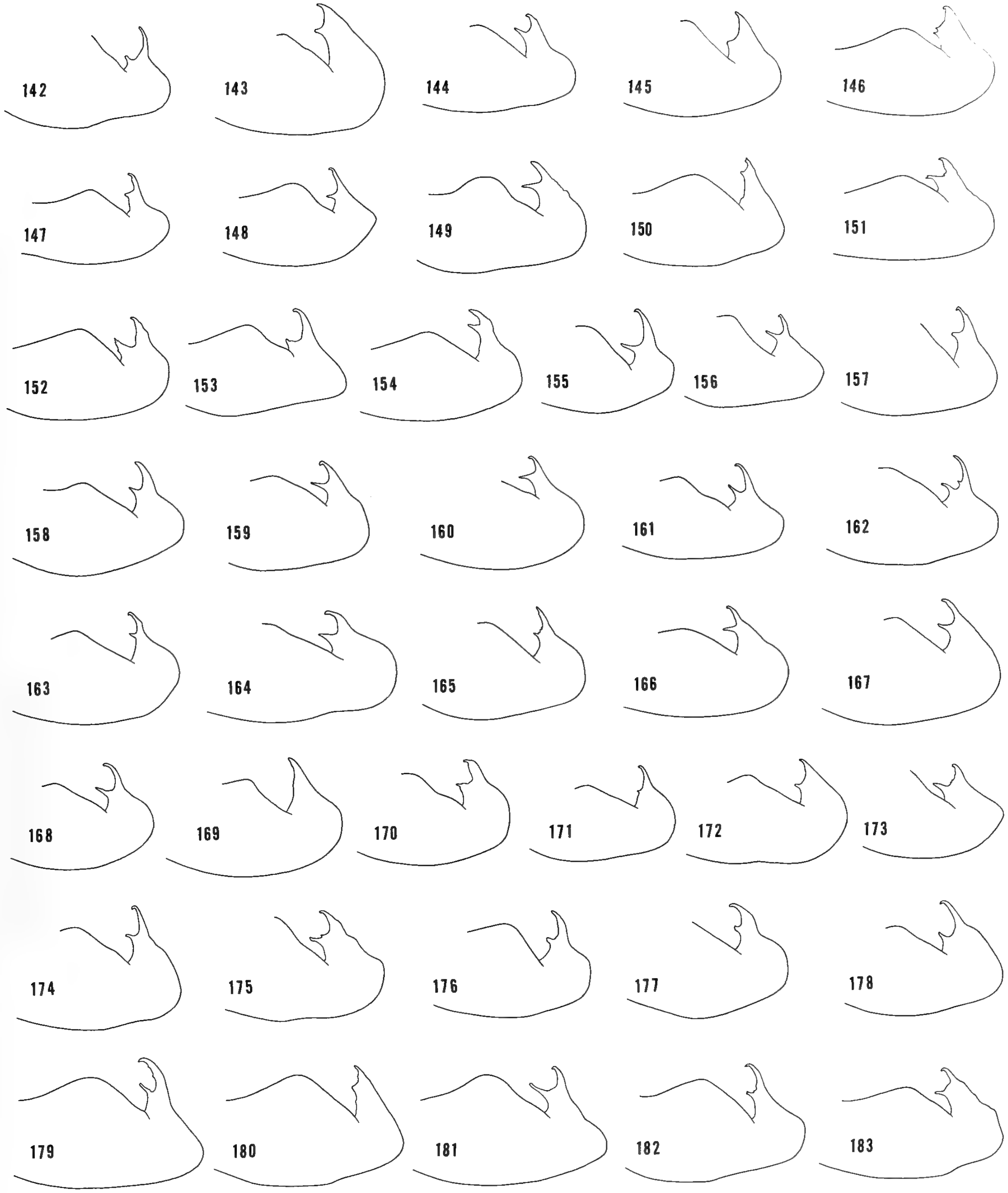
In the southwestern USA, where overlap is so extensive, some northern records of sympatry go further back in time. For example, at Ft. Wingate, McKinley County, New Mexico, *P. albescens* was taken on 18 June 1906 and *P. communis* on 19 July 1906 (AMNH); and at St. George, 2800 ft (855 m), Washington County, Utah, both species were taken on 10 June 1919 by T. Spalding (AMNH). Defying a strictly lowland pattern, *albescens* (1 ♂) flew with *communis* (11 ♂ in all) at Loop Camp, 7400 ft (2255 m), 13 mi (21 km) southwest of Grantsville, Tooele County, in northern Utah between 16 & 20 July 1958, F., P., & J. Rindge (AMNH). In a large majority of cases, the sympatry of *P. communis* and *P. albescens* indicated by half-dots in Figs. 21 and 22 has also involved synchrony.

Where *P. communis* and *P. albescens* coexist, their mutual spatial relations are no doubt dynamic and, therefore, rather unpredictable. *Pyrgus communis* has long been known as a mobile species whose northern distributional limit fluctuates considerably. Both species regularly invade weedy, disturbed habitats. Though predominantly austral, *albescens* shows up high on the tops of various mountain islands (see Materials and Methods and Relevant Background for some specific examples). Even the Portal, Arizona, sample of *Pyrgus* (Figs. 23–141) shifts, over 26 days, from mostly *albescens* to mostly *communis*.

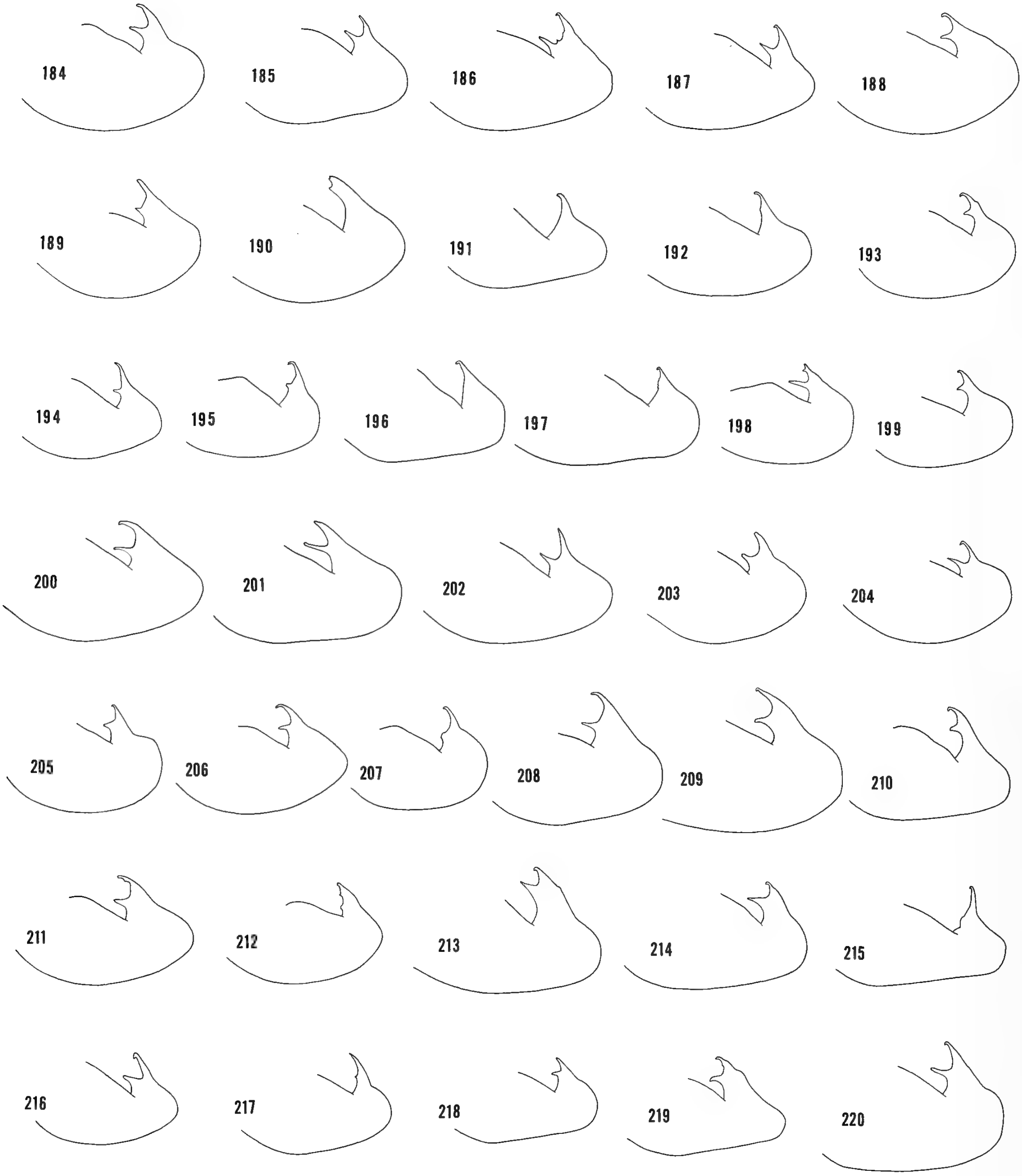
GENITALIC VARIATION

Although the rampant variation in the male genitalia of the Portal, Arizona, sample of *Pyrgus* (Figs. 23–141) may look continuous at first, it clusters about two distinct modes. The variation around each of these modes is extraordinary. In *P. communis*, with the higher, more massive valve, the diagnostic valval process varies so much in its length and width, and in the relative development of its paired, terminal prongs, that no two individuals are exactly alike. In some of the more extreme individuals, the lower terminal prong is weakly developed (Figs. 76, 100, 123, 137) or vestigial (Figs. 50, 120, 124) or completely missing (Figs. 23, 87, 113, 129, 139)—yet even then the resulting, simpler, one-prong process varies from narrow (Figs. 87, 129, 139) to intermediate (Fig. 113) to wide (Fig. 23). Occasionally, an extra terminal prong appears (Fig. 99). Most individuals express the typical two-prong process (Figs. 26, 30, 68, 69, 75, 83, 86, 88–90, 93, 95–98, 100–102, 105, 106, 108, 112, 114–119, 121, 122, 125–128, 130–136, 140, 141), but each in his own way; and in one, this process is uncommonly short (Fig. 138). It is no wonder that Lindsey (1939), in measuring four aspects of the valval process and its prongs in 100 males of *P. communis*, obtained such enormous coefficients of variation.

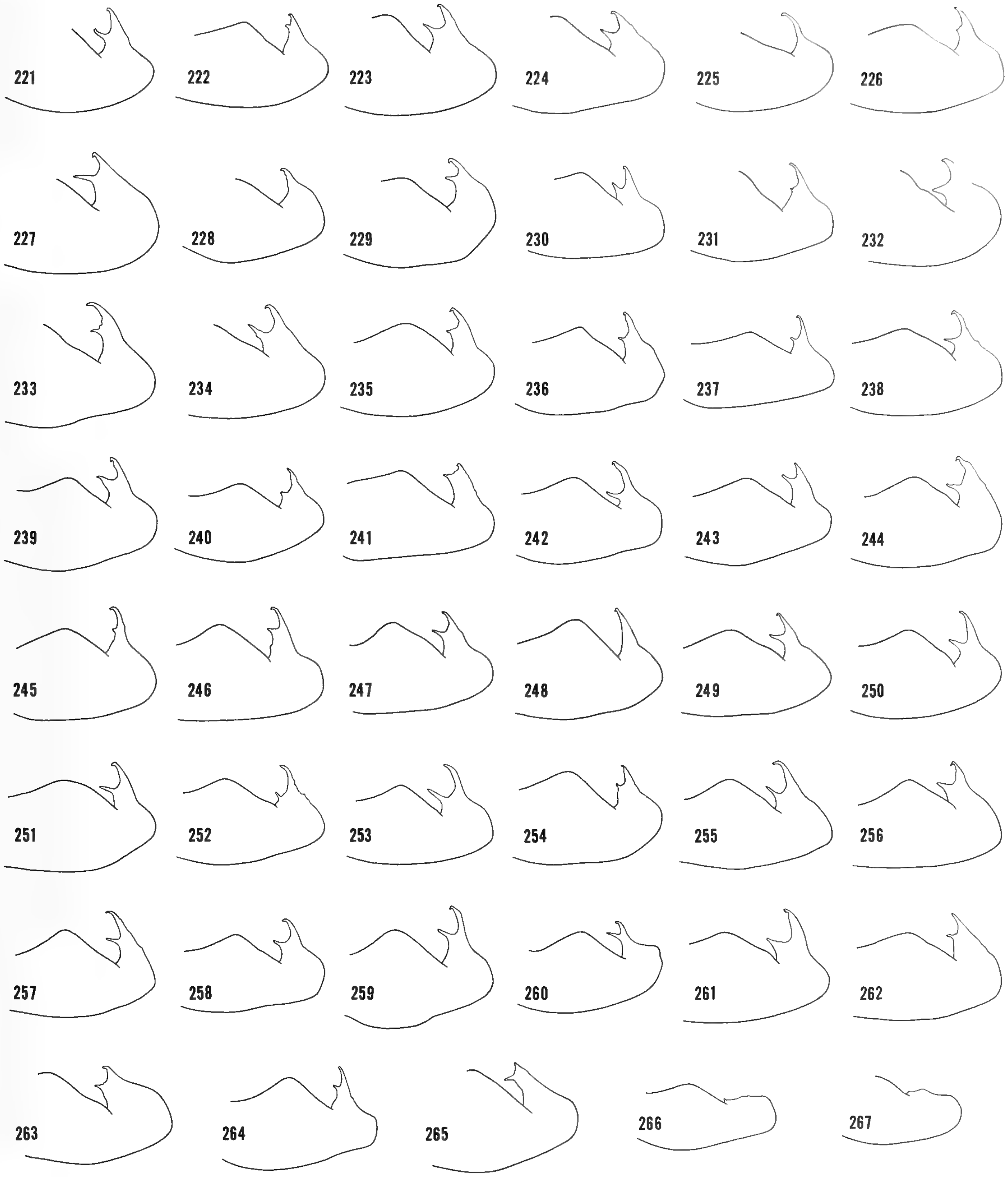
Again, in *P. albescens*, with its lower, leaner look, the variation in the valve is so great that every individual is visibly unique—but none occupies the gap between *albescens* and *communis*. The dorsodistal end of the valve, which rarely is fairly even (Figs. 49, 62), usually shows traces (Figs. 28, 32, 33, 38, 41, 42, 44, 47, 51, 52, 55, 61, 64, 70, 72, 73, 82, 84, 92, 94, 103, 104, 109–111) or real beginnings (Figs. 24, 27, 29, 31, 34, 45, 54, 56, 57, 60, 66, 74, 77, 79, 80, 85, 91, 107) or clear expressions (Figs. 25, 36, 37, 39, 40, 43, 46, 48, 53, 58, 59, 63, 65, 67, 78, 81) of one or two teeth, which rarely develop further into incipient but modest



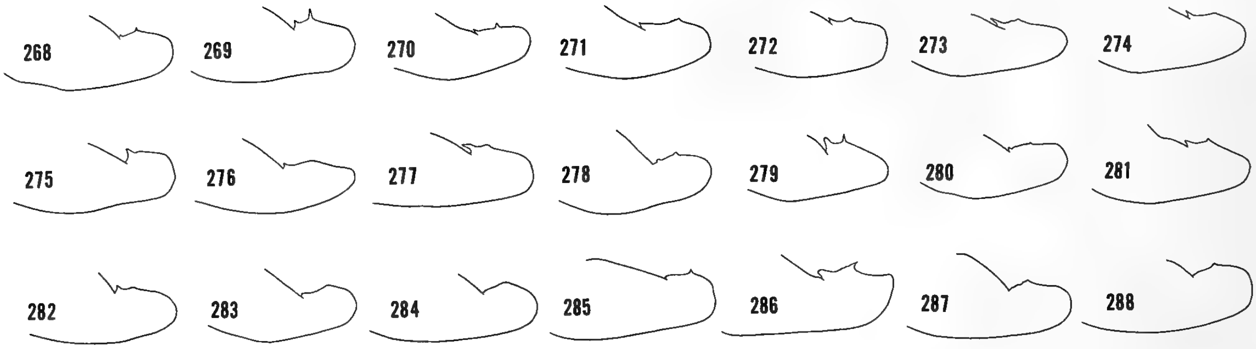
FIGS. 142–183. Genitalia of 42 ♂ *Pyrgus communis* from Galivants Ferry, Horry County, South Carolina, USA, 16 August 1957 to 27 September 1981, J. M. Burns (USNM); distal end of left valva in lateral view.



FIGS. 184–220. Genitalia of 37 ♂ *Pyrgus communis* from Meade County, South Dakota, USA, 27 to 30 July 1975 (USNM); distal end of left valva in lateral view.



FIGS. 221–267. Genitalia of 45 ♂ *Pyrgus communis* (3 March to 30 May 1966 and 30 April to 3 June 1967) plus 2 ♂ *P. albescens* (16 May and 3 June 1967) from Austin, Travis County, Texas, USA, J. M. Burns (USNM); distal end of left valva in lateral view.

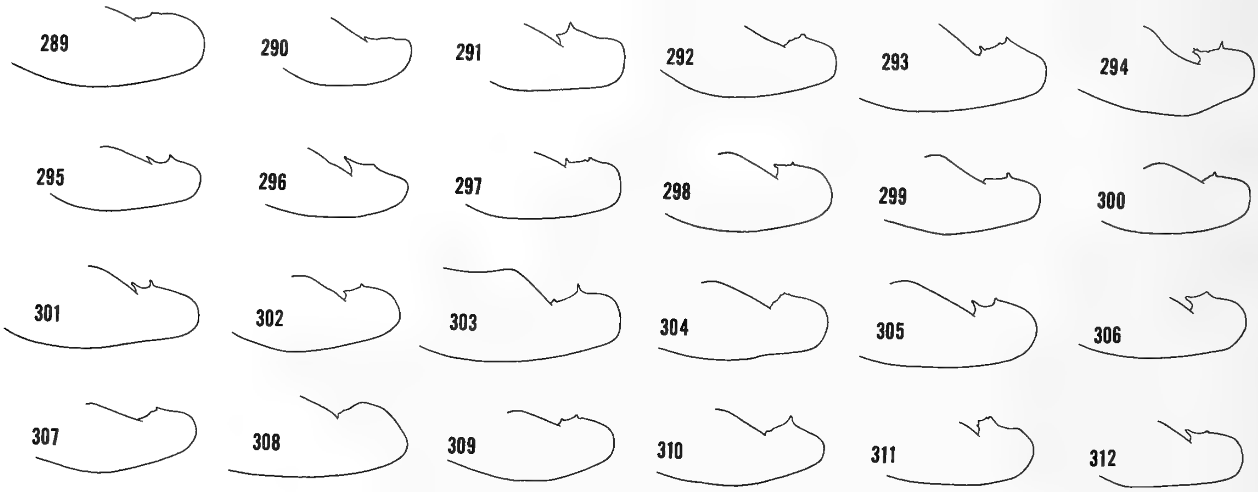


FIGS. 268–288. Genitalia of 21 ♂ *Pyrgus albescens* from Harlingen, Cameron County, Texas, USA, 8 December 1957 to 21 June 1958, J. Hunt (UCB); distal end of left valva in lateral view.

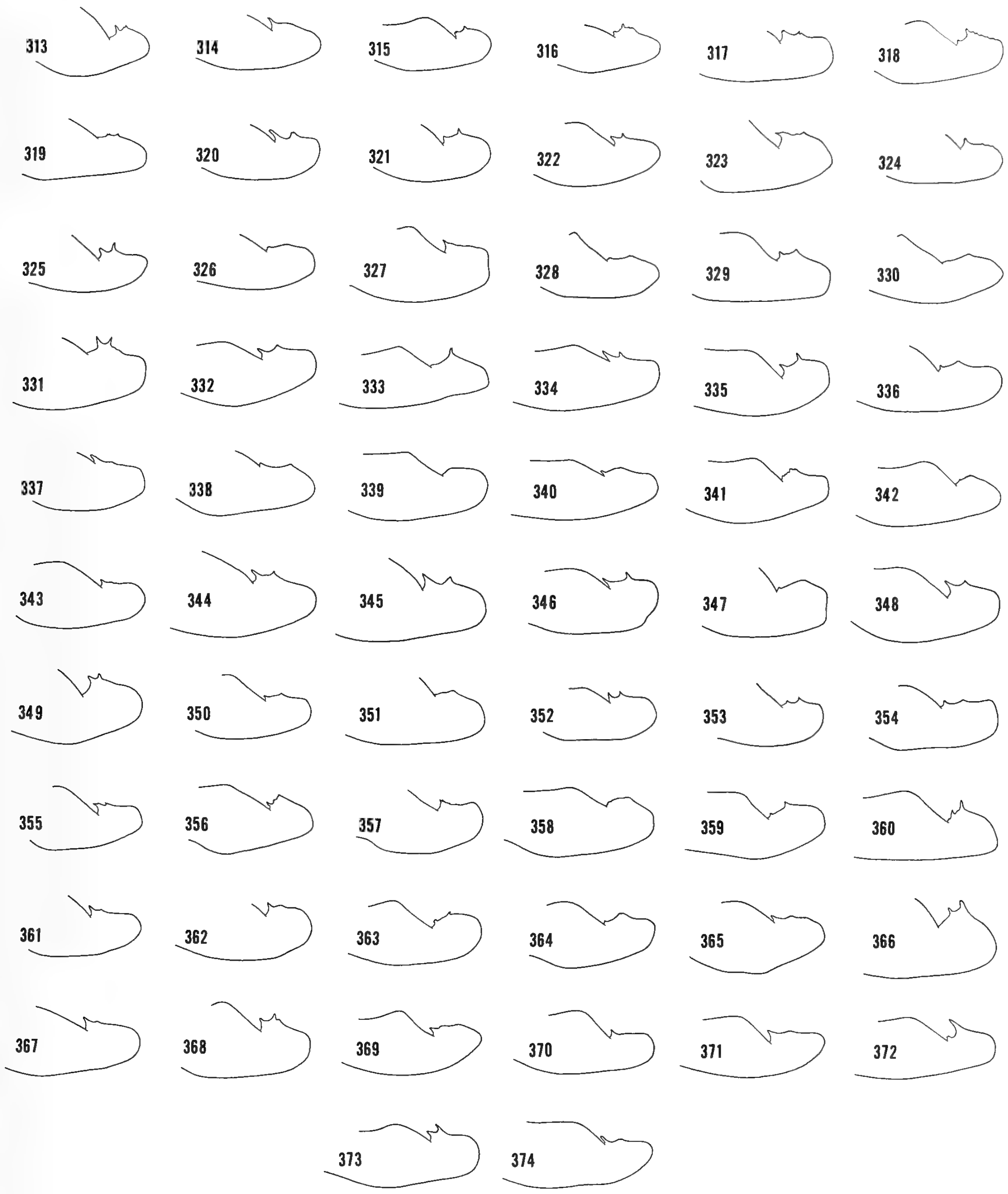
prongs (Figs. 35, 71). Although this variable expression of one or, more often, two teeth on the low distal end of the valve is perfectly normal for *albescens*, it has regularly been mistaken for intergradation toward the elevated, two-prong process of *communis*. The five valval figures called "intermediates" by Austin (1986:fig. 1), for example, are all unadulterated *albescens*.

Despite the bimodal variation, some will ask, How do you know that many of the more extreme variants are not intergrades reflecting genetic exchange between *communis* and *albescens*? The answer comes from studying and comparing genitalic variation throughout each species' geographic range. In so doing, I have found, within each species, fully as much genitalic variation in areas of separation as in areas of contact or overlap. In other words, wherever it occurs, *P. communis* runs the gamut of variation on its specific genitalic theme, whether *P. albescens* is present or not—and vice versa. The high level of genitalic variation is not the result of hybridization between differentiates; rather, it is inherent in each.

I can convey all this best by showing genitalic variation in sizable samples from a variety of situations. For *P. communis*, these are northeastern South Carolina (Figs. 142–183) and western South Dakota (Figs. 184–220), both of which are well removed (in different directions) from any contact with *albescens* (Fig. 21); plus Austin, Texas (Figs. 221–267), where *communis* predominates but *albescens* does occur. For *P. albescens*, these are Harlingen (Figs. 268–288), a town almost 300 mi (480 km) due south of Austin in southernmost Texas where *albescens* predominates but *communis* does occur; plus San Diego, California (Figs.



FIGS. 289–312. Genitalia of 24 ♂ *Pyrgus albescens* from San Diego, San Diego County, California, USA, 30 August 1891 to 25 May 1959, F. E. Blaisdell, G. H. Field, F. M. Jones, J. Powell, W. S. Wright (CAS, UCB, USNM); distal end of left valva in lateral view.



FIGS. 313–374. Genitalia of 62 ♂ *Pyrgus albescens* from the region of Laguna Chapala, Punta Prieta, Bahia de Los Angeles, Rancho Rosarito, and Mission San Borja in southern Baja California Norte, MEXICO, 28 March to 2 April 1973, J. Donohoe, J. Doyen, D. Patterson, J. Powell (CAS); distal end of left valva in lateral view.

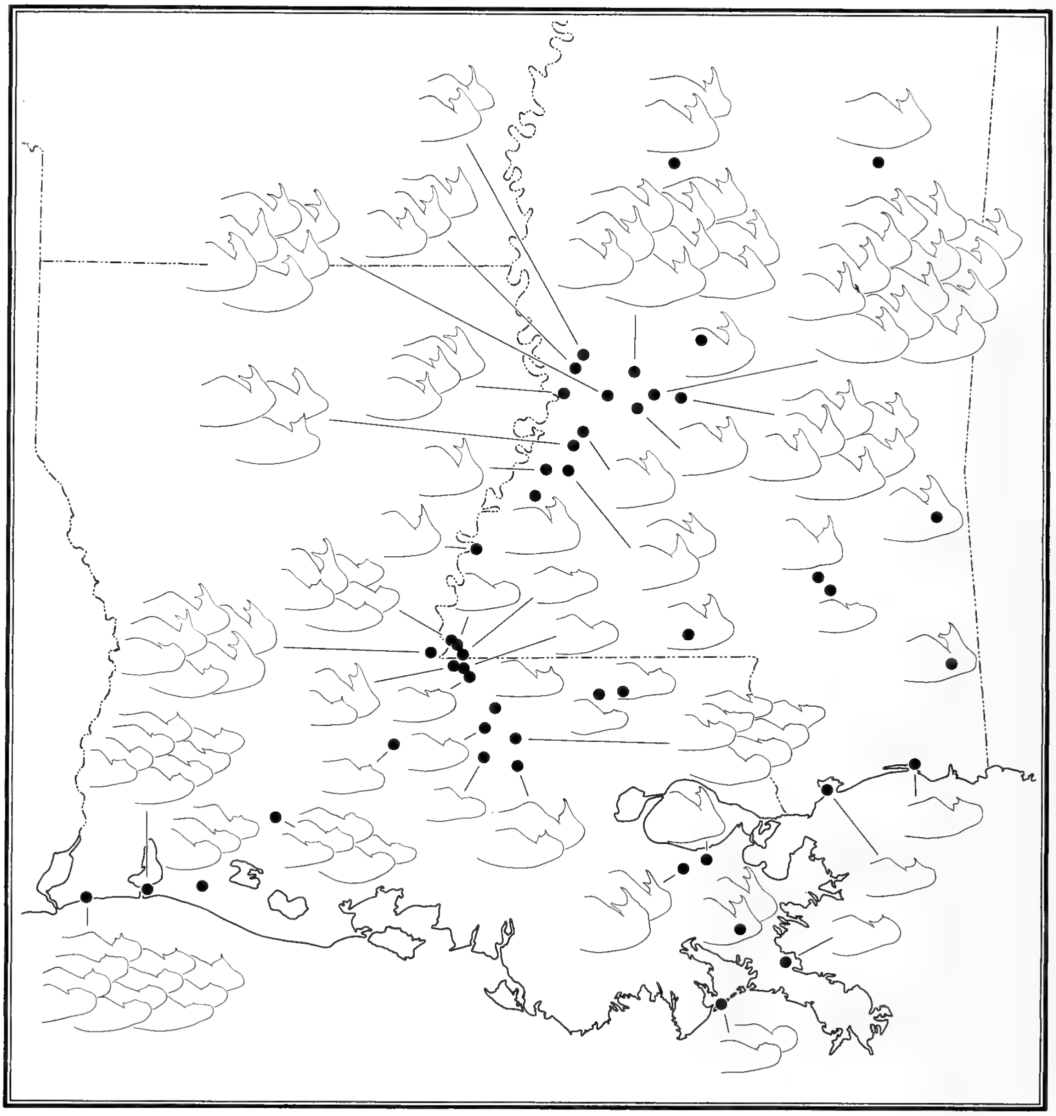
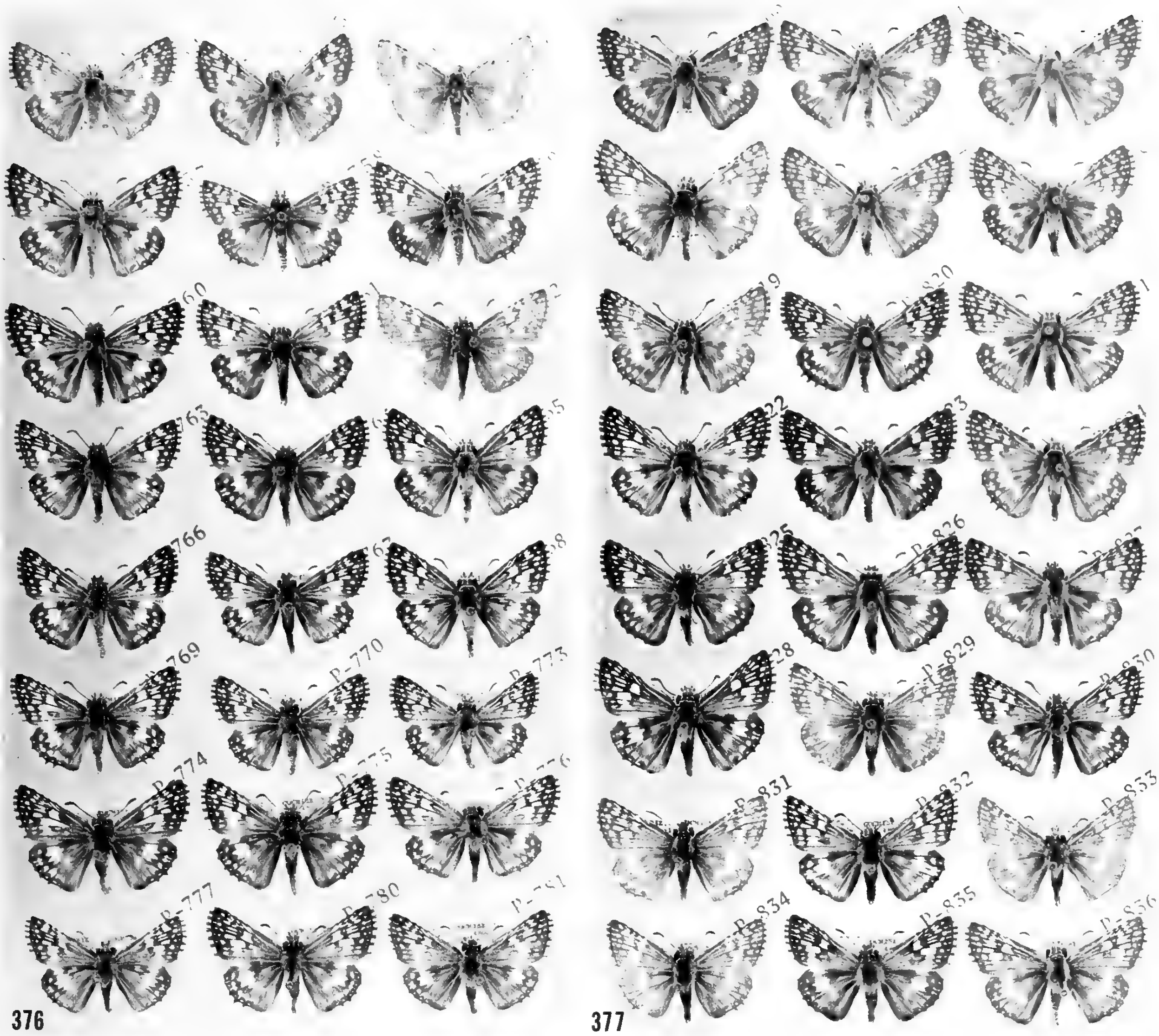


FIG. 375. Detailed geographic distribution of *Pyrgus communis* and *P. albescens* in Louisiana and Mississippi, USA, based on male genitalia, which appear (distal ends of left valvae) in lateral view.

289–312), and southern Baja California Norte (Figs. 313–374), both of which are well removed from any contact with *communis* (Figs. 21, 22). And, finally, for both species where they are in contact and narrowly sympatric, these are Louisiana and Mississippi (Fig. 375).

Most extreme among *P. communis* genitalic variants are those that have more or less lost the lower of the two prongs on the long valval process. Because I encountered a number of these individuals (Figs. 23, 50, 87, 113, 120, 124, 129, 139) in the Portal sample of mixed *Pyrgus*, it might be argued that loss of the prong reflects genetic input from *albescens*. But nothing would be further from the truth. Such one-prong variants have surfaced again and again in many different populations of *communis*—including not only those that are sympatric with *albescens* (as at Austin, Texas [Figs. 225, 228, 248]) but also those that are decidedly allopatric (as in South Carolina [Fig. 169] and, most notably, South Dakota [Figs. 191, 192, 196, 197, 212, 215, 217]).

Genitalic variants of *P. albescens* that tend most toward *P. communis* are those whose two teeth at the distal end of the valve are appreciably elevated as, for example, at Portal, Arizona (Figs. 36, 39, 58, 59, 67), and Harlingen, Texas (Figs. 269, 279)—both areas of



FIGS. 376, 377. 24 ♂ *Pyrgus albescens* (left) and 24 ♂ *P. communis* (right) from the same time and place (midsummer 1974, Portal, Chiricahua Mountains, 4800 ft [1465 m], Cochise County, Arizona, USA, J. M. & S. N. Burns [USNM]) arranged in pinning units of the same size to show the greater average wingspread of *P. communis*.

sympatry with *communis* and therefore of potential influence from it. But similar variants appear where *albescens* is well separated from *communis*, as at San Diego, California (Figs. 291, 294, 296, 311). Indeed, the most extreme variants of this kind have turned up in southern Baja California Norte (Figs. 325, 335, 344, 345, 348, 368, 373 and especially Figs. 331, 349, 366), where *albescens* is about as far removed and isolated from *communis* as it can be.

In light of this analysis, the picture of genitalic variation in Louisiana and Mississippi (Fig. 375) clearly shows *P. communis* and *P. albescens* meeting and slightly overlapping in space without genetically merging.

SIZE DIFFERENCE

It is always more satisfying to be able to bolster a difficult species separation based on subtle genitalic distinctions with evidence of another kind.

In his minimal original description of *P. occidentalis* (=*albescens*), Skinner (1906a:96) said, "This is a smaller . . . species than *tessellata*" (=*communis*); and, soon after, he claimed (Skinner 1906b:278)—with no

TABLE 1. Length (mm) of right forewing in *Pyrgus* males from Portal, Chiricahua Mountains, 4800 ft (1465 m), Cochise County, Arizona, USA, July to August 1974, J. M. & S. N. Burns (USNM).

Species	N	Range	Mean ± SE	SD	CV
albescens	63	12.0–14.9	13.72 ± 0.08	0.61	4.45
communis	54	13.2–15.6	14.58 ± 0.07	0.54	3.70

detail, explanation, or justification—"It expands in the ♂ 25 mm.; whereas *tessellata* expands 32 mm. This is an average size for the two." Tilden (1965:92) observed, "In long series, *P. communis* appears a bit larger. . . . *P. albescens* in series appears somewhat smaller. . . . The smaller average size . . . of *P. albescens* might be expected of a desert population, as compared with a related population living in a more temperate climate." But, like Skinner, he offered no supporting data.

In truth, *P. albescens* really is a little smaller than *P. communis*. The 1974 Portal, Arizona, sample is ideal for comparing size in these species because both were caught in numbers at the same time and place and presumably had weathered similar environmental conditions. A slight average difference in size becomes readily perceptible when the mounted, genitalically determined males of each species are segregated into adjacent, identical pinning units (Figs. 376, 377). Winglength measurements with a pair of vernier calipers show an average difference of 0.86 mm (Table 1).

A quarter century later, on 15 and 16 August 1999, Sarah and I caught 7 ♂ *P. albescens* and 21 ♂ *P. communis* at an elevation of 4000 ft (1220 m) in Sycamore Canyon, Santa Cruz County, Arizona. Mean forewing lengths of these coexisting *albescens* and *communis* are 13.41 mm and 14.25 mm, respectively—for an equivalent average difference of 0.84 mm.

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A NEW SPECIES OF *OMIODES* GUENÉE FROM SOUTH AMERICA (PYRALOIDEA: CRAMBIDAE)

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ABSTRACT. ***Omiodes pseudocuniculalis*, new species,** is described from South America where it is recorded from Peru, Ecuador, and Bolivia. Five males were examined, and no females are yet known. The male and its genitalia are illustrated showing the diagnostic character of short, protruding lobes located along the medial edges of the ventral groove of the uncus. The new species is most similar to *O. cuniculalis* Guenée and externally resembles other members of the "*cuniculalis* group" of *Omiodes* by the cinnamon or brown color of the adults, the beige or brown color of the ventral surface fo the the head, neck, thorax, and abdomen, and legs, and the brown color of the anal tuft. The key to the "*cuniculalis* group" is revised to include the new species.

Additional key words: Fabaceae, Western Hemisphere, genitalia morphology, parategumenal sclerites.

The genus *Omiodes* Guenée (Crambidae) was recently redescribed within the context of a study of the Pyraloidea of Costa Rica, and a checklist and key to New World species were developed (Gentili & Solis 1998). It consists of 74 species worldwide, 33 species in the Western Hemisphere, and includes *Omiodes indicata* (F.), a worldwide pest on many crops in the Fabaceae. Externally, the adults of this genus are diverse: "brown and noctuid-like, bluish and arctiid-like, and yellow reddish and pyraloid-like"; the forewing lengths vary from 7 to 26 mm long; the forewing is elongated, the termen straight, but the hindwing is usually round, in some species triangular; the thorax and abdomen in some species with bright-yellow areas, but generally same background color as wings (Gentili & Solis 1998).

During the study of Costa Rican *Omiodes* we also discovered a new species from northern South America, which we describe in this paper. The diagnosis and description of the new species is based on a comparison with all *Omiodes* species of the Western Hemisphere. The new species, *Omiodes pseudocuniculalis*, belongs to a group of closely related species that Gentili and Solis (1998) called the "*cuniculalis* group". This group includes *O. cuniculalis* Guenée, *O. fulvicauda* (Hampson), *O. anxiferalis* (Schaus), *O. alboanalis* Amsel, and *O. martini* Amsel. They are distinguished from species in other *Omiodes* groups by the cinnamon or brown color of the adults, the beige or brown color of the ventral surface of the head, neck, thorax, abdomen, and legs, the brown color of the anal tuft, the uncus head with a crest with erect hairlike setae and scale or spines in patches and lateral lobes pendant.

Omiodes pseudocuniculalis Solis and Gentili, new species

(Figs. 1, 4–8)

Diagnosis. Lobes along medial edges of ventral groove of uncus neck short and protruding.

Description. *Male. Head:* light brown. Antenna light brown. Labial palpus cream at base changing gradually to light brown at tip. Patagium ventrally cream. *Thorax:* light brown. Tegula reaching abdominal tergum II. Legs light brown, gradually lighter brown toward and including tarsi. Forewing length: 16.7–18.3 mm (n = 5). Forewing ground coloration light brown, slightly darker brown beyond postmedial line; wing pattern darker brown, postmedial line zigzag; fringe with proximal row of scales same as ground color and outer row lighter brown with area between 1A+2A and CuA$_2$ cream. Hindwing same ground color as forewing, darker beyond postmedial line; postmedial line zigzag with inner angles darker, giving impression of dots; fringe as in forewing, outer row of scales cream from apex to 1A+2A. *Abdomen:* light brown, ventrally lighter and shinier. Posterior margin of male tergum VI convex; anal tuft light brown. *Male genitalia:* uncus base slightly wider than neck; neck with ventral groove present medial edges of apical half with two well-delineated short, round, lobes with hairlike setae; head with crest, two tufts of erect scales; apical tip upturned with brush of hairlike setae; lateral lobes with hairlike setae. Ventral margin of valva at end of sacculus not swollen; hooklike process as long as sclerotized base along saccular margin; setose patch small. Transtilla continuous. Cornutus spine short, about half length of aedeagus; ductus ejaculatorius short. Parategumenal sclerites one-fourth surface area of valva [The term "coremata" was incorrectly used for this structure in Gentili & Solis (1998). To distinguish this structure from the "coremata" of the Arctiidae, Clavijo (1990) coined the term "parategumen sclerites" for these coremata-like structures in the Pyraustinae and defined them as: ". . . A pair of lateral sclerites located each in the basal region of the tegumen, typically containing long pencils or brushes of modified hair-like and/or

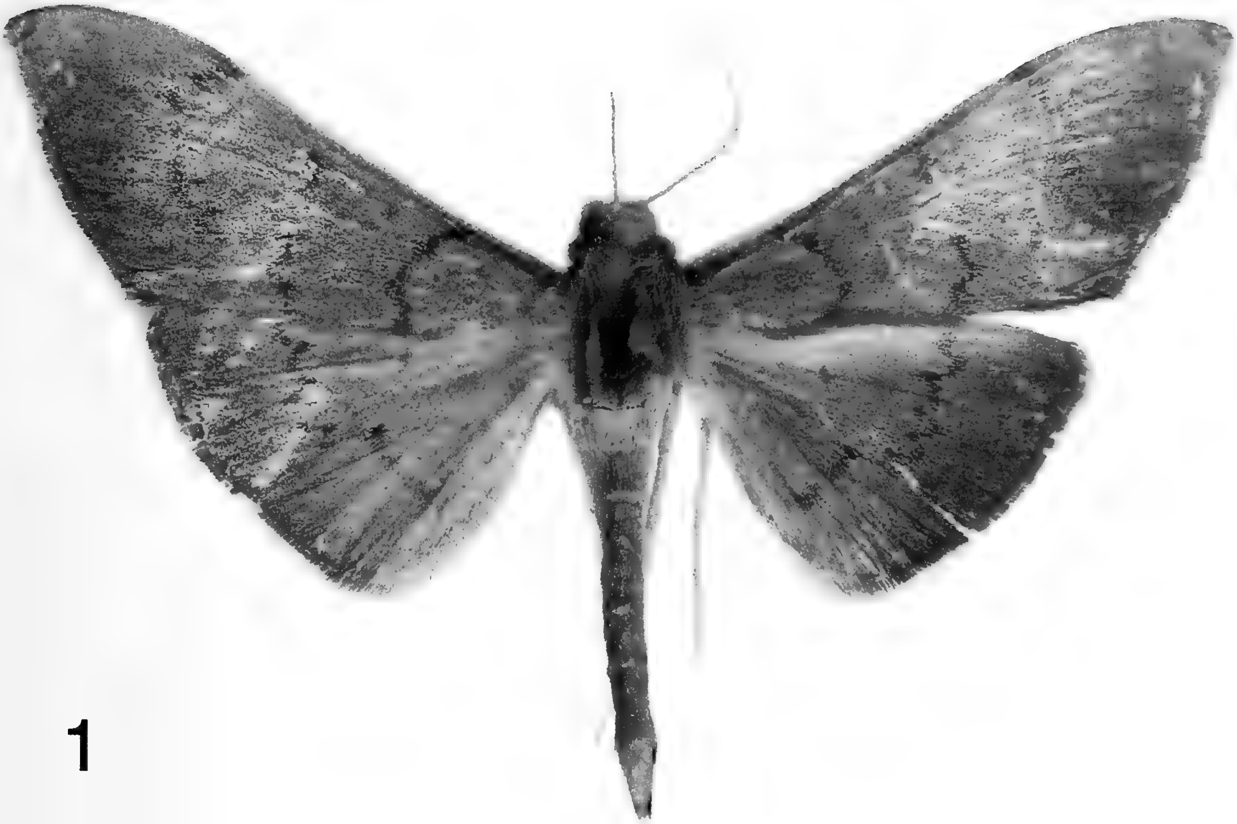

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FIG. 1. Paratype adult male of *Omiodes pseudocuniculalis*, Ecuador, Environs de Loja. Wing length = 16 mm.

spatulate scale, presumably for scent production and/or distribution."] *Female:* unknown.

Types: *Holotype:* ♂, ECUADOR: "Environs de Loja," "Equateur," "89-" "Dognin Collection," genitalia slide number 105,812 [USNM]. *Paratypes:* 4 paratypes: ECUADOR: 1 ♂, "Environs de Loja," "Equateur," "Dognin Collection," genitalia slide number 106,832 [BMNH]. PERU: 1 ♂ , no label data, "Peru," "Collection Wm. Schaus," genitalia slide number 105,811 [USNM]. BOLIVIA: 1 ♂, "Charuplaya," "Juin 1901," "Bolivie," "Saison sèche," "Dognin Collection," genitalia slide number 105,809 [USNM]. UNKNOWN LOCALITY: 1 ♂, "Dognin Collection," genitalia slide number 105,810, head slide number 106,735, wings slide number 106,737, legs slide number 106,736 [USNM]. Paratypes deposited in The Natural History Museum, London, England [BMNH] and The National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA [USNM].

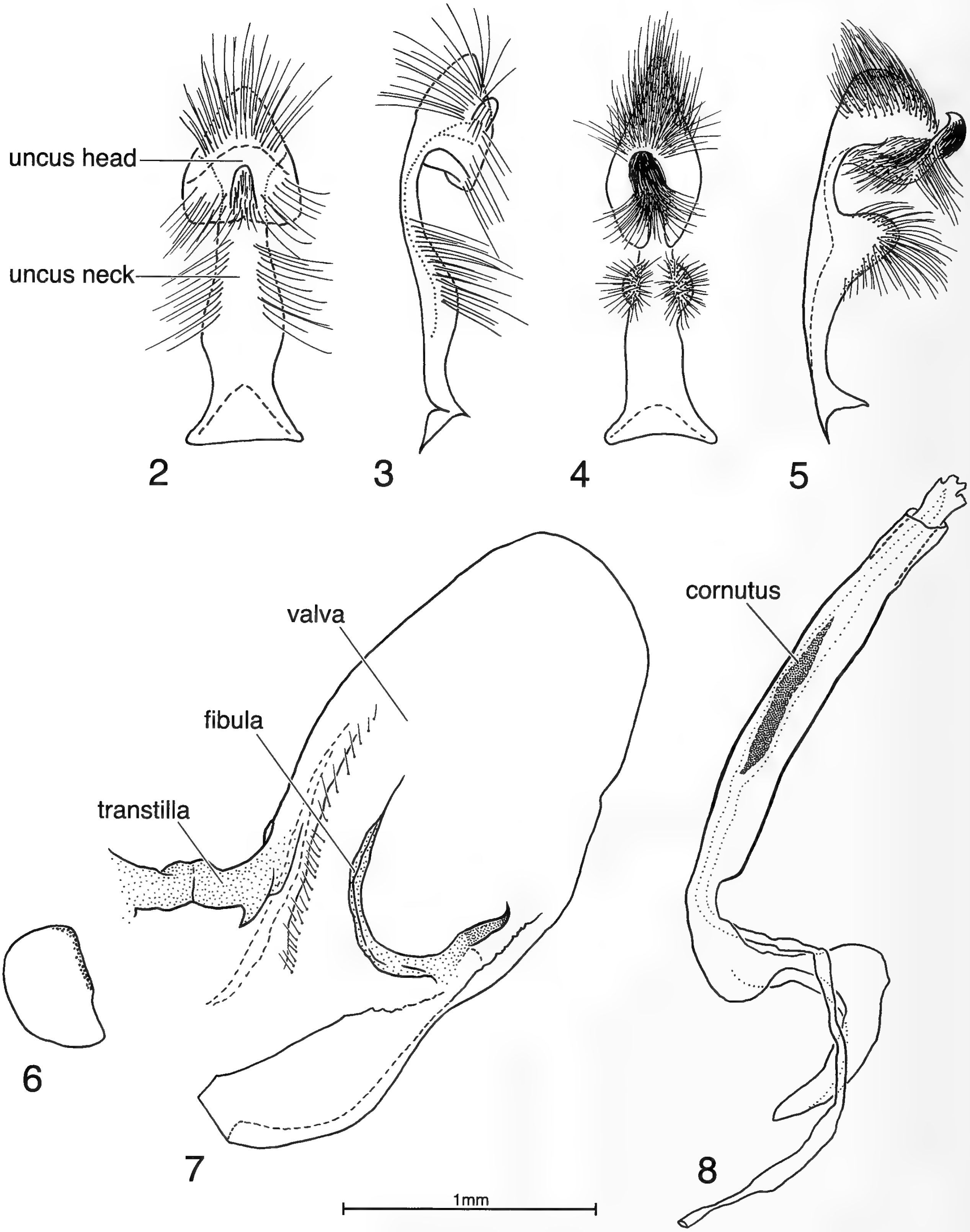
Remarks. *Omiodes pseudocuniculalis* is closely related to and could be confused externally with *O. cuniculalis*, a species that occurs from Mexico south to Brazil and Colombia, including the Caribbean; it is difficult to determine whether these species are sympatric because these areas are so poorly collected. Although we have not seen specimens of *O. cuniculalis* from Ecuador, Peru, or Bolivia, where *O. pseudocuniculalis* occurs.

We compared specimens with the types deposited at the BMNH of *O. cuniculalis*, a male from French Guiana. Externally *O. cuniculalis* and *O. pseudocuniculalis* are very similar in color and size. In both species the lobes on the medial edges of the ventral groove are round with hairlike setae, but in *O. cuniculalis* they occur on the basal half and are not well delineated while in *O. pseudocuniculalis* they occur on the apical half, are short, well delineated, and protruding.

Etymology. This species is named in reference to the close external resemblance to *O. cuniculalis*.

REVISED KEY TO SPECIES OF THE "*CUNICULALIS* GROUP" OF *OMIODES*

1. Ventral surface of body and legs light brown, never bright yellow, general body coloration cinnamon or brown, wing pattern darker brown, postmedial line zigzag, fringe ochraceous; uncus head with crest, medial edge of neck ventral groove without serrate area 2
   Ventral surface of body and legs bright yellow, some specimens with terga VII and VIII yellow, general body coloration dark brown, postmedial line not zigzag, lines slightly darker, fringe white; uncus head without crest, medial edge of neck ventral groove with serrate area . . . . *fulvicauda*
2. Cinnamon, homogeneous; uncus head with central patch of two tufts of erect scales, medial edge of neck ventral groove with lobes along edges 3
   Light to dark brown, sometimes forewing intermedial area cinnamon; uncus head with two lateral patches of short spines, medial edge of neck ventral groove without lobes 4
3. Medial edges of uncus neck ventral groove lacking well-delineated lobes along basal half (Figs. 2, 3) . . . . *cuniculalis*
   Medial edges of uncus neck ventral groove with well-delineated lobes along apical half (Figs. 4, 5) . . . . *pseudocuniculalis*
4. Wings unicolorous; medial edge of neck ventral groove with hairlike setae . . . . *alboanalis*



FIGS. 2–8. Male genitalia of *O. cuniculalis* and *O. pseudocuniculalis*. Scale line = 1.0 mm; **2,** ventral view of *O. cuniculalis* uncus, USNM slide 104,743; **3,** lateral view of *O. cuniculalis* uncus, USNM slide108,814; **4,** ventral view of *O. pseudocuniculalis* uncus, USNM slide106,832; **5,** lateral view of *O. pseudocuniculalis* uncus, USNM slide106,832; **6,** parategumenal sclerite of *O. pseudocuniculalis*, USNM slide106,832; **7,** valva and transtilla of *O. pseudocuniculalis*, USNM slide106,832; **8,** aedeagus of *O. pseudocuniculalis*, USNM slide106,832.

Wings not unicolorous, with intermedial area lighter in color; medial edge of ventral groove of neck without hairlike setae 5

5. Uncus head with lateral patches of spines almost completely meeting dorsomedially, crest conspicuous; transtilla continuous, same width throughout . . . . *anxiferalis*

Uncus head with lateral patches of spines not meeting dorsomedially, crest not conspicuous; transtilla divided, broad medially. . . . . *martini*

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BOOK REVIEWS

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REVISTA DE THECLINAE COLOMBIANOS/ REVIEW OF COLOMBIAN THECLINAE, by Museo de Historia de National de la Universidad de Caldas, Manizales, Museo de la Universidad Pedagógica Nacional, Santefé de Bogotá, Museo De La Salle de Ciencias Naturales, Santefé de Bogotá. Volumes 1 & 2, no actual date for publication is given, but the mailing date is given as 15 August 1997. Overall dimensions of both publications, 5 1/2 by 8 1/2 inches. Volume 1 contains 179 pages of text with numerous line drawings, 2 color plates, and 4 plates of black and white photos; volume 2 contains 178 pages of text with numerous line drawings, 6 color plates, and 6 plates of black and white photos. Text in English and Spanish. Soft covers. ISSN 0123-1677, free, available from Dr. Kurt Johnson, Environmental Affairs, The Ethical Culture Society, 53 Prospect Park West, Brooklyn, NY USA 11215.

According to the authors these two volumes are but the beginning of a series of volumes that will cover the entire spectrum of the Theclinae of Colombia with the goal of producing at least one volume per year. The title is a bit misleading in that both volumes are a collection of research works and papers, some previously unpublished, containing many newly described genera and species. Very little time or space is devoted to the many species previously named by others that occur in Colombia. Some of the described species in the many newly described genera do not occur in Colombia, but because they are a part of the original papers involved, appear in these volumes. One may readily determine the titles, the authors, and a brief of the contents of each paper on the outer back cover of each volume. There are 8 papers listed in volume 1, and 10 in volume 2.

A number of typographical errors and the incredibly disjointed and complex format of the entire text and illustrations make these volumes difficult to read and to follow logically and easily. To compound the entire matter, the size of the font is reduced in many instances for reasons that escape this reviewer.

It would be presumptuous of this reviewer to comment specifically on the array of new species and, more particularly on the many new genera that have been erected in this publication. I have collected rather extensively in South America and Panama (and yes, in Colombia) since 1962, and I am surprised to note that most, if not all, of the many specimens figured in these volumes with which I am familiar, now sport new specific names and even more amazing, belong to new and different genera, in many cases a new genus for each species!

As a case in point, the first work in volume 1 is the description of Strephonina, a "New Infratribe" of the Eumaenini. This is a new term to this reviewer and I can find no definition for it in this work. The Strephonina contains fourteen new genera. The only genus listed as containing more than a single species is *Strephonota* which contains 4 species. Some of the remainder contain more than a single species, but one has to search the text carefully in order to ascertain this fact.

In volume 2 another new infratribe carries the title of *Macusiina*. It appears to be a collection of very different and disparate species, especially when one looks at the array of genitalia sketches representing the various species. Again, one must search the text carefully in order to determine the species contained in each of these newly described genera. This is as good a place to mention this: there is no complete index of species or genera in either volume. If one wishes to locate a particular species or genus in either volume, one must search the entire volume, page by page. It is time consuming and frustrating.

Finally in volume 2, the species of *Strymon* illustrated and described as "new" left me shaking my head and wondering if I had read and viewed the descriptions and plates correctly. *Strymon melinus* (Hübner, 1813) herein named and figured as *Strymon caldasensis* is a dead ringer for any number of specimens in the collections of various individuals and museums I have observed and studied in the past 50 years. It is one of the most common and widespread eumaeines in the Western Hemisphere. Although not as common and widespread, three other examples of this distortion of names of familiar species are contained on the same color plate: *Strymon rufofusca* (Hewitson, 1877), named herein as *S. guanensis*; *Strymon bubastus* (Cramer, 1782), herein named *S. vividus*, and *Strymon gabatha* (Hewitson, 1870), herein named *S. alicia*. I have studied the descriptions and photos of these "newly described" species and can only surmise that the widely held and trusted concept of variation within a species is no longer a valid concept.

There are a number of disturbing factors in these two volumes, but the most glaring error noted in this cursory reading of the 2 volumes is to be found on photoplate XIV, figure H which bears the name *Strymon carmencitae* Le Crom & Johnson. The taxon figured here and elaborated upon in the text is not a *Strymon* and it does have a name — Hewitson named this species in 1868. This species does not bear the characteristic *Strymon* characters of the genital ring, valvae, aedeagus, or the scent pad on the forewing of the male. It is not a common species, but I have studied specimens from Brazil as well as Colombia

Finally, if one wishes to be overwhelmed by a profusion of new names for familiar species, then these two volumes will fit the bill. The appropriate text is difficult to read, the plates and line drawings are not in such a sequence as to be easily followed and related to the text, and there are no legend numbers or notes on the plate figures that allow easy cross reference to the appropriate text. These features, added to the lack of any index to the species and/or genera in either volume, make them difficult to use.

S. S. NICOLAY, *1500 Wakefield Drive, Virginia Beach, Virginia, 23455, USA.*

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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. 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*, Phil Schappert, Dept. Zoology, Univ. Texas, Austin, TX 78712. Requests to review books for the *Journal* and book review manuscripts should be sent to M. Alma Solis, Syst. Entomol. Lab, USDA, c/o National Museum of Natural History, MRC 127, Washington, DC 20560. *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. Authors are expected to provide a diskette copy of the *final accepted* manuscript in a standard PC or Macintosh-based word processing format.

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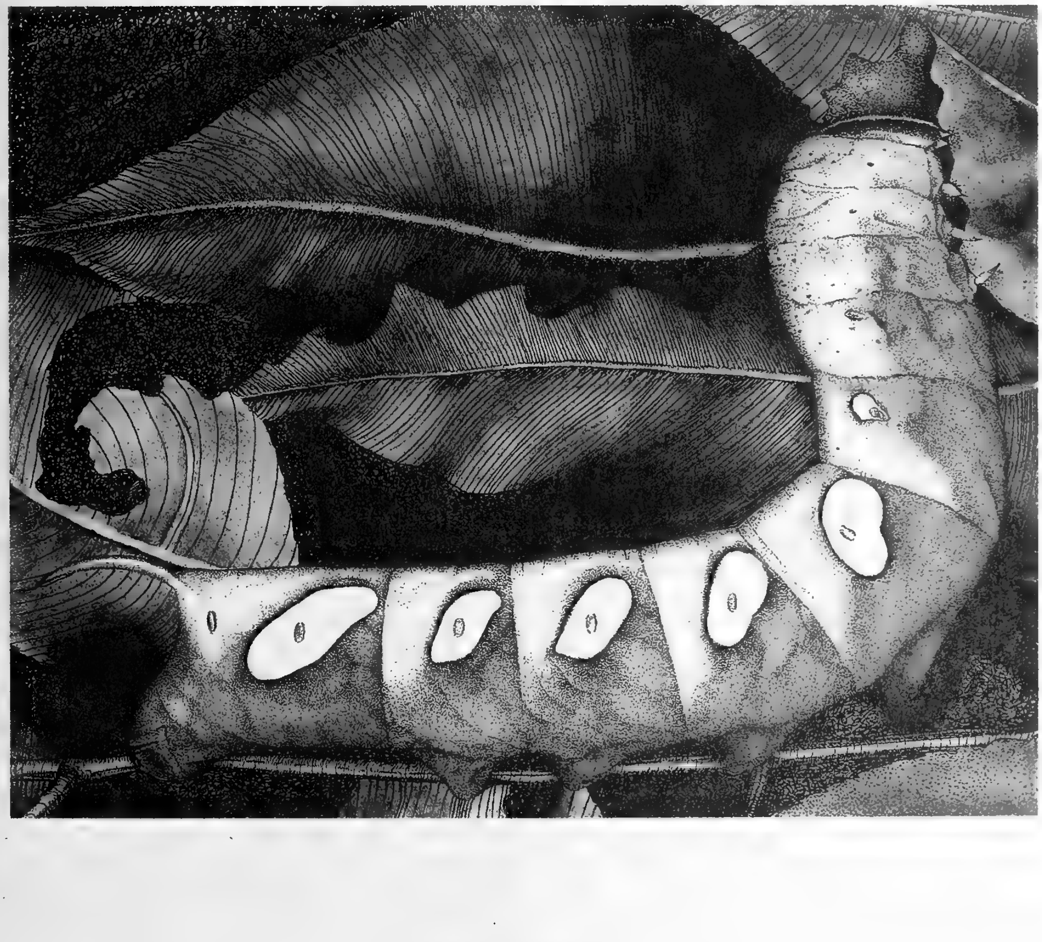

25 September 2001

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Cover illustration: Last instar larva of the Tomato Hornworm, *Manduca sexta* (Sphingidae). Ink drawing by Eowyn Burke, University of Colorado.

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ONTOGENETIC CHANGES IN LEAF SHELTER CONSTRUCTION BY LARVAE OF *EPARGYREUS CLARUS* (HESPERIIDAE), THE SILVER-SPOTTED SKIPPER

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ABSTRACT. In this paper we examine patterns of shelter construction by larvae of the Silver-spotted Skipper, *Epargyreus clarus* Cramer (Hesperiidae). Through observations of field and laboratory populations we characterize 1) the types of shelters constructed over larval ontogeny and their relationship to larval size and instar, and 2) the location of shelters on the host plant. We also describe various aspects of larval feeding behavior. Each larva builds and inhabits its own shelter, successively abandoning shelters and constructing new ones approximately five times across five instars. On kudzu (*Pueraria lobata;* Fabaceae), larvae produce shelters in four distinct styles that change predictably as the insects grow. Ontogenetic changes in style of shelter construction are likely to be related to larval size, needs, and physical capability.

Additional key words: leaf folder, caterpillar behavior.

Lepidopteran larvae in at least 18 families construct shelters from leaves that are rolled, folded, or tied and sealed with silk (Scoble 1992). These shelters are thought to provide a variety of advantages to the larvae, including protection from natural enemies (Damman 1987; Ruehlmann et al. 1988), creation of a favorable microhabitat (Henson 1958), increased leaf nutritional quality (Sagers 1992), or protection from phytotoxicity (Sandberg and Berenbaum 1989). Very little is known, however, about the pattern or process of leaf shelter construction (Clark 1936, Fraenkel and Fallil 1981, Ruehlman et al. 1988, Fitzgerald and Clark 1994).

The vast majority of skippers (Hesperiidae) live singly in a shelter constructed of host leaf material and silk (Moss 1949, Scoble 1992). Shelter styles vary among species, and also across larval ontogeny within a single species (Scudder 1889, Clark 1936, Moss 1949). The diversity of shelter styles includes leaf rolls, folds, peaked tents and perforated pockets (Scudder 1889, Moss 1949). Shelter construction may be initiated at the leaf margin or in the center of the leaf, and may involve a small portion of a leaflet, an entire leaf, or multiple leaves. For certain species on a given host plant, shelter size, style, and placement on the leaf can be diagnostic (H. Greeney pers. comm., J. Brock pers. comm.).

In this paper we describe the pattern of shelter construction by larvae of the Silver-spotted Skipper, *Epargyreus clarus* Cramer (Hesperiidae). Through observations of field and laboratory populations we characterize 1) the types of shelters constructed over larval ontogeny and their relationship to larval size and instar, and 2) the location of shelters on the host plant.

MATERIALS AND METHODS

Study organism. The Silver-spotted Skipper, *Epargyreus clarus*, ranges throughout North America from Saskatchewan in the north through Baja California, Texas, and Florida in the south (Scott, 1986). In the Washington, D.C. area these large skippers fly from mid-April through October, and commonly use black locust trees (*Robinia pseudoacacia*) and kudzu (*Pueraria lobata*) (both Fabaceae) as hosts (Clark & Clark 1951). In this study we used kudzu as our host plant because of its abundance, accessible vining growth form, and the longevity of cut leaves in the laboratory.

Caterpillars inhabit leaf shelters throughout their larval lives, leaving only to feed or to build a new shel-

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TABLE 1. Summary of *Epargyreus clarus* larval and shelter characteristics across 5 instars. Values are given as the mean (SE (sample size).

	Instar				
	1	2	3	4	5
Larval length, mm[a]	5.5 ± 0.1 (29)	8.4 ± 0.1 (25)	14.3 ± 0.4 (20)	26.4 ± 0.5 (21)	36.2 ± 1.2 (20)
Shelter length x width, mm (shelter type)[b]	7.1 ± 0.1 x 8.1 ± 0.2 {1} (69)	13.1 ± 0.4 x 14.7 ± 0.5 {1} (31)	18.8 ± 1.1 x 15.9 ± 0.8 {1} (15)	36.7 ± 1.6 x 18.4 ± 1.2 {2, 3, 4} (25)	46.5 ± 1.6 x 26.3 ± 2.2 {2, 3, 4} (15)
Shelter size / Larval length[c]	1.4	1.7	1.2	1.0	1.0
Distance to subsequent shelter, cm	5.4 ± 0.5 (55)	8.9 ± 0.8 (47)	11.4 ± 1.3 (20)	24.6 ± 11.2 (5)	--
Duration of feeding bout, minutes	3.4 ± 0.18 (97)	5.2 ± 1.2 (8)	5.1 ± 1.4 (3)	2.7 ± 0.2 (73)	4 ± 0.6 (11)
% daytime spent feeding	4.3 ± 0.4 (61)	3.7 ± 1.7 (14)	1.3 ± 0.7 (13)	2.1 ± 0.6 (11)	1.9 ± 1.1 (16)
Maximum feeding distance, cm	1.1 ± 0.2 (50)	1.9 ± 0.1 (20)	2.1 ± 0.2 (20)	7.0 ± 0.6 (15)	18.3 ± 1.9 (15)
Location of feeding site relative to shelter[d]	100% sll (40)	100% sll (37)	100% sll (45)	78% sll, 14% all, 8% alf (36)	4% sll, 20% all, 76% alf (25)

[a] Measurements taken of mid-instar larvae

[b] Measurements taken of only those shelter types indicated

[c] Ratio of (mean shelter width + length)/2 to mean larval length

[d] sll = same leaflet; all = adjacent leaflet, same leaf; alf = adjacent leaf

ter. Larvae do not feed within the shelter, although early instars feed close by (Table 1). Based on observations of many larvae in the field, we determined that during the day, caterpillars spend approximately 3% of their time feeding, and that the average feeding bout (time elapsed between a caterpillar's departure from and return to its shelter) lasts about 4 minutes (Table 1). Young larvae feed on the same leaflet that their shelter occupies, while older larvae may venture to an adjacent leaflet or leaf (Table 1).

Collection and care of larvae

Larvae were obtained from eggs of adults caught on the Georgetown University campus and from meadow habitats on the Eastern Shore of Maryland from June through October 1997 and 1998. After the first generation, the colony contained both lab-reared and field-collected adults. Butterflies were kept outdoors in 2 m^3 mesh cages, and were fed flowers of *Trifolium pratense* (Fabaceae), *Buddleja davidii* (Buddlejaceae), and *Lantana camara* (Verbenaceae), supplemented with 10% sucrose solution. Freshly cut kudzu leaves were provided for oviposition. Kudzu leaves containing eggs were collected from the outdoor cage each morning, brought into the lab, and placed in 13″ × 7.5″ × 4.25″ clear plastic boxes with opaque lids. Larvae were housed in these boxes and were given fresh cut kudzu leaves as needed until pupation.

1) Types of shelters constructed over larval ontogeny

To characterize patterns of shelter construction, we collected and examined over 600 leaf shelters constructed by larvae in field and lab populations, and identified the instar of the inhabitant. Based on our observations of shelter characteristics, we developed a classification of shelter types. We also measured the dimensions of a subset of shelters of each type, and determined the length of their larval inhabitants, using a Mitutoyo Absolute Digimatic caliper (±0.01 mm).

To determine how patterns in the size and shape of shelters relate to the timing of a molt to a later instar, fifteen newly hatched larvae were placed on fresh kudzu leaves in individual plastic boxes in the laboratory. Every other day, the boxes were opened and the larval instar and house type recorded. Care was taken not to touch or manipulate the larvae themselves.

2) Location of shelters on the host plant

In the field, we measured the height above ground of the shelter-bearing leaf for 36 first instar shelters. Height of first instar shelters is a good indication of height at which eggs are laid, because empty egg shells and first shelters are generally found on same leaflet (pers. obs.). We also divided the leaflet into four quadrants (quadrant 1 = right apex; 2 = left apex; 3 = left base; 4 = right base) and noted in which one a shelter was located, for 356

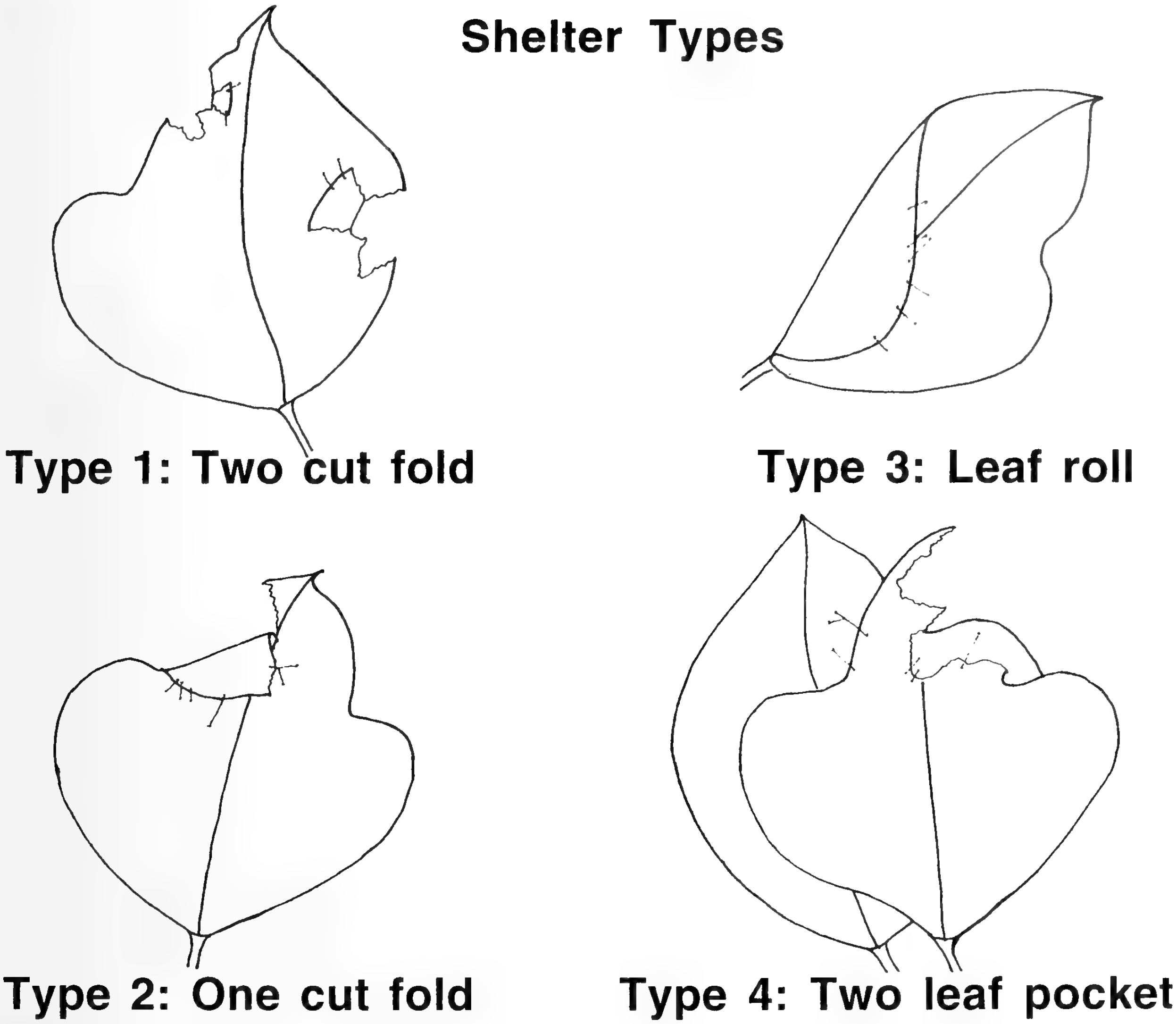

FIG. 1. *E. clarus* larvae construct 4 types of shelters over larval ontogeny. Lines connected to shelters represent silk guy wires.

shelters made by first, second and third instar larvae. We often encountered leaflets or leaves that contained three or four shelters which we inferred were constructed by a single larva, based on the predictable progression of shelter size and style. We used a ruler to measure the shortest linear distance between sequential shelters.

RESULTS

1) Types of shelters constructed over larval ontogeny

We found that *Epargyreus clarus* larvae construct shelters in four distinct styles (Fig. 1), designated types 1, 2, 3, and 4 for the approximate order in which they appear in larval life. For shelter type 1 ('two-cut folds'), the larva makes two cuts of precise length and orientation in from the margin of the leaflet, applies multiple strands of silk at corner 'hinges' to pull the triangular to rectangular flap over towards the center of the leaflet, and secures it to the leaf surface with silken 'guy-wires'. A peaked roof is formed by the tight silking of a small cut perpendicular to one of the main cuts. Type 2 shelters ('one-cut folds') are similar, but entail only one cut in from the leaflet margin. Type 3 shelters ('leaf folds') have no cuts; caterpillars fold the margin of some or all of a leaflet towards the center and secure it to the surface with long guy wires. Type 4 shelters ('two-leaf pockets') consist of two leaflets pulled together by silk strands to form a pocket.

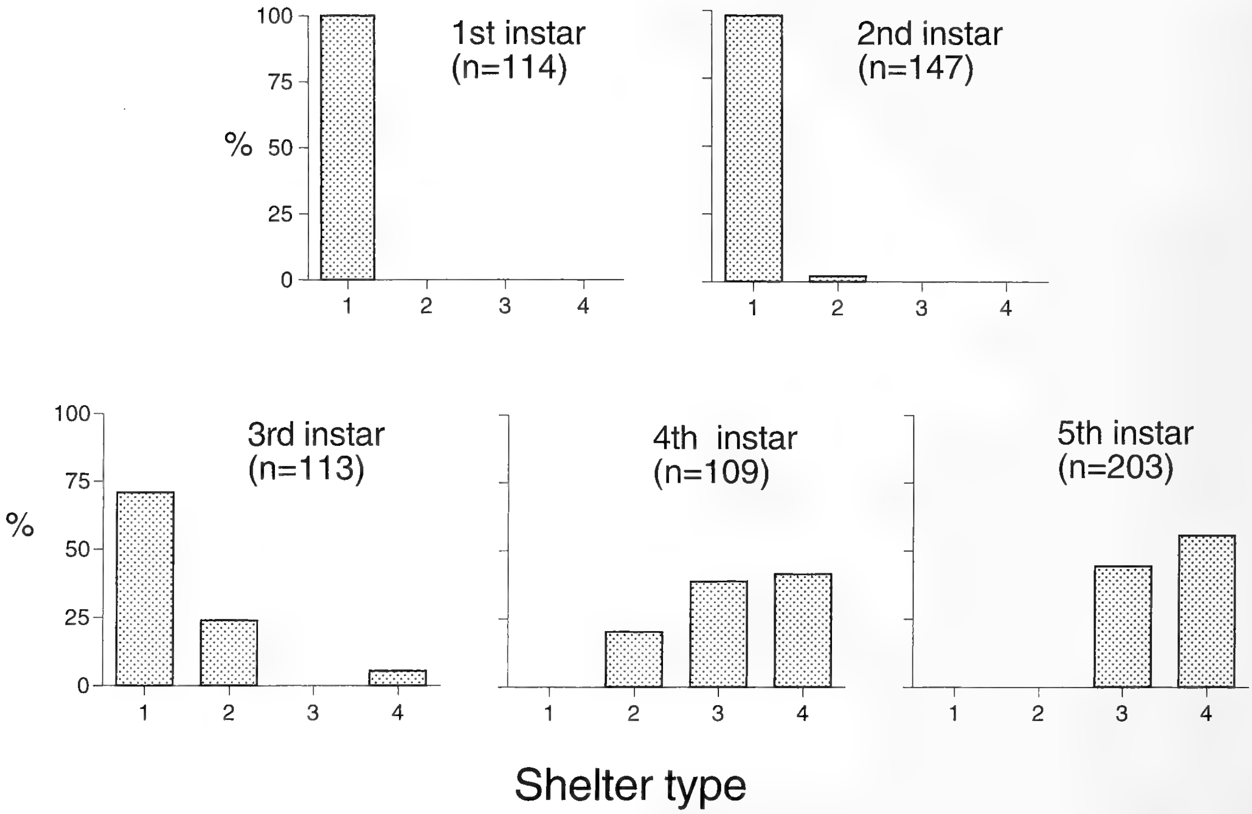

FIG. 2. Distribution of shelter types varies predictably across larval instars.

The style of shelter constructed varies predictably over larval ontogeny (Fig. 2). First and second instar caterpillars build type 1 shelters almost exclusively, while third instar larvae construct mostly type 1, some type 2, and rarely type 4 shelters. Fourth and fifth instars never build type 1 shelters; instead, they construct mostly shelter types 3 and 4.

Larger larvae build larger shelters, both across and within shelter types. That is, each successive shelter type is generally larger than the previous, and for a given shelter type, shelter size is positively correlated with larval size (Table 1). The relationship between larval length and shelter size is relatively constant across all five instars: the size of the shelter (approximated as (length + width)/2) ranges between 1.0 and 1.7 times the length of the larva (Table 1).

Laboratory-reared larvae allowed to change shelters at will built a mean 5.1 shelters (±0.24 SE; N = 15) over five instars. Larvae generally constructed a new shelter one to several days after molting within the previous shelter (mean ± SE = 1.7 ± 0.2 days after first molt; 1.6 ± 0.2 days after second molt; 2.8 ± 0.3 days after third molt; 4.0 ± 0.8 days after fourth molt). Only three out of 60 observed molts took place outside of a shelter.

2) Location of shelters on the host plant

The height above the ground of leaves bearing first instar shelters ranged from 0.25–1.25 m, with a mean ± SE of 0.65 ± 0.03 m. The distribution of shelters across the 4 quadrants differed significantly from random ($X^2 = 109.86$, 3 df, $p < 0.001$). Almost 50% of the shelters were located in quadrant 2, and together quadrants 1 and 2 (the apical half of the leaf) contained three-quarters of all shelters. As larvae grow, the distance between shelters increases. First, second, and third instar shelters are generally located on the same leaflet, while shelters constructed by fourth and fifth instar larvae are often constructed on an adjacent leaflet or leaf (Table 1).

DISCUSSION

Although larvae of many lepidopteran species fold, roll or tie leaves into shelters, it is not uncommon for these taxa to begin their larval lives with a radically different feeding habit, such as leaf-mining or boring (Gaston et al. 1991). Presumably, this is related to the small size of early-instar larvae. For example, *Caloptilia serotinella* (Gracillariidae), the cherry leaf-roller, is a leaf-miner in its early stages, while fourth and fifth instar larvae are leaf-rollers (Fitzgerald & Clark 1994). In a range of other taxa, hatchling and early instar larvae use a shelter made by another species, construct a communal shelter or silk canopy, or hide in a cranny, while late instar larvae build their own shelters (Doerksen & Neunzig 1976, Damman 1987, Cappuccino 1993, Loeffler 1994).

Like *E. clarus*, larvae in several other diverse taxa construct leaf shelters throughout larval life, and exhibit ontogenetic changes in style of shelter construction. The golden-banded skipper, *Rhabdoides* (=*Autochton*) *cellus*, builds shelters in a progression of styles very similar to that of *E. clarus* (Clark 1936). Shelters made by larvae of the skipper *Staphylus hayhurstii* are also similar to those of *E. clarus*, although the shelters lack a notch in the second cut and thus do not have a peaked roof (pers. obs). Larvae of the pyralid moth *Herpetogramma aeglealis* sequentially construct and inhabit shelters of three distinct types on fronds of Christmas fern (Ruehlmann et al. 1988). Early-stage *Nephopterix celtidella* (Pyralidae) larvae web two leaves flatly together, while last-stage larvae web a dead, curled leaf to the surface of a living leaf (Doerksen & Neunzig 1976).

Ontogenetic changes in shelter size and style may be due to the biological needs and/or physical capabilities of the larva. Certainly, to be fully enclosed and hidden from predators, larger larvae require larger shelters, so that while a small folded section of leaflet is sufficient to cover a first instar caterpillar, larger larvae need the increased area that a folded leaflet or two leaves silked together can provide. Perhaps, in addition, a fixed relationship between larval size and shelter size is necessary to maintain a particular internal microclimate, or to restrict access to predators.

Changes in shelter size and style may also reflect changes in the physical abilities of the larvae. A 3-mm-long *E. clarus* hatchling may not be able, even utilizing the axial retraction forces of stretched silk (Fitzgerald et al. 1991) to fold a large flap over itself or pull two leaflets together. It can, however, cut a small flap of leaf tissue and fashion it into a shelter. As the larva increases in size, it is able to manipulate larger pieces of leaves, and cutting eventually becomes unnecessary. Indeed, by the time larvae reach the fifth instar, they rarely cut leaves prior to constructing their shelters, and either fold over the entire edge of a leaflet or join two leaflets together with silk. Cuts made in leaves by late instar larvae might be counter-productive as well as unnecessary, as the weight of a fifth instar larva (~700 mg) could pull down or tear a leaf flap. Cutting leaf tissue may also cause the release of volatile compounds that could attract parasitoids (Turlings et al. 1995).

The types of shelters built by each larval instar may also reflect selection for speed and efficiency of construction, as leaf-rolling or leaf-tying insects are generally palatable to natural enemies (Bernays & Cornelius 1989), and exposed larvae are much more likely to be eaten than are sheltered ones (Damman 1987, Cappuccino 1993).

Little is known about the ontogenetic patterns of shelter construction for most taxa that fold, tie, or roll leaves to make a shelter. Some species, like *E. clarus* and *Herpetogramma aeglealis* (Pyralidae) (Ruehlmann et al. 1988), build very regular structures that change predictably in size and style over larval ontogeny, while others produce more variable shelters (pers. obs.). The relationship between insect size and shelter size is also likely to vary across taxa. Larvae that feed inside the shelter may make relatively larger shelters than those that venture out to eat, and those that retain frass in the shelter may also make larger shelters than those that eject their frass. Comparative studies of shelter-building taxa will help to elucidate the relative importance of various factors, including larval physical ability, feeding and defecation behavior, vulnerability to predators, leaf toughness, and internal microclimate, that may be involved in determining patterns of shelter construction.

The innate behavior patterns underlying the construction of different shelter styles are also worthy of further study. We have determined that the almost invariant size and shape of first instar shelters results from a prescribed pattern of larval movements and behaviors, in which larvae use their body length as a 'ruler', and lay down a silk 'blueprint' on the leaf surface prior to initiating cuts (Weiss et al. in prep.). We are currently investigating the behavior of *E. clarus* on leaves of different sizes and morphologies to determine the degree of plasticity in these seemingly hard-wired behaviors.

ACKNOWLEDGMENTS

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REPRODUCTIVE OUTPUT AND EGG MATURATION IN RELATION TO MATE-AVOIDANCE IN MONANDROUS FEMALES OF THE SMALL COPPER, *LYCAENA PHLAEAS* (LYCAENIDAE)

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ABSTRACT Females of the small copper, *Lycaena phlaeas*, were captured in the field and dissected to investigate their mating frequency and reproductive output. Spermatophore counts showed that most females were monandrous. A single spermatophore usually occupied about half of the bursa copulatrix, though the size of the spermatophore decreased with the female's age. Young females had 250 immature eggs in their ovaries and laid an estimated 150 eggs throughout the course of their lives. Mate avoidance behavior was frequently observed in both mated and virgin females. In laboratory experiments, virgin females contained a few mature eggs immediately after eclosion, and the number of mature eggs gradually increased with age. Ovaries of females accepting copulation contained significantly larger numbers of mature eggs than ovaries of females avoiding mating. Copula duration was about 16 min (at 30°C) irrespective of male age. Egg maturation in the ovaries is thus seen as important in the mating behavior of such monandrous species.

Additional key words: bursa copulatrix, egg load, *Lycaena phlaeas*, mate-avoidance, monogamous, spermatophore.

In butterflies, ejaculates from males during copulation are used in female egg production and/or somatic maintenance. Females may, therefore, benefit from mating more than once (Boggs 1981, Boggs & Gilbert 1979, Watanabe, 1988). One potential benefit of repeated matings for the female butterfly is the substantial increase of sperm supply (Lederhouse 1981). As a rule, however, males transfer a number of sperm in excess of that needed to inseminate all eggs at a single mating (Watanabe et al. 1998). Consequently, in cases in which a spermatophore is used only as a reservoir of sperm to fertilize eggs, females should benefit from mating only once. Re-mating may decrease the time available to females for egg-laying and foraging activities, and may increase the risk of predation while *in copula*. In the evolution of such species, therefore, natural selection should favor females who avoid males after mating. The mate refusal posture displayed by unreceptive females has been reported in many butterfly species (Shapiro 1970, Watanabe et al. 1997).

The small copper, *Lycaena phlaeas* (Linnaeus), is a multi-voltine butterfly that flies from spring to autumn in central Japan. Adults inhabit sunny areas such as forest margins, clearings, open fields with low vegetation, banks and roadsides (Suzuki 1976). Suzuki (1978) reported mate-avoidance behavior in females and suggested that females generally mate only once. However, there are few data on spermatophore counts in the bursa copulatrix of wild females, and few studies have been conducted on oviposition behavior, nor have any data on lifetime reproductive schedules been gathered.

In this paper, we clarify the mating frequency and fecundity of *L. phlaeas* in the field. Lifetime egg production and reproductive success are discussed. Since female monandrous butterflies may solicit courtship before copulation and actively avoid males after mating in order to allow time for oviposition (Wiklund 1982), we examined the relationship between mate-avoidance behavior and fecundity in the laboratory.

MATERIALS AND METHODS

The data presented in this paper were obtained primarily from summer generations of the small copper, *L. phlaeas,* in Shirouma in Nagano Prefecture, which is located in a cool-temperate zone of Japan. The major habitat consists of rice-fields and margins of deciduous forests where adults may feed on nectar plants, and larvae on host plants (primarily *Rumex japonicus*, Polygonaceae), during the summer. During the day, large numbers of males fly near the ground to gather nectar and search for mates. Chasing behavior between males and females was sometimes observed over the course of the summer. Females engaged in various activities such as feeding, roosting, flying, copulating and ovipositing, were collected from late July to early August of both 1995 and 1996. To examine mating frequency of females flying in natural populations, sampling was done on windless, sunny days (a total of 13 days). When females were captured, their abdomens were amputated and immersed in a solution of 50% ethyl alcohol, and their wing condition and forewing length were recorded. We classified individuals into 5 age groups, on the basis of the degree of wing damage, using a ranking from O to IV, following Watanabe and Ando's method (1993). The five age groups were as follows: O, newly emerged females with wings having lustrous scales and no visible damage; I, fine tears and fewer lustrous scales; II, tears and frayed scales; III, notched tears and frayed scales; and IV, broken or extensive tears and frayed scales. All females were examined for the number of spermatophores in their bursa copulatrix and the number of eggs stored in their ovaries.

The individuals of *L. phlaeas* used in the mating experiments were the offspring of females collected in the wild. They laid eggs in cages, and the hatching larvae were reared on the host plant, *R. japonicus,* in small chambers at 25°C, with 18 hours of light per day. A newly emerged virgin female was placed in a mating cage (30 × 40 × 45 cm) along with 10 virgin males (less than 10 days old) to allow matings. The cage was set in a greenhouse for two hours around noon (at ca 30°C). In the present study, 451 females emerged in the laboratory. Their average forewing length was 16.5 ± 0.6 mm (SD), which is not significantly different from that of the captured wild females (16.3 ± 0.9 mm, *U*-test, Z = 0.825, n.s.). Out of the 451 females, 147 were randomly selected for mating experiments.

The mating pairs were kept in small cages (24 × 30 × 38 cm) until they separated. The duration of copulation was recorded. After copulation terminated, females were dissected to examine the spermatophore and to count the number of eggs in ovaries. As a control, virgin females of various ages in stock culture were also dissected.

In the present study, many females introduced into the cages avoided or refused to copulate with males displaying courtship behavior, although the males repeatedly approached females in the course of two hours. These females were taken out of the cage and supplied with sugar solution in another small cage at ca. 25°C. On the following day, they were then placed back in the mating cage. In this way, the copulation trials for virgin females were repeated every day until the female engaged in copulation.

Since both the spermatophore and the bursa copulatrix are oval, their respective volumes were calculated as an ellipsoid. Although eggs in the ovaries could be classified into three groups (mature, submature, immature), those in the oviducts were primarily of the mature type. These oviduct eggs were large, pale green and sufficiently well-formed (with a semi-spherical shape and pronounced ribbing) to be ready for oviposition. The vitellarium of the ovaries contained mainly submature eggs; these were large but more lightly colored than the mature eggs. Immature eggs, which included oocytes, were found in the terminal filament, the germarium and part of the vitellarium of the ovarioles. Eggs in the ovarioles decreased in size toward the tip of the terminal filament filled with oocytes. Because oocytes do not contain yolk, they appear white, and we were able to count them using tweezers and a light microscope (40×).

RESULTS

Over the course of the two-year study period, we examined a total of 99 wild females from the study area. In 1995, more than half of the females captured were young (ages O and I), and no females of the oldest age class (age IV) were captured (Table 1). Five of 36 age-O and 2 of 20 age-I females were virgins, and 2 additional virgin females were captured at age I. In 1996, 3 age-I females were virgin. In both years, there were a few females that contained both an intact full-sized spermatophore and a spermatophore fragment, thus showing evidence of having mated twice as shown in Table 1. No females contained mating plugs blocking their genital openings.

TABLE 1. The frequency of spermatophore distribution in the bursa copulatrix of female *Lycaena phaeas* caught in the wild for 5 age classes (0 ~ IV) in the summer generation of 1995 and 1996.

Years	Number of spermatophores present	Age class				
		0	I	II	III	IV
	0	5	2	0	0	0
1995	1	29	16	7	1	0
	2	2	2	0	0	0
	0	2	1	0	0	0
1996	1	3	9	6	8	4
	2	0	0	1	0	1

In mated females, the spermatophore has been ejaculated into the bursa copulatrix and is filled with white secretion. The sperm sac is an elongated cone which occupies the bursal duct and has its opening at the end of the duct near the seminal duct. There is no appendix bursae in the female reproductive system.

In age-O females, the average volume of the spermatophore was about 0.05 mm^3, which occupied about 31% of the volume of the bursa copulatrix (Fig. 1). There was no significant difference in the size of the spermatophores among females of age O to III (F = 1.610, n.s.). Among females of these four age classes, the spermatophore occupied about 40% of the bursa copulatrix. In age-IV females, the spermatophore size significantly decreased ($p < 0.01$), compared with the spermatophore size of age-I ($U = 14$), age-II ($U = 6$) and age-III ($U = 3$) females, but still occupied about 45% of the bursa copulatrix.

The mean number of eggs (±SE) in wild-caught virgin females of age O was 41.7 ± 13.3 (n = 7), 19.1 ± 3.8 (n = 7) and 242.1 ± 39.3 (n = 7) for mature, submature and immature eggs, respectively. The mated females of age O contained means (±SE) of 261 ± 15 immature eggs (n = 29), which number was similar to that for virgin females. Therefore, the potential fecundity of *L. phlaeas* was estimated at about 300. Figure 2 shows the lifetime changes in the number of immature eggs in monandrous females. The number of immature eggs decreased with age. Since there were less than 20

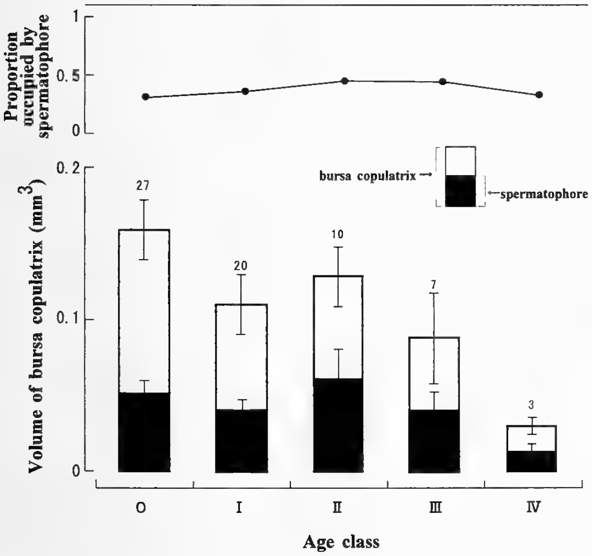

FIG. 1. Change in the volume of spermatophore in the bursa copulatrix and its proportion in wild monandrous females of *Lycaena phlaeas* for 5 age classes (O, I, II, III and IV). Each bar represents SE. The numbers above the bars show sample size.

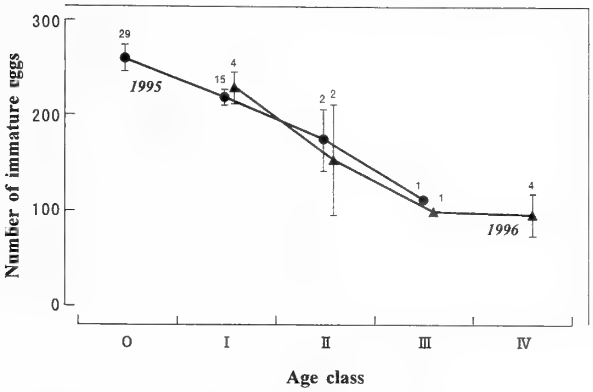

FIG. 2. Changes in the number of immature eggs of age O, I, II, III and IV wild monandrous females of *Lycaena phlaeas* in 1995 (circle) and 1996 (triangle). Each bar represents SE. The numbers above the symbols show sample size.

mature eggs in the ovaries of females of age IV, the decrease in immature eggs resulted from resorption or oviposition. However, no fused eggs were observed in the ovaries, suggesting that few eggs were consumed for somatic maintenance. In such cases, in which there is no addition of immature eggs during the adult stage, the decreasing number of immature eggs in the ovaries is thought to be due to oviposition. A monogamous female of age IV may thus have laid 150 eggs.

In the mating cages, all *L. phlaeas* males were seen perching, and would presumably mate with the females. We observed a total of 605 unsuccessful courtships, which can be described in terms of five distinct behavioral events. After approaching a female, the male tried to make initial contact. In 43% of unsuccessful courtships, females remained perched and ignored approaching males. Walking or flying away from males was seen in 29% and 14% of approaches, respectively. In some cases, females turned face-to-face with the male (9%) or fluttered (4%) until the male flew away. The latter two behaviors were considered to constitute mate-refusal behavior rather than mate-avoidance, although no females showed the pierid mate-refusal posture in which the wings are spread and the abdomen elevated (Shapiro, 1970). There was no significant difference between the forewing length of males failing to copulate (wing length = 15.2 ± 0.2 [SE] mm, n = 24) and that of males succeeding in copulation (wing length = 15.6 ± 0.2 mm [SE], n = 9) (*U*-test, Z = 0.788, n.s.).

Out of 77 virgin females aged 2-days at the first trial, only 22 engaged in copulation (28.6%). The other females were re-introduced to the mating experiment on the following day and 35.0% of them (7/20) copulated. In the third trial, 28.6% of the virgin females (2/7) copulated. The remaining virgin females did not copulate with males.

The copulation duration was about 16–17 min, regardless of the number of previous trials (Table 2). When the copulation terminated, most females were

TABLE 2. The number of eggs loaded in accepting and avoiding females during male courtship behavior (mean ± SE).

Females of 1st trial	Accepting	Avoiding	*U*-test
Number of females dissected	22	6	
Copula duration (min)	15′ 33″ ± 41″	—	
Number of mature eggs	62.6 ± 8.9	2.8 ± 2.6	Z = 3. 191, p < 0.01
Number of submature eggs	39.1 ± 3.8	20.8 ± 4.4	Z = 2. 715, p < 0.01
Number of immature eggs	254.7 ± 8.6	228.7 ± 20.1	Z = 1. 225, n.s.
Females of 2nd and 3rd trials	Accepting	Avoiding	*U*-test
Number of females dissected	9	6	
Copula duration (min)	16′ 45″ ± 1′ 22″	—	
Number of mature eggs	60.9 ± 12.8	30.3 ± 11.9	*U* = 8, 0.05 > p > 0.01
Number of submature eggs	32.8 ± 5.0	21.5 ± 5.0	*U* = 13.5, n.s.
Number of immature eggs	227.3 ± 12.3	241.7 ± 7.8	*U* = 18, n.s.

dissected, and their bursa copulatrix and the number of eggs in their ovaries were examined. Every female had a single spermatophore in the bursa copulatrix, though it was not completely solidified in any of the females. The average volume of the bursa copulatrix among mated females was 0.195 ± 0.017 [SE] mm^3 (n = 25), which was significantly larger than that of wild females of age O (*U*-test, Z = 3.182, $p < 0.01$). The average volume of the spermatophore was 0.145 ± 0.015 [SE] mm^3 (n = 20), which occupied 74% of the bursa copulatrix compared with 40% in wild females. Spermatophore volume was also significantly larger than that of wild-caught females of age O (*U*-test, $U = 37$, $p < 0.01$).

After the trial, a number of virgin females who had consistently avoided mating were also examined to determine the number of eggs in the ovaries. As shown in Table 2, females accepting mating at the first trial contained significantly more mature and submature eggs than those who avoided mating at the first trial. The number of immature eggs did not differ among female mating outcomes. At the second and the third trials, females with immature eggs were older and must therefore have further developed their eggs in the ovaries. However, mated females loaded about 60 mature eggs, which was significantly greater than that of the females avoiding mating (30 mature eggs) in Table 2. There was no significant difference in the numbers of submature or immature eggs between females accepting and avoiding mating in either the second or third trials.

Figure 3 shows the change in the number of mature eggs in females reared in the laboratory. Very few mature eggs were found in the ovaries of newly emerged females (0-day-old). It follows that maturation of eggs occurs with aging. About 50 mature eggs had accumulated one week after emergence. Figure 3 also shows that the number of mature eggs in mating females was above the mean number of mature eggs of virgin females, and that the number of females avoiding mating was below it. An increase in the number of mature eggs thus appears to facilitate female willingness to mate.

DISCUSSION

The mating frequency of *L. phlaeas* females was examined in terms of the number of spermatophores in the bursa copulatrix, because each mating generally results in the deposition of a single spermatophore. It is well known that the number of spermatophores in several butterfly species increases with female age (Lederhouse 1981, Watanabe & Nozato 1986, Watanabe & Ando 1993). However, there is little information on the mating frequency of female lycaenid butterflies (Burns 1968, Suzuki 1978). In the present study, most females (94%) of the small copper, *L. phlaeas*, had a single spermatophore in the bursa copulatrix irrespective of their age class. We found a few polyandrous females (6%) that had two spermatophores, one of normal size lying near to the site of sperm migration in the bursa copulatrix and the other being very small or consisting of fragments. Although we did not find any signs that the spermatophore had been absorbed by the female, the spermatophore just after copulation of laboratory-reared young females was larger than that of females of age class O, suggesting that females quickly absorbed the spermatophore. This means that wild-caught females had retained the remnants of the spermatophore. Therefore, the fragments of spermatophore must be derived from a small spermatophore, which might be transferred by old males (e.g., Lederhouse et al. 1989) or by recently mated males (Watanabe et al. 1997). When the first spermatophore is too small for females to avoid re-copulation, females must be exceptionally polyandrous.

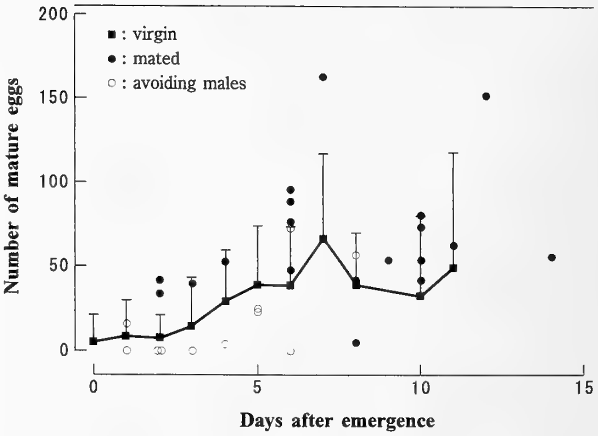

FIG. 3. Daily change in the number of mature eggs of virgin *Lycaena phlaeas* females (squares, + SD) and the number of mature eggs of females accepting copulation (closed circles) and of those avoiding males (open circles) in laboratory experiments.

Female reproductive success will depend on the amount of three potential resources available to female somatic maintenance or offspring. One is the nitrogenous reserves accumulated during their own larval feeding and stored in the fat body, which is usually depleted with egg development (e.g., Dunlap-Pianka et al. 1977). Another is nectar feeding during the adult stage (e.g., Boggs 1986, Watanabe 1992), though the nectar contains little nitrogen. The third resource is the contributions of the male ejaculate during copulation (e.g., Boggs & Watt 1981). Boggs and Gilbert (1979) showed that the ejaculates were used for egg development by females. In the present study, however, females seemed not to use the ejaculates to increase their fecundity. Bissoondath and Wiklund (1995) stated that both relative ejaculate mass and protein content in the spermatophore are low in monandrous species.

In this study, the small copper females had few mature eggs following eclosion, and they used their own energy or nectar to develop eggs without ejaculates from males. The lifetime reproductive output was estimated at about 150 eggs in the present study. Females feed on nectar as an energy source. On the basis of our experiments in which virgin females were kept in a flight cage and allowed to feed freely on nectar, such females live more than 3 weeks without mating. Boggs (1986) reported that females of the nymphalid butterfly, *Speyeria mormonia*, which is monandrous, survived for an average of 19 days in captivity, laying eggs for 14 days on average.

The present study showed that the ratio of spermatophore volume to the volume of the bursa copulatrix was stable, regardless of the spermatophore size. Sugawara (1979) showed that a certain volume of spermatophore is perceived by the stretch receptors which stimulate the mate refusal posture of the female white butterfly, *Pieris rapae*. The stretch receptors in the bursa copulatrix may also operate in the small copper to induce mate-avoidance behavior over the course of the insect's life, and thereby maintain female monandry.

The present study suggests that the number of mature eggs determines the mating behavior of the female butterflies. This means that there is a period of sexual immaturity and avoidance or refusal of males after eclosion. Therefore, females of this species have a pre-mating adult period, during which they mature initial eggs. One possible explanation for this phenomenon is that it allows females to be more particular in their choice of mate, since the small copper is a perching species, in which males spend part of the day sitting on some object waiting for passing females who are then pursued and courted. Such behavior may be particularly advantageous in a monandrous species. Wiklund (1977) showed that female monogamy in the pierid butterfly, *Leptidea sinapis*, is maintained by the females simply remaining quiescent during courtship, without any kind of mate-refusal posture. However, there is no quantitative information on the diurnal activity of females of the small copper or on their choosing of mates in the field. A detailed study of preferential mating will be required for the monandrous small copper.

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DESCRIPTIONS OF THE IMMATURE STAGES AND OVIPOSTION BEHAVIOR OF *PYRRHOGYRA OTOLAIS* (NYMPHALIDAE)

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ABSTRACT. The morphology and behavior of the immature stages of *Pyrrhogyra otolais* (Nymphalidae) are described. The early stages are compared with those of *Pyrrhogyra crameri.* An unidentified species of *Serjania* (Sapindaceae) is the larval host plant in Ecuador. The oviposition behavior and habits of the adults are discussed.

Additional key words: Ecuador, larva, pupa, *Serjania*, Sapindaceae.

The entirely neotropical genus *Pyrrhogyra* Hübner encompasses between nine and twelve species (D'Abrera 1987) distributed from Mexico through Central and South America, with the highest diversity in northern South America. At least four species occur in our study area. Our current understanding of species relationships within this genus is poor (D'Abrera 1987) and larval descriptions and hostplant relationships will provide useful information for correctly separating species. Adults are fast flyers and are frequently encountered in forest light gaps where they feed on dung, fruit (DeVries 1987) and carrion (pers. obs.). Known host plants are all within the family Sapindaceae (DeVries 1987) and the larvae show close behavioral and morphological affinities to such genera as *Catonephele* Hübner, *Nessaea* Hübner, *Callicore* Hübner, *Diaethria* Billberg, *Temenis* Hübner, *Eunica* Hübner, and *Epiphile* Doubleday (DeVries 1987).

Pyrrhogyra otolais Bates is distributed from Mexico to Peru, and seems confined to wet forests of lower elevations. Despite this widespread butterfly's formal description nearly 150 years ago, its early stages and hostplant relationships have remained undescribed. This study presents observations on hostplant use, larval morphology and behavior, as well as oviposition behavior.

Materials and Methods

All observations and rearings were conducted at the La Selva Biological Station located in the Sucumbios providence of eastern Ecuador. The station is located approximately 75 km east-south-east of Coca at an elevation of approximately 250 m. All studies were conducted adjacent to the oxbow lake Garza Cocha. The forest in this area is predominantly intact, though some areas have been clear-cut for coffee and manioc plantations.

On 14 November 1997, at 1330, two female *P. otolais* were observed to oviposit on a small seedling of an unidentified species of *Serjania* Mill. (Sapindaceae). Six eggs and a second instar were collected by cutting off the leaves to which they were attached. Larvae were reared in individual plastic cups. Fresh leaves were added and frass was removed semi-daily. Subsequently, larvae in various stadia were found and reared in a similar fashion. Vouchers of each stadium were preserved. Seven larvae were reared to adults. All head capsules, pupal exuviae, and vouchers are in the personal collection of the senior author.

Results

Larval host plant. *Serjania* sp. (Sapindaceae) is the larval host plant of *P. otolais* at our study site in eastern Ecuador. The strikingly colored, new, red leaves of this plant are easily seen in light-gap areas of the forest and in the forest understory. New leaves are present from November to January. The fact that adult *P. otolais* are present for most of the year in this area and can be quite common, suggests that adults are fairly long-lived.

Oviposition behavior. Upon locating a potentially suitable oviposition plant, the two observed females began flying rapidly in tight circles around the plant. During this period they landed on leaves of any plant in the vicinity. After several minutes they began landing more and more frequently on the host plant. While on the plant they walked about for several seconds rapidly tapping their forelegs on the leaf. After a single egg was laid, they repeated the rapid flight and leaf-tapping sequence for about 30 seconds before laying another egg. Eggs were always laid singly on the fresh red leaves of new shoots, but multiple eggs were eventually placed on the same leaf. Most commonly, eggs were placed dorsally along the mid-rib of the leaf, but were occasionally placed at the base of the petiole or on the stem nearby.

Egg. (n = 20+, Fig. 1a). Pale-yellow to white, darkening slowly after being laid, shape a truncated cone with strong longitudinal ridges and many closely spaced cross

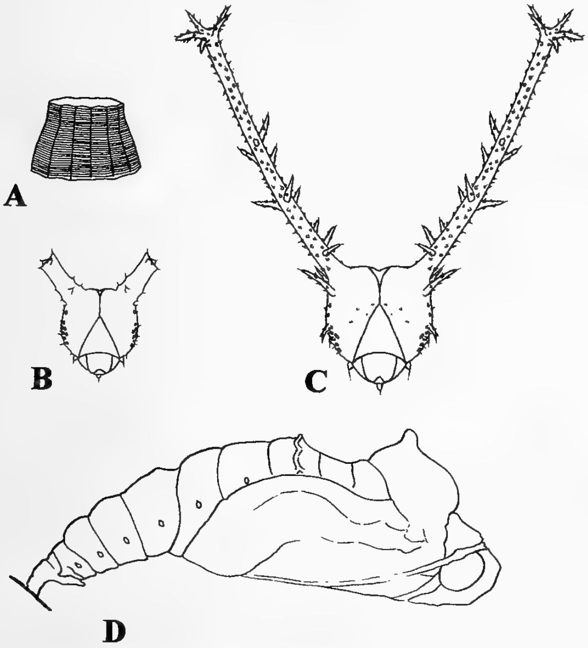

FIG. 1. Egg and larval head capsules of *P. otolais*. (a) egg: not drawn to scale (b) Second instar (c) Fourth instar (d) Pupa: not drawn to scale.

ribs, a slight constriction near the top gives them almost a bell shape. First instars hatch by flipping open the entire top of the egg like a lid. Larvae were never observed to eat the egg shell upon emergence.

Larva. *First instar* (n = 6). Head dark brown and devoid of scoli; body light yellow with dark setae. *Second instar* (n = 9, Fig. 1b). Head black with dorso-lateral scoli; body same color as first instar, all segments with pairs of short, rounded scoli dorsally, all with bulbous tips, brown at base and white at apex; A7 and A8 with middorsal scoli formed by rosettes of 3 and 5 spines respectively. *Early third instar* (n = 7). Head black with dorso-lateral scoli curving backwards, each scolus with several irregularly placed chalazae along the shaft and ending in a rosette of five spines, shaft of each scolus white immediately below apical rosette; body dull yellow, T3–A6 dorsally dark greenish-gray color with fine white patterning; A1–A6 with a pair of small white spots dorsally on either side of midline, all segments with dorsal, bifid scoli on either side of midline forming a row along the body, similar rows of single scoli laterally and ventro-laterally; T1 with single middorsal scolus; T2 with three-pronged middorsal scolus; T3 with five-pronged middorsal scolus; A2–A8 each with single, bifid, middorsal scolus; A9 with middorsal rosette of four scoli; A7 with middorsal, three-branched scolus in addition to the bifid scolus; A8 with additional five branched scolus; all scoli black and sparsely covered with small chalazae. *Late third instar* (n = 7+). Similar to early third instar but with orange bodies, dorsal portions of T3–A7 pale yellow with dark brown markings. *Fourth instar*. (n = 10+, Fig. 1c) Head as described for third instars; body as above with the addition of small, single scoli near the base of each proleg. *Fifth instar* (n = 17). Head bright orange except for the scoli and all spines, no white patch below the rosette at the tip of the scoli; body differs from fourth instar in being more brightly orange and the dorsal areas of segments T3-A7 bright yellow with dark brown or black markings.

Pupa. (n = 11, Fig. 1d) Mostly lime-green with brown markings along the ridges, cremaster dark brown, strong thoracic keel coming to an abrupt peak around the mesothorax, strong ridge along the dorsal edge of the wing pads extending onto the head and eyes, another strong ridge across the dorsum of the second abdominal segment. All individuals that pupated in the laboratory did so on the side of the container and were attached at nearly right angles to the sides of the container but curved downward. Only one pupa was found in the field, and this was attached to the near-horizontal surface of the hostplant leaf.

Larval behavior. Typical of other nymphalid genera, first and second instar larvae rest on "frass chains" built from the edge of the leaf (DeVries 1987, Otero & Aiello 1996). Later instars rest along the midrib of the leaf when not feeding. They rest with the head oriented towards the apex of the leaf, and angled so that the scoli project forwards. When disturbed, larvae rear back onto their prolegs and thrash wildly about, occasionally raising their terminal abdominal segments simultaneously.

DISCUSSON

As noted for other species of *Pyrrhogyra* (DeVries 1987), the early stages of *P. otolais* show affinities to the early stages of other sapindaceous feeders such as *Temenis* Hübner and *Epiphile* Doubleday (Nymphalidae). First, second, and early third instars are almost identical to those of *P. crameri* Aurivillius, which can be found during the same time of year in this area. *Pyrrhogyra crameri* larvae, however, feed on *Paullinia* Linn. (Sapindaceae). The second and third instars can be separated from those of *P. otolais* by the presence of only three spines in the middorsal rosette of segment A8. The behavior of these two species while resting as larvae on their host plant and as adults is very similar. Adults of both species are seen frequently patrolling light gaps, usually perching several meters from the ground.

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EFFECTS OF ADULT FEEDING AND TEMPERATURE REGIME ON FECUNDITY AND LONGEVITY IN THE BUTTERFLY *LYCAENA HIPPOTHOE* (LYCAENIDAE)

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ABSTRACT. When fed highly concentrated sucrose solution, adult females of the Purple-Edged Copper butterfly *Lycaena hippothoe* L. laid significantly more eggs (mean = 464) than those individuals given water only (mean = 65). Longevity was also three to five times greater, whereas hatching rate of the eggs was not affected by the mother's nutrient intake. Stored resources acquired during the larval stage supported realization of only 14% of the fecundity of the fed females. Hence, *L. hippothoe* butterflies depend far more on adult-derived resources than other nectar-feeding butterflies for which comparable data exist. These findings may be important for the population dynamics of the species, as reduced availability of nectar sources presumably constrains realized fecundity.

Additional key words: Adult diet, reproduction, nutritional ecology, population dynamics.

Oogenesis in insects is typically a nutrient-limited process, triggered only if sufficient nourishment is available (Wheeler 1996). The required resources can be acquired during the larval or adult stage (or both), depending on the insects' life cycle (Boggs 1997a). In the holometabolous Lepidoptera, resources for reproductive investment may stem from the herbivorous larval stage or from the adult stage, during which they collect liquid food such as nectar (Wheeler 1996). Although it is generally thought that butterflies and moths usually rely more on reserves accumulated during the larval stage to supply egg production (Wheeler 1996), there is broad variation with regard to the importance of adult feeding (Hill 1989, Murphy et al. 1983). Many adult moths do not feed at all and rely completely on reserves accumulated during the larval stages ("capital breeders" sensu Tammaru & Haukioja 1996). At the other extreme, female *Heliconius* butterflies collect protein-rich pollen which supports the laying of eggs through the adult life span of several months (Gilbert 1972, Dunlap-Pianka et al. 1977). Such species can be referred to as "income breeders" (Tammaru & Haukioja 1996), for which successful reproduction is essentially mediated by resources available to the adults.

In many temperate-zone nectar-feeding butterflies (cf. Boggs & Ross 1993, David & Gardiner 1962, Karlsson & Wickman 1990, Labine 1968, Murphy et al. 1983, Stern & Smith 1960) and at least some moths (Adler 1989, Cheng 1970, Leahy & Andow 1994, Leather 1984, Miller 1989), even though substantial protein is not acquired after adult eclosion, carbohydrate ingestion can profoundly affect longevity and fecundity. Certain tropical butterflies even appear to supplement their nitrogen budget by visiting protein-rich mud-puddles (Beck et al. 1999). The degree of dependence on nectar, however, varies between species (e.g., Boggs 1997b). The majority of previous studies are concerned with analyzing correlations between butterfly abundance and availability or diversity of potential nectar sources (e.g., Douwes 1975, Grossmueller & Lederhouse 1987, Hill 1992, Loertscher at al. 1996, Schultz & Dlugosch 1999). Controlled experimental studies, in contrast, are available only for a small range of taxa.

With far more than 5000 extant species, the Lycaenidae are the second-largest family of true butterflies in the world (Heppner 1991). However, hitherto almost no experimental data on the role of adult feeding in lycaenid butterflies are available (with exception of the Australian species *Jalmenus evagoras*; Hill & Pierce 1989). This paper reports the effects of different feeding and temperature regimes on fecundity, survival and hatching rate of the Purple-Edged Copper butterfly *Lycaena hippothoe*, in order to assess the relative importance of income vs. stored resources. Furthermore, we discuss the relevance of our results for the population dynamics of this species.

STUDY ORGANISM, MATERIAL AND METHODS

Lycaena hippothoe is a widespread butterfly ranging from northern Spain in the west throughout much of the northern Palaearctic region eastwards to the easternmost parts of Siberia and China (Ebert & Rennwald 1991, Lukhtanov & Lukhtanov 1994). In Central Europe, adults fly in one generation from about mid-June through late July (Fischer 1998). The species inhabits different kinds of wetland as well as unimproved grassland. The principal larval hostplant is *Rumex acetosa* L. (Polygonaceae), a common and widespread perennial herb occurring in various types of grassland. Recent declines of *L. hippothoe* populations stimulated concern among nature conservation authorities and resulted in the inclusion of this species into "Red Data Lists" in various European countries (cf. Marttila et al. 1999, Pretscher 1998, SBN 1987, Tax 1989).

In June 1997 and 1998, respectively, freshly emerged females (not older than one or two days, judged by wing wear) of *L. hippothoe* were caught in the Westerwald area (western Germany; see Fischer

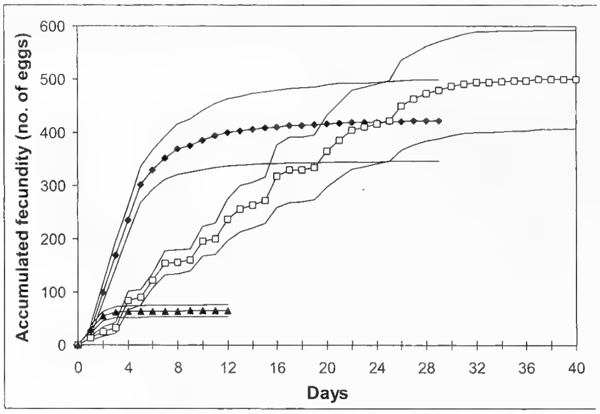

FIG. 1. Mean accumulated fecundity (solid lines without symbols: ±SE of respective means) of *Lycaena hippothoe* over time under different feeding and temperature regimes (rhombuses: "fed 25°C", squares: "fed", triangles "water").

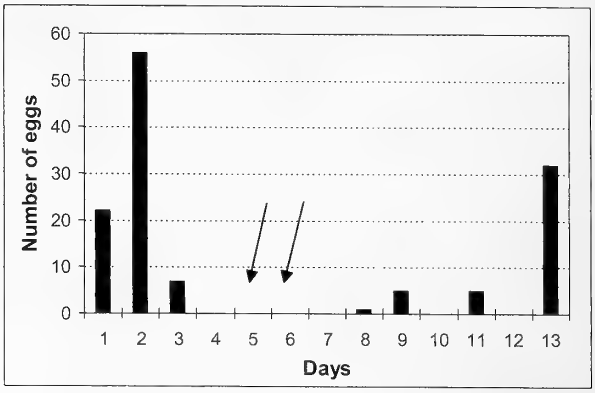

FIG. 2. Fecundity in a single female *Lycaena hippothoe* provided with water only. On two occasions (indicated by arrows) the female was allowed to feed on highly concentrated sucrose solution for about half an hour each time.

1998) for rearing experiments and to provide the foundation of a captive breeding stock. Females were placed individually in glass jars (1 L) containing moistened filter paper and the jars covered with gauze. Each jar contained a bunch of the larval foodplant *R. acetosa* (in H_2O) as oviposition substrate.

For measuring the effects of feeding and temperature regime three experimental treatments were used. (1) Ambient daylight and temperature conditions (from mid-June to mid-July 1997, wild-caught females), butterflies fed with a highly concentrated sucrose solution. (2) Conditions as before (from mid-June to mid-July 1998, wild-caught females), but butterflies were provided with water only. (3) In an environmental chamber at a constant temperature (25°C) and a photoperiod of L18:D6 (in 1998), fed with a highly concentrated sucrose solution (these females originated from captive breeding stock, F_1-generation). The three treatments are hereafter referred to as "fed" (1), "water" (2), and "fed 25°C" (3). For egg-laying under ambient conditions glass jars were put on a table outside in a sheltered area. The day-night regime during the periods was about L16.30:D7.30 (time between sunrise and sundown excluding civil twilight).

In the morning (i.e., before onset of oviposition activities) of each day eggs were removed and counted. Eggs were then exposed to a constant temperature of 20°C (photoperiod L18:D6) to assess hatching rate. Females were dissected after death occurred, and the number of mature oocytes remaining in their ovaries was determined under a stereomicroscope. Furthermore, 10 freshly emerged and unfed females from captive breeding stock were dissected to analyze the status of oogenesis at emergence. Only already yolked oocytes with a diameter of at least 0.5 mm were counted.

Differences in mean values were tested using the Mann-Whitney *U*-test and the Tukey-Kramer post-hoc comparison after the non-parametric Kruskal-Wallis H-test (Sachs 1997), since data distributions deviated strongly from normality. Throughout the text all means are given ±1 SD.

RESULTS

Egg production and hatching rate. Total lifetime egg production was strongly affected by access to nutrients, but not by temperature regime (see below). Females fed highly concentrated sucrose solution in both treatments laid significantly more eggs than those individuals given water only ($H_{2df} = 14.3$, $p = 0.0008$; Table 1). The latter achieved, on average, only 14.0 % of the fecundity of the fed individuals (64.9 ± 30.1 vs. 464.2 ± 207.1 eggs, data for "fed" and "fed 25°C" pooled). The number of eggs laid in the "water"-group coincides with the well developed oocytes at emergence (mean 60.9 ± 18.8, n = 10; *U*-test: z = 0.44, p = 0.66, n.s.). Likewise, total potential fecundity (measured as the total number of eggs laid plus mature oocytes remaining after death) was much reduced in the water-only treatment, but did not differ between the two sugar-feeding treatments.

In females with no access to carbohydrate sources, substantial oviposition occurred only during the first three days of the experiment (Fig. 1). One of those butterflies was provided with sucrose solution on two days, after which it resumed laying eggs again (Fig. 2). These eggs laid after sucrose feeding were excluded from further data analysis.

No significant difference in egg production was found between females fed at a constant temperature of 25°C compared to those fed under ambient tem-

Table 1. Fecundity, hatching rate and longevity (means ± SD) of female *Lycaena hippothoe* under different feeding and temperature regimes ("fed 25°C": in environmental chamber at a constant temperature of 25°C, fed with sucrose solution; "fed": ambient temperature conditions, fed with sucrose solution; "water": ambient temperature conditions, access to water only). Figures within one row followed by the same letter do not differ significantly (Tukey-Kramer post-hoc comparison after Kruskal-Wallis H-test, threshold for significance $p < 0.05$).

	Fed 25°C	Fed	Water
Number of females	6	7	8
Number of eggs laid	422.3 ± 187.9^{a}	500.1 ± 245.7^{a}	64.9 ± 32.1^{b}
Range (eggs laid)	165–690	126–808	9–102
Highest egg number/day	98	110	65
Number of oocytes	43.0 ± 41.0^{a}	26.9 ± 23.1^{a}	28.5 ± 22.8^{a}
Number of eggs and oocytes	465.3 ± 163.7^{a}	527.1 ± 240.4^{a}	93.4 ± 14.9^{b}
Relative realized fecundity [%]	88.1 ± 11.9^{a}	93.0 ± 6.4^{a}	66.6 ± 29.8^{a}
Hatching rate of eggs [%]	83.0 ± 11.9^{a}	81.3 ± 17.8^{a}	84.1 ± 11.8^{a}
Female longevity [days]	16.8 ± 7.8^{a}	31.7 ± 9.7^{b}	6.1 ± 3.6^{c}
Oviposition period [days]	10.8 ± 8.2^{a}	28.0 ± 10.1^{b}	4.0 ± 1.5^{c}

perature conditions (Table 1). However, under the ambient temperature regime it took the females far longer to reach saturation of the fecundity curve (about 30 compared to 10 days; Fig. 1). The "steps" in the fecundity curve of the individuals fed under an ambient temperature regime are caused by days with adverse weather conditions and hence no egg-laying.

Realized relative fecundity, expressed as the ratio of eggs laid relative to the total number of eggs laid plus remaining mature oocytes after death, was high in fed individuals and lower, though not significantly so, in the water-fed butterflies ($H_{2df} = 4.5$, $p = 0.1$; Table 1). In contrast, hatching rate of eggs was invariably high (80–85 %) and not affected by adult feeding ($H_{2df} = 0.1$, $p = 0.95$). As all females produced viable eggs, they obviously were mated.

Longevity. Feeding as well as temperature regime strongly influenced longevity (Table 1). Sucrose-fed females (both treatments) lived three to five times longer than water-fed individuals ($H_{2df} = 14.5$, $p = 0.0007$). Furthermore, sucrose-fed individuals under ambient climatic regime survived twice as long as the group fed at 25°C. Extended survival also distinctly increased the duration of an individual's oviposition period ($H_{2df} = 15.1$, $p = 0.0005$). Compared to females provided with water only, among sucrose-fed butterflies the period over which eggs were laid increased by a factor of 2 (at 25°C) to 7 (at ambient temperature conditions).

DISCUSSION

Our data demonstrate the exceptional importance of adult feeding for reproduction in female *L. hippothoe*. Overall, fecundity in our experiments was much higher than suggested for this species in the literature (Bink 1992), and sucrose-feeding increased total egg production, oviposition period as well as longevity. Therefore, nourishment from nectar sources is essential for maintenance of basic metabolic functions as well as for egg production.

Adult-derived resources seem to be even more important for egg production and longevity than in many other butterfly species. For example, in *Pararge aegeria* (Nymphalidae) egg number is approximately four times higher after sugar-feeding than after water-feeding (Karlsson & Wickman 1990). In the checkerspot butterfly, *Euphydryas editha* (Nymphalidae), as well as in *Jalmenus evagoras* (Lycaenidae), sugar-feeding roughly doubles egg production and longevity relative to individuals kept with no access to food or supplied with water only (Murphy et al. 1983, Hill & Pierce 1989). In *L. hippothoe*, in contrast, the increase in fecundity was seven-fold, and longevity was three to five times greater. Obviously, substantial egg production in *L. hippothoe* relies strongly on adult-derived rather than larval-derived carbohydrates. Thus, in the continuum between capital and income breeders the species is positioned far to the latter side. Until recently, carbohydrate intake was largely regarded as a means of acquiring flight fuel, and its importance for oogenesis was not clear (Wheeler 1996). But now the incorporation of carbohydrates into developing oocytes has been confirmed directly by radiotracer studies (Boggs 1997a), and our results further corroborate the relevance of sugar-feeding for egg production in butterflies.

Surprisingly, hatching rate was not affected by adult feeding. We conclude that unfed females are able to lay those eggs only, in which development is already under way at adult emergence (cf. Boggs & Ross 1993). This is supported by the coincidence between the number of well developed oocytes found in females at emergence with the total egg production in the water-fed group (cf. Hill & Pierce 1989, Watanabe 1992). Oogenesis of those eggs must rely exclusively on nourishment gathered during larval stage (probably supplemented by male-derived nutrients received by the female at mating; cf. Boggs 1990, 1997a). The production or maturation of additional eggs is apparently severely constrained in *L.*

hippothoe butterflies without adult carbohydrate intake. In contrast to the sucrose-fed females, most oocytes remaining after death were poorly developed in the water-fed individuals. Obviously, females are supplied with a rather small amount of stored carbohydrates, which are abundantly available from adult nectar resources. On the other hand nitrogenous compounds, which are scarce in the diet of most (temperate-zone) adult butterflies, are commonly capital reserves acquired more or less entirely during the larval stages (but see Beck et al. 1999, Erhardt & Rusterholz 1998). These stored reserves are used throughout adult life (Boggs 1997a), whereas larval-derived carbohydrates decline rapidly and need to be complemented by income.

Our findings could be of importance for the population dynamics of *L. hippothoe* in at least two ways. As the number of eggs laid obviously depends on adult resources in this species, adverse weather conditions can influence population dynamics not only through a higher adult or larval mortality (e.g., Singer & Ehrlich 1979, Pollard et al. 1997), but also through a decrease in fecundity. A high incidence of rainy or overcast days would limit not only the time available for egg-laying, but also for feeding. Unlike factors affecting oviposition rate only, there is no compensation for a reduced egg production caused by lack of nourishment (Gossard & Jones 1977), as nutrient limitations should impede compensation of time limitations through an increase in oviposition rate. In contrast to other species able to produce substantial egg numbers even without any adult feeding (e.g., *Euphydryas editha*; Murphy et al. 1983), population dynamics of *L. hippothoe* should be far more affected if access to adult nutrient resources is limited.

Second, modern agricultural techniques lead to a reduction of nectar sources (i.e., flowers) through a high mowing frequency and recurrent application of fertilizers (Barabasz 1994, Ellenberg 1996, Erhardt 1995, Nigmann 1997). Taking into account the dramatic loss of traditionally managed hay meadows in central European landscapes (e.g., Erhardt 1995, Erhardt & Thomas 1991), the concomitant reduction of flower availability could be an important factor for regional declines in this sedentary species.

Our study revealed that *L. hippothoe* butterflies must be regarded, to an unexpected degree, as income breeders. It remains to be tested whether other temperate-zone lycaenids rely in a similar manner on nectar resources for reproduction. If this were the case, this could explain the decline of other lycaenid species with common and widespread hostplants (e.g., *L. tityrus* Poda, *L. virgaureae* L., sharing the same hostplant, *Rumex acetosa*, with *L. hippothoe*) in modern European landscapes. Hence, the importance of the availability of adult resources for the reproductive biology and persistence of butterfly populations, which is most commonly inferred from field data on spatial distributions (e.g., Hill 1992, Douwes 1975, Loertscher et al. 1996), deserves more experimental studies on a broader range of taxa.

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GENERAL NOTES

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NOTES ON THE BEHAVIOR OF *SPEYERIA IDALIA* (DRURY) (NYMPHALIDAE) LARVAE WITH IMPLICATIONS THAT THEY ARE DIURNAL FORAGERS.

Additional key words: *Speyeria idalia*, diurnal feeding behavior, tallgrass prairie, Kansas.

Populations of the regal fritillary, *Speyeria idalia* (Drury), are in decline throughout its range (Hammond & McCorkle 1983, Debinski & Kelly 1998). This decline has heightened interest in the study of the life history of this butterfly species, especially the juvenile stages. Understanding the larval behavior of *S. idalia* is an important step in understanding the butterfly's overall life history and ultimately, implementing management plans to protect it along with the remaining tracts of native tallgrass prairie. Scudder (1889) was the first to note our lack of knowledge of the natural history of *S. idalia* larvae. Much of what is known, such as the daily feeding patterns, is anecdotal and has not yet been corroborated by laboratory experiments. Larvae of the genus *Speyeria* have been reported to feed on violet plants (*Viola* spp.) at night and remain hidden during the day, away from their host plants (Holland 1931, Ehrlich & Ehrlich 1961, Royer 1988). In Kansas, *S. idalia* feeds primarily on two species of violet: *V. pedatifida* G. Don (the prairie violet) and, to a lesser extent, *V. pratincola* Greene (the blue prairie violet). If the larval strategy is to leave their host plant during the day, the larvae must either relocate the host plant upon which they last fed or find a new one. We studied larval *S. idalia* both in the field and in the laboratory to determine their daily activity patterns.

We first attempted to rear the larvae according to the procedure of Mattoon et al. (1971), but survivorship was very low. Therefore, it was necessary to collect larvae in the field. Field studies were conducted in a native tallgrass prairie (dominated by little bluestem, *Schizachyrium scoparius* Michx.; Indian grass, *Sorghastrum nutans* (L.) Nash; and big bluestem, *Andropogon gerardii* (Vitman) 8.0 km west of the town of Wamego, in Pottawatomie Co., Kansas (TIOS, R9E, Sec. 1)). For a more through description of the study site, see Kopper (1997). Searching violet plants at night proved useless. We spent most of our time searching for larvae on and around violet plants during the day in mid-April and early May. Even in the day larvae were exceedingly difficult to find, resulting in the small number (n = 12) used in this study. Where the larvae were found and the behavior that they exhibited prior to collection was recorded (Table 1).

Of the 12 field-collected larvae available, three were parasitized by Hymenoptera and three died from unknown causes, leaving us with six larvae to use for bioassays. We released one 4th instar larva back to the prairie and observed it continuously for 24 hours beginning at 0900 CST. Additional studies were conducted in the greenhouse. Larvae (n = 5) were released into a prairie plot located in the Kansas State University greenhouses. This plot consisted of a portion of native tallgrass prairie (slated for road development) that was dug out to a depth of 40 cm and transplanted into an open-top plywood box (1.83 × 1.22 m). The temperature within the greenhouse was maintained as close to field conditions as possible (28°C during the day, 18°C during the night; 60% RH). The plot was watered once a week. Natural light was used for illumination, so the photoperiod also mirrored field conditions. The larvae were observed every other hour over staggered eight-hour blocks of time to continuously monitor the larvae for 1 week.

We also obtained three larvae from eggs that we reared in the lab and used to film larval behavior. A sand-filled arena (24 cm diameter desiccation chamber) was used for the assay; violet leaves were placed into water vessels, which were buried in the sand. The density of violet leaves in the arena was similar to densities observed in the field. The bioassay was kept at ~20°C and 60% RH. A continuously operating, red low intensity (25 w.) incandescent light source permitted us to film and observe larval behaviors during the scotophase (dark period). The ratio of photoperiod:scotophase that the larvae would experience in the field was maintained in the laboratory, but the phases were reversed. Larvae were held for 1 week under these conditions to allow them to entrain to the new light regimen prior to the bioassay. The larvae were filmed and observed bihourly over various times of the day for 1 week.

We found that, in the field, the larvae were considerably more active during the day and inactive throughout most of the night. When inactive, the early instar (1st–early 3rd) larvae could be found in the curls of the young violet leaves, whereas the later instar (late 3rd–6th) larvae were found at the base of the violet plant. These results may be biased, because we spent a great deal of time searching for larvae in violet clumps. During the day (1000–1600 hours), larvae were feeding, walking, or inactive. When not at the base of violet plants, larvae were found feeding on violet plants (both leaves and flowers) and walking in curved directional paths.

We calculated the probability that larvae would move from one behavior to another by observing larvae (laboratory larvae were observed bi-hourly for one week and the field larva was observed over a 24-hour period) and assessing the change in larval behavior. Larval behavior was characterized into three categories: moving, inactive, and feeding. The change in larval behavior was pooled separately for larvae in both laboratory and field observations. Because of the low sample size (n = 3 for the laboratory assay and n = 1 for the field assay) used for these observations, these results should be interpreted with caution. Also, any differences between laboratory and field data may be due to the nature of the laboratory bioassay, such as a greater likelihood of running into leaves in the arena than finding a plant in the field. Furthermore, temperature or time of day was regrettably not recorded and which may have also influenced larval behavior. Following a period of inactivity, the larvae often started to move as opposed to feeding (52.4% and 75.0% laboratory and field, respec-

TABLE 1. Behavior of larvae found in the wild. All larvae were collected during daylight hours. Time, when recorded, is expressed in military time. nr = not recorded.

Individual	Date	Time	Instar	Behavior when found
1	4/16/97	nr	4th	Inactive at the base of *V. pratincola*.
2	4/22/97	nr	3rd	Inactive at the base of *V. pedatifida*.
3	4/23/97	10:00–10:30 h	3rd	Inactive at the base of *V. pedatifida*.
4	4/23/97	10:00–10:30 h	4th	Inactive at the base of *V. pedatifida*.
5	4/24/97	10:00–11:00 h	3rd	Inactive at the base of *V. pedatifida*.
6	4/28/97	11:00–12:00 h	3rd	Feeding on *V. pedatifida* leaves.
7	4/28/97	11:00–12:00 h	3rd	Inactive at the base of *V. pedatifida*.
8	5/1/97	nr	3rd	Feeding on *V. pedatifida* flower.
9	5/8/97	10:30–11:30 h	4th	Inactive at the base of *V. pedatifida*.
10	5/9/97	nr	5th	Walking towards *V. pedatifida*.
11	5/9/97	nr	5th	Inactive at the base of *V. pedatifida*.
12	5/9/97	nr	5th	Feeding on *V. pedatifida* leaves.

tively). After moving, the larvae typically became inactive again, only feeding 27.8% in the laboratory and 25.5% in the field. However, in the field, encountering food is not guaranteed, and these percentages do not take into account distance traveled. Once a larva in the field had fed, it would either remain inactive or move with equal probability. However, larvae in the laboratory would remain inactive after feeding 81.3% of the time.

Larvae would eat the violet leaves rapidly during feeding bouts and, when not feeding, larvae would hide in clumps of grass or walk. McCorkle and Hammond (1988) observed similar feeding behavior for *S. zerene hippolyta*. The fifth instar larva that was released back to the prairie walked in a curved path (25.40 m over a 24 hour period) and fed only on violet plants that were in its path (although it walked past violet plants as close as a centimeter away and apparently did not perceive them). Wind direction did not seem to matter as the larvae walked equally close to violets up and down wind without noticing them. As the sun set, the larva walked and fed progressively less, until it became inactive at the base of a grass clump and remained there until the following morning. The larvae studied in the laboratory and greenhouse displayed a similar diurnal feeding pattern. The inactivity associated with nightfall may be due to a reduction in temperature, however temperature does not drop substantially as soon as the sun sets in eastern Kansas, leading us to believe that light is a more important cue for activity than temperature.

This study of a small sample of *S. idalia* larvae in Kansas tallgrass prairie indicates that they do not forage entirely at night. More study is needed covering a larger geographic region in order to determine how widespread this behavior is within *S. idalia* and the genus *Speyeria*.

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BIOLOGY OF *ADELPHA MYTHRA* FEEDING ON ASTERACEAE, A NOVEL PLANT FAMILY FOR THE NEOTROPICAL LIMENITIDINAE (NYMPHALIDAE), AND NEW DATA ON *ADELPHA* "SPECIES-GROUP VII"

Additional key words: *Adelpha syma*, *Adelpha cocala*, life history, Rosaceae, Rubiaceae.

The Neotropical genus *Adelpha* Hübner (Nymphalidae) includes about 85 species (Keith Willmott pers. comm.) spread from western USA to Uruguay, and occurring in a wide variety of habitats and vegetation types (Aiello 1984). Species determination is very difficult in some *Adelpha* groups, and the natural divisions of the genus are not yet fully resolved, although a number of species relationships have been proposed on the basis of the immatures (Aiello 1984). Unfortunately, immatures are known for only 32 species of *Adelpha*, solely 21 of which have some portion of the early stages illustrated. Thus, although a cladistic analysis of the genus is needed, it would be impossible at this time. Because information on additional species is essential to a better understanding of the genus (DeVries 1987; Aiello 1991), it is important that any new data about *Adelpha* immatures be reported (Otero & Aiello 1996).

This paper describes the immature stages of *Adelpha mythra* (Godart 1824) and *A. syma* (Godart 1824), reports their larval host plants, and discusses the position of both species within *Adelpha*, based on their immatures.

Study sites and methods. *Adelpha mythra*, a montane species in southeast Brazil, is one of 16 species of *Adelpha* known in the Santa Genebra Forest Reserve (22°44′S, 47°06′W, altitude 600–630 m), a 250 ha fragment of semideciduous forest in Campinas, São Paulo State, SE Brazil (see additional information on the area in Morellato and Leitão-Filho 1995). In January 1999, a female *A. mythra* was observed there ovipositing on the scandent vine, *Mutisia coccinea* St. Hil. (Asteraceae). The egg did not hatch, so this very unusual "record" was thought to be an oviposition mistake of this female. However, from February to April 1999, *A. mythra* was reared from first to fourth instars collected on the same plant species and also on *Bathysa meridionalis* (Rubiaceae) in several parts of the Serra do Japi (23°11′S, 46°52′W), a mountain range (700–1300 m altitude) covered by semideciduous forest, in Jundiai, São Paulo State, SE Brazil (Brown 1992). Immatures of *Adelpha syma* were also found on *Rubus* (Rosaceae) in the Serra do Japi, and immatures of *A. cocala* were discovered feeding on a Rubiaceae in the Parque Ecológico do Voturuá (46°22′W, 23°57′S, altitude 20–100 m), a 200 ha fragment of lowland subtropical rainforest in the city of São Vicente, coastal São Paulo State, SE Brazil.

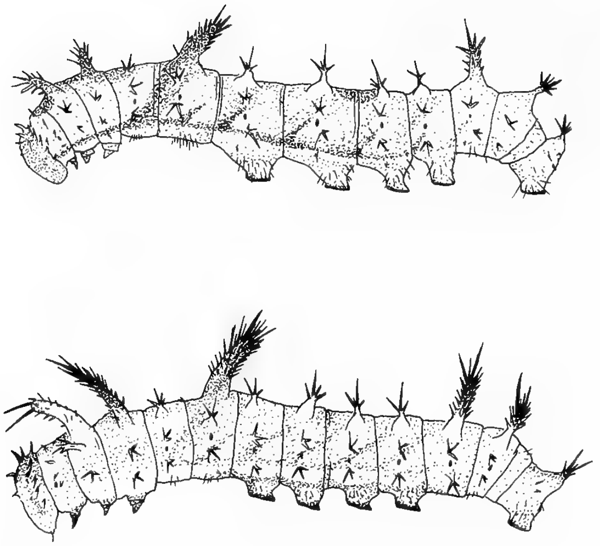

FIG. 1. Fifth instar larvae of *Adelpha syma* (above) and *A. mythra* (below)

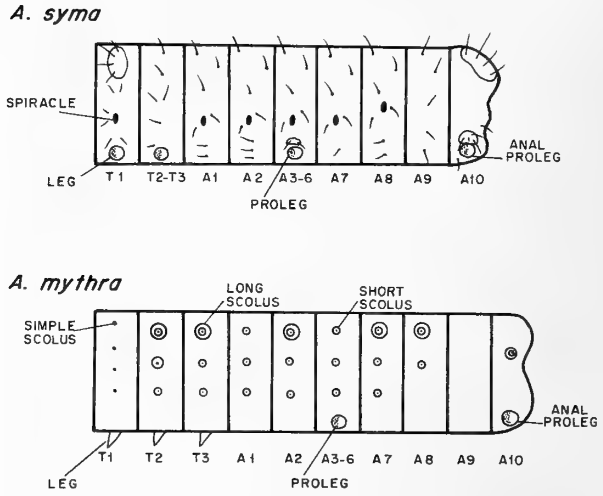

FIG. 2. Above, Chaetotaxy of first instar larva of *Adelpha syma*. Below, Distribution of scoli in a fifth instar larva of *A. mythra*.

Larvae were reared in plastic cages cleaned daily, following Freitas (1991). Adults, head capsules and pupal skins are in the collection of the first author. Larval food plant vouchers, identified by Dr. Jorge Tamashiro, have been deposited in the herbarium of the Universidade Estadual de Campinas.

Descriptions of immatures and host plants of *Adelpha mythra*. The only egg observed was greenish brown, sculptured with hexagonal pits, with spines arising from the pit junctions, consistent with eggs described for other species of *Adelpha*. The egg was placed on the upper surface of the leaf, near the apex. It was laid rapidly by a startled female, and did not hatch.

First and second instars were not described in detail. The third instar had conspicuous head scoli and a faintly visible variegated pattern that, with few changes, was maintained and intensified through the remaining larval stadia. The fifth instar (Fig. 1) was variegated green, with a pattern of oblique lateral stripes. The green areas changed to light orange as the larvae neared pupation. In the final larval stadium, the body scoli were short and thick, with a dense covering of spines; the scoli on A2 were arched posteriorly. The distribution of the scoli (Fig. 2) was the same as for most *Adelpha* species. The mature larva was about 25 mm long.

The first through fourth instars initiated feeding at the apex of a leaflet, leaving the midvein intact and extending it with fecula and silk to form "frass chains" (Aiello 1984). They rested upon these structures when not feeding. In addition, they attached dead leaf fragments and clumps of fecula to the base of the chains. When feeding on *Bathysa meridionalis*, larvae built "frass chains" on other parts of the same large leaf.

The pupa (Fig. 3A) showed an elongated general profile (about 17 mm long), with segment A2 produced and curved anteriorly, and segment T2 pointed and directed posteriorly. The head horns were pointed and shaped like tiny asymmetrical leaves, curving out from the sides of the head. The general color was brown, with dark lines on the wing pads and no reflective areas.

Mutisia coccinea (Asteraceae), a scandent shrub common in wet second growth habitats, was observed as the larval food plant of *Adelpha mythra* both in Santa Genebra and in the Serra do Japi. In the latter site, *A. mythra* was also reared on *Bathysa meridionalis* L. B. Smith & Downs (Rubiaceae), a plant with enormous leaves (up to 1m in length and width), of montane habitats, where it occurs most often near watercourses. *Bathysa meridionalis* is used by many other *Adelpha* species in that site (Brown 1992 and AVLF pers. obs.).

Immatures and host plants of *Adelpha syma*. The egg was greenish brown, with sculpturing and ornamentation as described for other species of *Adelpha*, placed on the upper surface of the leaf, near the apex. The height and diameter were about 0.8 mm; the duration was not determined.

The first instar was entirely brown, with pale body setae about 0.06 mm long, arranged as in Fig. 2. The head capsule was pale brown without ornamentation. The final body length was 4 mm. The second instar was entirely brown, with a spiny brown head. The body bore short stubby scoli. The final body length was 6 mm. The third and fourth instars showed a clearly visible variegated pattern, with head spines longer. The final lengths were 9 mm in the third and 15 mm in the fourth larval stadia. The fourth and fifth instars had the same general pattern. The fifth instar (Fig. 1) was variegated with green, cream and brown, showing a general pattern of oblique lateral stripes. The green areas change to light orange before pupation. The body scoli were short and thick, with dense spines, and the scoli of A2 arching posteriorly. The distribution of the scoli was the same as in *A. mythra*. The fully grown larva was 25 mm long. Data on head capsule widths for all instars are in Table 1. The first through fourth instars constructed frass chains and had a behavior similar to that described for *A. mythra*.

The pupa (Fig. 3B) showed an elongated general profile (about 18 mm long), with segment A2 projecting and curved anteriorly, and segment T2 pointed and directed posteriorly. The head horns were very small and pointed, curved out from the sides of the head. The general color was brown, with dark lines on the wing pads and no reflective areas.

The host plant in the Serra do Japi was *Rubus brasiliensis* Mart. (Rosaceae), a common blackberry of sunny second growth habitats, especially in montane sites. *Rubus rosifolius* Sm., an introduced species, is also used as larval food in other montane sites in SE Brazil.

Positions within *Adelpha*. The scolus shape and the general pattern of the larvae, and the general form of the pupae, suggest

TABLE 1. Head capsule widths of *Adelpha syma*

Larval instar	Range (mm)	Mean	SD	n
1°	0.56–0.58	0.57	0.011	7
2°	0.78–0.82	0.80	0.014	5
3°	1.18–1.22	1.18	0.042	6
4°	1.64–2.03	1.81	0.151	13
5°	2.73–3.12	2.89	0.133	11

that both *Adelpha mythra* and *A. syma* belong to the Species-Group VII of Aiello (1984). The immatures of both species are very similar to those of *A. cocala*, the main difference being that the A2 process of the pupa is much longer in *A. mythra* and more arched in *A. syma* than in *A. cocala* (Fig. 3C). In *A. mythra*, the length of the A2 projection approaches the condition observed in *A. phylaca* (as described by Müller 1886) (Fig. 3D), a species belonging to Group II of Aiello (1984). However, the T2 projections of *A. mythra* and *A. syma* are sloped posteriorly, and not curved upward as in Group II pupae, giving pupae in the two groups distinctive general appearances. The pupal head horns of *A. mythra* (Fig. 3A) are similar in shape to those of *A. cocala* (Fig. 3C), but are farther apart at their bases and are more tapered. The head horns of *A. syma* (Fig. 3B) are similar to those of *A. phylaca* (Fig. 3D), but are more curved.

Additional species of *Adelpha* need to be reared in order to clarify the scenario based on the morphology of the immatures and to make a cladistic analysis possible. Some species groups are based on only one, two or three species, and the immatures of many common species remain to be discovered, or their descriptions are not sufficiently detailed to permit assignment to a species-group. Additional descriptions of *Adelpha* immatures with figures are important, especially when they show apparent deviations from the eight known species groups (Aiello 1984, Otero & Aiello 1996).

Host plant use. Among the Nymphalidae, the association with Asteraceae as larval food plants is found in only a few groups (especially Melitaeinae and Acraeinae) (Ackery 1988, Freitas 1991). The record of Asteraceae as a larval host of the Limenitidinae represents a new plant family for neotropical *Adelpha*. Larvae of *Adelpha* species have been recorded as feeding on Aquifoliaceae, Asteraceae, Bombacaceae, Caprifoliaceae, Combretaceae, Ericaceae, Fagaceae, Flacourtiaceae, Icacinaceae, Malpighiaceae, Melastomataceae, Moraceae, Ochnaceae, Piperaceae, Rosaceae, Rubiaceae, Tiliaceae, Ulmaceae, Urticaceae, Verbenaceae and Vochysiaceae (Jones & Moore 1883, Müller 1886, Moss 1933, Biezanko et al. 1966, Aiello 1984, 1991, DeVries 1987, Ackery 1988, Brown 1992, Otero & Aiello 1996, Diniz & Moraes 1997, Constantino 1998, and this work). Some themes may be recognized in the different species-groups (Aiello 1984). Basically the species of *Adelpha* can be sorted into rubiaceous feeders and non-rubiaceous feeders. Four examples of species feeding on both Rubiaceae and other families have been reported (*A. serpa*, *A. boreas tizona*, *A. syma* and *A. cocala*), and *A. mythra* is the fifth recorded case. Although interesting, this pattern must be considered with caution, because some plant identifications need to be confirmed by additional field observations.

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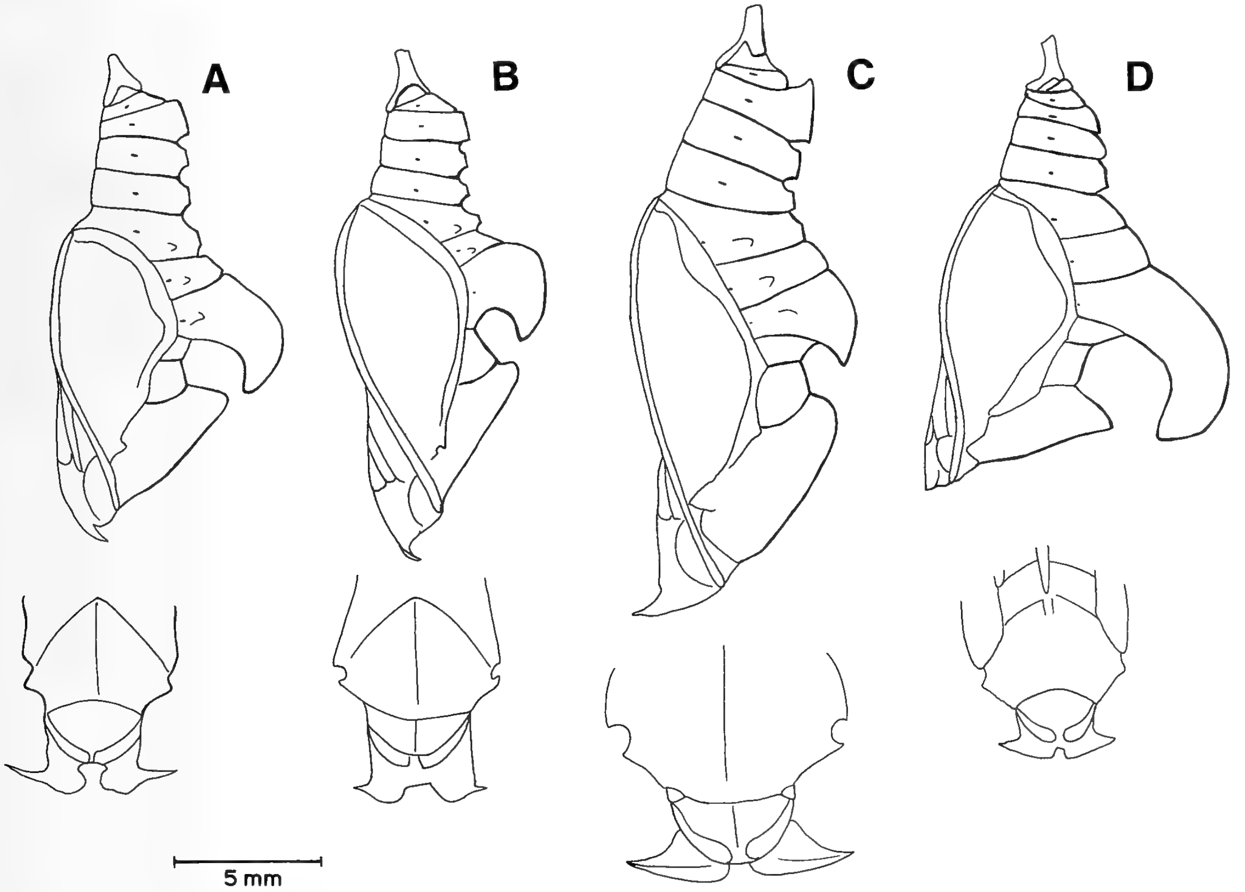

FIG. 3. Pupae of *Adelpha mythra* (A), *A. syma* (B), *A. cocala* (C) and *A. phylaca* (D) (*A. phylaca* redrawn from Aiello, 1984, in a different scale; the bar means 7.3 mm).

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BOOK REVIEWS

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HAWKMOTHS OF THE WORLD: AN ANNOTATED AND ILLUSTRATED REVISIONARY CHECKLIST (LEPIDOPTERA: SPHINGIDAE), by Ian J. Kitching and Jean-Marie Cadiou. Published by The Natural History Museum, London and Cornell University Press, Ithaca, New York. 226 pp., 8 color plates. Hardcover, 8.8 × 11.3 inches, ISBN 0-801437-34-2. Available from the publisher, Price $95.

Description: This large-format book documents the current nomenclatorial status of more than 3800 species and genus-group names for the Sphingidae. Kitching and Cadiou recognize 203 genera and 1272 species as valid, and include all known available and unavailable synonyms in the checklist. The authors are to be congratulated for their encyclopedic scholarship in updating and correcting sphingid nomenclature and their comprehensive and critical review of the status of species and generic names. Nevertheless, as the authors acknowledge, there is still much work to be done on this charismatic moth family, including a full revision and a thorough phylogenetic analysis.

The book begins with a 34-page introduction containing short sections on morphology of adults and early stages, natural history, economic impact, rarity, and conservation (the authors argue that sphingid species are not necessarily as rare as they may seem). There is a brief sketch of the history of higher-level classification, and a table presenting a partially ordered "current best estimate" classification based on unpublished cladistic analyses by Kitching. This is followed by notes on biogeography, and a description of prior faunal lists and catalogs (some of the most important or recent are Rothschild and Jordan (1903, *A revision of the lepidopterous family Sphingidae*, Novitates Zoologicae, 9 (suppl.):1–972.), Hodges (1971, *Sphingoidea*, Moths of America North of Mexico including Greenland, 21:1–158), d'Abrera (1987, *Sphingidae Mundi, Hawk moths of the world*, E. W. Classey, Farringdon, U.K., 226 pp.), Bridges (1993, *Catalog of the family-group, genus-group and species-group names of the Sphingidae of the world*, C. A. Bridges, Urbana, Ilinois, 282 pp.), Pittaway (1993, *The Hawkmoths of the Western Palaearctic*, Harley Books, Colchester, U.K., 240 pp.), Carcasson and Heppner (1996, *Sphingoidea*, 118, *Sphingidae*. *In* J. B. Heppner, ed., Atlas of Neotropical Lepidoptera, checklist. 4B. Drepanoidea, Bombycoidea, Sphingoidea. Association for Tropical Lepidoptera, Gainesville Florida, pp. 50–60, 62.), Zhu and Wang (1997, *Lepidoptera Sphingidae*. Fauna Sinica (Insecta) 11:1–410) and Danner, Eitschberger and Surholt (1998. *Die Schwärmer der westlichen Palaearktis, Bausteine zu einer Revision (Lepidoptera: Sphingidae)*. Textband. Herbipolania 4(1):1–368; Tafelband. Herbipolania 4(2):1–720). A section on methodology describes the authors' concepts of genus, species and subspecies, and explains their differences of opinion on circumscription of taxa with respect to Danner et al.'s (1998, op.cit.) more finely split treatment of the Palearctic fauna. The introduction ends with instructions on how to interpret abbreviations and annotations to the checklist itself.

The checklist is organized in nested alphabetical order, first by genus, then by species within each genus, then by subspecies within species. Synonyms, infrasubspecific names, and *nomina nuda* are listed beneath the valid species or subspecies name to which they correspond. Author and year of publication are given for each name, and all original descriptions are included in the References Cited section. There are eight good-quality color plates: six illustrate pinned specimens of 48 species (including six holotypes, two paratypes, and two lectotypes), and two show photos of living specimens at rest in the wild. The latter are slightly grainy and the color reproduction seems a bit saturated. The dust jacket is illustrated with rather dark images of five species named after either Cadiou or Kitching which are not reproduced elsewhere in the book.

The bulk of the text comprises 627 nomenclatorial notes. These range from short reports on lectotype designations, transcriptions of data labels and other rather dry taxonomic minutia, to long and sometimes fascinating detective stories surrounding cases of mistaken identity, nomenclatorial squabbles that are reminiscent of Francis Hemming's pronouncements (Hemming 1967, *The generic names of the butterflies and their type-species (Lepidoptera: Rhopalocera)*. Bull. BM(NH) Ent. Suppl. 9:1–509), and philosophical explorations of the ICZN Code (1985, International Commission on Zoological Nomenclature, International Code of Zoological Nomenclature, International Trust for Zoological Nomenclature and the British Museum (Natural History), London.)) and its relation to species concepts.

The book concludes with a comprehensive Literature Cited section, descriptions of two newly-recognized species and two new subspecies, a one-page Addenda section, and good subject and taxonomic indices. Two of the four descriptions of new taxa are nomenclatorial corrections of discrepancies between current concepts and old nominal types, the third gives a differentiated geographical form subspecific status and the last is a previously unrecognized species. Only two of the new taxa are illustrated.

In general, the book seems well-organized and error-free. I noticed only one error (a misnumbered footnote reference), which is quite remarkable given the complex cross-referencing between the checklist and the notes.

Two Criticisms: As the authors state (p. 24), "*Sphingidae Mundi* [d'Abrera 1985, *op.cit.*] remains the only readily available color guide to adult hawkmoths on a global basis . . . and will continue to be used to identify these moths." They justify their checklist as a means to correct the numerous nomenclatorial and identification errors in that work, (as well as a means to forestall entry into the literature of the "almost 1000 errors" in the Bridges' [1993, *op.cit.*] catalog). Although it exhibits impressive scholarly rigor, in my view Kitching and Cadiou's book will not be of much use or interest to the casual reader, or even to the serious amateur, because the practical information it contains is almost completely inaccessible, buried in the midst of a jumble of nomenclatorial notes that are arranged in the alphabetical order of the checklist. For example, suppose you identify a specimen as *Oxyambulyx placida* Moore by comparing it to the pictures in d'Abrera's book. To discover that d'Abrera's specimen was misidentified, you would need to stumble upon Kitching and Cadiou's footnote 56 (to *Ambulyx semiplacida* Inoue), which is not cross-referenced to either the synonym *Oxambulyx* Rothschild & Jordan, nor the species *A. placida* (Moore). Given the authors' acknowledgment of the continuing importance of d'Abrera's book to sphingid workers, two extremely practical sections to have included in Kitching and Cadiou would have been, 1) a concise list of corrigenda to d'Abrera's nomenclature and identifications, and 2) supplemental illustrations of the 200+ taxa d'Abrera excluded from *Sphingidae Mundi*.

A sign of our mercenary times is the Natural History Museum's promotion of what is essentially a rather narrowly-focussed monograph as a trade book. The inclusion of color plates (and of the term, "Illustrated" on the glossy dust jacket) is a lure that will entice many hawkmoth fanciers to buy this book, but I suspect that most of them will find its contents largely impenetrable. Once upon a time, the British Museum (Natural History) published scholarly nomenclatorial works in its Bulletin (e.g., Hemming 1967), and distributed them free of cost. Nowadays, the more revenue-oriented Natural History Museum encourages its systematists to produce marketable products: another recent example is Malcolm Scoble's geometrid catalog (1999. *Geometrid Moths of the World: a catalogue*. CSIRO Publications, Melbourne, 1400 pp., $395). I can think of no better way to prolong the lepidopterological imperialism of wealthy western nations than by publishing catalogs and checklists of global faunas in prohibitively expensive formats that the researchers from countries where most of the taxa occur generally cannot afford. It is onerous enough for Ecuadorean lepidopterists to have to go to London to see the holotypes of Ecuadorean moths. The least the Natural History Museum could do is to give something back to the "type localities" by making the knowledge derived from its holdings accessible at moderate cost, or better yet, free on the WWW.

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CHECKLIST OF THE GEOMETRIDAE (LEPIDOPTERA) OF THE FORMER U.S.S.R., by Jaan Viidalepp. 1996. Published by Apollo Books Aps., Kirkeby Sand 19, DK-5771 Stenstrup, Denmark. 111 pages. Soft cover, 25 × 17 cm., ISBN 87-88757-05-6. Price DKK 200.

This small book is a sequentially numbered annotated distributional checklist of the 1486 species of Geometridae recorded from the former U.S.S.R. and updates Jaan Viidalepp's previous list of 1247 species (1976–1979, *A list of Geometridae (Lepidoptera) of the USSR*. I–IV. Entomol. Obozrenie, 55 (4): 842–852, 56 (3): 564–576, 57 (4): 752–761, 58 (4): 782–798. (in Russian)). This is one of the author's first publications in English.

In a brief forward Viidalepp explains the checklist represents a personal effort to summarize his own fieldwork (1961–1992) and compile information previously published in regional faunas. A list of included geopolitical regions and their corresponding faunistic literature follows. The short reference list includes 39 systematic and faunistic papers published between 1976 and 1996 and 35 of these are in Russian or German. For literature prior to 1976 the reader is referred to the author's previous published list (Viidalepp, *op. cit.*). Following the 83 page checklist, two indices are provided, the first to higher categories, and the second to species group names.

The region covered by *Checklist of the Geometidae of the Former U.S.S.R.* includes the large Russian Federation extending from eastern Europe to the Pacific and north to the Arctic Ocean, the Baltics, Belarus, Ukraine, Moldova, Georgia, Armenia, Azerbaijan, Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, and Uzbekistan. To present distributional information for this vast and politically challenged segment of the world Viidalepp utilizes an unconventional combination of political names and physical geographic features. For Asia in particular emphasis is placed on stable geomorphic features such as mountain ranges. Unfortunately the author does not provide a gazetteer or map to familiarize the reader with this geographically complex region. For many species entries extralimital distributional information is also provided with neighboring states listed when distributions extend outside the territory of the former U.S.S.R. For holarctic species, North America is sometimes included in the extralimital distribution but inconsistently so. Many well known holarctic geometrids such as *Epirrhoe alternata* (Müller), *Rheumaptera (Hydria) undulata* (Linnaeus), and *Ectropis crepuscularia* (Denis and Schiffermüller) as well as palearctic introductions to North America including *Thera juniperata* (Linnaeus), *Operophtera brumata* (Linnaeus), *Pasiphila* [*Rhinoprora* in this list; *Chloroclystis* in North American lists] *rectangulata* (Linnaeus), *Aplocera plagiata* (Linnaeus) and *Hemithea aestivaria* (Hübner) are not acknowledged to occur on the North American continent.

The geometrid fauna Viidalepp treats includes the following subfamilies followed by the number of species listed (the corresponding number of North American species recorded north of Mexico is given second for comparison based on the list compiled by D. C. Ferguson (pp. 88–107 *In* R. W. Hodges et al., 1983, *Check List of the Lepidoptera of America North of Mexico*, E. W. Classey, Ltd., London, England, 284 pp.): Archiearine (4/2), Alsophilinae (Oenochrominae *sensu lato*, part) (14/3), Larentiinae (706/467), Sterrhinae (204/96), Geometrinae (66 / 76), Ennominae (488/760), and Orthostixinae (4/0). At least some of the genera included in the last subfamily by Viidalepp and others might be more appropriately placed in the Ennominae but their placement remains unresolved and they cannot be included in a strict concept of Oenochrominae (see Müller, B., 1996, Geometridae pp. 218–249 *In* O. Karsholt & J. Razowski (eds.), *The Lepidoptera of Europe*, Apollo Books, Stenstrup, Denmark, 380 pp.; and Holloway, J. D., 1996, *The Moths of Borneo Part 9: Family Geometridae, Subfamilies Oenochrominae, Desmobathrinae and Geometrinae*, Malayan Nature Journal 49: 147–326, published by Southdene Sdn. Bhd., Kuala Lumpur, Malaysia). The total geometrid fauna catalogued by Viidalepp (1486 sequentially numbered entries; doubtful records also included within the list but not numbered) is comparable to the total number of geometrid species in North America north of Mexico (1404). However in the Eurasian fauna the subfamilies Larentiinae and Sterrhinae are disproportionately represented as exemplified by 253 species of *Eupithecia* Curtis and 69 species of *Idaea* Treitschke in the Viidalepp list (corresponding figures for North America north of Mexico are 157 and 26 respectively). Although Viidalepp's checklist provides distributional information for each species, an overview of faunistic affinities and biogeographic distributional patterns within Eurasia is not provided.

It is unfortunate Viidalepp does not discuss or more completely reference recent systematic literature. Approximately 200 species group and over 20 generic names listed in the *Checklist of the Geometidae of the Former U.S.S.R* were published since 1970 reflecting considerable recent systematic effort especially in Asian countries. Species group and generic synonymies are incomplete and only selectively provided. Many recent new combinations, new synonymies, status changes, and revivals cannot be traced using this checklist alone. In an attempt to be inclusive, a number of unpublished taxa are listed with notations such as "sp. n. (in print)" [=in press?] and "sp. n. (in prep.)". Even more tentative is larentiine species number 185: "G. nov. sp. n." listed in the tribe Cidariini. The tribe "Hierochthoniini (trib. n.)" appears on page 61 of the list and includes the geometrine genera *Hierochthonia* Prout and *Hissarica* Viidalepp but without description of the new higher category.

In summary the *Checklist of the Geometidae of the Former U.S.S.R* is a distributional list that also serves as an introduction to the geometrid fauna of a large and diverse region. Lepidopterists unfamiliar with the Eurasian fauna and its biogeography can delve further with the aid of the Zoological Record, a good atlas, and the references provided. English speaking geometrid specialists eagerly await additional faunistic and systematic publications treating the Geometridae found within the former U.S.S.R.

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THE MOTHS OF BORNEO, Part 9, Family Geometridae (incl. Orthostixini), subfamilies Oenochrominae, Desmobathrinae, Geometrinae, and Ennominae addenda, by Jeremy Daniel Holloway. 1996. Malayan Nature Journal 49: 147–326. Published in the Malayan Nature Journal and also produced in paper covers by Southdene Sdn. Bhd., Kuala Lumpur, Malaysia. 427 figures, 12 color plates. Soft cover, sewn binding, 17.9 × 25.3 cm., ISBN: 983-99915-3-1. Available from Southdene Sdn. Bhd., P.O. Box 10139, 50704 Kuala Lumpur, Malaysia; Phone: 603-4022-2643; FAX: 603-4022-2267; e-mail: hsbar@pc.jaring.my; website: www.edi.co.uk/barlow; Price $26.00, £18.00 (including surface mail overseas).

THE MOTHS OF BORNEO, Part 10, Family Geometridae, subfamilies Sterrhinae, Larentiinae, and addenda to other subfamilies, by Jeremy Daniel Holloway. 1997. Malayan Nature Journal 51: 1– 242. Published in the Malayan Nature Journal and also produced in paper covers by Southdene Sdn. Bhd., Kuala Lumpur, Malaysia. 608 figures, 12 color plates. Soft cover, sewn binding, 17.9 × 25.3 cm., ISBN: 983-99915-4-1. Available from Southdene Sdn. Bhd., P.O. Box 10139, 50704 Kuala Lumpur, Malaysia; Phone: 603-4022-2643; FAX: 603-4022-2267; e-mail: hsbar@pc.jaring.my; website: www.edi.co.uk/barlow. Price $30.00, £20.00 (including surface mail overseas).

These volumes are the eighth and ninth of an estimated eighteen part series documenting the macrolepidoptera of the second largest non-continental island, Borneo. For the family Geometidae alone this is an ambitious effort. Together with part 11 of the series (Ennominae, published in 1994), a fauna of 1079 species is treated, equivalent to approximately one-quarter of the estimated geometrid fauna in the Oriental region. The author, Jeremy Holloway, has been working on the faunistics and biogeography of Indo-Australian Lepidoptera for decades and in 1995 was awarded the Karl Jordan Medal of the Lepidopterists' Society for his many contributions.

Borneo is an important piece of the large Indo-Australian biogeographic puzzle that has fascinated biogeographers since Alfred Wallace. In a broad sense understanding the fauna of Borneo requires consideration of taxa that range from Africa to Oceanea, and from Australia to the Himalayan region. Holloway's contribution to the higher classification of the Geometridae as outlined in this series extends well beyond the region to the global level as evident in more recent systematic treatments of the family (see Minet, J. & M. J. Scoble, 1999, The Drepanoid / Geometroid Assemblage, pp. 301–320, *In* N. P. Kristensen (ed.), *Handbook of Zoology, Volume IV Arthropoda: Insecta, Part 35 Lepidoptera, Moths and Butterflies, Volume 1: Evolution, Systematics, and Biogeography*, Walter de Gruyter, Berlin and New York, and Scoble, M. J. (ed.), M. S. Parsons, M. R. Honey, L. M. Pitkin, & B. R. Pitkin, 1999, *Geometrid Moths of the World: a Catalogue (Lepidoptera, Geometridae)*, CSIRO Publishing and Apollo Books in association with The Natural History Museum, London, England; Collingwood, Australia and Stenstrup, Denmark, 2 volumes). Of the 1079 species of Geometridae treated in *The Moths of Borneo* series, 17% are newly described, 11% contribute new synonymy, and 4% are revived from synonymy. The lowland forests of Borneo harbor many endemic species and the upper montane forests are rich in endemic Larentiinae, especially the tribe Trichopterygini.

Parts 9 and 10 of *The Moths of Borneo* are similar in format. The introduction of part 9 is a world review of the family group names previously referred to subfamilies Oenochrominae *sensu lato* and Geometrinae as well as a discussion of the classification of these subfamilies. The introduction of part 10 includes a synopsis of the diversity of Bornean Geometridae with analysis of ecological and biogeographic affinities. A brief section offering a tentative classification of the world Geometridae follows. Family group names and subfamily classification are reviewed in the systematic accounts of the Sterrhinae and Larentiinae.

Within the systematic accounts each genus is cited with its author, type species (including type locality), and synonyms. A generic description follows based primarily on adult external features and genitalia. Brief descriptions of the early stages are provided where known (not illustrated except for a few color photos in the plates), larval hosts enumerated, and the geographic distribution of the genus summarized. Particularly for new or revived genera, extralimital taxa are listed as new combinations. Species accounts include synonymy, citation of original descriptions, diagnosis, taxonomic notes, geographical distribution, habitat notes, and where known, biology and larval hosts. Recent systematic and biological literature is often cited and considerable biological information is published here for the first time. The total number of new taxa published in parts 9 and 10 attest to Holloway's effort to document the fauna (22 genera, 108 species, and 3 subspecies). At the conclusion of each part useful appendices include lists of new taxa, new combinations, new synonyms, and status changes and revivals. Finally, a checklist of Bornean taxa is provided and annotated with general distribution and habitat information. The checklists serve as indices to the pages on which species accounts appear, a general index is not provided. The extensive literature cited should appeal to the geometrid bibliophile.

With the exception of the first four figures of part 9 (line drawings of wing venation) and the first two text figures of part 10, all figures are photographs of male and female genitalia. Legends are listed separately in the pages that precede the genitalia figures. The genitalia photographs vary in size and are arranged in a loose "cut and paste" format. Figures are not always sequentially numbered. Quality of the preparations and clarity of the photographs varies. Central structures of the male genital capsule and the female sterigma are not always optimally displayed and aedeagi are often photographed without vesica inflation. All to frequently the aedeagus is not illustrated or only the male genitalia are figured even when female material was available for study. I confess a preference for line drawings of genitalia but this would be prohibitive in a series of this magnitude. Nevertheless, selective use of line drawings can serve to differentiate close taxa as well as illustrate important generic and family group characters. The color plates of both parts are of reasonable quality. For smaller moths photographic enlargement would have enhanced details of maculation. It is difficult to judge color fidelity without specimens for comparison. Some plates of the green geometrids in part 9 appear color shifted toward blue or show reflections (perhaps attributable to scale wear) and many plates of part 10 are dominated by yellow tints. Specimens depicted on the color cover of part 10 appear crisper and show better color balance than photographs of the same specimens on the corresponding plates.

For the remainder of this review I will overview Holloway's contribution to geometrid systematics in *The Moths of Borneo* at the subfamily, generic, and specific levels.

Present higher classification of the Geometridae is far from satisfactory and requires revision on a world basis. While it is accepted that traditional groups such as the Oenochrominae *sensu lato* are unnatural assemblages (see Minet & Scoble 1999, *op. cit.*), satisfactory phylogenetic classification is elusive. Holloway's proposed classification might best be viewed as provisional, and is based largely on similarities of adult structures, especially those of the abdomen. Holloway appreciates that careful comparative study of the early stages is needed to shed further light on geometrid systematics.

In the Bornean fauna, only the robust bodied members of *Sarcinodes* Guenée are included in the Oenochrominae *sensu sticto*. Holloway revives the subfamily name Desmobathrinae to encompass "delicately built 'oenochromine' genera with elongate, slender appendages." This subfamily includes a number of cosmopolitan mostly tropical genera placed in the tribe Desmobathrini and the monobasic Indo-Australian tribe Eumeleini. Two genera, *Heteralex* Warren, and *Naxa* Walker, traditionally referred to Oenochrominae are tentatively transferred to Ennominae with the latter genus (along with *Orthostixis* Hübner) included in the tribe Orthostixini. The larvae of *Naxa* are colonial and known to feed on Oleaceae with the larvae and pupae suspended in extensive silken webs. In part 10 Holloway publishes new biological information *regarding Naxa guttulata* Warren observed feeding on a fern (*Diplazium* sp.); color photographs of the larva and pupa suspended in their silken web are recorded on plate 4. In his review of 'oenochromine' family group names Holloway concludes the Holarctic genus *Alsophila* Hübner should be placed in a separate subfamily, Alsophilinae, a decision accepted by Minet and Scoble (1999, *op. cit.*).

The Geometrinae of Indo-Australia include groups quite unfamiliar to Lepidopterists of the Northern Hemisphere. Holloway retains the robust bodied aposematic moths of the genus *Dysphania* Hübner within the subfamily but emphasizes the distance of this unique group from the remainder of the Geometrinae by dividing the subfamily into two tribes, Dysphaniini and Geometrini. In turn it is proposed, though with some reservation, that all geometrine family groups other than Dysphaniini be assigned as subtribes of Geometrini and given names ending in "-iti". Many genera of Bornean Geometrini are robust bodied moths with falcate forewings or gray and brown moths with boarmiine facies.

A number of Bornean Sterrhinae should be more familiar to northern Lepidopterists with the genera *Scopula* Schrank, *Idaea* Treitschke, and *Cyclophora* Hübner well represented. Holloway reviews evidence for viewing the sterrhines as two broad lineages (Timandrini / Cosymbinii and Scopulini / Sterrhini / Rhodostrophiini) based on characters of both the adult and early stages. He further argues for inclusion of the Neotropical tribe Cyllopodini in the latter lineage, and places the Old World tribe Rhodometrini in the former, at least in his phylogenetic diagram (Part 10, Fig. 2).

Given the absence of many recognized tribes of Larentiinae in the tropics, Holloway's discussion of higher classification of this subfamily is less inclusive. It is suggested that the Trichopterygini may represent a sister group for the remainder of the Larentiinae. Four Australian and Oriental larentiine genera (two newly described by

Holloway) cannot be placed in presently recognized tribes indicative of the unsettled state of higher classification for the subfamily.

On the generic level, Holloway's revisionary work establishes a large number of new combinations and many new genera. As pointed out by Scoble et al. (1999, *op.cit.*), restricting the definition of previously large and overly inclusive genera such as the larentiine genus *Chloroclystis* Hübner based on study of a regional fauna may strand unstudied extralimital taxa not corresponding to new generic concepts. Holloway both revived and erected new genera in his treatment of *Chloroclystis sensu lato* and reassigned many Indo-Australian species. Some reassignments are hasty and seem premature. For example, eight species are formally transferred to the larentiine genus *Bosara* Walker without study of the genitalia even though Holloway admits final placement awaits confirmation by dissection. A number of unplaced species now reside in the provisional genus "*Chloroclystis*" of the Scoble, et al. (1999, *op.cit.*) catalog.

At the species level, documenting the macro-fauna of a diverse tropical landmass such as Borneo is daunting but Holloway pulls off a commando performance. Many factors contribute to the difficult task of determining specific limits including allopatry in the insular realm of Indo-Australia, lack of sufficient study material, ambiguous association of sexes, and inadequate old descriptions. Holloway acknowledges that some treatments are provisional. To identify species considerable reliance is placed on brief diagnoses and discussion of similar species. Keys to genera and species are not provided even though this would certainly aid in the sorting and recognition of taxa especially for speciose groups. For many species only the male genitalia or the male genital capsule are illustrated. A number of new species and genera are described in the absence of description and illustration or even mention of the male aedeagus. This frequently occurs in the green geometrids. Even if the aedeagus lacks diagnostic characters, that fact should be demonstrated.

Access to the enviable store of type material in The Natural History Museum, London, and other European museums has enabled Holloway to place many Indo-Australian taxa and recognize undescribed species. Although synonymies are listed for each species, useful type information such as type locality, repository, condition, sex, and lectotype designation is frequently lacking. Unless otherwise noted, holotypes of species described in *The Moths of Borneo* are deposited in The Natural History Museum.

Holloway rejects the stipulation of the Code of Zoological Nomenclature that requires species group names to agree in gender with genus group names and gives all specific names the orthography of the original description. This convention is also adopted in the Scoble catalog for the geometrid fauna of the world, a convenience that I sincerely hope will become standard practice.

I cannot overstress the ambitious nature of the project Jeremy Holloway has undertaken. Borneo harbors a geometrid fauna equal to 77% of the number of species known from America north of Mexico, a fauna better understood as a consequence of Holloway's studies. Lepidopterists interested in the faunistics, biogeography, and biology of Indo-Australian Lepidoptera will want to add *The Moths of Borneo* to their library. The parts treating the Geometridae are of particular value to geometrid specialists worldwide and will inform and inspire future systematic efforts.

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NOTICE TO CONTRIBUTORS

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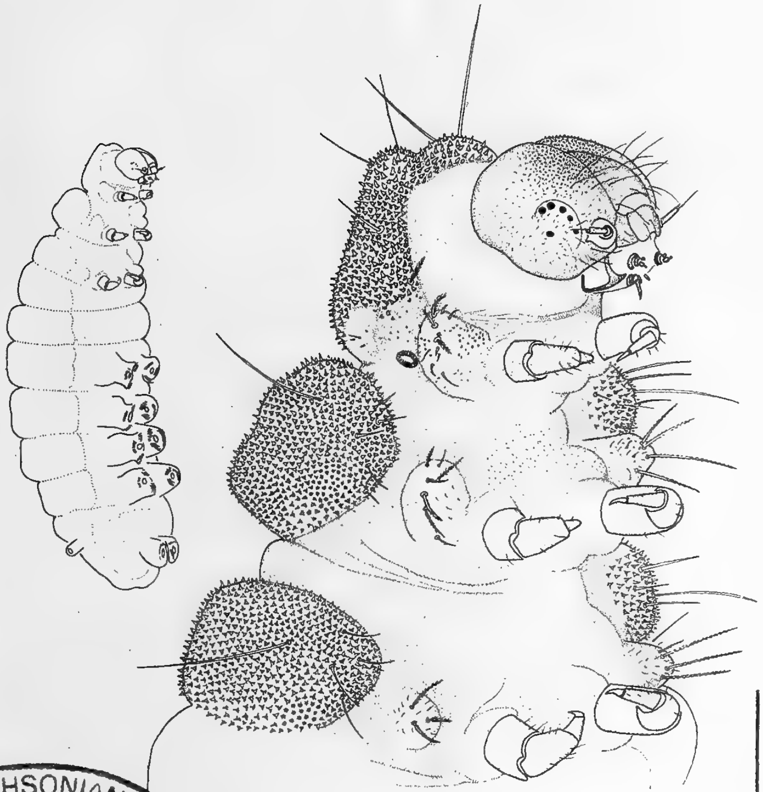

10 December 2001

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Cover illustration: *Alesa amesis* (Riodinidae), fifth instar, detail of the thorax with an insert showing entire larva. Scale line = 1 mm. This species is from Ecuador, Sucumbios, Garza Cocha. Drawing by C. M. Penz.

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IMMATURE STAGES OF THE MARBLED UNDERWING, *CATOCALA MARMORATA* (NOCTUIDAE)

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ABSTRACT. The immature stages of *C. marmorata* are described and illustrated for the first time, along with biological and foodplant notes.

Additional key words: underwing moths, Indiana, life history, *Populus heterophylla*.

The Marbled Underwing, *Catocala marmorata* Edwards 1864, is generally an uncommon species whose present center of distribution is the central and south central United States east of the Mississippi River (Fig. 1d). Historically, the range of *C. marmorata* extended somewhat farther to the north, as far as southern New England (open circles in Fig. 1d; see Holland 1903, Barnes & McDunnough 1918, Sargent 1976), but the species has not been recorded from these localities in the past 50 years, and the reasons for its apparent range contraction remain unknown.

We are not aware of any previously published information on the early stages or larval foodplant(s) for *C. marmorata*. The foodplant has long been suspected to be willow (*Salix*) or poplar (*Populus*) (Salicaceae), based on the external morphology and wing pattern of the adults. In his recent studies on this species, Willis (1991) was unable to obtain viable ova from numerous captive females, even from one female that was kept alive for 81 days. He dissected 40 females that died in captivity, and concluded that females may not regularly oviposit until September or October, which is six to eight weeks after their emergence in the field.

Here we report on the successful rearing of *C. marmorata*, from ova deposited by a wild-caught female from southern Indiana, and offer suggestions on a potential wild larval foodplant for this species.

REARING NOTES

Ova were secured from a worn female *C. marmorata* collected at a baited tree at 2300 CST on 11 September 1994, in Point Twp., Posey Co., Indiana. The habitat is mesic lowland flatwoods, with internal swamps of two types: (1) buttonbush (*Cephalanthus occidentalis* L.) (Rubiaceae), cypress (*Taxodium distichum* L. (Richaud)) (Taxodiaceae), and swamp cottonwood (*Populus heterophylla* L.); and (2) overcup oak (*Quercus lyrata* Walt.) (Fagaceae) and swamp cottonwood. The female was confined in a large grocery bag (17.8 × 30.5 × 43.2 cm) on a shaded porch at outside ambient temperature (15–30°C). She was offered a 20% sucrose solution daily on a small piece of sponge; a new sponge piece with solution was provided every other day. The female moth lived until 4 October 1994 (24 days), during which time she deposited 404 ova on the sides and bottom of the bag, and on the sponges. Ova were removed daily and placed onto filter paper in empty plastic film containers, and slightly moistened every 2–3 days. Ova were overwintered in the film containers at ambient outside temperatures (–2 to 10°C) until 23 January 1995, when they were transferred to a refrigerator and kept at 5°C until April 1995. Refrigerated ova were removed and misted lightly once every two weeks before being returned to cold storage.

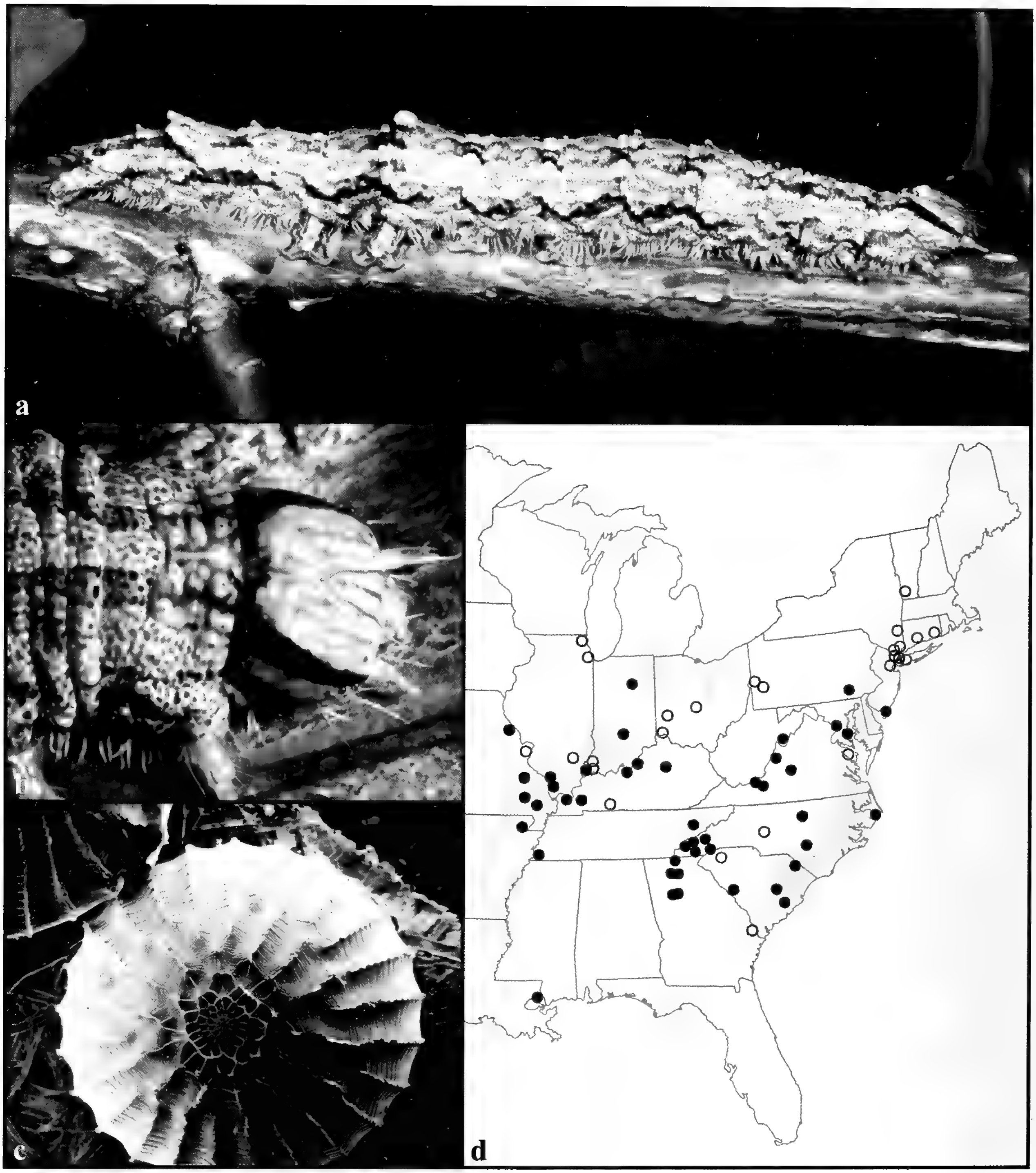

FIG. 1. Immature stages and distribution of *Catocala marmorata*. **a,** lateral view of 5th (last) instar larva. **b,** closeup of head capsule of 5th instar larva. **c,** dorsal view of egg as revealed by scanning electron microscopy (60×). **d,** distribution of *C. marmorata* in North America; open circles, pre-1950 records; filled circles, post-1950 records; each circle represents a county in which the species has been recorded; shading represents distribution of *Populus heterophylla* (after Little 1977 and McCormac 1993).

On 13 and 27 April 1995, batches of ova were removed from the refrigerator and held at 22°C. First instar larvae began emerging 13–19 days after the ova were removed from the refrigerator. A total of only 23 of 404 ova survived winter storage to produce larvae. The duration between 5% and 95% total first instar emergence from a single clutch of eggs, a measure to assess hatch synchronization as it pertains to life history strategies of *Catocala* (D. F. Schweitzer & L. F. Gall, unpubl. data), was 4 days for this clutch. Newly emerged larvae were placed individually in petri dishes on moistened filter paper, and presented with fresh leaves of sandbar willow (*Salix exigua* Nutt.) and cottonwood (*Populus deltoides* Bartr.). Although no precise data were kept, the larvae appeared to eat both foods equally well, and their development was comparable on both plants, with little apparent difference in the duration of larval instars and pupae, or adult size. The larvae were reared indoors at 20–24°C through the fourth instar using fresh cut foliage that was collected daily. Most of the ultimate (5th) instar larvae were placed in fine-mesh nylon sleeves on field grown willow or cottonwood saplings to complete development. Thirteen of the original 23 larvae survived to the adult stage. The average duration for each stage was as follows: ova, 15 days; 1st instar, 4 days; 2nd instar, 4.5 days; 3rd instar, 4.7 days; 4th instar, 5 days; 5th instar, 7.6 days; pupa, 26.1 days. A description of the mature larva is as follows:

5th (final) instar larva. Fig. 1a, b. Length 9 cm; head capsule width 4 mm; body color light mousy brown tinged with pink; dorsal tubercles pink; spiracles pinkish brown; finely dispersed black to brown specks forming interrupted but nearly complete dorsal and lateral lines along length of body, most apparent in the vicinity of the dorsal tubercles; 5th abdominal segment with slightly elevated, 2 mm wide transverse protuberance, slightly lighter than body color, with a lateral "saddle patch" slightly darker brown than body color, all lines formed by specks being darker and more prominent on this segment; 8th abdominal segment with a pair of ventrally projecting, 2 mm long tubercles; lateral filaments present along entire length of body, pink, dense, 1–2 mm in length, simple (not bifurcate or multifurcate); ventral surface of body segments dirty pink, with black spots on each abdominal segment, edged and overlayed with orange on 4th through 7th abdominal segments; capitad surface of head capsule flattened but not strongly produced addorsally, with two 1–2 mm wide, dark, nearly continuous lateral stripes from antennae to dorsal margins; antennae and true legs pinkish; setae on head capsule and body pinkish, sparse.

On 16 September 1996, two additional female *C. marmorata* were captured at the Posey Co. site, and confined for ova. The protocols for handling these females and their ova and larvae were largely as described above. These two females together laid several hundred ova, with subsequent first instar hatches again of only several dozen larvae. Measures of hatch synchronization for first instar larvae from these broods were 6 and 12 days, respectively. Larvae of each brood were reared indoors successfully on *Populus deltoides.*

DISCUSSION

It is unlikely that either of the laboratory foodplants, *Populus deltoides* and *Salix exigua,* is the wild larval foodplant of *C. marmorata* at the Indiana site. *S. exigua* was not located anywhere in the area where the adult females were taken, and *P. deltoides* occurs only rarely in the general vicinity, and then not in close proximity to the female collection site. However, both black willow, *S. nigra* Marsh, and swamp cottonwood, *P. heterophylla,* occur within 200 m of the female collection site. *S. nigra* is common and widely distributed in the eastern United States, as is *P. deltoides,* and both of their geographic ranges greatly exceed that of *C. marmorata.* The indeterminate foliating schedule of *S. nigra* leaves is considerably longer than that of most *Populus* species, and the egg hatch synchronization measures of 4, 6, and 12 for *C. marmorata* are comparable to *Catocala* species that are known to use the more determinate-foliating *Populus* as opposed to *Salix* as their principal wild larval foodplants (D. F. Schweitzer & L. F. Gall, unpubl. data). During 1995 and 1996, many adult *C. marmorata,* particularly females in September, rested in close proximity to *P. heterophylla* trees at the Indiana site, and the overall geographic range of *P. heterophylla* better approximates that of *C. marmorata* (Fig. 1d; but note this tree is not present in the central Appalachian Mountains). These facts suggest that *P. heterophylla* is more plausible than either *S. nigra* or *P. deltoides* as a possible wild foodplant.

Adult *C. marmorata* were fairly common at the Indiana site in 1995, with a total of 18 moths observed in 48 hours, both on baited trees and in bait traps at night, and on tree trunks during daylight hours. On warm days, adults were seen resting head up from 0.5 to 2 m above the ground on the trunks of large, gray-barked trees, especially overcup oak (*Quercus lyrata*). These observations accord well with those of Willis (1991), who collected most of his *C. marmorata* by tapping large trees with light-colored bark, including white oak (*Q. alba* L.), red oak (*Q. rubrum* L.), maple (*Acer* spp.) (Aceraceae), hickory (*Carya* spp.) (Juglandaceae), white pine (*Pinus strobus* L.) (Pinaceae) and tulip poplar (*Liriodendron tulipifera* L.) (Magnoliaceae). Although both Holland (1903) and Sargent (1976) considered *C. marmorata* "rare," and Covell (1984) considered it "uncommon to rare," Willis (1991) is more probably correct in describing the species as "not as rare as sometimes implied . . . but rather . . . [with] a somewhat localized distribution."

We suspect our success in obtaining viable ova was in part the result of utilizing female *C. marmorata* collected late in the season. It is possible that female *C. marmorata* mate many weeks after emergence, and/or undergo a period of reproductive diapause from the time of initial emergence in July and August, as is true for some western willow-poplar feeding *Catocala* species (D. C. Hawks, pers. comm.). Irrespective, our poor success at obtaining hatchable *C. marmorata* eggs contrasts sharply with the more typical 90–100% hatching success with most other *Catocala* species, and suggests that at least some aspects of the handling and/or overwintering biology of *C. marmorata* remain incompletely understood.

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This study was facilitated by the generous assistance of John Shuey who introduced JWP to the Indiana site. Both he and Tom Carr helped with the collection of female moths. Valerie Giles and David Wagner provided the larval photographs, and John Furlough (Ohio State Museum of Biological Diversity) identified the *Salix exigua*.

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TAXONOMIC CLARIFICATION OF *NOTOCELIA ROSAECOLANA* (DOUBLEDAY) AND *N. TRIMACULANA* (HAWORTH) (TORTRICIDAE)

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ABSTRACT. The strikingly similar Old World olethreutines *Notocelia rosaecolana* (Doubleday) and *N. trimaculana* (Haworth) have long been differentiated with seven structural and wing-pattern characters. Because these characters are quantitative and difficult to apply, it is unclear whether one or both taxa were accidentally introduced into North America. We evaluate the seven characters by examining each one (y) relative to forewing length (x), a surrogate for body size, in a basic sample of 60 specimens of both taxa from two continents, using the allometric equation $y = a(x^b)$. All seven characters proved to be body-size dependent and to lack discontinuities necessary for discrete states, thus rendering them diagnostically inadequate. Fortunately, a new qualitative diagnostic character emerged from this study: presence or absence of melanic sex scales near the base of the male hindwing hair pencil. These scales were absent in the putative type of *N. trimaculana* but present in those of *N. rosaecolana*, thus clarifying species identities and showing that *N. rosaecolana* is the only member of the pair thus far present in North America.

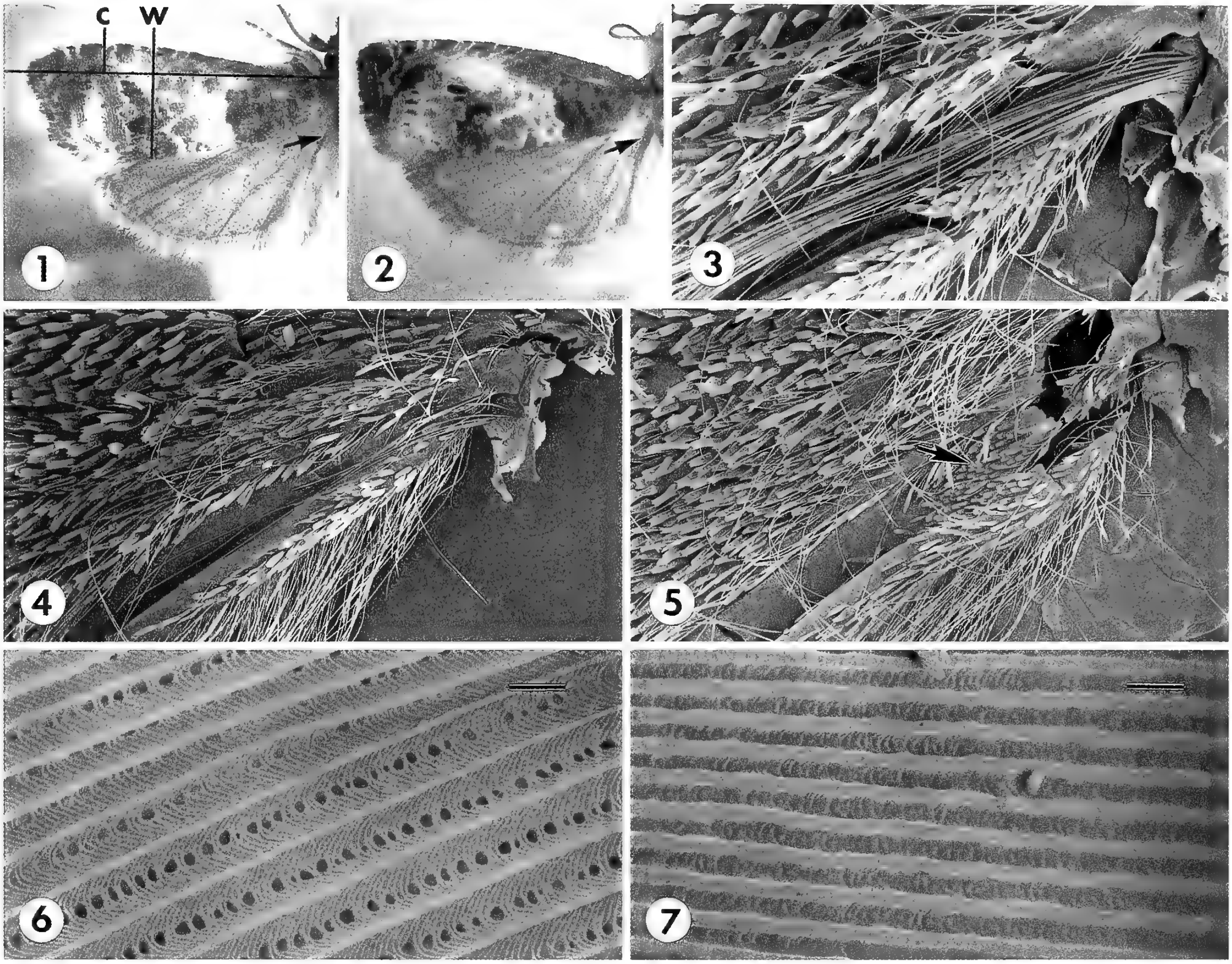
Additional key words: Olethreutinae, allometry, body size, Rosaceae, nitrogen.

Although strikingly similar, the olethreutines *Notocelia rosaecolana* (Doubleday 1850) and *N. trimaculana* (Haworth 1811) are considered separate entities in the Old World (Benander 1950, Bentinck & Diakonoff 1968, Bradley et al. 1979, Hannemann 1961, Kuznetsov 1987, Nasu 1980, Obraztsov 1965, Razowski 1987, Van Deurs 1956). The similarity, which encompasses genitalia as well as wing pattern, is acknowledged by most authors, with Hannemann (1961) adding that the taxa cannot be separated with certainty. Wing patterns (Figs. 1, 2) demonstrate the diagnostic difficulty, the illustrated specimens having been reliably identified by a newly discovered qualitative structural character introduced later in this paper.

The close similarity of these taxa has posed a problem in North America because it is unclear whether one or both are invading immigrants. The first American record is Kearfott's (1910) report from New Jersey of what he called *Eucosma suffusana* ([Lienig &] Zeller), a junior synonym of *Notocelia trimaculana*. This and subsequent specimen records were verified or reported by Brown (1973), Heinrich (1923), and Procter (1946). Later, Bradley et al. (1979) asserted that *N. rosaecolana* is the correct name for the taxon in North America. Their claim presumably rests on the fact that the reported larval foodplant in North America is *Rosa* (Rosaceae) (Ferguson 1975, Heinrich 1923, Kearfott 1910), which is the foodplant of putative *N. rosaecolana* in Eurasia. Doubleday (1850) described this species from specimens that developed on *Rosa*, probably the same specimens Douglas (1849) reared shortly before. In announcing the discovery of putative *N. rosaecolana* in Quebec, Landry (1995) used the nomenclature of Bradley et al. (1979), but suggested that both taxa might be present in North America.

The adult characters purported in the past to differentiate the two taxa are quantitative, and hence potentially ambiguous. These traditional characters consist of four structural and three wing-pattern traits. The states of these characters diagnosing *N. rosaecolana* and *N. trimaculana*, respectively, are: (1) strong vs. weak forewing costal curvature; (2) more vs. less obliqueness of forewing costal strigulae; (3) more (5–7) vs. fewer (4–5) pairs of forewing costal strigulae; (4) male forewing costal fold two-fifths of forewing length vs. one-half; (5) wide vs. narrow forewing width; (6) lighter vs. darker forewing coloration; (7) long and narrow vs. short and broad male socii (Benander 1950, Bentinck & Diakonoff 1968, Bradley et al. 1979, Hannemann 1961, Kuznetsov 1987, Nasu 1980, Razowski 1987, Van Deurs 1956). The *N. rosaecolana* states of characters (1), (2), and (6) were noted in the original description (Doubleday 1850). States of an eighth quantitative structural character mentioned by Bentinck and Diakonoff (1968)—thickness of male valval neck—contradict their illustrations, so this character is not considered further here.

The above sources give range of wing span or forewing length for both taxa as body size indicators.



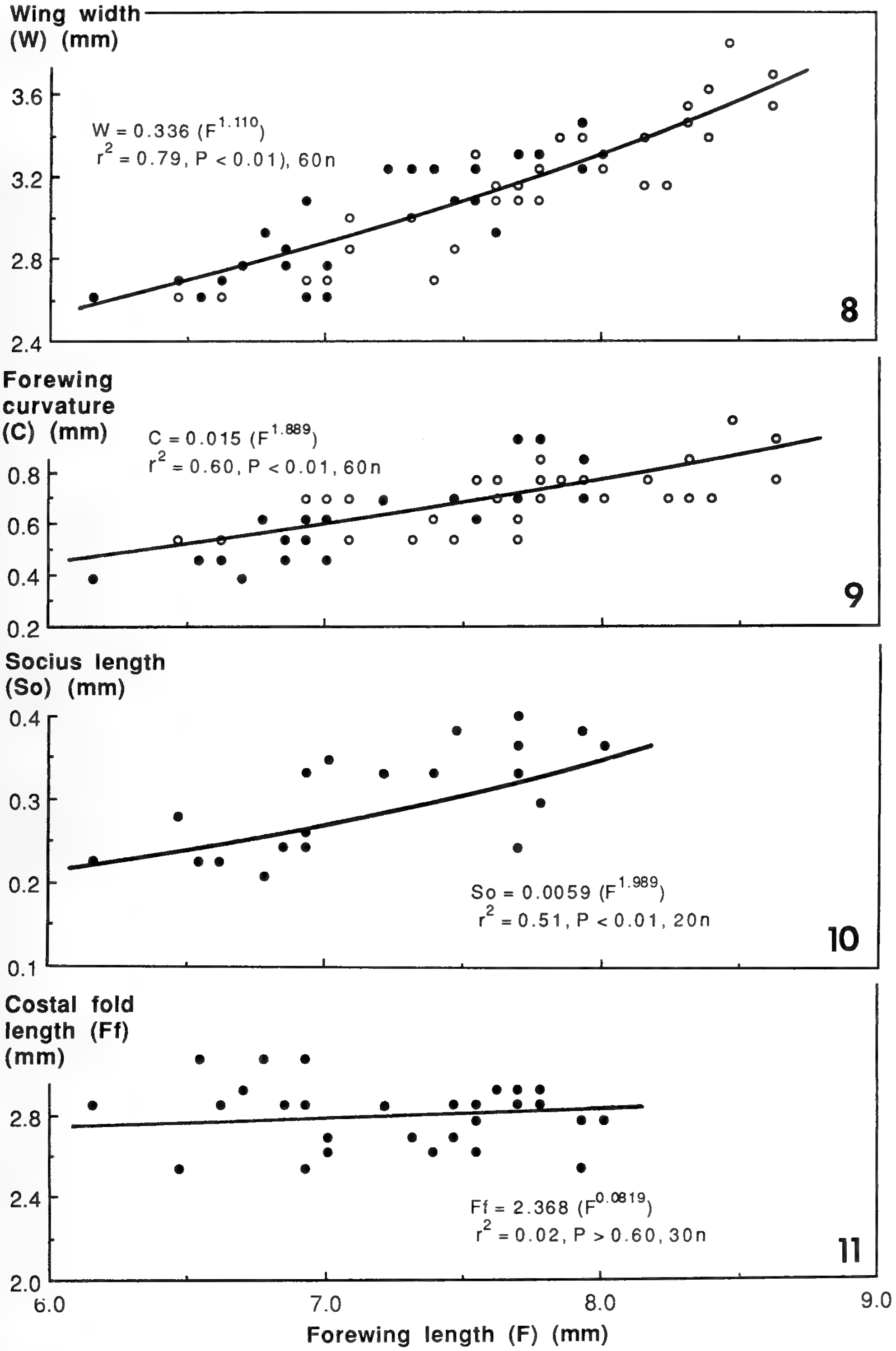
FIGS. 1–7. *Notocelia* wings and wing details. 1, *N. rosaecolana* male from St. Johns, Newfoundland (CNC) showing where forewing width (W) and curvature (C) were measured. Arrow points to barely visible hindwing anal fold containing hair pencil. Melanic sex scales, not visible, are present near base of the hair pencil. Forewing length 7.7 mm. 2, *N. trimaculana* male from "England" (Hodgkinson Coll., No. 54698) (BMNH). Arrow points to barely visible hindwing anal fold containing hair pencil. Melanic sex scales are absent near base of the hair pencil. Forewing length 6.9 mm. 3, Hair pencil in hindwing anal fold of male *N. trimaculana* from "Germany" (MEM), with melanic sex scales absent near the base of the hair pencil. 4, Hindwing anal fold of male *N. trimaculana* from "Germany" (MEM) with hair pencil removed to show absence of melanic sex scales. 5, Hindwing anal fold of male *N. rosaecolana* from Ithaca, NY (MEM) with hair pencil removed to show presence of melanic sex scales (arrow). Blackness of melanic sex scales is not evident in scanning electron micrographs. 6, Surface of normal scale adjacent to hindwing anal fold and hair pencil of male *N. rosaecolana* from Ithaca, NY (MEM). Bar = 2 microns. 7, Surface of melanic sex scale in anal fold beneath hair pencil of male *N. rosaecolana* from Ithaca, NY (MEM). Bar = 2 microns.

There is fairly close agreement in forewing length among the sources after spans are converted to lengths by an empirically derived equation (Miller 1977). The resulting ranges for putative *N. trimaculana* and putative *N. rosaecolana* are, respectively, 6.8–8.3 mm, and 7.3–9.1 mm. The larger body size of *N. rosaecolana* was noted in its original description (Doubleday 1850).

None of the seven traditional characters has been shown to be independent of body size. If characters are body-size dependent without discontinuities, they may erroneously appear to assume dichotomous states at different ends of the body-size spectrum, more so if they are positively allometric relative to body size. We examine the seven characters with respect to body size to decide whether they are sufficient for differentiating *N. rosaecolana* and *N. trimaculana.* Also, we introduce and elucidate a new qualitative structural character that for the first time clearly differentiates the taxa.

MATERIALS AND METHODS

We gathered data on the seven traditional characters from 60 pinned specimens of combined *N. rosaecolana* and *N. trimaculana,* half male and half female, which are referred to as the basic sample. To



FIGS. 8–11. Relations of structural character measurements to forewing length in 30 females and 19–30 males of combined *N. trimaculana*-*N. rosaecolana*. 8, Wing width. 9, Forewing curvature. 10, Socius length. 11, Costal fold length. Solid circles are males, hollow circles females. Some points represent more than one observation.

avoid accidentally including closely related taxa such as *N. roborana* (Denis & Schiffermüller), we used only pristine specimens with well preserved wing patterns. Using standard procedures, we made genitalia preparations of nearly half of the basic sample. To count presence and absence of melanic scaling associated with the male hindwing hair pencil—the new character—and to measure respective forewing lengths, we more than quadrupled the number of males in the basic sample, creating what is referred to as the augmented sample. Specimens of the basic sample originated in the U.K., France, Germany, the U.S. (Connecticut, Maryland, Massachusetts, Michigan, New Jersey, New York, Pennsylvania, Vermont), and Canada (Newfoundland, Ontario, Quebec); specimens of the augmented sample had the same origins plus Japan. We labeled each specimen of the basic sample "Voucher, Miller-Brown-Tuck 2001."

To gather character data from specimens, we measured dimensions, and categorized wing patterns, as follows: (1) Forewing width of both sexes in mm at W in Fig. 1; (2) Forewing curvature of both sexes measured in mm from costal edge at C in Fig. 1 to the perpendicular reference line; (3) Male socius length in mm from tip to cleft at the uncus; (4) Male forewing costal fold length in mm; (5) Number of pairs of strigulae in one forewing of females only, as the costal fold interfered with counting such strigulae in males; (6) Maximum slant of female forewing costal strigulae scored subjectively from 1 for slight to 4 for extreme; (7) Proportion of white or near white in the forewings of both sexes estimated subjectively to the nearest 10%.

We measured maximum length of one forewing as a surrogate for body size, including fringe and excluding tegula. Forewing length is a sensitive and reliable index of body size, with body mass in olethreutine adults increasing approximately as the cube of forewing length (Miller 1977). In the basic sample, using an ocular micrometer, we measured wing variables to the nearest 0.08 mm at nominal 10.5× magnification, and socius length to the nearest 0.02 mm at nominal 45× magnification. In the augmented sample, we measured wing length to the nearest 0.5 mm with a ruler.

To examine character measurements (y) relative to forewing length (x), we used the power or nonlinear form of the allometric equation, $y = a(x^b)$, where a and b are parameters (Smith 1980). We obtained parameter values using the Quasi-Newton method of estimation for nonlinear models (SYSTAT 1992). Because r^2 values in SYSTAT nonlinear output are rounded to one decimal place (nearest 10%), we obtained more precise r^2 values with the exponential regression option of StatWorks (Rafferty et al. 1985), which produced trend lines virtually identical to those of the allometric equation. We used absolute male forewing costal-fold length in the analysis rather than fold/wing length ratio to avoid the statistical complication of fold length appearing on both sides of the equation.

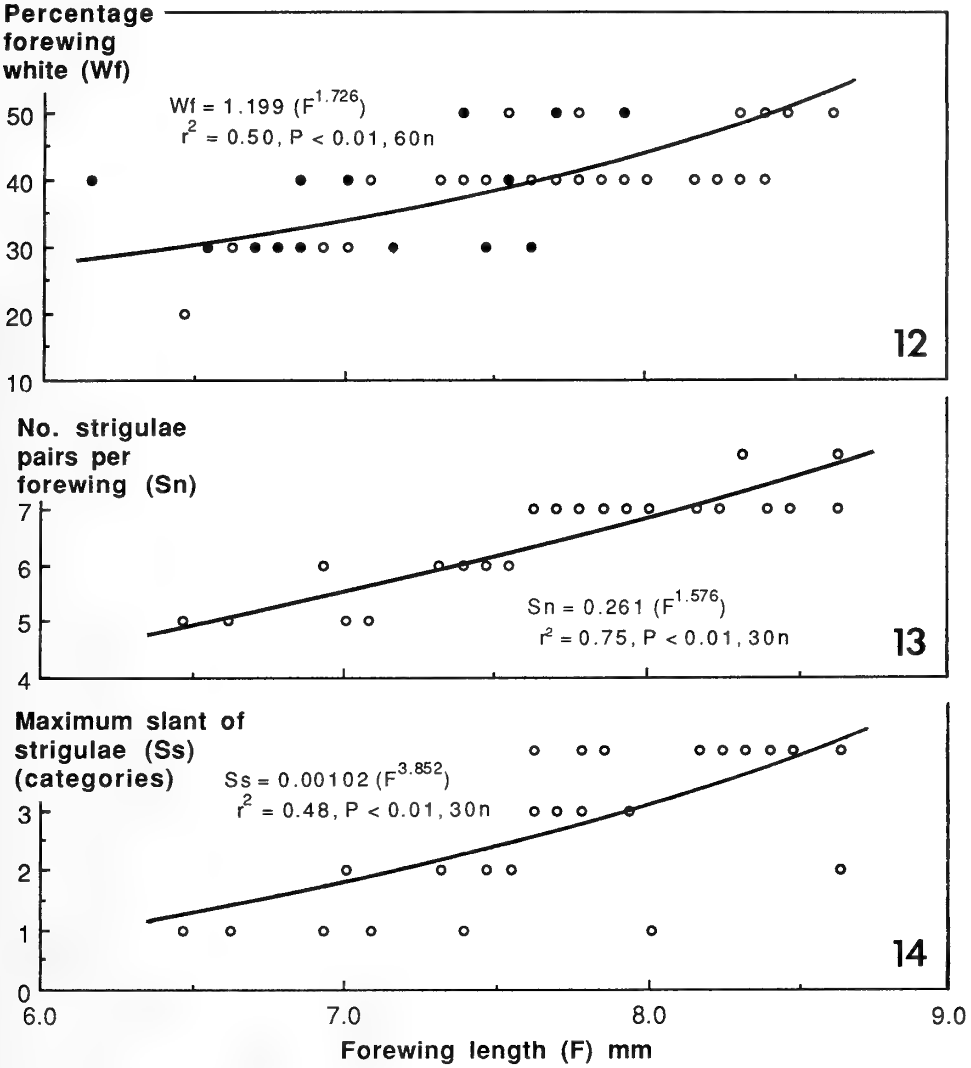
Male hindwing anal folds and associated structures were photographed with a LEO S 360 scanning electron microscope at an acceleration voltage of 15.0 kV. Specimen preparation for scanning electron microscopy followed Adamski and Brown (1987).

Museum and collection abbreviations are as follows: AMNH, American Museum of Natural History, New York, NY; BL, collection of B. Landry, Ottawa, ON; BMNH, Natural History Museum, London, UK; CAES, Connecticut Agricultural Experiment Station, New Haven, CT; CMP, Carnegie Museum, Pittsburgh, PA; CNC, Canadian National Collection, Ottawa, ON; JDG collection of J. D. Glaser, Baltimore, MD; LDG, collection of L. D. Gibson, Florence, KY; MEM, Mississippi Entomological Museum, Mississippi State, MS; MNHP, Muséum National d'Histoire Naturelle, Paris, France; UMC, University of Missouri, Columbia, MO; UMSP, University of Minnesota Entomology Museum, St. Paul, MN; USNM, National Museum of Natural History, Washington, DC; WDA, Washington State Dept. of Agriculture, Olympia, WA.

RESULTS

All seven traditional characters proved to be body-size dependent in their expressions, and to lack discontinuities necessary for discrete character states (Figs. 8–14). The size dependency of three structural characters—forewing width, forewing curvature, and male socius length—is direct, with forewing length explaining from 51 to 79% of character variability (Figs. 8–10). The size dependency of the remaining structural character, length of male forewing costal fold, is indirect; fold length is stable at a mean 2.8 mm regardless of forewing length (Fig. 11). Thus relative fold length is greater at shorter forewing lengths, and less at longer forewing lengths. Toward the shorter end at 6.5 mm of forewing length, the costal fold/wing length ratio is 0.43 (2.8 / 6.5 = 0.43)—near that for putative *N. trimaculana*—whereas toward the longer end at 8.0 mm of forewing length, the ratio is 0.35 (2.8 / 8.0 = 0.35)—near that for putative *N. rosaecolana*. In all the wing pattern characters, body-size dependency is direct, with forewing length explaining from 48 to 75% of character variability (Figs. 12–14). There were no pronounced sexual differences in characters measured on both sexes (Figs. 8, 9, 12).

Allometry is evident in several characters. Allometry refers to the numerical change in one body part or



FIGS. 12–14. Relations of scale pattern character measurements to forewing length in 30 females and 30 males of combined *N. trimaculana-N. rosaecolana*. 12, Percentage forewing white. 13, No. strigulae pairs per forewing. 14, Maximum slant of strigulae. Solid circles are males, hollow circles females. Some points represent more than one observation.

character relative to that in overall body size or in another body part or character (Smith 1980). If the exponent b in the allometric equation is >1, positive allometry is indicated; if it is <1, negative allometry is indicated; and if it is ≈1, isometry is indicated. Thus wing width, with a rounded exponent of 1.1, is essentially isometric (Fig. 8). Forewing curvature, male socius length, and number of pairs of forewing strigulae, with rounded exponents of 1.9, 2.0, and 1.6, respectively, are positively allometric (Figs. 9, 10, 13). Length of male costal fold, with a rounded exponent of 0.08, is negatively allometric (Fig. 11). Percentage forewing white (Fig. 12) and maximum slant of forewing strigulae (Fig. 14) may also exhibit positive allometry, but less definitely so because these variables were arbitrarily scaled. Allometry increases the apparent contrast in character states at opposite ends of the body-size spectrum. Incidentally, the visual impact of some of these relations is reduced because their vertical axes were compressed for economy of reproduction.

In contrast to the traditional characters, all seven of which are quantitative, the new diagnostic character discovered during this study is qualitative. It consists of melanic scales which are possessed by one taxon but not the other. When present, these scales occur in a fold between hindwing vein 3A and the anal wing margin near the base of a hair pencil lying in the fold (Figs. 3–5). The scales are assumed to have a sexual function.

The hair pencils of both species are similar except for their bases, the base appearing thicker and darker when the melanic scales are present. Hair pencil coloration ranges from brown to black in each species, perhaps depending on degree of exposure to light and fading. In the basic sample, the melanic sex scales were present in 10 males, and absent in the remaining 20.

In both species, ordinary scales on either side of the fold in which the hair pencil lies exhibit definable fenestrae, cross ribs, and scutes on longitudinal ridges (Fig. 6) and are similar to ordinary wing scales in the anal and cubital regions of other olethreutines (Brown & Miller 1983). In contrast, the melanic sex scales are coated with a substance that can be seen extruding from some fenestrae (Fig. 7). Similar coatings on melanic sex scales in males of the olethreutine *Cydia caryana* (Fitch) are removable by solvents, and have been postulated to be accreted glandular scent components (Brown & Miller 1983). The melanic sex scales reported here could be important in isolating males of one *Notocelia* species from females of the other.

The ability to separate males based on the new character enabled us to verify more subtle differences between the two taxa. We believe the following character states apply more often than not, and that they may be useful for separating females until a qualitative diagnostic character emerges for them: The forewing pattern is more precisely defined in *N. trimaculana*, with the dark markings having more definite boundaries than in *N. rosaecolana;* the forewing apex is more acute in *N. trimaculana*, and the apical scales more reddish brown than in *N. rosaecolana;* and the transverse silvery bars of the forewing ocellus are closer together in *N. trimaculana* than in *N. rosaecolana.*

Based on the augmented sample, the mean, computed standard deviation, and range of forewing lengths of males with and without melanic sex scales are, respectively, 7.9 ± 0.5 mm (6.5–9 mm) ($n = 76$) and 7.3 ± 0.5 mm (6–8.5 mm) ($n = 59$). Despite a broad overlap, the mean difference, 0.6 mm, is highly significant ($P < 0.001$, Student *t*-test).

In the basic sample, range in forewing length (6.1–8.6 mm) ($n = 60$) is similar to that published for the combined taxa (6.8–9.1 mm). Range interval of forewing length (higher range limit minus lower range limit) in the basic sample ($8.6 - 6.1 = 2.5$ mm) is likewise similar to that published for the combined taxa ($9.1 - 6.8 = 2.3$ mm). In the augmented sample, forewing length range (6–9 mm) and range interval ($9 - 6 = 3$ mm) ($n = 135$) are similar to the corresponding published values for the combined taxa (6.8–9.1 mm and 2.3 mm).

The new diagnostic character begs a review of names currently used for the two species. Presence or absence of melanic sex scales should enable species identities to be clearly established from the respective male primary type specimens. Besides *trimaculana* Haworth, 1811, and *rosaecolana* Doubleday, 1850, the name *suffusana* Duponchel (1843) is used instead of *trimaculana* by some modern authors apparently because Obraztsov (1965) considered *trimaculana* of Haworth to be a misidentification. Further complicating matters, the name *suffusana* was known for many years in collections as "*suffusana* Kuhlwein." Kuhlwein never published the name even though credited as the author by [Lienig &] Zeller (1846) who also reported *Crataegus* as its foodplant. The name *suffusana* [Lienig &] Zeller was originally used for the taxon introduced into North America, but *suffusana* [Lienig &] Zeller is a junior homonym of *suffusana* Duponchel. In addition, *suffusana* [Lienig &] Zeller is inferred to be a junior synonym of *trimaculana* Haworth because of the *Crataegus* rather than *Rosa* foodplant, and the liklihood that Duponchel also used Kuhlwein's name for his *suffusana.*

According to Horn et al. (1935–37), the collections of Haworth and Doubleday are in BMNH, and that of Duponchel in MNHP. Searches of those collections did indeed reveal male examples presumably used in describing the three taxa. Specimens of such vintage are usually considered types, in the present case a holotype each for *trimaculana* Haworth and *suffusana* Duponchel, and several syntypes of *rosaecolana* Doubleday. These examples of *trimaculana* and *suffusana* were found to lack melanic sex scales, while those of *rosaecolana* had them.

The present known North American distribution by states and provinces of the taxon possessing the melanic sex scales—*N. rosaecolana*—is Alabama, Connecticut, Delaware, Kentucky, Maine, Maryland, Massachusetts, Michigan, Missouri, New Jersey, New York, Newfoundland, Nova Scotia, Ohio, Ontario, Pennsylvania, Quebec, Tennessee, Vermont, Virginia, Washington state, and West Virginia (AMNH, BL, CAES, CMP, CNC, JDG, LDG, MEM, UMC, UMSP, USNM, WDA). None of our North American male specimens lacked the melanic sex scales ($n = 49$).

DISCUSSION

The demonstration that all seven traditional characters used to distinguish *N. rosaecolana* and *N. trimaculana* are governed by body size, and that they lack discontinuities with change in body size, renders them inadequate for diagnostic use. Analogous situations have been demonstrated in other olethreutine genera, such as *Endothenia* (Miller 1983) and *Epiblema* (Miller & Pogue 1984). As for the larvae, Swatschek (1958) does not explicitly differentiate *N. rosaecolana* and *N. trimaculana*, but his key separates them by head color. MacKay (1959), however, considered head color a dubious diagnostic character for olethreutine larvae. Comparisons of forewing length range and range interval of study specimens with published values for the two taxa show that body size in the study specimens is representative.

Were it not for the new qualitative diagnostic character discovered during this study, results of the analysis of the seven traditional characters would cast doubt on whether *N. rosaecolana* and *N. trimaculana* are in fact different species. Although the new character distinguishes males only, it is sufficient to confirm that the two taxa are indeed separate entities. Females thus far cannot be reliably diagnosed, but certain wing characters verified in males enable tentative separation of some females.

The difference in mean body size between the taxa may be explainable by foodplant differences. Larvae of both are said to feed on terminal foliage of their respective foodplants: *N. rosaecolana* on the shrub genus *Rosa,* and *N. trimaculana* on the arboreal genera *Crataegus, Prunus,* and *Pyrus* (Rosaceae) (Benander 1950, Bradley et al. 1979, Hannemann 1961, Kuznetsov 1987, Nasu 1980, Razowski 1987, Swatschek 1958, Van Deurs 1956). These four plant genera differ in foliar nutrient quality. Nitrogen concentration in foodplant tissues is positively linked to growth in phytophagous insects (Mattson & Scriber 1987). Concentrations of foliar nitrogen in the three arboreal genera range from 1.7 to 2.9%, with one high outlier at 3.4% (Blinn & Buckner 1989, Cannon et al. 1960, Chase & Young 1978, Gerloff et al. 1964, Henry 1972, Vang-Petersen 1973). In contrast, concentrations of foliar nitrogen in the shrub genus *Rosa* under regimes of cultivation and fertilization range from about 3.0 to 5.6%, with one low outlier at 2.2% (Armitage & Tsujita 1979, Di Benedetto et al. 1995, Johansson 1979a, 1979b). Thus the foliage of cultivated *Rosa* can often be a third or more richer in nitrogen than the foliage of the arboreal foodplant genera. Significantly, Bradley et al. (1979) state that in the U.K., the larger bodied *N. rosaecolana* occurs especially on cultivated roses. Interestingly, elevated foliar nitrogen in *Rosa* may be an artifact of cultivation because foliar nitrogen reported for wild *Rosa* ranges from 1.5 to 2.2% (Henry 1972)—essentially the same as for the arboreal genera. Thus the body size difference between the two *Notocelia* taxa could also be an artifact.

Five reared adults available to us approximated body size expectations. All North American in origin, two males and two females developed on *Rosa* (CAES, USNM). These range in forewing length from 7.0 to 8.2 mm, which places them among the largest two-thirds of the basic sample. Both males possess the melanic sex scales of *N. rosaecolana.* The fifth specimen developed on *Robinia pseudoacacia* L. (Leguminosae) (CAES), which constitutes a new foodplant record for the *N. rosaecolana-trimaculana* group. This adult, which cannot be identified with certainty because it is a female, measures 7.4 mm in forewing length, and thus also falls among the largest two-thirds of the basic sample. Foliar nitrogen values for *Robinia* range from 3.1 to 4.0% (Blinn & Buckner 1989, Day & Monk 1977), which is in the foliar nitrogen range of cultivated *Rosa.*

Results of examining the putative types for melanic sex scales confirm the currently prevailing nomenclature of the two species, while clearly making *suffusana* Duponchel a junior synonym of *trimaculana* Haworth. The results also show that males of the invading species in North America are *N. rosaecolana* rather than *N. trimaculana.* Of course, the absence thus far of *N. trimaculana* males in North America makes it likely that North American females of the complex are also *N. rosaecolana.*

In conclusion, we would underscore that invalidating traditional but unreliable diagnostic characters can have the positive effect of fostering fruitful searches for new and strong diagnostic characters.

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THE GENUS *HYPOPHYLLA* BOISDUVAL, 1836 (RIODINIDAE) WITH DESCRIPTIONS OF NEW TAXA

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ABSTRACT. The genus *Hypophylla* Boisduval, 1836 is reinstated as the genus of a monophyletic group of riodinid butterflies previously included in the genus *Calospila* Geyer, 1832. Two new species, *Hypophylla caldensis*, **n. sp.** and *Hypophylla idae*, **n. sp.** are described from Colombia. Additional taxa included in the genus *Hypophylla* are *H. zeurippa* Boisduval, 1836; *H. lasthenes* (Hewitson, 1870), **reinst. stat., n. comb.**; *H. flora* (Staudinger, 1887), **n. comb.**; *H. martia* (Godman, 1903), *n. comb.; H. sudias* (Hewitson, [1858]), **n. comb.**; *H. sudias callaghani* (Constantino and Salazar), 1998, **n. comb., n. stat.**; and *H. argenissa* (Stoll, [1790]) **n. comb.** Notes are provided on the habitats, distribution, behavior, systematics of individual species, as well as keys for the determination of both males and females.

Additional key words: Trans-Andean region, México, Guatemala, Honduras, Nicaragua, Costa Rica, Panamá, Colombia, perching behavior, morphology.

Over the many years in which I have been studying the riodinids of the inter-Andean valleys and western coastal regions of Colombia, I collected a number of specimens of the genus *Calospila,* two of which I recognized as being undescribed taxa. My interest thus having been aroused, I examined other similar species of the genus *Calospila.* My conclusion was that these taxa form a distinct monophyletic group that belongs to the genus *Hypophylla* Boisduval. The purpose of this review is to 1) re-describe the genus *Hypophylla* Boisduval, 2) present morphological and biological information on each species comprising the genus and near relatives, 3) describe two new species in the genus, and 4) provide a key to the identification of both males and females.

MATERIALS AND METHODS

During course of the study I examined material at the Museo de la Universidad de Caldas, Manizales, Colombia, the Musée National d'Histoire Natural, Paris (MNHN), the Universidad Nacional Autonoma de México (MZFC), the collections of Dr. Schmidt-Mumm, Bogotá, and Dr. Francisco Delgado of Santiago, Veraguas, Panamá (FD) and of myself (CJC). I studied the relevant type material at the British Museum (Natural History), and the Humboldt Universitat, Berlin. I examined 167 specimens and made 46 genitalia preparations. Measurements were made with an ocular micrometer and calipers. Reference to wing cells and veins follows the Comstock-Needham system in Miller (1969) and the genitalia terminology is from Klots (1970). My field trips in Colombia, Costa Rica and Panamá over a 25 year period provided data on the habitats and adult habits of *Hypophylla.*

HYPOPHYLLA Boisduval, 1836, **reinstated genus**

Type species. *Hypophylla zeurippa* Boisduval, 1836
Description. Male (Figs 26, 27)—Average Fw length = 16.5 mm. Forewing costa slightly curved to apex, apex slightly falcate, distal margin slightly convex; hindwing with costa straight, distal margin rounded. Venation (Fig. 6), forewing with 4 radial veins, R1 and R2 branching before, and R3 after the discal cell, and Cu1 branching before. On the hindwing Rs branches before and Cu1 at the end of the discal cell, Vein 3A extends to the tornus. Dorsal surface wing ground color reddish-brown. Forewing costal margin dark brown to apex, wing dull purple from middle of cell to apex and to tornus, rest of wing reddish-brown; a reddish-brown line at end of discal cell and two more inside with two additional black lines in cell Cu2–1A+2A below; an irregular median band of connected reddish-brown spots reaches from the costa to Cu1, then is displaced basad such that it is closer to the cell, reaching 1A+2A; a submarginal black band extends from the apex to the inner margin, widest from costa to M3; fringe black. Hindwing reddish-brown above 1A+2A and anal margin light grey, and distal margin from tornus to Cu1 dark yellow-orange, fringe black. Some specimens have variable blue scaling at apex. Maculation includes a black spot on the costa, with a black line at end and two within the discal cell, and two more below in cell Cu2–1A+2A, median band of unconnected spots, one on costa slightly offset basad from next 4 in a straight row to Cu1, then two more offset basad to 1A+2A. Long hair-like scales are scattered in cell Cu2–2A. Ventral surface ground color dark grey-brown with black markings. Forewing with black markings as on dorsal surface. Hindwing pattern same as dorsal surface, but with a faint submarginal band reaching from apex to tornus, distad of which is a row of faint spots between the veins, those at the apex and tornus with more extensive variable black scaling.

Head, thorax, abdomen dark reddish-brown dorsad, uniform white scaling ventrad, antennae brown, ventrad with white scales between sections, club weak; orbit white, frontoclypeus white ventrad, with light brown scaling above; labial palpi (Fig. 1) dark brown, with short, dense scaling, last segment 0.32 of second, protruding beyond face when viewed dorsally. Forelegs (Fig. 3) white, with coxa thin and wedge-shaped, trochanter branching off slightly more than half way to the tip, tarsus unimerous; middle (Fig. 4) and hind legs with a tibial spur and a group of 3 spines on distal tip of tarsal segments.

Genitalia (Fig. 8)—Uncus deeply bifurcated and lobes rounded; vinculum narrow, widening medially, broad at base, connected to wide, spade-like saccus; valvae as two caudad projecting rounded processes, connected with a broad transtilla which has two long, thin caudad projecting processes, the right side (looking cephalad) longer; pedicel squared caudad; bifurcated process on transtilla short, reaching slightly beyond the end of the aedeagus; aedeagus pointed with one cornuti; posterior edge of 8th sternite slightly bifurcated.

Female (Figs. 28, 29)—Average forewing length 15.5 mm. Forewing height to length 1:1.44. Dorsal surface wing ground color light brown with ventral maculation appearing through. Forewing with 3.0 mm wide uneven pale yellow band reaching from costa almost to tornus, enclosing a variable spot of brown scaling at anal angle, band slightly jagged at end of cell. Ventral surface forewing apical area dark brown, bordered basad by pale yellow area

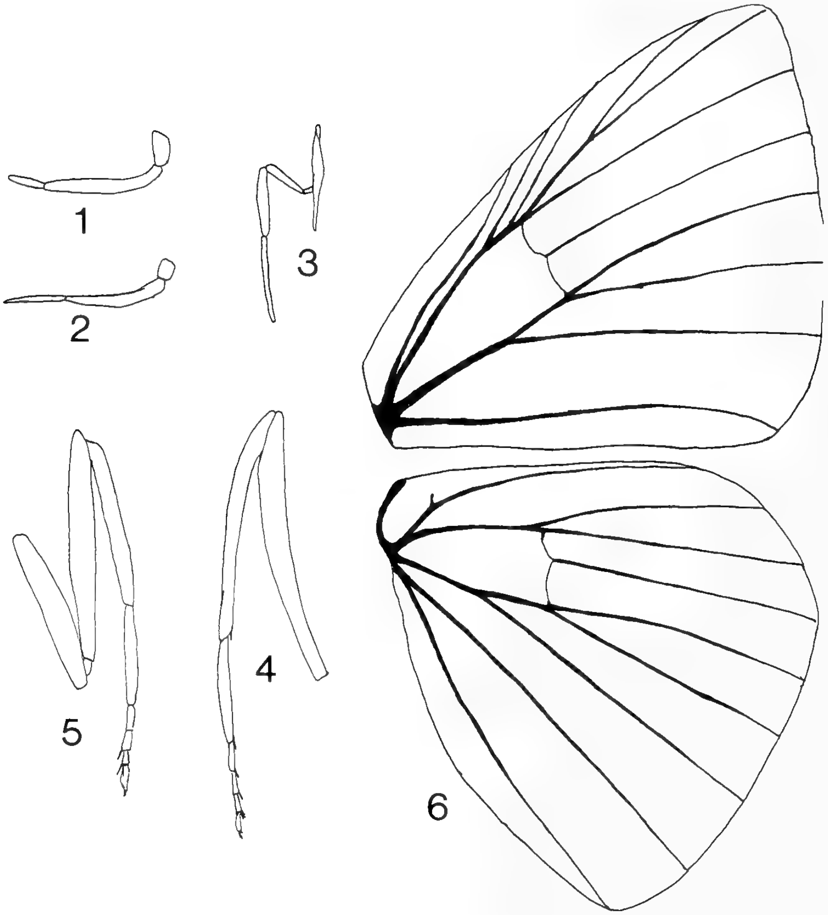


Fig. 1. Male palpi. Fig. 2. Female palpi. Fig. 3. Male foreleg. Fig. 4. Male middle leg. Fig. 5. Female foreleg. Fig. 6. Venation of *Hypophylla.*

corresponding to dorsal band, which extends along costa to base and stops slightly short of tornus. Submedian to base lighter grey-brown with brown maculation corresponding to that of male. Hindwing grey-brown, darker on submarginal area with same maculation as male.

Head, thorax and abdomen dark brown dorsad, white scaling ventrad; frons white basad, labial palpi (Fig. 2) dimorphic, longer than male, third segment 0.62 of second. Forelegs (Fig. 2) normal.

Genitalia (Fig. 18)—Papillae anales blade-like, rounded, setose, with a small point between lobes; ostium bursae opening as a wide funnel with the top folded dorsad and a small sclerotized ridge, ductus seminalis joins at the left side of the base, looking ventrad; corpus bursae with the signa as two slightly invaginated sclerotized patches.

Systematics: Most of the species proposed for the genus *Hypophylla* were originally described in the genus *Lemonias.* In his revision of that genus, Stichel (1911) resurrected the genus *Polystichtis* (Hubner 1816) for these and other butterflies, with the genus type being *Lemonias parthaon* (Dalman 1823). As the name *Polystichtis* was invalid as a subjective junior synonym of *Emesis* Fabricius, 1807, Hemming (1967) placed these butterflies under the next available name, *Calospila* Geyer, 1832.

As defined by Stichel, the genus *Calospila* includes at least two morphologically distinct groups; a section of species related to *C. parthaon,* the type of *Calospila* (including *C. gygas* (Stichel 1911) and *C. zeanger* (Stoll 1790)), and part of another section called the Argenissiforms by Stichel (1911), containing the species in this study. *Hypophylla* is related to *Calospila,* with which it shares venation (which probably led Stichel to include both under *Polystichtis*), sexually dimorphic labial palpi, and the slightly indented eighth abdominal sternite in the male.

Morphological synapomorphies which support the monophyly of *Hypophylla* are 1) the long, thin asymmetric posterior projecting processes of the transtilla of the male genitalia, 2) the branching of the ductus seminalis from the left side of the base of the ductus bursae of the female genitalia, 3) the formation of the opening of the ostium bursae which is folded over as a thin short membrane and with a variable internal flange, and 4) the signa in the corpus bursae as two slightly invaginated round sclerotized patches in all but one species.

In addition to the foregoing, the members of *Hypophylla* can be separated from those of *Calospila* by the general structure of the ostium bursae (compare Figs. 17 and 18), the separation of the male valvae and the male pedicel which is uniform and not inflated at the base (compare Figs. 7 and 8). Superficially, members of *Hypophylla* may be recognized by their generally larger size, dull blue coloration on the male dorsal forewing and orange-yellow at the tornus and submarginal areas of the hindwing.

Among the Stichel's Argenissiforms, there are two that do not belong. *Calospila candace* H. Druce (1904), from southeast Brazil, is a typical *Calospila,* as I verified through examination of the male and female genitalia. The other is *Calospila fannia* (Godman 1903), which is likewise a *Calospila.* (J. Hall, pers. comm.).

The male, and, especially female, genitalia show consistent phenotypic variation and are a good basis for the separation of species.

Important characters in the male include the shape of the uncus, shape of the valvae and caudad projecting process on the transtilla, shape of the pedicel, rami and the adeagus. In females, important characters include the shape of the ostium bursae, position of the ductus seminalis and the signa in the corpus bursae.

With the changes and new species proposed in this review, the following synonymic list summarizes the classification of *Hypophylla:*

HYPOPHYLLA Boisduval, 1836
zeurippa zeurippa Boisduval, 1836,
  eumedes Doubleday, 1847, nom. nud.
lasthenes (Hewitson, 1870), **reinst. stat., n. comb.**
martia (Godman, 1903), **n. comb.**
caldensis Callaghan, **n. species**
flora (Staudinger, 1887), **n. comb.**
idea Callaghan, **n. species**
sudias sudias (Hewitson, [1858]), **n. comb.**
  sudias callaghani (Constantino and Salazar), 1998, **n. comb., n. stat.**
argenissa (Stoll, [1790]), **n. comb.**
    petronius (Fabricius, 1793)
    staudingeri (Godman, 1903)

ECOLOGY AND BEHAVIOR

Distribution and habitat. Members of *Hypophylla* exclusively inhabit the transandean region, from México (Chihuahua, Guerrero, Chiapas, Oaxaca, Veracruz) through Central America to Colombia (Cordillera Oriental, west slope to the Pacific coast) and western Ecuador. The genus is not recorded from the eastern (Amazonian) slope of the Cordillera Oriental. It shows its greatest radiation in Colombia, with six species recorded. Four species are found in Costa Rica (DeVries 1997) and southern Nicaragua, while two are found in Mexico, and one in Ecuador (J. Hall, pers. comm.). The assertion in Seitz (1917) that it is found in Venezuela needs verification. In the MNHN in Paris there is a typical *H. lasthenes* male from "Surinam", which I suspect is a mislabelling.

The majority of the species inhabit tropical lowland Tropical Humid Forest and Very Wet Humid forests (Holdridge 1947) below 900 m. Two species in Colombia are found in Premontane Humid Forest zone in the Coffee belt, between 900 and 1800 m.

Wing pattern and predation. The males of all species but one have bright yellow patches on the distal hindwing to attract predators to that part of their anatomy, as suggested by captured specimens with beak-bite marks on the hindwing. Females mimic day flying moths with a yellow band on the forewing, particularly Geometridae (Laurentiinae, Sterrhinae) and Arctiidae (Lithosiinae) (DeVries 1997; pers obs.)

Mating behavior. All species of *Hypophylla* use perching as mate locating behavior. Perch localities as well as male behavior differ among species. The males of six taxa perch inside woods edges, streams or treefalls, resting with outspread wings on ventral leaf surfaces, and three, *H. caldensis, H. sudias callaghani* and *H. idae* I found exclusively on hilltops, resting on the dorsal leaf surfaces (Fig. 52). When disturbed, all species fly with a rapid, loping flight similar to *Eurybia,* or a satyrid, returning shortly to their original perches. When not perching, both sexes rest under leaves with the wings flat.

SPECIES ACCOUNTS

Hypophylla zeurippa Boisduval, 1836
(Figs. 26, 27, 28, 29)

eumedes Doubleday, 1847, nom. nud.

Hypopylla zeurippa was described from a male from Mexico and as the type of the genus *Hypophylla* . Boisduval's type was discovered in the British Museum (Natural History) by Dr. Gerardo Lamas. The specimen is similar to the *H. zeurippa* population from the Pacific coast (Guerrero), which is distinct from the southern and gulf coast populations.

Diagnosis. The similarity of the male genitalia place *H. zeurippa* in a group comprising *H. martia, H. lasthenes* and *H. caldensis.* In fact, I initially considered these four to be conspecific. However, the distinct female genitalia and consistently different wing patterns and coloration, and lack of intergrades, as well as *H. lathenes* and *H. martia* being sympatric in Costa Rica and Panamá, convinced me otherwise. The males of *H. zeurippa* are easily distinguished by the dark orange color of the uniform submarginal band on the hind wing (in some individuals it may be entirely lacking) coupled with the weak markings on the ventral surface. The females have a narrow yellow subapical band on the forewing, a characteristic shared with *H. martia;* however they may be separated by the post median row of spots between Rs and Cu1 ventral hindwing being in a straight line. *H. zeurippa* male specimens from Guerrero have more extensive blue on the forewing, and a wider yellow forewing band on the females.

Range. *Hypophylla zeurippa* ranges from Mexico (Colima, Guerrero, Veracruz) south through Guatemala, Honduras, Belize to central Nicaragua(?).

Material examined. MÉXICO: 1 ♂ Santa Marta, Oaxaca, 500 m, 1 June 1970 (CJC); 8 ♂♂ 1♀ Candelaria, Loxiche, Oaxaca, 500 m, 10 Aug.,(CJC); 2 ♂♂ same locality, Aug. Oct. 1988 (MZFC); 2 ♂♂ Chacalapilla, Candelaria, Loxiche, Oaxaca, 24 July 1990, (MZFC); 10♂♂,7♀♀ Las Parotas, Atoyac de Alvarez, Guerrero, 25 Oct. 1985; 11 Sept. 1988, 20 Jan. 1987, 25 Nov. 1985, 4 May 1985, 25 Oct. 1985, 11 Sept. 1985, (MZFC); 8♂♂, 8♀♀ Río Santiago, Atoyac de Alvarez, Guerrero, 20 March 1987, 10 Sept. 1985, 6 July 1985, 23 Oct. 1985, 9 July 1985, 26 Nov. 1985, 22 July 1984, 23 Oct. 1985, 28 July 1984, 25 July 1984, 5 May 1985, 8 Aug. 1985, (MZFC); 1♂ Camino a Tonina, Ocosingo, Chiapas, 14 July 1991, (MZFC); 1♀ Ojo de Agua, Madrid, Tecoman, Colima, 29 Oct. 1982 (MZFC); Baden de Neixpa, Lazaro Cadenas, Michoacan, 15 Feb. 1996, (MZFC); 1♂ Metates San Miguel Aloapam, Oaxaca, Aug. 1991, (MZFC); GUATEMALA: 1♂ Guatemala, (MNHN).

Hypophylla lasthenes (Hewitson, 1870)
(Figs. 30, 31, 32, 33)

Hewitson described *Lemonias lasthenes* from a male from Chontales, Nicaragua. Godman and Salvin (1886) extended its range to Costa Rica and Panamá, and Stichel (1911) placed this taxon as a subspecies of *Polystichtis zeurippa.* Some confusion exists regarding the type. The specimen in the British Museum (Natural History) bearing the type label from "Chontales" is typical of southern Mexican specimens of *H. zeurippa.* Comparison of this specimen with the original description suggests that it is not the type, especially with reference to the size of the orange spot on the dorsal hindwing. It is possible that both phenotypes occurred at Chontales, but is impossible to verify as forest habitat there no longer exists.

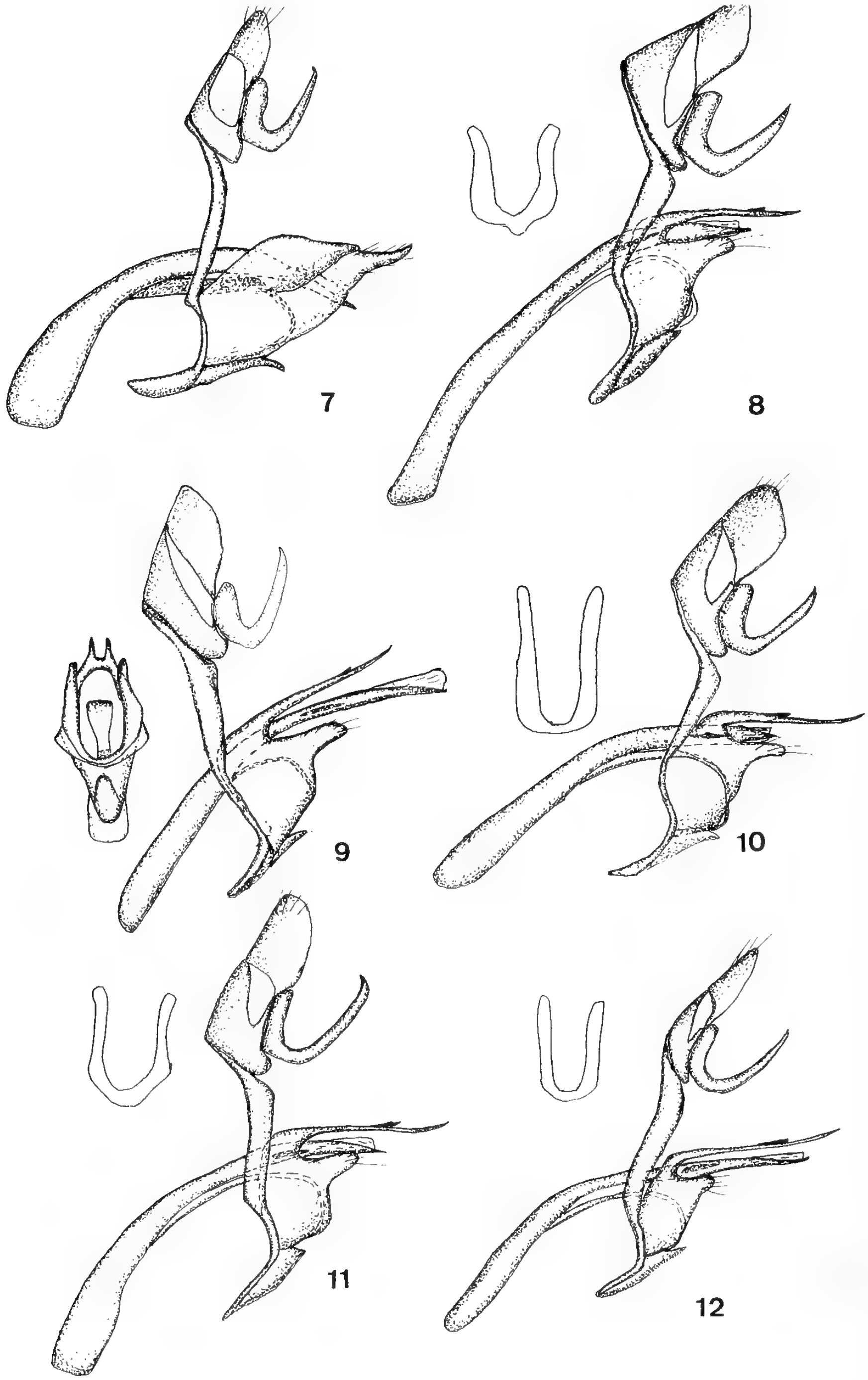


FIG. 7. *Calospila parthaon*, male genitalia. FIG. 8. *Hypophylla zeurippa*, male genitalia. FIG. 9. *Hypophylla lasthenes*, male genitalia. FIG. 10. *Hypophylla martia*, male genitalia. FIG. 11. *Hypophylla caldensis*, male genitalia. FIG. 12. *Hypophylla flora*, male genitalia.

Diagnosis. A comparison of *H. zeurippa* and *H. lasthenes* suggests that they are separate species. Their populations are apparently allopatric with no intergrades, the male genitalia are similar, but *H. lasthenes* has more parallel and longer valvae (Fig. 9). The female genitalia of *H. lasthenes* (Fig. 19) have the ductus bursae more swollen and a sclerotized patch opposite the base of the ductus seminalis. Superficially, *H. lasthenes* males are separated from *H. zeurippa* and *H. martia* by the wider, more rounded and more brightly colored orange patch on the hindwing that extends from M2 to the inner margin, with a wavy basal edge. The ground color is lighter, the maculation bolder on the ventral surface, and the females have a wider, more even forewing band.

Material examined. COSTA RICA: 1♂, 2♀♀ Chilamate, 100 m, Heredia, 30 June 1992, leg. Callaghan. (CJC); PANAMÁ: 1♂, 2♀♀ Colón, Puerto Bello, Rio Cuango, 26 April 1991, 1 Aug. 1991 leg. Delgado (FD); 2 ♂♂, 6♀♀ Colón, Coclesito, 50 m, 9 Sept. 1988,

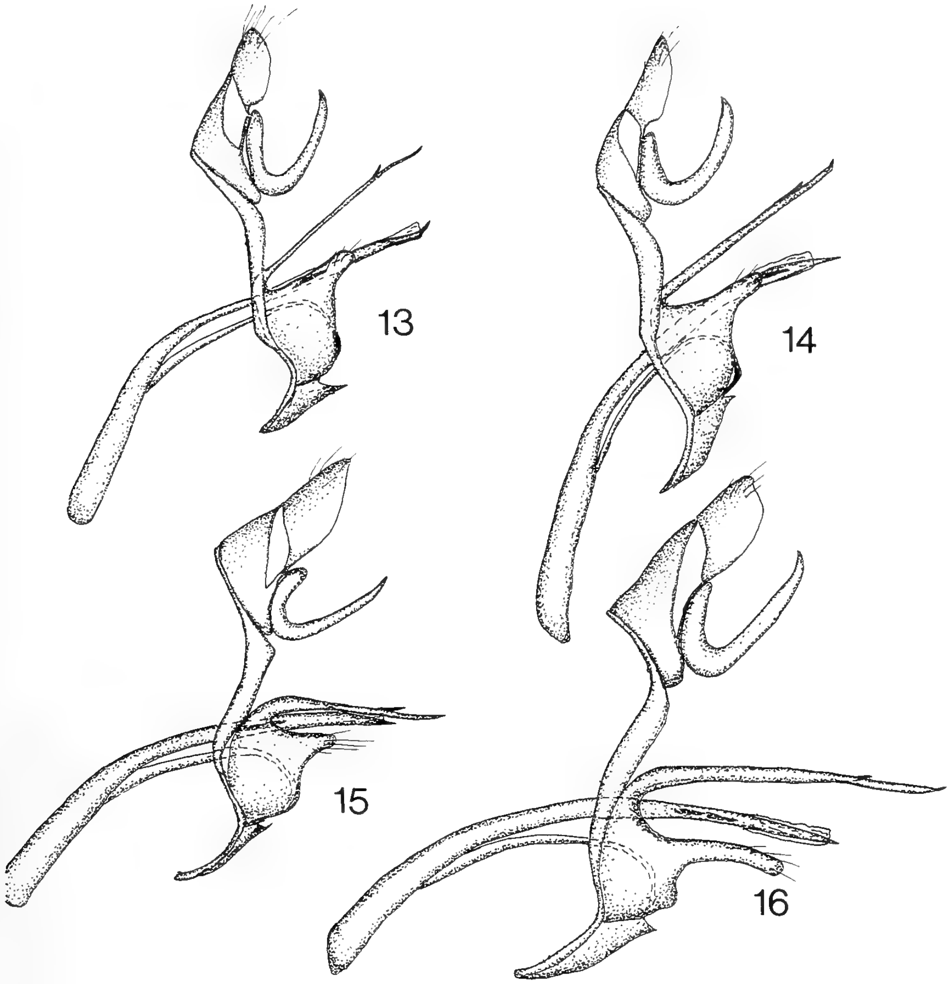


FIG. 13. *Hypophylla idae,* male genitalia. FIG. 14. *Hypophylla sudias callaghani,* male genitalia. FIG. 15. *Hypophylla sudias sudias,* male genitalia. FIG. 16. *Hypophylla argenissa,* male genitalia.

4 Sept.1988, 13 Jan. 1989, 22 Feb. 1989, 18 March 1994, 16 June 1988, leg. Delgado (FD); 1♂ Santa Fé, Belém, 13 March 1987, leg. Delgado (FD); 1♀ Alto de Piedra, Santa Fé de Veraguas, 28 Sept. 1989, leg. Delgado, (FD); 1♂ "Surinam" (MNHN); 1♂ no data (MNHN); 1♀ Panamá, (MNHN); 1♀ Chiriqui, Panamá (MNHN).

Range and habits. This species is recorded only from northern Costa Rica to the Caribbean coast in Panamá. DeVries (1997) reports this phenotype from Costa Rica on both Atlantic and Pacific slopes near sea level in mangrove habitats. My experience with this butterfly in Costa Rica is in Very Humid Tropical Rainforest (Holdridge 1947) on the edge on a small hilltop near Chilamate, Heredia (100 m). Two females were captured at 1000 hours resting with wings outspread on the underside of leaves. At 1230, a male was taken on the same hilltop likewise resting under a leaf with wings spread. It is rare in Costa Rica, more common in Panamá.

Hypophylla martia (Godman, 1903), **n. comb.**
(Figs. 34, 35, 36, 37)

This species was described from a male originating from San Pablo on the Río San Juan, Chocó, Colombia. The type is in the British Museum (Natural History).

Diagnosis. *H. martia* males resemble *H. zeurippa* in the extent of blue on the forewing and the uniform dark orange submarginal band along the distal margin of the hindwing, reaching from the tornus to M2. *H. martia* may be separated by the much darker maculation of both wing surfaces, generally thinner submarginal line on the forewing apex, and more pointed forewing. The male genitalia (Fig. 10) differ in the shorter, thinner valvae and a more truncated process on the transtilla. The female forewing band, while approximately the same width, is sharper on *H. martia,* is not bordered basad by the end of the discal cell and terminates on the distal margin. The ductus bursae (Fig. 20) is wider in *H. martia* and dilated at the base of the ductus seminalis.

Range and habits. This species ranges from Costa Rica to the west coast of Colombia. In Costa Rica, there is one record for this species from Magsaysay in the lowland Atlantic rainforest (DeVries 1997). This species is very rare in Colombia, the only specimen I have seen from there is the type. It appears to be more common in Panamá, where it is sympatric with *H. lasthenes.* From my data, the habitat of this species is lowland tropical rain forest.

Material examined. PANAMÁ: 1♂ Gamboa, 5 Jan. 1979, (CJC); 1♂ same locality, 16 Dec. 1979, (CJC); 1♂ Los Rios, 4 Jan.1971, leg. King (CJC); 1♀ Barro Colorado Island, July 13, 1977, leg. R. Robbins (CJC); 1♂, 2♀♀ Chepo Island, Majé, March 1989 leg.

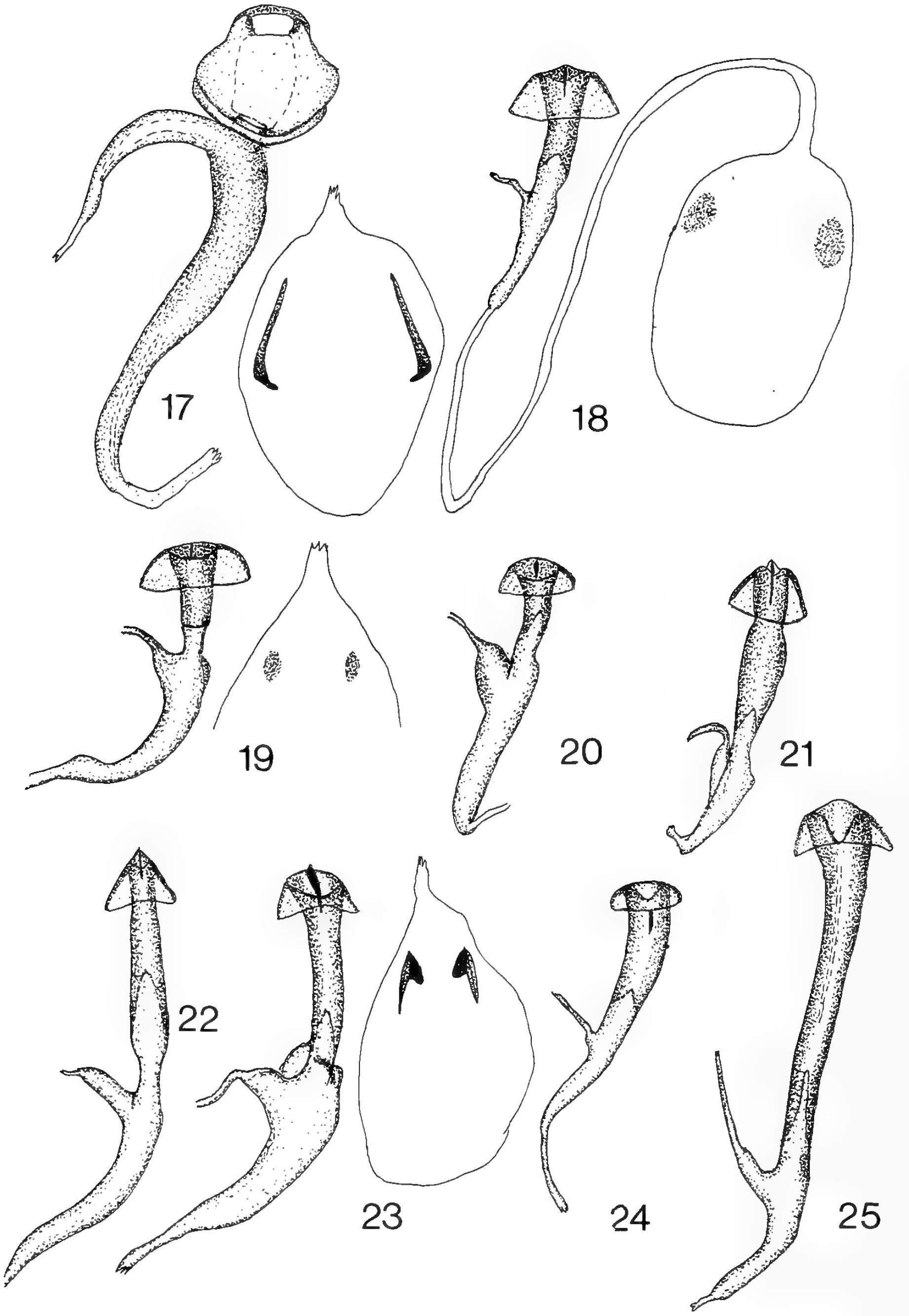


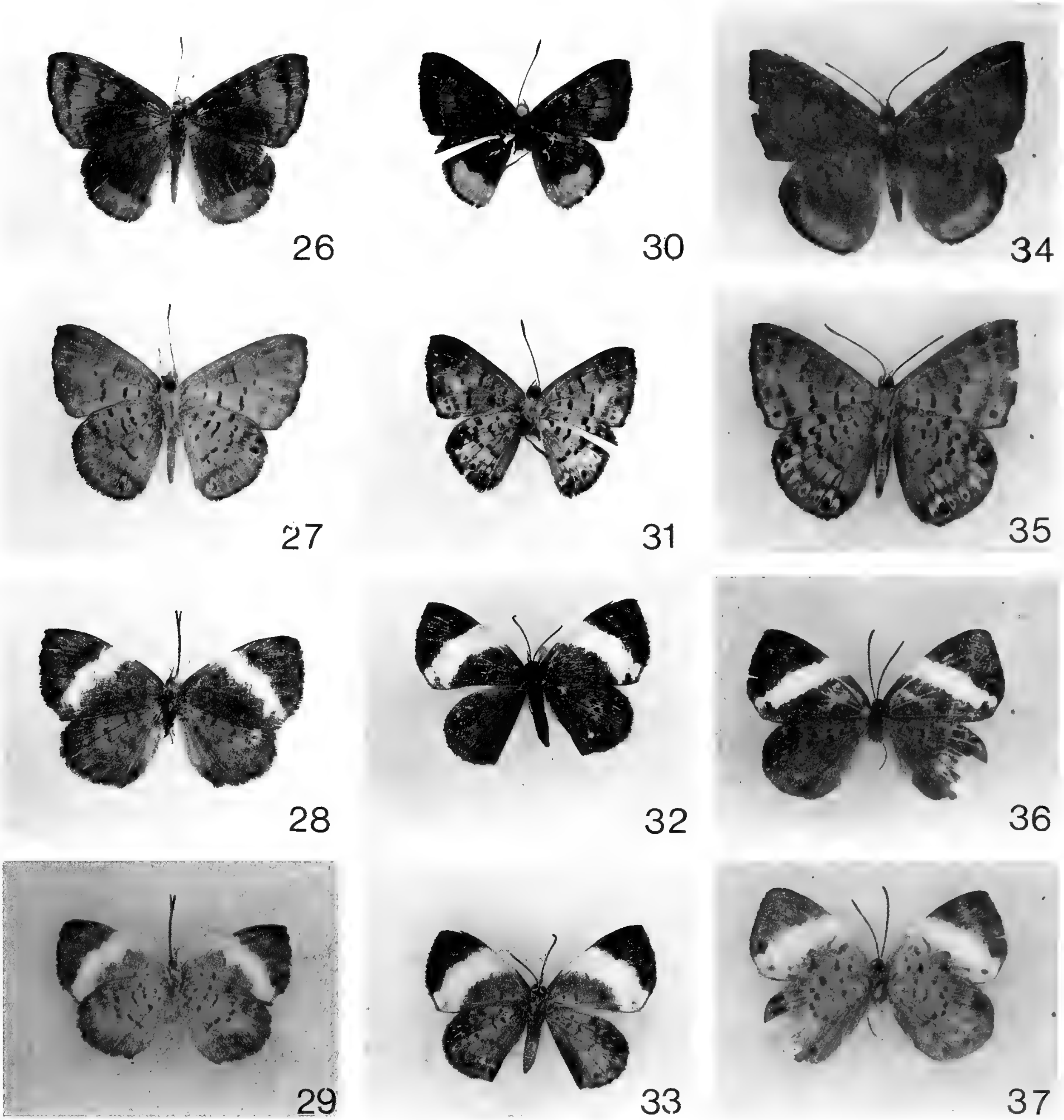
FIG. 17. *Calospila parthaon,* female genitalia. FIG. 18. *Hypophylla zeurippa,* female genitalia. FIG. 19. *Hypophylla lasthenes,* female genitalia. FIG. 20. *Hypophylla martia,* female genitalia. FIG. 21. *Hypophylla flora,* female genitalia. FIG. 22. *Hypophylla idae,* female genitalia. FIG. 23. *Hypophylla caldensis,* female genitalia. FIG. 24. *Hypophylla sudias,* female genitalia. FIG. 25. *Hypophylla argenissa,* female genitalia..

Delgado, (FD); 2♂♂, 3♀♀ Colón, Coclesito, 23 Jan. 1988, 15 April 1990, 26 Aug. 1988 leg. Delgado, (FD); 1♂, 2♀♀ Colón, Puerto Bello, Río Cuango, 26 April 1991, leg. Delgado (FD).

Hypophylla caldensis Callaghan, new sp.

(Figs. 38, 39, 40, 41)

Description. Male (Figs. 38, 39)—Forewing length of Holotype 16.5 mm and paratypes 16.2 mm. Forewing costa slightly curved to apex, apex rounded, distal margin slightly convex; hindwing with costa straight, distal margin rounded. Forewing costa dark brown to apex; dull, light purple from end of discal cell to apex and to tornus, rest of wing reddish-brown; a reddish-brown line at end of discal cell and two more inside, two additional black lines in cell Cu2–1A+2A below; a median band of connected dark brown spots reaches from the costa to Cu1, then is displaced basad such that it forms a continuous band with the end of the cell to 1A+2A; a marginal black band extends from the apex to the inner margin, widest from costa to M3; fringe black. Hindwing costa above M1 to apex dark brown with two black spots above discal cell and faint irregular blue spot just before



FIGS. 26, 27. *Hypophylla zeurippa,* male, dorsal/ventral view. FIGS. 28, 29. *Hypophylla zeurippa,* female, dorsal/ventral view. FIGS. 30, 31. *Hypophylla lasthenes,* male, dorsal/ventral view. FIGS. 32, 33. *Hypophylla lasthenes,* female, dorsal/ventral view. FIGS. 34, 35. *Hypophylla martia,* male, dorsal/ventral view. FIGS. 36, 37. *Hypophylla martia,* female, dorsal/ventral view.

apex, base to median above 1A+2A reddish brown and anal margin light grey, postmedial area and distal margins yellow-orange, fringe black. Discal cell includes a black line at end and two within, and two below in cell Cu2–1A+2A, median band of unconnected, bold spots, one on costa slightly offset distad from next 4 in a straight row to yellow-orange area. Ventral surface ground color dirty white with black markings. Forewing slightly darker at apex and margin, black markings as on dorsal surface. Hindwing maculation as on dorsal surface, and yellow-orange area same, but paler, with a darker marginal area containing a row of variable marginal black spots, those at anal angle and two at apex larger; a post median row of spots continues below Cu1, offset basad and nearly parallel to those above.

Head, thorax, abdomen dark reddish-brown dorsad, uniform white scaling ventrad, antennae brown dorsad, with white scales ventrad between sections, club long, weak; orbit white, frontoclypeus white ventrad, with light brown scaling above; labial palpi scaled, protruding beyond face when viewed dorsally.

Genitalia (Fig. 10)—uncus bilobed and rounded, valvae rounded, narrower and straighter than *H. zeurippa,* process of transtilla slightly longer and thinner, posterior edge of 8th sternite slightly bifurcated, aedeagus pointed with unsclerotized sheath, and a wedge-shaped cornuti.

Female (Figs. 40, 41)—forewing length 15.5 mm. Dorsal wing ground color light brown with ventral maculation appearing through. Forewing with a 3 mm wide uneven pale yellow band from costa almost to tornus, enclosing a variable spot of brown scaling at anal angle, band slightly jagged at end of cell. Ventral forewing apical area dark brown, bordered basad by pale yellow area reflecting the dorsal band, base light grey with indistinct brown maculation corresponding to that of male. Hindwing light grey with dark brown apex and brown maculation as on male. Head, thorax and abdomen dark brown dorsad, white scaling ventrad; frons white basad, labial palpi sexually dimorphic, third segment longer than on male.

Genitalia (Fig. 23)—ostium bursae as a long, sclerotized tube, slightly wider at opening where the rim is folded dorsad, and with a high, sclerotized flange in the middle dorsad; base of tube very broad where the ductus seminalis separates; corpus bursae elongated with two well developed, invaginated, pointed signa.

Types. Holotype male COLOMBIA: Cerro Aguacatal, Río Súcio, 1600 m, Caldas 21 March 1997 leg. Callaghan. Paratypes. 3♂♂ same data as holotype, and 2♂♂ same locality, 30 April 1994 leg. J. Salazar (CJC), and 1♂ 12 km west of Otanché, Boyacá, 700 m (ex collection E. Schmidt-Mumm), and 1♂ Río Cali, Valle, 1100 m, 12 October, 1981 leg. Callaghan (CJC). 1♀ Aguas Claras 100 m, Río Anchicayá, 6 June 1982, leg. Callaghan, (CJC); 1♂ Caucathal, 1000 m, (MNHN). The Holotype is deposited in the Museum of the Universidad Nacional , Bogotá, and paratypes in the author's collection and the NMNH, Washington, D.C.

Etymology. The species is named after the Department in Colombia where the type locality is located.

Diagnosis. The males of *H. caldensis* differ from *H. zeurippa* and *H. martia* in the greater extent and lighter yellow color of the distal half of the dorsal hindwing and the lighter ground color and darker maculation on the ventral surface, and from *H. lasthenes* by the expanded yellow on the hindwing. On the ventral forewing, the post median spots below Cu1 form a continuous line with the end of the discal cell. The ventral surface is less strongly marked than *H. lasthenes.* The genitalia are very close to *H. zeurippa* but with slightly shorter valvae.

A female captured at Aguas Claras (Tatabro) Chocó, 100 m is tentatively described as the female of this species. The unique morphology of the genitalia (Fig. 23), in particular the fully developed invaginated sclerotized signae instead of the sclerotized patch does not associate it with any other species. It shares certain characters with *H. caldensis* males, such as a spot on the tornus of the forewing and the beginning of the medial band in line with the end of the cell. However, the specimen was captured in a completely different biotype from the males that are not known from the Chocó. Therefore, until more material can be examined, the specimen will be maintained as the female of *H. caldensis.*

Range and habits. *H. caldensis* ranges from 700 to 1800 m in the Cauca and Magdalena river drainage of Colombia, and possibly to the Chocó. Its habitat is in the coffee zone characterized as Premontane very humid forest with rainfall between 2000 and 4000 mm. (Espial & Montenegro 1977). The species is probably more widespread than suggested by the few records known. Males perch on hilltops from 1300 to 1500, where they fly with a bouncing flight like a small satyrid, resting on leaf dorsal surfaces 1–2 meters above the ground (Fig. 52). The Río Cali specimen was found in the woods by the river at 1130.

Hypophylla flora (Staudinger, 1887), **n. comb.**
(Figs. 42, 43, 44, 45)

Lemonias flora was described from a male captured near the Rio San Juan, Chocó, in western Colombia. The type is in the Humboldt Museum, Berlin.

Diagnosis. The male of *H. flora* can be easily separated from its congeners by the shape of the orange-yellow spot on the distal half of the hindwing, which is rounded at the tornus and culminates in a point at M1; ventral surface dark grey, markings indistinct, apex of ventral hindwing has three black triangular marks bordered basad with white between the veins. The male genitalia (Fig. 12) has an uncus similar to *H. zeurippa,* but the valvae are extremely truncated. The aedeagus extends far beyond end of valvae, and is same length as left process of the transtilla, only slightly shorter than the right one. The female has a 4 mm. wide yellow band reaching from the costa to the distal margin. The band of *H. idae* is likewise wide, but ends on the inner margin. In the female genitalia (Fig. 21), the ductus bursae is a narrow sclerotized tube, wider in the middle and slightly wider at the ostium bursae where the rim is folded dorsad, with a high dorsal sclerotized flange in the middle reaching above the rim. The ductus bursae is slightly broader where the ductus seminalis separates; the signa in the corpus bursae are two slightly invaginated sclerotized patches.

Range and habits. *Hypophylla flora* is known from the Chocó region on the Colombian west coast to western Ecuador (Tinalandia, Paramba, Palmar, in northwest Ecuador. J. Hall, pers. comm.), from sea level to 300 m. Seitz' (1917) assertion that it ranges to Venezuela was possibly based on mislabelled material. I have observed this species perching on the underside of leaves along forest trails and along streams in primary rainforest. It is rare.

Material examined. COLOMBIA: 4♂♂ Río Tatabro (Aguas Claras), Río Anchicayá, Valle, 100–200 m 11 Nov. 1989, leg. Callaghan (CJC); 1♀ Río Tatabro, Valle, July 1992, leg. Salazar. (CJC); 2♂♂ Caucathal, 1000 m (MNHN).

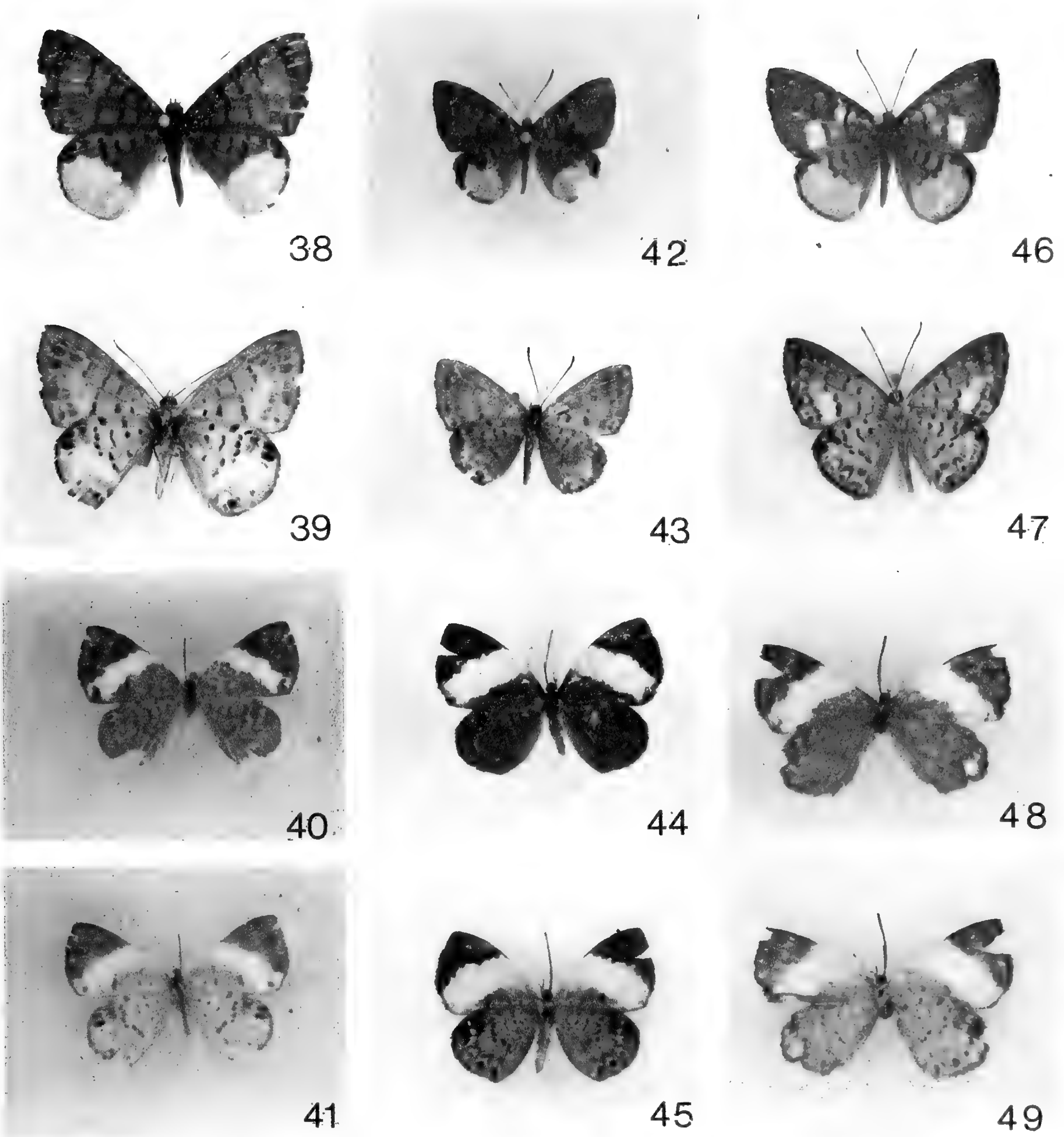
Hypophylla idae Callaghan, new species
(Figs. 46, 47, 48, 49)

Description. Male (Figs 46, 47)—forewing length of holotype and paratypes 16.7 mm (N = 5). Forewing costa slightly curved to apex, apex pointed, distal margin slightly convex, hindwing with costa straight, distal margin rounded. Dorsal wing ground color reddish brown with dull purple and yellow-orange scaling. Forewing discal cell with orange scaling and black bars at end, middle and base, and two more cell Cu2–1A+2A below; costa and post medial area above M3 and distad of cell end to apex and to tornus dull purple, with a row of faint marginal spots; base to slightly beyond end of cell below M3 reddish-brown with some orange scaling distad, and bordered distad with a black bar; postmedian area between M3 and 1A+2A with a yellow-orange spot; below 1A+2A to base reddish-brown, fringe black. Hindwing base, discal area reddish-brown with black markings at end, middle and base of discal cell, two black spots on costal margin and a medial row of spots between RS and 1A+2A, the first four in a straight line, the last two offset basad; apex and fringe to tornus black, postmedial area to margin yellow-orange; fringe black. Ventral surface ground color dark grey, maculation as on dorsal surface, dorsal yellow-orange areas ventrally light pink. Forewing with marginal row of black spots between the veins bordered basad with white, that continues along the hindwing margin, the two spots at the apex being the largest.

Head, thorax and abdomen reddish-brown dorsad, mixed white-brown scaling ventrad, appendages white, antennae brown dorsad, ventrad with white scales between sections, club weak, orbit white, frontoclypeus brown; palpi scaled, protruding beyond face when viewed dorsally.

Genitalia (Fig. 13)—uncus deeply bifurcated, lobes squared; vinculum thin, slightly wider in middle; saccus rounded, valvae tips rounded, transtilla with two very long, thin processes, left slightly shorter than right; aedeagus long, pointed with tip turned up, and internal cornuti; pedicel rounded, posterior margin of 8th sternite slightly bifurcated.

Female (Figs. 48, 49)—forewing length 16.8 mm. Forewing elongated, height to length 1:1.52. Dorsal wing ground color light brown with ventral maculation appearing faintly. Forewing with 5 mm wide uniform yellow band from costa to just before tornus and inner angle, enclosing a tiny spot at tornus. Ventral forewing apical area dark brown with two rows of faint white marginal spots and bordered basad by pale yellow area corresponding to dorsal band, base light grey with indistinct brown maculation corresponding to that of male. Hindwing light grey with dark brown apex and brown maculation as on male.



FIGS. 38, 39. *Hypophylla caldensis,* Holotype male, dorsal/ventral view. FIGS. 40, 41. *Hypophylla caldensis*, female, dorsal/ventral view FIGS. 42, 43. *Hypophylla flora,* male, dorsal/ventral view. FIGS. 44, 45. *Hypophylla flora*, female, dorsal/ventral view. FIGS. 46, 47. *Hypophylla idaii,* Holotype male, dorsal/ventral view. FIGS. 48, 49. *Hypophylla idae*, female, dorsal/ventral view.

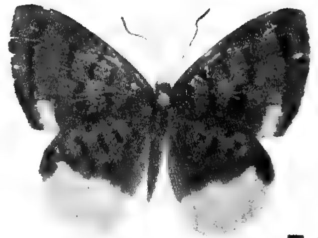
Head, thorax and abdomen dark brown dorsad, white scaling ventrad; palpi sexually dimorphic, longer than male.

Genitalia (Fig. 22) – Ductus bursae as a narrow, long funnel, narrowing slightly at the pointed opening, with the top doubled over and a small internal sclerotized flange, ductus seminalis joining at the left side of base; the signa on the corpus bursae are represented by two very weakly sclerotized patches.

Types. Holotype male: COLOMBIA, Quebrada Valle Sol, km. 104, Bogotá-Medellin, Antioquia, leg. Keith S. Brown Jr. Paratypes. 1♀ with same data as holotype; 1♀ Río Calima (Calima Dam) 800 m, Valle, 27 Oct. 1982, leg. C. Callaghan, (CJC); 2♂♂, 1♀ Río Claro 700 m, 5°50′N 74°52′W, Antioquia, Nov. 4, 1989, leg. Callaghan, (CJC); 1♂ Río Calderas, 700 m Cocoruá, Antioquia, Jan. 4, 1996, leg. Salazar, (CJC). The Holotype is deposited in the Museo de la Universidad Nacional, Bogotá, and paratypes are deposited in the author's collection and the NMNH, Washington DC, USA.

Etymology. This lovely species is named for my wife, whom I met near the type locality.

Diagnosis. Male *H. idae* are easily separated from its cogeners by the orange spot at the postmedian area of the forewing. The gen-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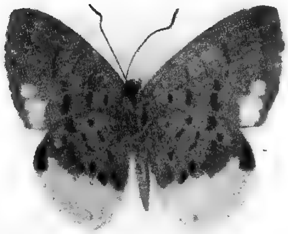
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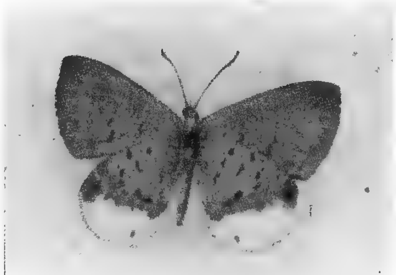
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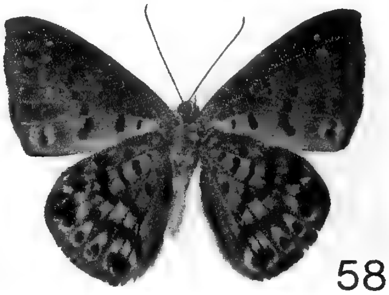
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FIGS. 50, 51. *Hypophylla sudias callaghani*, male, dorsal/ventral view. FIG. 52. *Hypophylla caldensis* male perching on hilltop, Río Súcio, Caldas. FIGS. 53, 54. *Hypophylla sudias sudias*, male, dorsal/ventral view. FIGS. 55, 56. *Hypophylla sudias sudias*, female, dorsal/ventral view. FIGS. 57, 58. *Hypophylla argenissa*, male, dorsal/ventral view. FIGS. 59, 60. *Hypophylla argenissa*, female, dorsal/ventral view.

italia differs from *H. zeurippa* in the squared lobes of the uncus, longer, thinner process on the transtilla and rounded pedicel. The female differs in the elongated forewing and 5 mm broad forewing band that terminates mainly on the inner margin instead of the distal margin.

Range and habits. The type locality is a disturbed forest hilltop off the Medellin-Bogotá highway in the Central Cordillera. The vegetation is Pre-montane very humid forest and Very humid tropical forest (Espial & Montenegro 1977). All male specimens were observed perching on hilltops between 1100 and 1200 on the upper surfaces of leaves with their wings slightly raised. The females were discovered in nearby woods.

Hypophylla sudias sudias (Hewitson, [1858]), **n. comb.**
(Figs. 53, 54, 55, 56)

Lemonias sudias was described from a male from Honduras. The holotype is located in the British Museum (Natural History).

Diagnosis. The males of *H. sudias* may be easily separated by the purple scaling covering the dorsal forewing to Cu2–1A+2A with the postmedian area of the hindwing yellow-orange reaching from M3 to the tornus with yellow fringe, and the slightly falcate apex of the forewing. The ventral surface ground color is grey-brown and the black markings are weak, not appearing above vein Cu1; the yellow band appears on the ventral surface and the fringe is yellow. Some specimens from the gulf coast of México (Popocatóptl, Vera Cruz) have some yellow scaling on the tornus of the dorsal forewing, similar to *H . s. callaghani* (see below). Specimens form Panamá differ in having a uniform marginal black band on the forewing and heavier markings on the ventral surface, intermediate to *H .s. callaghani.* In the male genitalia (Fig. 15), the uncus is deeply bifurcated and the lobes pointed; the valvae are only slightly shorter than *H. zeurippa* and the aedeagus is the same length as the right process of the transtilla. *H. sudias* females are distinguished by a 5 mm wide white band on the forewing which reaches from the costa nearly to the distal margin, then curves into the inner margin narrowing to a point. In the female genitalia (Fig. 24), the ductus bursae is a short, wide sclerotized tube, slightly wider at the ostium bursae opening where the rim is folded dorsad, with a deep V-shaped notch in the rim, the sclerotized flange in the dorsal middle is reduced, not reaching the rim. The ductus bursae is only slightly broader where the ductus seminalis separates; the signa in the corpus bursae are two barely sclerotized patches.

Range and habits. *H. sudias sudias* ranges from northern México (Chihuahua) down the Gulf Coast to Oaxaca and Chiapas, then south to Panamá, inhabiting lowland tropical forest. There is one record in the Allyn Museum of Entomology from San Quintin, BCN which needs verification. The species is known from Costa Rica from a single specimen (DeVries 1997). J. Hall (pers. comm.) reports *H. sudias* males at Lake Petén, Guatemala perching one meter high under leaves inside the forest edge at 1630.

Material examined. MÉXICO 1♂, 1♀ Chiapas, San Filipe, 3000”, Pasta, 6 Aug. 1974. leg. R.Wind, (CJC); 1♂, 1♀ Monumento Natural Yaxachilán, Ocosingo, 5 Abr. 1998, Sept. 1948 (MZFC); 2♂♂, 3♀ Ocosingo, Chiapas, Sept. 1948, June 1940, (MZFC); 1♂ Sierra de Juárez, Oaxaca, July 1982, (MZFC); 1♂ San Juan Chamula Chiapas, 19 July 1993, (MZFC); 1♂ Cerro del Coconá, Teapa, Tabasco, 20 April 1995, (MZFC); Ojo de Agua, Michoacan, 17 Nov. 1981 (MZFC); 8♂, 2♀ Puerto eligio, Oaxaca, 6 Oct. 1986, 12 Aug.1986, 6 Oct. 1986, 31 Oct. 1987, 11 May, 1980, 10 Aug. 1986 (MZFC); 4♂♂ 30 July 1982 (MZFC); 3♂, 8♀ Popoctépetl, San Andres Tuxtla, Veracruz, July 1982, 24 Sept. 1982, 9 July 1982, 20 Aug. 1982, (MZFC); 1♂, 1♀ Tapalapan, 5 Aug. 1982, (MZFC); 1♀ Santa Rosa Comitán,Chiapas, Oct. 1982 (MZFC); 3♀♀ Metates, San Miguel, Aloapam, Oaxaca, 16 Sept. 1987, 22 July 1979 (MZFC); GUATEMALA: 1♂ Las Cajas, El Petén, 250 m, (CJC); PANAMÁ. 1♀ Alto de Piedra, Santa Fé de Veraguas 840 m, 23 Feb.1987 (FD).

Hypophylla sudias callaghani
(Constantino & Salazar, 1998), **n. comb., n. stat.**
(Figs. 50, 51)

The male of *H. sudias callaghani* was described from Tatabro, Río Anchicayá, 100 m, Chocó, Colombia, as a species, *Calospila callaghani.* The Holotype is deposited in the Museo de Historia Natural de la Universidad de Caldas, Manizales. Examination of the phenotype and the female suggests, however, that it is a subspecies of *H. sudias.*

Diagnosis. Males are easily distinguished from the nominate subspecies and other *Hypophylla* by the yellow-orange spot at the tornus of the forewing combined with the heavy maculation on both wing surfaces. The male genitala (Fig. 14) of the two subspecies are slightly different, with the uncus of *H. sudias callaghani* more pointed, and the valvae and processes of the transtilla longer and narrower. The female of *H. sudias callaghani* is illustrated in D'Abrera (1994) on page 1032 from a specimen in the BMNH from the Río San Juan, Chocó, misidentified as the female of *H. argenissa.* The females differ from the nominate subspecies in the slightly more truncated white band on the forewing, and appear to be very rare.

Range and habits. The habitat of this subspecies is coastal tropical rain forest in the Chocó region of western Colombia. Males can be encountered rarely on hilltops after 1530 where they fly in circles with a bouncing flight like a small satyrid, resting on leaf dorsal surfaces 2–3 meters above the ground.

Material examined. COLOMBIA: 1♂ Quebrada Bendición,Valle 7 July 1987 leg. Keith Brown Jr. (CJC); 2♂♂ Aguas Claras, Río Anchicayá, 100 m, 16 June 1982 leg. Callaghan (CJC); 1♂ Aguas Claras, Jan. 17, 1982, leg. Callaghan (CJC); 1♂ Quibdó, Chocó, June 17, 1993, leg. K.B.Brown Jr.

Note: The locality Aguas Claras is also known as Tatabro, located on the Río Anchicayá east of Buenaventura.

Hypophylla argenissa (Stoll, [1790]), **n. comb.**
(Figs. 57, 58, 59, 60)

=*petronius* (Fabricius, 1793) (Hesperia)
=*staudingeri* (Godman, 1903) (Lemonias)

Stoll described *Papilio argenissa* from material supposedly from Surinam. This may be in error, as to my knowledge this species has not been recorded east of the Cordillera Occidental in Colombia. This led Godman (1903) to describe *Lemonias staudingeri* from a misidentified figure based on a western Colombian specimen in Staudinger's Exotische Schmetterlinge, which was in fact *P. argenissa.* The type of *L. staudingeri* is in BMNH. I was unable to locate Stoll's type during my searches at the museum at Leiden, The Netherlands, so it is apparently lost. However, the distinct morphology of this butterfly precludes the necessity of designating a neotype.

Diagnosis. This species can be confused with no other. The ground color of the male dorsal surface is uniform dark blue with black markings. On the ventral surface, the ground color is dark brown with black markings and infusion of white scaling on the hindwing. In the male genitalia (Fig. 16) the uncus is bifurcated with a narrow notch and the lobes are pointed, the valvae are long and narrow, and the adeagus contains two cornuti. The females are easily distinguished from other members of the genus by the yellow forewing band with a straight basal border and a distal border that is curved towards the tornus. In the female genitalia (Fig. 25) the ductus bursae is a long, narrow, funnel shaped, sclerotized tube, bulbous where the ductus seminalis separates and wider at the ostium bursae where the rim is folded dorsad, with a minuscule, sclerotized flange in the middle and a U-shaped notch; the signa in the corpus bursae are two elongated sclerotized patches.

Range and habits. *Hypophylla argenissa* ranges from Costa Rica to Colombia, where it inhabits west coast (Chocó) from sea level to about 300 m. In Panamá and Costa Rica, this species is found on both Pacific and Atlantic slopes to 1000 m (DeVries 1997, pers. obs.). Both sexes perch on hilltops, in treefalls and on forest edges from 1100 to 1500, resting on ventral leaf surfaces with wings outspread.

Material examined. COLOMBIA: 2♂♂ Aguas Claras, Río Anchicayá, Valle, 17 Jan. 1982, leg Callaghan (CJC); 1♀ same locality, July 1990 leg. Salazar (CJC); 1♀ same locality, 1 Aug. 1981, leg. Callaghan (CJC); 1♀ same locality, May 24, 1982, leg. Callaghan (CJC); 2♂♂, 1♀ same locality, 20 Feb.1982, leg. Callaghan (CJC); PANAMÁ: 1♀ Canal Zone, Gatún, 26 April 1989, leg. Callaghan (CJC); 1♂ Colón (Santa Rita) 500 m, 7 Jan. 1975, leg. Nicolay (CJC); 2♂♂ Gamboa, 17 May 1979 (CJC); 3♂♂, 1♀ Colón, Río Cuango, 25 Oct. 1992, 15 Febr. 1995, 20 Sept. 1991, leg. Delgado (FD); 9♂♂, 3♀♀ Colón, Coclesito, 18 June 1988, 27 Aug.1988, 27 June 1986, 27 Nov. 1986, 11 Sept. 1988, 13 March 1989, 30 Nov. 1988, leg. Delgado (FD); 1♀ Alto de Piedra, Santa Fé de Veraguas, 10 Sept. 1981, leg. Delgado (FD).COSTA RICA:1♂, 2♀♀ Chilamate, Heredia, 30 June 1992 leg. Callaghan (CJC);

KEY TO MALES OF *HYPOPHYLLA*

1a. Dorsal wing surface with orange areas 2
1b. Dorsal wing surface blue with no orange areas . . . . *argenissa*

2a. Orange on hindwing limited to a uniform submarginal 4 mm wide band 3
2b. Orange on hindwing wider than 4 mm 4

3a. Ventral hindwing post median row of spots between Rs and Cu1 in a straight line . . . . *zeurippa*
3b. Ventral hindwing post median row of spots between Rs and Cu1 not in a sraight line . . . . *martia*

4a. Fringe on hindwing yellow 5
4b. Fringe on hindwing brown 6

5a. Maculation heavy, tornus forewing always with an orange spot . . . . *callaghani*
5b. Maculation reduced, tornus of forewing rarely with an orange spot . . . . *sudias*

6a. Orange-yellow markings on disal area of forewing . . . . . *idae*
6b. Orange-yellow markings absent from forewing 7

7a. Submarginal black line on forewing thin and discontinuous; ventral surface ground color dark gray . . *flora*
7b. Submarginal black line on forewing wide near apex, thinner to tornus; ventral surface ground color light gray . . 8

8a. Yellow orange area on hindwing wide, reaching nearly halfway from margin to base; black marks between forewing veins Cu1 and 1A+2A form continuous line with end of cell . . . . *caldensis*
8b. Yellow orange area on hind wing narrower, reaching only a third of the distance from margin to base; black marks between forewing veins Cu1 and 1A+2A do not form continuous line with end of cell . . . . *lasthenes*

KEY TO THE FEMALES OF *HYPOPHYLLA*

1a. Dorsal forewing band yellow 2
1b. Dorsal forewing band white . . . . *sudias*

2a. Dorsal forewing band narrow, not exceeding 4 mm 6
2b. Dorsal forewing band wide, greater then 4 mm 3

3a. Dorsal forewing band more or less constant width 4
3b. Dorsal forewing band convex distad from costa, ending in a point, followed by an irregular, variable patch of yellow scaling before distal margin . . . . *argenissa*

4a. Dorsal forewing band ends opposite distal margin . . . . *florus*
4b. Dorsal forewing band ends opposite tornus and inner margin 5

5a. Ventral forewing band more extensive, filling cell and reaching base; forewing elongated . . . . *idaii*
5b. Ventral forewing band reaches base only along costal margin; forewing not elongated . . . . *lasthenes*

6a. Ventral ground color gray-brown, forewing band bordered basad by line at end of cell . . . . *zeurippa*
6b. Ventral ground color gray or white, forewing band not bordered basad by line at end of cell 7

7a. Ventral hindwing post median row of spots between Rs and Cu1 in a straight line . . . . *caldensis*
7b. Ventral hindwing post median row of spots between Rs and Cu1 not in a straight line . . . . *martia*

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SUITABILITY OF FOUR FAMILIES OF FLORIDA "BAY" SPECIES FOR *PAPILIO PALAMEDES* AND *P. GLAUCUS* (PAPILIONIDAE)

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ABSTRACT. We tested the suitability of four Florida "bay" plant species for larval growth and adult oviposition preferences for two swallowtail butterfly species, *P. palamedes* and *P. glaucus.* Much confusion exists about the host plant records for these butterflies in the literature. We confirmed that of the four bay species tested, only red bay (*Persea borbonia*) of the Lauraceae was suitable to support larval survival and growth of *P. palamedes.* All *P. palamedes* larvae offered sweetbay (*Magnolia virginiana* of the Magnoliaceae), Loblolly bay (*Gordonia lasianthus* of the Theaceae) or Southern Bayberry (*Myrica cerifera* of the Myricaceae) died as neonates. Conversely, only sweet bay (*Magnolia*) was suitable for supporting survival of neonate *P. glaucus* larvae, with red bay, loblolly bay and bayberry unacceptable or toxic. Oviposition preferences (individually assessed in a revolving four-choice arena) were strongly in favor of the most suitable host for each species: sweet bay received 93.9% of the total *P. glaucus* eggs and red bay received 54.2% of the total *P. palamedes* eggs. The generally low level of adaptation of the *Lauraceae* specialized spicebush swallowtail, *Papilo troilus,* to red bay was evident in that all nine Florida females refused to oviposit on any of the four "bays" (including red bay).

Additional key words: herbivore-plant interactions, tiger swallowtail butterfly, palamedes swallowtail, spicebush swallowtail, Lauraceae, Magnoliaceae, Theaceae, Myricaceae.

Largely because of its distinctive plant species and geographic isolation as a peninsula, Florida harbors some unique and rare butterfly and moth species (Minnow & Emmel 1992; Emmel 1995). The phytochemical constraints and ecological opportunities affecting host selection and use by various Lepidoptera (Feeny 1995) are of general interest. Some of these unique biochemical, physiological, behavioral and ecological adaptations of Lepidoptera to Florida's local host plants have been documented for the sweet bay silkmoth, *Callosamia securifera* (Peigler 1976, Scriber 1983, Johnson et al. 1996) and three different species of swallowtail butterflies (Scriber 1986, Nitao et al. 1991, Scriber et al. 1991, 1995, Lederhouse et al. 1992, Bossart & Scriber 1995a, 1995b, Frankfater & Scriber 1999a, 1999b). We have examined population fluctuations and the relative densities of *Papilio palamedes, P. troilus,* and *P. glaucus* in central Florida hammocks and bay forests for the past decade (Scriber et al. 1998a). Field observations and lab studies suggest close affinities in preference for either Magnoliaceae or Lauraceae, but not both.

Nonetheless, one of the most confusing examples of uncertainty in host plant records for Lepidoptera exists for *Papilio troilus, P. palamedes,* and *P. glaucus.* Early food plant references for *Papilio* species in the literature are especially unclear about the Florida hosts since the use of the term "bay" (Mitchell & Zim 1964, Scriber 1984) could refer to several species in four different families: 1) Red bay (*Persea borbonia* (L.) Spreng) of the Lauraceae family, 2) Sweet bay or white bay (*Magnolia virginiana* (L.) of the Magnoliaceae family, 3) Loblolly Bay (*Gordonia lasianthus* (L.) Ellis) of the Theaceae family, 4) or Southern Bayberry (*Myrica cerifera* L.) of the Myricaceae family. For example, it has been stated that "*Papilio palamedes*. . . larvae feed on magnolias in the Bay Tree hammocks of the Everglades" (Young 1955). While loblolly bay occurs throughout Highlands County and in each Florida county north of Lake Okeechobee and into Georgia; red bay, sweet bay, and southern bayberry occur in every county of Florida including the southern ones down to the Keys (Little 1978, Nelson 1994).

In a study of latitudinal and geographic variation in host plant records for the 560+ species of swallowtail butterflies, Scriber (1973, 1984) lists numerous citations that report both the Magnoliaceae and Lauraceae families as host plants for the *Papilio troilus, P. palamedes,* and *P. glaucus* butterfly species. No specific records of bayberry (or other Myricaceae) nor *Gordonia* (or other Theaceae) were listed as hosts or foods for these *Papilio.* However, since all four "bay" species frequently coexist in swamps, hammocks and floodplain forests of southern Florida, we were inter-

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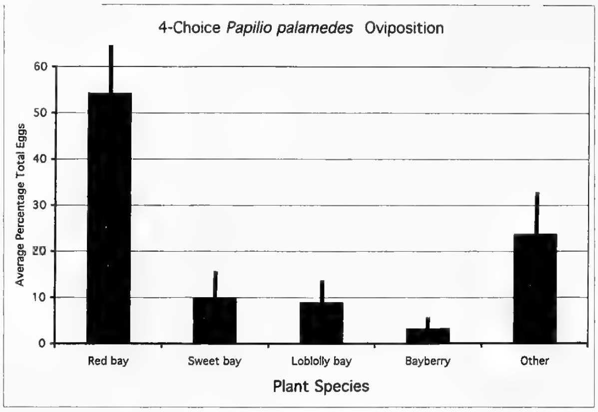

FIG. 1. The 4-choice oviposition preferences (mean ± SE) of eight Florida *P. palamedes* females on four "bay" species or "other" (on paper lining or plastic arena) (red bay, Lauraceae; sweet bay, Magnoliaceae; loblolly bay, Theaceae; southern bayberry, Myricaceae). The average eggs per female was 45 ± 16 (SE).

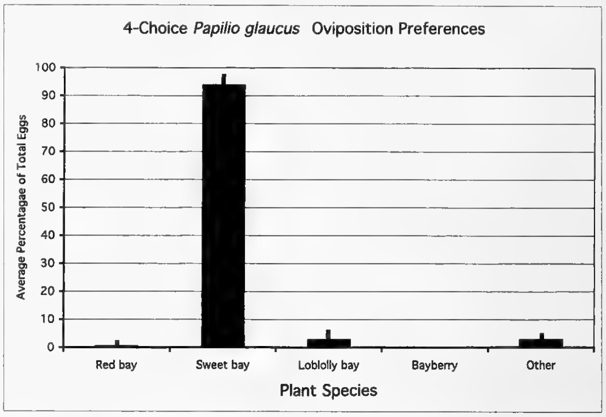

FIG. 2. The 4-choice oviposition preferences (mean ± SE) of five Florida *Papilio glaucus* females on four "bay" species (see Fig. 1). The average total eggs per females was 84 ± 36 (SE).

ested in determining which of these four were used (or capable of being used) for oviposition and/or for larval food. We conducted our multichoice oviposition and larval survival and growth studies in Highlands County, Florida, at the Archbold Biological Station and some bioassays were conducted with material sent to Michigan State University.

Clarification of uncertain adult oviposition and larval food plant records is critically important for understanding the relationships between insects and plants in ecological and evolutionary time (Ehrlich & Raven 1964, Feeny 1995). A procedure for reporting host plants or food plant observations was provided by Shields et al. (1969), and they explained how misidentification of either the insect or plant species can lead to errors that get transmitted in textbooks, guidebooks, and other scientific literature for decades. In our case, it has been suspected that *P. palamedes* only feeds on members of Lauraceae and not on members of Magnoliaceae (Brooks 1962, Scriber 1986); however sweet bay (*Magnolia virginiana,* previously described as *Magnolia glauca*) or Magnoliaceae is listed as hosts for *P. palamedes* by numerous authors (Jordan 1907, Young 1955, Klots 1958, Forbes 1960, Ehrlich & Ehrlich 1961, Kimball 1965, Harris 1972, Tietz 1972, Tyler 1975, Pyle 1981, Okano 1983, Beutelspacher-Baights & Howe 1984, Opler & Krizek 1984, Pyle 1997). While still other authors do not list sweet bay magnolia as a host for *P. palamedes* they do list it as a host for *P. troilus* (Scudder 1889, Shapiro 1974, Howe 1975, Scott 1986, Tilden & Smith 1986), which is also very unlikely (Scriber 1986, Scriber et al. 1991, Nitao et al. 1992).

Our study was conducted with *P. palamedes* and *P. glaucus* in order to determine both the adult female oviposition preferences in 4-choice arenas and the neonate larval survival abilities of both of these swallowtail butterfly species in no-choice bioassays with four "bay" species of Highlands County, Florida. While we intended to include *Papilio troilus* larvae in these studies, we were not successful in obtaining oviposition from the females (n = 9) we did secure.

METHODS

Adult females of *Papilio palamedes, P. troilus,* and *P. glaucus* captured in Florida (Highlands, Levy and Columbia Counties) were set up in 4-choice oviposition arenas to assess host preferences via contact chemoreception. The arenas are round plastic boxes that revolve 10 times per hour on a mechanized platform in front of incandescent lights. Leaves of each bay species were supported in water-filled floral aquapics and draped along the side and bottom of the dish as described by Scriber (1993). The four bay species, *Persea borbonia* (red bay = RB), *Magnolia virginiana* (sweet bay = SB), *Gordonia lasianthus* (loblolly bay = LB), and *Myrica cerifera* (southern bayberry = BB), were collected from the area west of Istokpoga Lake near the city of Lake Placid, Florida. The oviposition arenas were inside the invertebrate biology laboratory of Mark Deyrup at the Archbold Biological Station. Herbarium vouchers of these plant species have been deposited in the Michigan State University research collection (JMS).

Each day, eggs were collected and the number of eggs placed on each "bay" by individual females was recorded as were the few eggs sometimes placed on the side of the plastic dish. Adult females were fed each day (with the exception of two periods of 48-hour intervals over our four week study period). Some eggs of *P. palamedes* and *P. glaucus* were sent by overnight express mail with leaves of the bay species to our laboratory at Michigan State University. When received, the eggs were immediately placed in a growth chamber set at 26° and 18 L: 6D photoperiod. The leaves were placed in refrigeration at about 4°C in order to maintain their freshness. Subsequent shipments of leaves were sent via overnight mail, and put under refrigeration. A majority of these eggs and neonate larvae of *Papilio* were maintained in Florida at the Archbold Biological Station (at room temperature) for parallel and simultaneous bioassays (n = 70 *P. palamedes* and n = 140 *P. glaucus*). Eggs were checked at least twice a day so that neonates could be placed on leaves within hours of eclosion at each location. 150 × 25 mm petri dishes were set up with a circle of paper towel in the bottom and with an aquapic filled with water in which to place the leaves to prevent them from drying out. The maternal source from which the larvae came was recorded for each bioassay treatment. When larvae hatched, they were allocated equally among the four types of bay leaves, three larvae per dish. Larvae were gently placed on the leaves using a camelhair brush. All work surfaces and the camelhair brush used were cleaned with a 5% bleach/95% water solution before and after uses. Larvae were kept in the same growth chamber and were monitored daily to determine survival through the first instar. Survivors were reared to pupation on their host plant treatment.

RESULTS

It was absolutely clear that three of the "bay" species (sweet bay, loblolly bay and bayberry) were unsuitable for larvae of *P. palamedes*. All *P. palamedes* larvae placed on these hosts died with little or no eating and no frass production within a few days during the first larval instar stage, while survival and growth was very good on red bay, (*Persea borbonia*). The red bay survival for the neonates of six different families at Michigan State University was: 100%, 100%, 80%, 60%, 44% and 14% (n = 3, 2, 10, 5, 16, and 7 respectively). Similar results were obtained with sibling *P. palamedes* larvae from one mother larva bioassayed on each of the four treatment plant species in Florida at the Archbold Biological Station: 37 of 40 neonates reached the second instar on red bay and all neonates on the other 3 "bay" species died (n = 10 larvae each) without evidence of eating or feces.

In contrast, *Papilio glaucus* neonates all died (with no eating or frass) on red bay as well as on loblolly bay and bayberry. Sweet bay (*Magnolia virginiana*) was the only suitable host for these tiger swallowtail larvae in the Florida studies. All larvae on red bay (n = 16), loblolly bay (n = 16), and bayberry (n = 16) refused to eat and died, whereas 77 of 94 larvae (82%) survived to the second instar on sweet bay. Similarly, the smaller subset of eggs shipped overnight to Michigan had a 50% larval survival on sweetbay and 0% survival on each of the other species.

The 4-choice oviposition preferences of the adult females of *P. palamedes* favored red bay over the other 3 "bays" in 7 of 8 females that laid more than 10 eggs. The other female *palamedes* oviposited on the dish or paper lining more than all of the four "bay" choices together. A total of sixteen other females of *P. palamedes* laid fewer than 10 eggs each in their four-choice arenas and were excluded from analyses.

In contrast, five adult females of *Papilio glaucus* selected the sweet bay (the only suitable larval host) for the majority of their oviposition choices in the 4-choice arena (four of these selected SB for more than 93% of their eggs). A total of 28 other female *P. glaucus* laid fewer than 10 eggs.

All females (n = 9) of the Florida *P. troilus* refused to lay any eggs in the 4-choice oviposition arenas (five from Highlands County in the south and two each from Levy County and Columbia County in the north). While we were unable to bioassay *P. troilus* larval survival on the four "bay" species in this study, it was of interest that those females of the spicebush swallowtail all refused to lay any eggs, even with the (Lauraceae) red bay presented as one of the choices.

DISCUSSION

It was clear that not even sympatric Florida populations of the *palamedes* swallowtail butterfly could survive on three of the four "bays" of Florida: only red bay of the Lauraceae supported larval survival and growth. Neither sweet bay (Magnoliaceae), loblolly bay (Theaceae), nor southern bayberry (Myricaceae) were eaten in no-choice bioassays and all neonate larvae tested from six different families died. It has been shown previously that sweet bay was toxic to *P. palamedes* larvae (Scriber 1986) due to toxic neolignans from *Magnolia virginiana* leaves (Nitao et al. 1992) but nothing is known about the specific deterrent/toxin mechanisms for loblolly bay nor Southern bayberry.

It was also observed that larvae of Florida tiger swallowtail butterflies, *P. glaucus*, could not survive the neonate (first instar) stage on any of the "bays" other than *Magnolia virginiana* (sweet bay) of the Magnoliaceae. All larvae died on (and refused to even eat) leaves of red bay, loblolly bay, and southern bayberry in no-choice bioassays. The toxicity of red bay to *P. glaucus* was suggested earlier (Scriber 1986) but the phytochemical cause is still not known for this plant or the other two bay species bioassayed here. It is unusual that larvae of this polyphagous species refused to even nibble on the leaves since it is known that neonates often eat small trenches in the edge of toxic plants from many families (Hagen 1986, Scriber 1988, Scriber et al. 1991, Scriber et al. 1999).

Oviposition preferences of these two different *Papilio* were generally for the bay species that was the only suitable host (red bay for *P. palamedes,* and sweet bay for *P. glaucus*). The few scattered eggs on other plants is not surprising, perhaps because the experimental 4-choice oviposition arenas do not provide enough space to prevent co-mingling of volatile chemicals (e.g., stimulants and deterrents). Contact chemosensory stimulations are the key cues used by Lauraceae-specialized *Papilio* (Carter & Feeny 1999, Carter et al. 1999, Frankfater & Scriber 2001) and the deterrents in the Lauraceae (red bay) for *Papilio glaucus* females (Frankfater & Scriber 1999). These strong tarsal contact and oviposition stimulation/deterrency reactions to red bay phytochemicals could explain the dominant patterns of single host recognition and preference in our arenas. Adult preference and larval performance in these four bay species seem to be clearly related for both *P. palamedes* and *P. glaucus* for host or non-host. However, there are many ecological reasons why such a physiological and behavioral "preference/performance" correlation (whether or not genetically based) might not always be expected within a species (Thompson & Pellmyr 1991, Thompson 1995, Bossart & Scriber 1999). For example, Florida populations of *P. glaucus* survive better and grow faster than Georgia, Ohio, and Michigan populations on sweet bay, which reflects significant differences in behavioral and physiological adaptations of local populations (Scriber 1986, Scriber et al. 1991). It is interesting that, despite ecologically significant divergence among *P. glaucus* populations of these four states, no detectable genetic divergence in allozyme frequencies were observed (Bossart & Scriber 1995b).

The fact that *P. troilus* females refused to lay any eggs in the 4-choice oviposition arenas (even on red bay) is interesting, since most *palamedes* females did. In southern Florida, the only Lauraceous host plant for *P. troilus* appears to be red bay, *Persea borbonia.* However, throughout their geographic range north of Gainesville, *P. troilus* females prefer sassafras (*Sassafras albidum*) or spicebush (*Lindera benzoin*). Local larval adaptation of southern Florida *P. troilus* populations to red bay, their only host species in Highlands County, has been demonstrated to have a genetic basis (Nitao et al. 1991, Nitao 1995). Five of the nine *P. troilus* females were from Highlands County (four were from the north). Perhaps the recognition of red bay in the 4-choice oviposition array is less well developed for *P. troilus* in general compared to *P. palamedes,* especially since this is the case for larval survival and growth on red bay (Scriber et al. 1991, Lederhouse et al. 1992, Nitao 1995). Larval survival on red bay was 77% for *P. palamedes* (n = 30 families, 562 larvae) and only 47% for *P. troilus* (8 families, 119 larvae) while larval survival on spicebush is basically reversed; 28% for *P. palamedes* (20 families, 165 larvae) and 86% for *P. troilus* (7 families, 156 larvae; Scriber et al. 1991). For two other Lauraceae species, larval survival on sassafras (78% and 79%) and camphor tree (52% and 50%) is basically the same for *P. palamedes* and *P. troilus,* respectively.

Despite their close co-occurrence in Florida swamps, wetlands, hammocks, and forests, the four "bay" species from four different plant families analyzed in our studies are clearly recognized as host and non-hosts for *P. palamedes* and *P. glaucus.* Only red bay is a host for *P. palamedes* and only sweet (white) bay as a host for *P. glaucus.* When early literature records are incorrect, mistakes can be passed on from one to another (Shields et al. 1969). We believe this issue has largely been clarified for Florida "bays" (Young 1955, Mitchell & Zim 1964, Scriber 1984) by our oviposition and larval bioassays here.

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ON THE USE OF ULTRAVIOLET PHOTOGRAPHY AND ULTRAVIOLET WING PATTERNS IN BUTTERFLY MORPHOLOGY AND TAXONOMY

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ABSTRACT. In a series of feeding experiments we found that, depending on the larval food plant species or part of food plant ingested, individuals of the blue butterfly *Polyommatus icarus* (Lycaenidae) exhibit broad variation of wing patterns in the ultraviolet (UV) range of wavelengths which is invisible to humans. Such intraspecific variability in UV wing patterns has been underestimated thus far due to the rather demanding approach needed to study these patterns. We discuss methodological problems with the assessment of butterfly UV wing patterns by UV photography. Given proper standardization, UV photography is a suitable method to qualitatively assess UV wing patterns for possible use in morphology or systematics. Spectrophotometry should preferably be used as quantitative method when considering UV wing patterns in a communication context. No higher value should be attached to UV wing patterns as compared to human visible wing patterns.

Additional key words: *Polyommatus*, ultraviolet light, visual communication, color, phenotypic plasticity.

Ultraviolet (UV) wing patterns have been widely used in butterfly systematics. Differences in UV reflectance patterns of butterfly wings proved helpful in the revision of otherwise morphologically very similar taxa, such as the genera *Colias* (Ferris 1973, Silberglied & Taylor 1973, 1978, Kudrna 1992) and *Gonepteryx* (Nekrutenko 1964, Kudrna 1975, Brunton et al. 1996). Differing UV wing patterns were suspected to act as "isolating mechanisms" between closely related species, e.g., by Meyer-Rochow (1991) in *Lycaena,* or shown to be involved in mate choice of several species (e.g., Silberglied & Taylor 1973, 1978, Rutowski 1977, 1981).

Butterflies, in general, perceive UV light and UV vision is an integral part of their visual capabilities (Eguchi et al. 1982, Silberglied 1984, Lunau & Maier 1995, Tovée 1995, Kelber & Pfaff 1999). The same is true for many visually guided butterfly predators such as birds, lizards, and robberflies (Menzel & Backhaus 1991, Jacobs 1992, Fleishman et al. 1993, Tovée 1995). Therefore, UV coloration of butterfly wings has to be considered as an essential part of overall wing patterns in the spectral range of 300 nm to 700 nm, i.e., the entire range of visual communication (Endler 1990, Cuthill & Bennett 1993, Bennett et al. 1994b). Human observers cannot perceive UV light directly. This may be the reason why many researchers implicitly or explicitly attached an extraordinary meaning to the coloration of butterfly wings in the UV range of wavelengths as compared to the human visible range. In the New Zealand *Lycaena salustius* (Lycaenidae) species complex, for example, distinction of species based on human-visible wing patterns and morphology of genitalia is possible (Gibbs 1980), yet the discovery of marked differences in UV reflectance patterns was taken even as evidence to suggest the existence of UV wing pattern-based isolating mechanisms (Meyer-Rochow 1991; for another case study in the genus *Lycaena* see Schaider (1988) versus van Oorschot & de Prins (1989)). Human lack of UV perception, and the processing of visual stimuli in other animals by nervous systems which are completely different from our own, make it very hard for the researcher to imagine what the world may look like for other animals. But it seems as if the lack of UV vision in humans and many other mammals is the exception rather than the rule in the animal kingdom (cf. Tovée 1995).

In this paper we compare UV photography and spectrophotometry as methods for assessing butterfly UV wing patterns. In particular, we discuss some methodological problems with the assessment of butterfly UV wing patterns by UV photography. Finally, we point out an underestimate of individual variability in UV wing patterns which may result from such methodological problems as well as from the neglect of environmentally driven phenotypic plasticity.

MATERIALS AND METHODS

Feeding experiments. Mated females of *Polyommatus icarus* (Rottemburg, 1775) (Lycaenidae) were caught in summer 1997 at two locations in Northern Bavaria, Germany and allowed to lay eggs. Caterpillars used in this study were from the F1 or F2 generations of these females. All larvae were reared in the same climate chamber (25°C, 18 h light, 6 h dark). We kept the larvae in transparent plastic boxes (125 ml) lined with moist pa-

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per tissue. Fresh food plant material was available *ad libitum* and was supplied at least every two days. Food plants were either grown outside in a garden (*Medicago sativa* L. leaves) or collected locally from natural populations (flowers of *Trifolium repens* L., flowers and leaves of *Lotus corniculatus* L.) (all Fabaceae). We killed the emerging butterflies with either HCN or by deep freezing. We measured spectral reflectance of the wings of these specimens and took UV photographs.

Ultraviolet photography. UV photographs were taken with a Pentax Asahi Ultra-Achromatic-Takumar 85 mm/f 4,5 UV transmitting lens and Novoflex Auto-Bellows on Agfapan APX 100 film. To exclude all but ultraviolet light a combination of 3 mm Schott UG1 and 2 mm Schott BG38 filters was placed in front of the lens for UV photographs. Illumination was provided by two Metz Mecablitz 45 CT1 flash lights in manual mode so that the same amount of light was available for every exposure. Emission spectra of these flash lights reach far enough into the UV range for the purpose of this study (data not shown). Photographic processing and development of film material was standardized as much as possible. Films were developed for 5 min in 10% Agfa Neutol and fixed for 4 min in Tetenal fixing agent at 21°C.

To examine the effect of using different grades of paper on the appearance of prints to be used for comparing UV patterns, we produced prints on different grades of Agfa Broviro Speed glossy paper. These prints were then developed for 3 min with 10% Agfa Neutol and fixed for 15 min with Tetenal fixing agent at 21°C.

For purposes of comparison we took color photographs of all objects on Kodak Elite II 100 slide film. We used the same equipment as above but without the filters and with one flash light only.

Spectrophotometry. We measured wing reflectance with a L.O.T. Oriel spectrometer system (InstaSpec II diode array detector, MS 125 spectrograph with 400 l/mm grating, sighting optic) equipped with a Zeiss Ultrafluar 10/0.20 UV transmitting objective at a right angle to the wing surface. Measuring spot diameter was 0.2 mm, numerical aperture of the measuring beam was 0.14. The measuring spot was illuminated at an angle of 45° to the wing surface via liquid light guide by an Osram XBO 75 W/2 OFR lamp powered by a L.O.T. Oriel 68806 power supply. Numerical aperture of the illumination was 0.08. Wings were oriented so that they were all illuminated from the same apical direction. With this setup we were able to record spectral reflectance of individual wing spots in the range of 300 nm to 700 nm with a resolution of approx. 0.5 nm. A Spectralon™ 99 reflectance standard was assumed as having 100% reflectance. For further details of methods see Knüttel and Fiedler (2001).

RESULTS

UV patterns strongly varied in both sexes of the European common blue butterfly, *Polyommatus icarus* (Figs. 1, 2). We found consistent differences of UV reflectance among individuals that were fed different plant species or plant parts during their larval stages. Reflectance in the UV was much lower for animals reared on flowers of *Trifolium repens* and flowers or leaves of *Lotus corniculatus,* as compared to animals reared on leaves of *Medicago sativa* (Figs. 1, 2). These differences were most pronounced in the white spots (as seen with human eyes) but were apparent in the underside ground coloration, too (Fig. 1). Overall, judging from the UV photographs (Fig. 1), one might be tempted to assign highly UV-reflecting specimens reared on *M. sativa* foliage to a different 'species'. No differences in UV reflectance were found for the upper sides, the orange spots, and the black spots (Knüttel & Fiedler 1999).

Altering photographic processing had a strong effect on the appearance of the resulting prints, a phenomenon well known to any photographer. The influence of using photographic paper of differing grades is illustrated in Fig. 3. Even if processed from the identical negative using the same chemicals, the resulting prints of UV photographs may be quite different. We therefore included a calibrated gray scale, made from thick chromatography paper and dyed with various dilutions of black India ink, in every photograph. Spectral reflectance of the steps of the gray scale is illustrated in Fig. 4. Parts of a given photographic print that are of similar brightness, compared to the gray scale, will have a similar reflectance value (Figs. 1 and 3).

The differences in wing patterns in the UV range, among individuals reared on different plant species or plant parts, emerged from UV photographs and spectrophotometric measurements alike. However, more subtle or gradual host plant-dependent color differences could better be visualized in the reflectance spectra (Fig. 2). For example, only by studying the spectra is one able to identify the wavelength ranges where individuals reared on *M. sativa* foliage converge into the variation seen in individuals fed other food plants. Moreover, the small but consistent differences between food treatments in the human-visible range were also only noticeable using spectrophotometric measurement data.

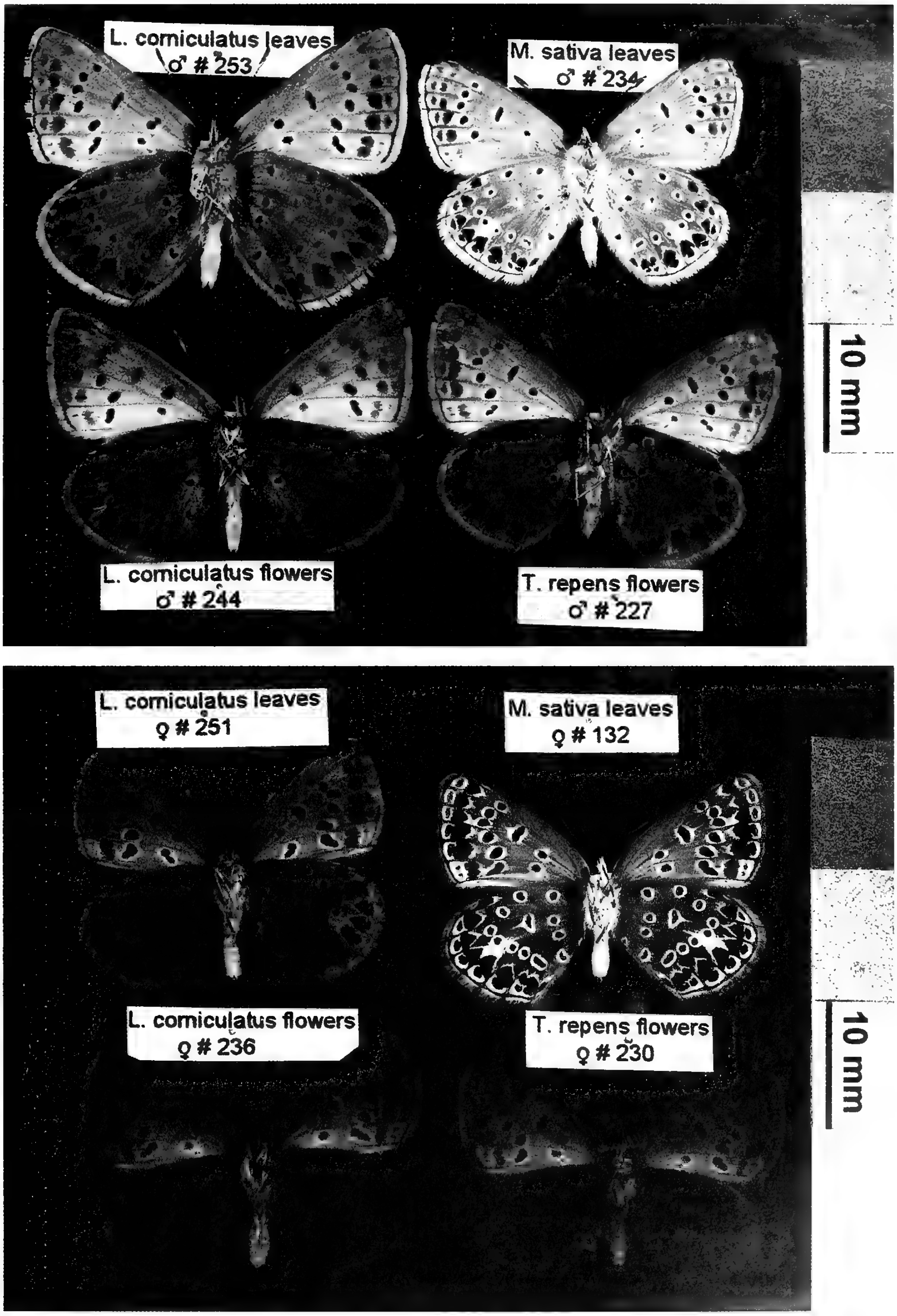

FIG. 1. UV photographs of the undersides of *Polyommatus icarus* reared on different food plants. Differences in UV patterns seen in these individuals are representative for larger series. Individuals were reared on leaves of *Lotus corniculatus* (upper left), leaves of *Medicago sativa* (upper right), flowers of *Lotus corniculatus* (lower left), and flowers of *Trifolium repens* (lower right). *Upper photograph:* males, *lower photograph:* females.

Discussion

1. Underestimate of individual variability in UV coloration

Butterfly systematists are well aware of the large extent of intraspecific variation in wing patterns and coloration within the human visible spectral range. In contrast, intraspecific variability in UV reflection patterns has been underestimated so far. We feel that this mainly arises from the difficulty in studying UV wing patterns, making the comparison of large series of specimens more laborious and demanding compared to patterns seen in the human visible range. Since in most studies UV photography applied to small samples was used to assess UV wing reflectance, subtle differences in UV reflectance of individuals may have frequently been missed.

Though only studied for a small range of butterfly species thus far, intraspecific variation of UV patterns may be as pronounced as, or even larger than that in other ranges of wavelengths visible to humans (Brunton & Majerus 1995, Knüttel & Fiedler 1999, 2001, this work). Yet, minor differences in UV patterns have been sometimes taken as evidence for erecting new species or subspecies (e.g., Nekrutenko 1968, Schaider 1988, but see van Ooorschot & de Prins 1989), or as a later confirmation of taxonomic hypotheses originally proposed on the grounds of other data (e.g., Meyer-Rochow 1991, Coutsis & Ghavalas 1996).

Differences in UV wing patterns may be due to genetic or environmental reasons, but only genetically determined UV wing patterns are of systematic importance. We demonstrated that high intraspecific variation in UV wing patterns in *Polyommatus icarus* can be caused by different larval food plants under otherwise identical rearing conditions among individuals from the same parents.

Flavonoids are a class of secondary plant compounds that highly absorb UV light (Harborne 1991, 1999). Some *Polyommatus* species sequester flavonoids from their larval food plants, and these pigments are deposited in the wings during metamorphosis (Wilson 1987, Wiesen et al. 1994, Geuder et al. 1997, Kornmaier 1999). Using artificial diets which only differed in their flavonoid content but were otherwise identical in their chemical composition, Knüttel & Fiedler (1999, 2001) showed that flavonoids sequestered by the larvae alter wing reflectance mainly in the UV range. In the polyphagous *P. icarus* the types and amounts of flavonoids that are taken up and stored by the larvae vary strongly depending on the larval food plants (Wiesen et al. 1994, Burghardt et al. 1997, 2001, Schittko et al. 1999). Therefore, it seems very likely that flavonoids are involved in mediating variation in UV wing patterns of *P. icarus* feeding on different food plants in nature.

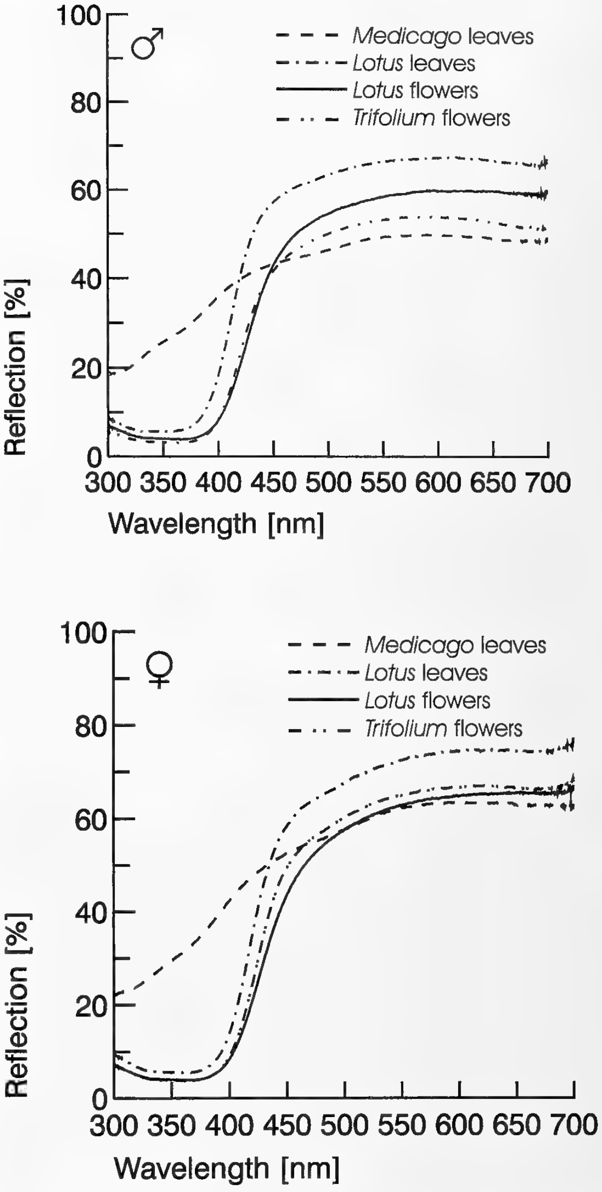

FIG. 2. Spectral reflection of the white spots of the undersides of the hindwings of *Polyommatus icarus* reared on different food plants. Each curve is the mean of the measurements of 5 to 10 spots of a hind wing of one of the individuals illustrated in Fig. 1. Individuals were reared on leaves of *Lotus corniculatus* (_ .), leaves of *Medicago sativa* (_ _), flowers of *Lotus corniculatus* (__), and flowers of *Trifolium repens* (_ _ . .). *Upper part:* males, *Lower part:* females. Conventions as in Fig. 1.

It is important to emphasize that intraspecific variability in UV reflectance in *P. icarus* appears to be caused by chemical variation in the host plants, while variation in UV reflectance may be caused by structural colors in other species (e.g., *Colias eurytheme* (Brunton & Majerus 1995)). UV pattern variation in *P. icarus* therefore must be regarded as a host-plant derived, environmentally shaped form of phenotypic plasticity, although heritable components cannot be fully excluded. As different food plant species or plant parts are of varying value as a food source to *P. icarus,* it seems likely that UV wing patterns may be used in intraspecific visual communication, indicating other food plant-derived properties of individuals, such as nitrogen content (Burghardt et al. 2001). Males of *P. icarus* discriminate between flavonoid-rich and flavonoid-free female dummies, preferring UV-absorbing, flavonoid-rich dummies (Burghardt et al. 2000, Knüttel & Fiedler 2001).

The differences shown here in the UV photographs (Fig. 1) and quantitatively demonstrated in the accompanying reflectance spectra (Fig. 2) very much resemble the differences in UV reflectance claimed by Coutsis & Ghavalas (1996) as characters separating *Polyommatus icarus* and the recently described *P. andronicus* Coutsis & Ghavalas, 1995. As differences of such magnitude can be found within one species and even among offspring of the same parents, they are unlikely to be sufficient to differentiate between species. No quantitative data on spectral wing reflectance are available for *P. andronicus,* and the range of individual variation has not been documented statistically. Therefore we cannot presently assess whether significant differences in UV patterns may exist between *P. andronicus* and *P. icarus.* However, based on the UV photographs in Coutsis & Ghavalas (1996) it seems unlikely that UV reflectance in *P. andronicus* falls outside the range observed in the highly variable species *P. icarus.*

2. Problems related to the technical visualization of UV patterns

As humans cannot see ultraviolet light, UV wing patterns must be translated into a form of information that is accessible to us. This must be accomplished by appropriate technical means. UV photography or UV videoviewing was chosen in most studies of UV wing patterns known to us (e.g., Ferris 1973, Rutowski 1977, 1981, Bowden & Kay 1979, Meyer-Rochow 1991, Kudrna 1992, Coutsis & Ghavalas 1996). Both methods yield comparable spatial pattern information but almost no spectral information. Ultraviolet light from a broad range of wavelengths is reduced to a single brightness value for every point or pixel in the picture. Usually the spectral response of the picture-generating system is unknown. Alternatively, wing reflectance can be measured by spectrophotometry (Ghiradella et al. 1972, Endler 1990, Brunton & Majerus 1995).

Both UV photography and spectrophotometry have advantages and disadvantages in their practical use. When selecting a method to study UV wing patterns the first step must be to answer the questions "What is the purpose of the study? What is it that UV patterns should actually tell me?" Not all studies have adequately addressed these questions. However, different conclusions may have to be drawn from the use of different methods. Therefore it is important to be clear about the purpose of the study before choosing the method.

UV patterns may be considered as a morphological feature like any other character. UV patterns result from wing areas that differ from each other in UV reflectance due to their physical and chemical constitution. There is no conceptual difference to the reflections or colors in the human-visible range. Therefore, UV wing patterns may be used as regular morphological characters in systematics, if they are assessed appropriately. For example, if individuals within a species exhibit substantial variation in UV wing patterns, such as we found in *P. icarus,* then UV wing patters may not be appropriate systematic characters. UV photography done in the right way (see below) seems a perfectly acceptable means for the description of UV wing patterns in this context.

On the other hand, UV wing patterns may serve as signals in a behavioral context. They may be important in mimetic or aposematic coloration (e.g., Beccaloni 1997) or in sexual selection (e.g., Brunton & Majerus 1995), to give examples. But it is not sufficient to simply assume that UV patterns do have a function, for example in mate recognition. This has to be proven in separate studies reaching farther than assessing differences in UV reflectance only. When considering the visual physiology of butterflies (e.g., Eguchi et al. 1982) or other visually guided species interacting with butterflies (e.g., Bennett et al. 1994a) it seems likely that UV light is important in the species' interactions. But this is so only because UV sensitivity is an integral part of these species' visual systems and is not a consequence of some putative special quality of UV light or vision in the UV range. The mere possibility that UV patterns serve a function in communication gives them no special or "higher" value in systematic reasoning (see e.g., Meyer-Rochow 1991, Brunton et al. 1996). The same is true when comparing UV patterns to human-visible color patterns.

To emphasize this point: There is no reason at all to assign a higher value to UV patterns than to human-

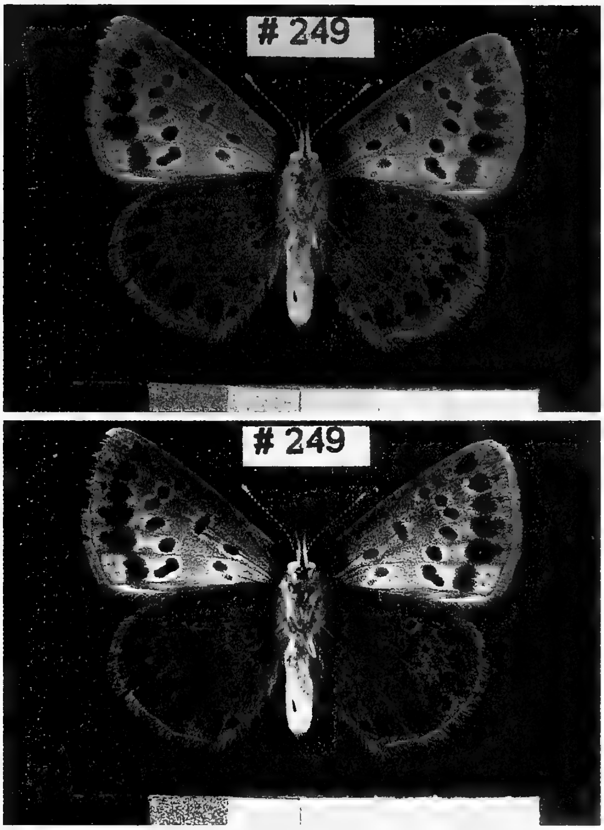

FIG. 3. UV photograph of the underside of one female *Polyommatus icarus* reared on leaves of *Lotus corniculatus*. Both prints were produced from the same negative but on photographic paper of differing grades and accordingly illuminated for different time periods. They illustrate the influence of a minor change in photographic processing. A calibrated gray scale (cf. Fig. 4) included in the photographs allows for a comparison up to a certain degree despite the different appearance of the prints. Width of a step of the gray scale is 5 mm. *Upper print:* Illumination for 5.5 sec, aperture 5.6 on grade 1 paper. *Lower print:* Illumination for 10 sec, aperture 5.6 on grade 5 paper.

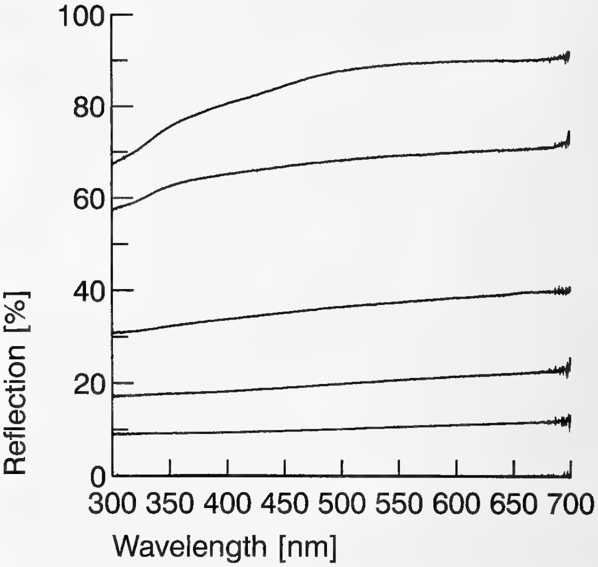

FIG. 4. Spectral reflection of the steps of the gray scale shown in Figs. 1 and 3. The higher the reflectance values the brighter the areas appear in the photographs. The curve for the darkest step almost falls in line with the abscissa. Mean spectral reflection for any given range of wavelengths may easily be obtained from the very flat, almost horizontal curves. The UV range is from 300 nm to 400 nm and the visible range is from 400 nm to 700 nm. *Abscissa:* Wavelength in nanometers. *Ordinate:* Reflection in %, i.e., the amount of light reflected at a given wavelength as compared to a white standard assumed to reflect 100%.

visible wing patterns. And there is no reason to presuppose a special function of UV wing patterns as a signal in visual communication.

More elaborate techniques must be applied when studying UV wing patterns as signals used in visual communication. Only when there are very strong differences, without intermediates in UV reflectance, will UV photography be useful in such a context. This might be the case when comparing wing patterns with and without strongly reflecting structural colors. However, even then UV photography will provide rather coarse qualitative results only and individual variability of UV reflectance may be missed (cf. Endler 1990, Brunton & Majerus 1995, this study). Variation in spectral information within the UV range that may be important in communication will also not be apparent with UV photography. For these reasons, in the study of communication or sexual selection (Bennett et al. 1994b), the method of choice is reflectance spectrophotometry. The whole range of 300 nm to 700 nm needs to be covered by the measurements, that is from the ultraviolet to the red. Comparison of obtained spectra can be done by appropriate statistical procedures (Endler 1990, Cuthill et al. 1999, Knüttel & Fiedler 2001). So far, for only very few species is information available on the physiology of photoreceptors and associated neurons. For these species a physiological model closer to the processes occurring in the organisms may allow to calculate a classification of colors. More details on the assessment of colors in animal communication systems may be found in the excellent works of Endler (1990), Cuthill and Bennett (1993), and Bennett et al. (1994b).

UV photography provides an easy method to assess the spatial distribution of areas of differing UV reflectance. Yet, in the majority of studies qualitative rather than quantitative results were obtained. This means that wing areas were mostly classified as UV-reflecting vs. not UV-reflecting. However, reflectance is a continuous measure that may not easily be assessed in discrete steps (cf. Fig. 2).

Moreover, comparisons between different photographs and/or studies may be difficult without proper standardization. Brightness and contrast in photographic prints depend on a number of parameters, not all of which might be under the control of the investigator. Important parameters that contribute to variation are amount and spectral composition of illuminating light, spectral transmission of photographic lenses and of UV transmitting filters, the film type, and all kinds of influences on photographic processing including printing during publication. Variation in the appearance of UV photographs may arise from a minor difference in photographic processing as illustrated in Fig. 3. Therefore, a detailed description of optical instrumentation, processing and film material should be given and, as a minimum standard, a gray scale of known UV reflectance should be part of every UV photograph. Such a gray scale will allow comparisons between photographs up to a certain degree because it provides a set of reflectance standards revealing intentional and unintentional differences in brightness or contrast between photographs (Figs. 1 and 3). This method is beautifully described in the pioneering work of Daumer (1958) on the UV patterns of flowers.

UV spectrophotometry yields very accurate quantitative data but requires expensive equipment not available to most systematists and a fair amount of computational data processing. Spectrophotometry is superior whenever spectral information will be required to answer biological questions. However, in contrast to UV photography, spectrophotometry will not provide easily comprehensible spatial pattern information. Hence, for taxonomic purposes where the recognition and documentation of qualitative similarities and discrepancies in wing patterns is usually the most important goal, properly standardized UV photography will continue to be the preferred method, though at the cost of loss of quantitative information.

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GENERAL NOTES

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LARVAL DESCRIPTION AND HOSTPLANT RECORD FOR *ITHOMIA DIASIA* HEWITSON (NYMPHALIDAE: ITHOMIINAE) IN PANAMA

Additional key words: pupa, *hippocrenis, Witheringia,* Solanaceae.

Despite the fact that butterflies in the genus *Ithomia* Hübner participate in well documented mimicry rings (e.g., Beccaloni 1997) and are therefore important players in community level interactions that characterize the Neotropics, information on their larval biology is scarce. All known *Ithomia* immatures feed on Solanaceae (Table 1, Brown and Freitas 1994, G. Beccaloni pers. comm.). We found no published host plants records for the remaining Central American species of *Ithomia,* and brief descriptions of immatures are available only for *I. patilla* and *I. heraldica* (see DeVries 1987).

On 18 February 1995 (dry season) we collected a fourth instar larva of *Ithomia diasia hippocrenis* Bates on *Witheringia asterotricha* (Standl.) (Solanaceae) on the Atlantic slope just below the Continental Divide near El Cope, Panama (800 m elevation). The range of *I. diasia hippocrenis* includes Panama and Costa Rica, and in Costa Rica it is distributed from sea-level to 1,400 m on the Atlantic slope, reaching greater abundance in the dry season (DeVries 1987). On 2 March 1995, an adult male emerged from the pupa, and was subsequently compared to specimens in the collection of the Natural History Museum, London (BMNH). The emerged male was similar to two specimens from highland Panama except for the black (rather than brown) triangular marking from the forewing costal margin to the distal end of the discal cell in the ventral surface of the forewing (see photograph of *I. diasia* in DeVries 1987). Of the 20–30 specimens of *I. diasia hippocrenis* at the BMNH, only one from Costa Rica also had the same black triangular marking, and we expect that this represents a rare variant of the phenotype.

The host plant, *Witheringia asterotricha,* occurs in moist upland forest, and the plants have a purplish appearance caused by purplish dendroid hairs on stems and leaves (visible in Fig. 2) and a bluish cast to the epidermis (D'Arcy 1973). D'Arcy (1973) considered *Witheringia asterotricha* to be a variety, of *W. solanaceae.* Hybrids of these two species are reported to occur in disturbed areas (D'Arcy 1973).

In the laboratory the larva was reared in a plastic container at ca. 23°C, and fed *ad libitum* on leaves that were kept in a plastic bag in the refrigerator. Note that developmental time in the laboratory is probably distinct from that in nature due to differences in temperature regime.

TABLE 1. Host plant records of *Ithomia* from Central America.

Species	Host plant	References
I. patilla	*Witherengia solanacea*	Drummond & Brown 1987
	Witherengia sp.	Drummond & Brown 1987
	Lycianthes multiflora	Drummond & Brown 1987
I. xenos	*W. cuneata*	Drummond & Brown 1987
	Acnistus arborescens	Drummond & Brown 1987
	Cuatresia riparia	Drummond & Brown 1987
I. iphianassa	*C. riparia*	Drummond & Brown 1987
	C. morii	Drummond & Brown 1987
	A. arborescens	Drummond & Brown 1987
I. celemia	*C. riparia*	Drummond & Brown 1987
I. diasia	*L. heteroclita*	DeVries 1985
	W. solanacea	Drummond & Brown 1987
	W. asterotricha	Srygley & Penz 2000

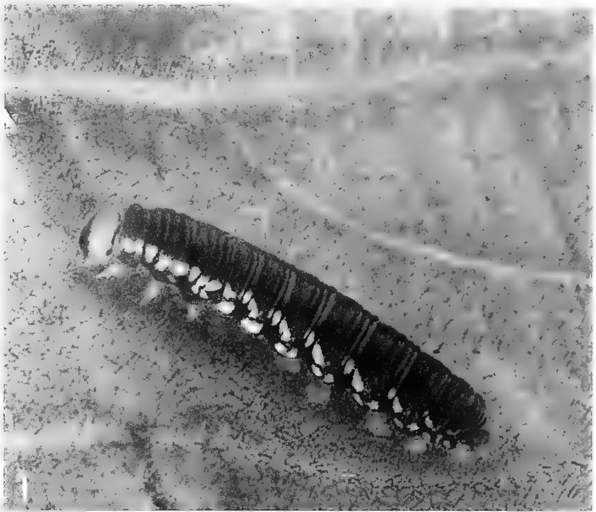

FIG. 1. Fifth instar larva of *Ithomia diasia* from Panama. FIG. 2. Pupa of *Ithomia diasia* from Panama.

Larva. *Fourth instar* (4 days, n = 1). Head light gray with a black transverse stripe that starts above front and ends below stemmata, stemmata black, mandibles brown; body translucent gray with broad, opaque, light gray markings across segments resulting in banded pattern; broken, longitudinal yellow spiracular line composed of color patches of uneven size; spiracles black; ventrally transparent (tracheal system visible); thoracic legs and prolegs translucent gray. *Fifth instar* (Fig 1, 3 days, n = 1). Head same as fourth instar although more translucent in color; body black with faint banded pattern on the posterior portion of each segment, three wrinkles across segments T2–A8; broken, longitudinal yellow spiracular line composed of color patches of uneven size; anal cap gray; ventrally translucent gray; thoracic legs and prolegs translucent gray.

Pupa (Fig. 2, 5 days, n = 1). Short, slightly compressed laterally, translucent green with patches of iridescent gold. Head with two small gold bumps just above eye; sutures of mouthparts and antennae dark brown; antennae with dark brown spots on each segment; T2 with gold dorsal keel and a pair of brown, dorso-lateral spots; gold patches laterally on T1–3; brown spots at the base and in the center of wing pad; four brown spots near distal margin of wing pad; T3–A8 with a pair of brown dorso-lateral spots; abdomen with gold dorsal midline band; large lateral gold patches on A1–3; spiracles brown; cremaster brown.

The broad black frontal stripe present in *I. diasia* fifth instar also occurs in other species of *Ithomia;* the broken sublateral band in the fifth instar and partially bent pupa are characteristic of the Ithomiinae tribes Ithomiini, Napeogenini and Oleriini (A. Freitas pers. comm.).

We thank G. Beccaloni for helping with identification of the adult, and G. Beccaloni and A. Freitas for commenting on the manuscript. Autoridad Nacional del Ambiente (ANAM) graciously granted permission to collect butterflies in the Republic of Panama. The adult voucher has been deposited in the Museo Fairchild of the Universidad de Panamá. This research was supported by the National Geographic Society (to RBS), a Smithsonian Tropical Research Institute (a pre-doctoral fellowship to CMP), and the National Science Foundation (NSF DEB-9806779 to CMP).

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BOOK REVIEWS

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INSECTORUM SIVE MINIMORUM ANIMALIUM THEATRUM: THE BUTTERFLIES AND MOTHS, by George Thomson. Published in 2000. Page size 7 3/4 by 11 1/2 inches. (2) + 66 pages, with numerous line illustrations and two colored plates pasted in. Hard covers, with dust wrapper. No ISBN, price £65 (approx $100). Limited edition, privately published by the author, and obtainable from Dr George Thomson, 2 Ravenhill, Lochmaben, Lockerbie, Scotland DG11 1QZ, UK.

Despite its many shortcomings, Thomas Moufet's *Insectorum Theatrum* is important as being the first entomology book to have been published in Britain, appearing in its original Latin version in 1634, and in English translation in 1658 although the original manuscript dates from the late 16th century. That the work is effectively the product of several authors, including Gesner, Penny and Wotton, is well known and has been widely discussed before, and we are fortunate that the original manuscript of the book is still extant in the British Library.

Thomson has here attempted to give an introduction to the book and its history, with a particular study of the adult Lepidoptera, which form only a small part of the whole *Theatrum.* He begins with a section on the manuscript and its origins, an account of Thomas Moufet and the other contributors, and a brief note on the illustrations. These are followed by the text of the English translation of the "Butterflies" chapter of the book, with the illustrations inserted in their correct places. Thomson has made useful comparisons of the mostly rather crude published woodcuts with the often very accurate and beautiful original paintings that are pasted in the margins of the manuscript. Each illustration is annotated with its modern scientific and common name, with a note on its occurrence in the original manuscript, the Latin text and the English text. After a brief bibliography a facsimile of the Latin version of the "De Papilionibus" chapter occupies 22 pages, and the book ends with a note about a butterfly specimen found between two pages of the original manuscript.

Although Thomson mentions that two chapters of Moufet's book contain many descriptions of lepidopterous larvae he does not include them, which is a sad omission as many could have been easily identified. He rightly states that the adults are not given names, but omits to state that many of the larvae *are* named, and they provide a useful insight into the origins of scientific names later given to some species.

The 82 forms described in the original work comprise 56 species, consisting of 30 moths, 25 butterflies, and one unidentifiable taxon. Five of the species are not found in Britain, although four of these occur elsewhere in Europe. The exception is the well-known North American *Papilio glaucus,* and a colored reproduction of John White's watercolour painting of this species forms a frontispiece to Thomson's book.

The historical sections of this book are all based on secondary sources, such as Lisney (1960) and Raven (1947), and, excellent though these books are, they are no substitute for more detailed works such as the study of Thomas Penny by W. Gardner (1930. A Lancashire entomologist in the time of Queen Elizabeth. *Transactions of the Lancashire and Cheshire Entomological Society* **1931**: 31–52) which is not mentioned here. Thomson's paraphrasing of secondary sources has led to ludicrous errors, such as stating that Moufet "accompanied Peregrine Bertie and Lord Willoughby to Elsinore" without realizing that these "two" men are one and the same!

Having described Rowland's English translation (published by Topsell) of the *Theatrum* as "somewhat inaccurate" and "rather poor" we might take this to mean that Thomson could have improved on it; however, he gives the translation in full without comment and we have to assume that his critical remarks on Topsell's edition are merely quoted from other sources.

This is a privately published book of 500 copies, well printed on good quality paper in an attractive binding, and it is inevitable that such a limited edition book will sell for a high price. However, readers expect a certain quality of content for their money and unfortunately this book falls into the familiar trap of many privately printed works in that it would clearly have benefited from professional editing. There are too many errors to list in this review; some are minor typographical mistakes but others cannot be so easily ignored and are very prominent. For example, the section on Theodore Mayerne bears the heading "Sir Thomas Mayerne", a name by which he was never known (this even appears in the contents list!). The two pages outlining Thomas Moufet's life have at least nine mistakes, and even the transcription of the Topsell translation contains a great many errors, with several misspelled scientific names (*Aglais* is spelled three different ways) and even the wrong authorship of one species (*Euphydryas aurinia,* mis-spelled *aurinea,* is attributed to Linnaeus rather than Rottemburg). Altogether I have noted over 60 errors in 42 pages of text (not including the facsimile section) which is unacceptably high in such an expensive book.

The final brief note on a butterfly found between the pages of the manuscript is accompanied by a colored illustration of the specimen. Thomson speculates on the possibility that the specimen may be contemporary with the manuscript, and he makes comparisons of the style of preservation with some known early collections such as that of James Petiver. Unfortunately he seems to be unaware of the published work on these collections, e.g., M. Fitton and P. Gilbert (1994. Insect collections. *In* A. MacGregor (ed.), *Sir Hans Sloane.* British Museum Press, London: pp. 112–122).

When I first picked up this book I had high hopes that it would be an original and stimulating work, but sadly those hopes have not been fulfilled. If the author had confined himself to describing the Lepidoptera in the *Theatrum* then this book would have had some value, but even then more care should have been taken with accuracy, and the inclusion of the larval chapters would have enhanced it considerably. But as a supposed historical study it has so many errors that it will be a disappointment to the expert, and potentially misleading to the novice.

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MICROLEPIDOPTERA OF EUROPE, VOLUME 2, SCYTHRIDIDAE, by Bengt Å. Bengtsson. 1997. Published by Apollo Books, Stenstrup, Denmark. 301 pp, 14 color plates, 419 text figures. Hard cover, 25 × 17 cm, ISBN 87-88757-11-0. Available from Apollo Books ApS, Kirkeby Sand 19, DK-5771, Denmark, fax +45 62 26 37 80, www.apollobooks.com. 550 Danish Kroners + postage.

Fifteen years ago, Bengtsson published a monograph of the Scythrididae of northern Europe (1984, *Fauna Entomologica Scandinavica,* v. 13), which treated a limited fauna of 33 species. With this new book, the second in the excellent series *Microlepidoptera of Europe*, Bengtsson has expanded his coverage to include the entire European fauna east of the Urals, the Mediterranean basin, Turkey, and the Canary Islands. The Scythrididae have thus been the object of two major works in the span of 15 years, both by the same author, which is rather remarkable for a family of (figuratively and actually) small and obscure moths.

The present treatment includes 237 species in 7 genera, with 40 species described as new. A number of new synonyms are also introduced. The book begins with a general introductory section with parts about Scythrididae morphology, practical hints for identification, genitalia preparation and collecting, biology, as well as brief comments on classification and geographical distribution of the family. This is followed with a checklist of all taxa treated with full synonymy, and then the systematic treatment, which makes up the bulk of the work. Individual species treatments include a diagnosis, a brief description of genitalia of both sexes, and a summary of known geographical distribution and biology. The host plant and biology of very few species is known. The geographical distribution of all species is conveniently summarized in a dense table placed at the end of the systematic section and lists occurrences by country; the table is useful albeit somewhat difficult to read with its 53 columns and 237 lines. The book concludes with an extensive reference list and an index to taxon names.

The most remarkable feature of the book is the 14 color plates, which present 258 superb watercolor paintings of adults (body and set right wings), painted by the author. Scythrids are rather dull-colored moths, many have dark brown coloration with a metallic sheen whose hue varies with the species and with the lighting, making these moths a real challenge to illustrate. The fine rendering of all subtle shades of greys, browns, beiges, off-whites as well as metallic hues is simply remarkable and attests to the great artistic talent of Bengtsson. I can only marvel at the countless hours that were required to produce all these watercolors, a benedictine labor of love.

The genitalia of all species are illustrated with line drawings (419 of them!). Many scythrid species are confusingly similar moths with strikingly different genitalia; conversely several species display a great amount of color variation depending on seasonality and region. Thus genitalia examination will be essential for species identification in many cases, unless one has a fair amount of experience with these moths and their subtle color differences. Curiously, however, the line drawings in this book are of a lesser quality than those produced by Bentgsson in his 1984 work on the northern European species. Generally, the drawings do not render the impression of depth and structural complexity exhibited by the genitalia of scythrids, although they display diagnostic features sufficiently well for species recognition, including arrows pointing at specific features on many. Most illustrations of male genitalia were drawn from standard flattened, dorso-ventral slide mounts, which are often inadequate for preserving the highly tri-dimensional, and fused scythrid genitalia because they result in a fair amount of distortion making interpretation of parts difficult.

A conspicuous omission in this otherwise fine work is an identification key. This is a significant deficiency considering the large number of species treated (237), most of which belong to the genus *Scythris* Hübner (204 spp.). Species are arranged into species-groups for which diagnoses are provided, but the user wanting to identify specimens has little choice but to wade through the entire set of illustrations to try to match specimens at hand, then go to the diagnoses to read diagnostic features. In some species-groups where similarities among species are high, the process is laborious.

The arrangement of the taxa is somewhat perplexing. On p. 14, paragraph 2, it is stated that species are arranged alphabetically which, although debatable in its value, is understandable. However, this is contradicted largely by the broad arrangement of the genus *Scythris*, by far the largest genus, for which the author states that a "logical order" was used to arrange the species. Actually, the alphabetical order is found only within species-groups. Bengtsson explains his so-called "logical order" as follows (bottom of p. 13): "In order to arrange species in a logical order, the author has based the classification on male genital structure together with the female genital structure and other characters when known." It is not clear what "logical order" means in biological classification.

The short section entitled "Systematics and classification" on pp. 13–14 explains the arrangement of taxa in the book. One is left with the impression that the author could have either expanded some of the points mentioned or omitted them altogether. For example, the statement that (p. 14) "Some of the remaining genera will probably be synonymized in the future when the whole world fauna can be analysed" is difficult to appreciate by the reader because there is little in the book itself to help evaluate this. Bengtsson also discusses his undocumented and unsatisfactory attempt at cladistic analysis: "In addition, species-groups are introduced, based on assumed synapomorphies or similarities of uncertain phylogenetic value. The author has used the computer program Hennig86 for analysis of the phylogeny, including a limited number of species at each evaluation. Starting with a complex and detailed data matrix the author has successively simplified the matrix until the most parsimonious tree structure approximately agreed with the intuitive opinion. Even so, the number of possible trees produced is very high.[. . .] . . . the phylogeny of the Scythrididae is extremely complicated. Instead of trying to utilise a systematic sequence in the present work, I have dealt with the species in alphabetic order." Because none of the data are presented, we are left with no basis to appreciate how the classification was developed. However, this is an academic point unlikely to bother the average user.

The English style is not always standard, being a little awkward in places and occasionally muddling the intended meaning or clarity, however, I did not find that this reduced the usability of the book. The book is of high quality, printed on glossy paper, clearly typeset, and has an attractive cover. The Smythe-sown binding allows the book to lay flat-open and will contribute to its durability.

Despite the criticisms expressed above, I can only praise Bengtsson for his accomplishment. I recommend unconditionally the book to any serious lepidopterist, if only because it provides a comprehensive treatment of a family for a large geographical region of the world and is part of a series (*Microlepidoptera of Europe*) that is akin to a counterpart of the *Moths of North America* (MONA) series.

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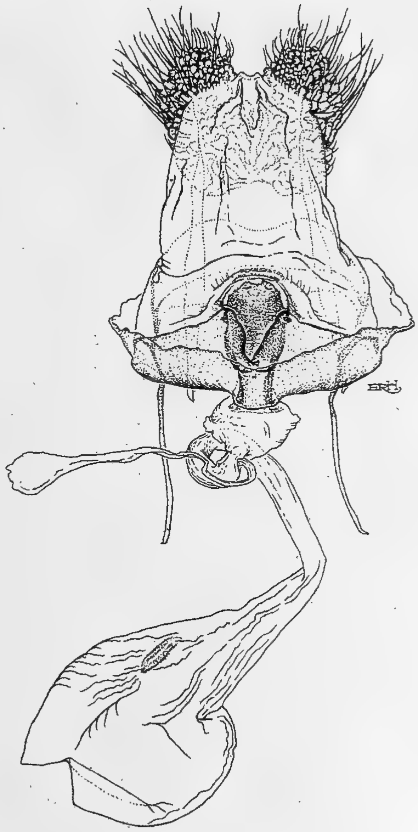

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PRESIDENTIAL ADDRESS, 2000: NOMENCLATURAL NONSENSE—FLYING IN THE FACE OF A FARCICAL CODE

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[The following is a modified transcript of the presidential address delivered at the annual meeting of the Lepidopterists' Society, Wake Forest University, Winston-Salem, North Carolina, 29 July 2000. The original title was "Everything You Always Wanted to Know About Nomenclature, But Were Afraid to Ask." You may recreate the mood of the banquet by waiting until late in the evening, eating a large meal, and drinking several glasses of wine before reading.]

The presidential address typically represents one of those points in the meeting when time . . . seems . . . to . . . stand . . . still, especially for spouses and others who have been coerced into attending the meeting, or at least the banquet. And you know who you are. Well, I'll try my best to be mercifully brief. But I'll warn you right now, you're going to have to pay attention because there are a couple quizzes during the talk and there's a test at the end.

Well, if you ask any biology student what the most boring and mundane topic is that he or she has had to endure as part of his or her undergraduate or graduate career, most will answer with little hesitation that nomenclature and/or taxonomy are absolutely the worst. I mean, what could be more boring than studying the rules, regulations, and recommendations governing the formation and use of scientific names . . . in Latin? Well, this evening I hope to demonstrate to you that although the study and practice of taxonomy and nomenclature may seem boring, it actually may be joyous, intriguing, fascinating, and entertaining . . . or at least not as boring as it seems. So, if I can have the first carousel we'll get started. Don't worry, there's only one carousel. Actually, there's only about 50 slides; so, if you want, you can keep track of how near we are to the end.

Well, before I get started, allow me to digress . . . but just briefly, of course. Well, nowadays everybody uses a software package called PowerPoint® to make spiffy slides for presentations (Fig. 1), and I'm no different. And when I'm preparing my slides for a talk, the first thing I do is try to match the subject matter of my talk and the type of audience with the appropriate background pattern or color scheme, and this can be quite challenging because PowerPoint gives you a ton of snappy templates upon which to build your presentation. So, for example, if my talk is going to be real sciency, I might use a template like Fig. 2, matching the intellectual quality and scholarly content of the presentation. To me this slide just reeks "Trust me, I'm a doctor, I know what I'm talking about." If my talk has a more evolutionary, ecological, or biogeographic bend, then I might use something like Fig. 3. Here we've got these green and yellow eco-colors going for us; and we've got this faint silhouette of a tree in the background. This template says "I'm concerned with the environment; I'm eclectic; I think globally." If my subject matter is going to be more high-tech, maybe using mathematical modeling or statistics (as if), I might use a template like Fig. 4—simple but contemporary. What I'm looking for here is a slide that says "Hey, I got 1600 on the math part of my SATs and I know a lot more about statistics than you do." Well, finally, if I'm just going to give a regular old talk to a diverse audience, I might choose a template like Fig. 5—sort of plain and unpretentious, kind of understated. Well, after carefully reviewing these and other templates, I selected Fig. 6. Here we've got this little bald guy up in the corner, obviously apprehensive about the subject matter of the talk, but we also have this confetti action going on here, indicating that we're going have a good time. Okay, now back to the talk.

Well, T. S. Eliot must have been a great lover of cats, as illustrated by his book *Old Possum's Book of Practical Cats* (Eliot 1939). And this is the first stanza of a poem from that book entitled "The Naming of Cats." And I'll read it to you.

The naming of cats is a difficult matter,
It isn't just one of your holiday games;
You may think at first I'm mad as a hatter
When I tell you a cat must have three different names.

Well if old T. S. had been a lepidopterist rather than a cat-lover, this poem may not have been that much different, and it might have gone something like this:

The naming of *moths* is a difficult matter,
It isn't just one of your holiday games;
You may think at first I'm mad as a hatter
When I tell you a *moth* must have *two* different names.

Actually, he might have left it as three if he had worked on butterflies . . . but we won't go there.

The beginning of the "modern era" of scientific nomenclature is typically defined by Linnaeus' classic treatment, *Systema Naturae* 10th edition, published in 1758, long before the time of T. S. Eliot. Linnaeus' consistent use of Latin binomials—that is two names, a genus and a species—for all organisms in *Systema Naturae* established it as the "starting point" for our modern taxonomy. If you think about it, its really pretty remarkable to have such a well defined milestone for any advancement in science, literature, or art. And probably because of this, Linnaeus has been dubbed "the father of modern biology"—so this binomial thing was really a pretty big deal.

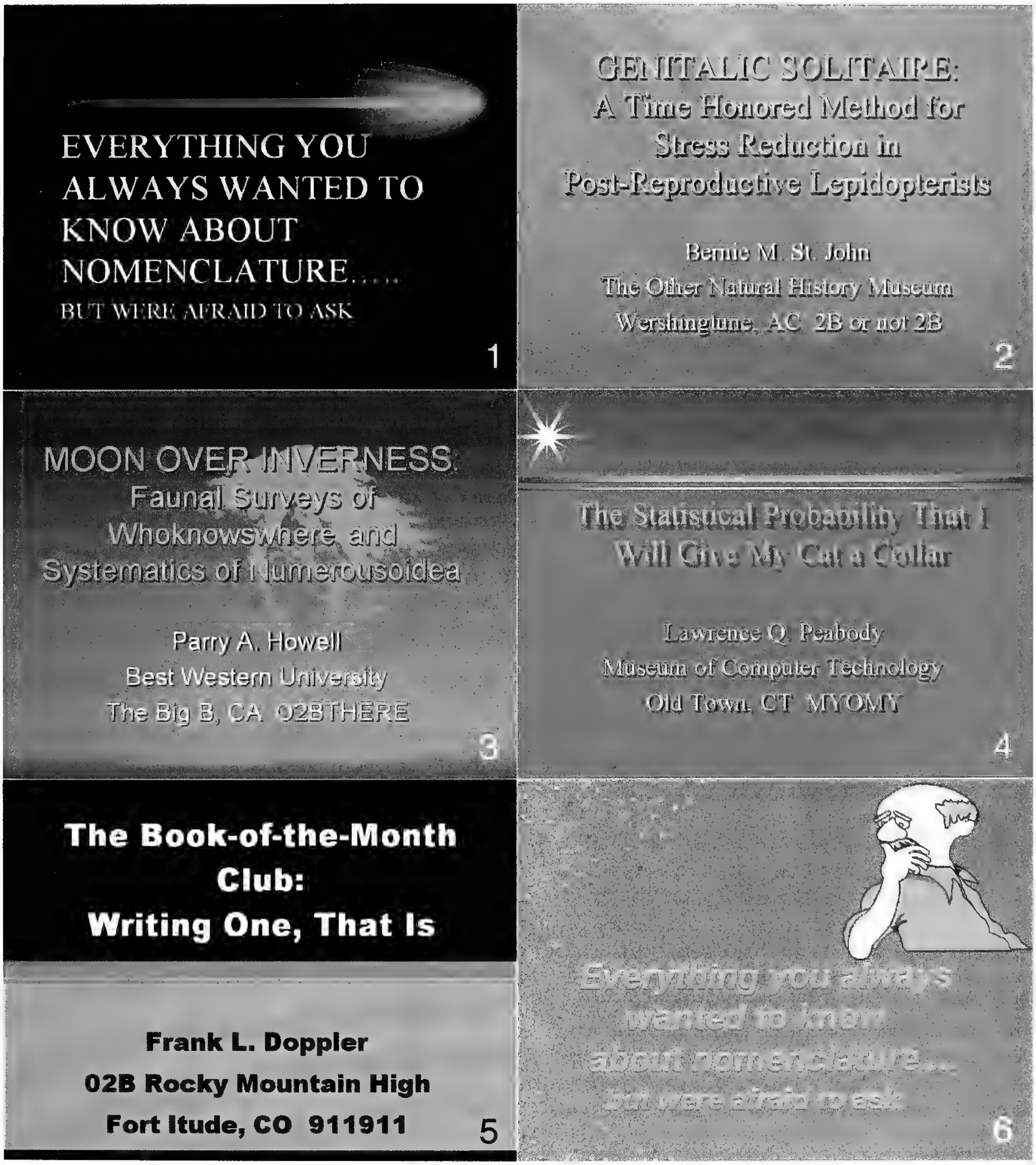
But as you can imagine, it took a while for everyone to get on-board with this two-name taxonomy; and it wasn't until 1905 that a group of systematists drafted the first set of rules to guide the use of scientific names: [Fanfare] The *International Code of Zoological Nomenclature.* Over the past 100 or so years, these rules have become more standardized and rigorous through successive editions of the *Code,* four in all. A new and improved version of the Code was published just last year. It's a little larger than the previous edition, and the cover is a little greener. I'm not exactly sure what the significance of the change in color is, but you can bet that it was a hotly debated issue, as are all issues associated with changes in the *Code.* We now have this complete *Code* clearly describing what constitutes a valid name; defining priority, synonymy, and homonymy; detailing what constitutes publication; and addressing a host of other complications that may be encountered. There is actually a Commission of Zoological Nomenclature that reviews proposals and makes decisions regarding specific cases of usage when controversy arises.

Scientific names are supposed to be Latin or at least "latinized," which is fine for those with a classic education that included Latin. But for some of us cretins whose only experience with Latin is pig-Latin (in grade school), conformance with this tradition may be a major chore. Fortunately, over the years our nomenclature has become contaminated with names of various origins, including Greek, Spanish, English, and so forth, some of which are described, even by their authors, as "arbitrary combinations of letters" and by their critics as just plain nonsense. These authors have paved the way for those of us with limited skills in, and knowledge of Latin to propose new names for animals that may not be ideal, but are recognized as valid, nonetheless. Well, finally we get to the purpose of this address, and that is to provide you with a brief glimpse into the rules and recommendations that apply to the naming of animals, not just cats, relying primarily, of course, on Lepidoptera. We're going to examine three areas: patronyms, synonyms, and inappropriate names. So here we go. [Slide of a playground slide] Hmmm. Well this is obviously the wrong slide.

Here we are. Let's start with Recommendation 25C: Responsibility of authors forming new names. "Authors should exercise reasonable care and consideration in forming new names to ensure that they are chosen with their subsequent users in mind and that, as far as possible [and this is the good part], they are appropriate, compact, euphonius [i.e., pleasant to the ear], memorable, and do not cause offence." Its this last phrase that I want you to remember for the test. Okay, here comes the meat.

WHAT IS A PATRONYM?

A patronym is a scientific name that honors a person by incorporating that person's name into the name of a genus, species, or subspecies. Here's one of the rules you need to follow. Article 31.1.2. "A species-group name . . . is to be formed by adding to the stem of that name 'i' if the personal name is that of a man, 'orum' if of men or man (men) and woman (women) together, 'ae' if of a woman, and 'arum' if of women . . ." This is one of the easiest ways to come up with latinized names for species, and I used it liberally when I started describing Lepidoptera about 20 years ago. For example, I named *Habrodais poodiae* for my wife



EVERYTHING YOU
ALWAYS WANTED TO
KNOW ABOUT
NOMENCLATURE.....
BUT WERE AFRAID TO ASK

1

GENITALIC SOLITAIRE:
A Time Honored Method for
Stress Reduction in
Post-Reproductive Lepidopterists

Bernie M. St. John
The Other Natural History Museum
Wershinglune, AC 2B or not 2B

2

MOON OVER INVERNESS:
Faunal Surveys of
Whoknowswhere and
Systematics of Numerousoidea

Parry A. Howell
Best Western University
The Big B, CA 02BTHERE

3

The Statistical Probability That I
Will Give My Cat a Collar

Lawrence Q. Peabody
Museum of Computer Technology
Old Town, CT MYOMY

4

The Book-of-the-Month
Club:
Writing One, That Is

Frank L. Doppler
02B Rocky Mountain High
Fort Itude, CO 911911

5

Everything you always
wanted to know
about nomenclature...
but were afraid to ask

6

FIGS. 1–6. PowerPoint slides illustrating templates for various types of talks (see text for explanation).

Poody Brown, *Mitoura thornei* for one of my early mentors (Fred T. Thorne), and *Euphyes vestris harbisoni* (hmm, three names, must be a butterfly) for another of my early mentors—Charles Harbison. In later years I even became clever enough to use the "orum" form, so this species, *Cuproxena duckworthorum*, is named for Donald and Sandra Duckworth. (Just sort of on the side, if your last name was Duckworth, would you name your son Donald? Isn't that a little like having the last name of Butterworth and naming your daughter Mrs.? Or having the last name of Wonderland and naming your daughter Allisen?) Anyway . . .

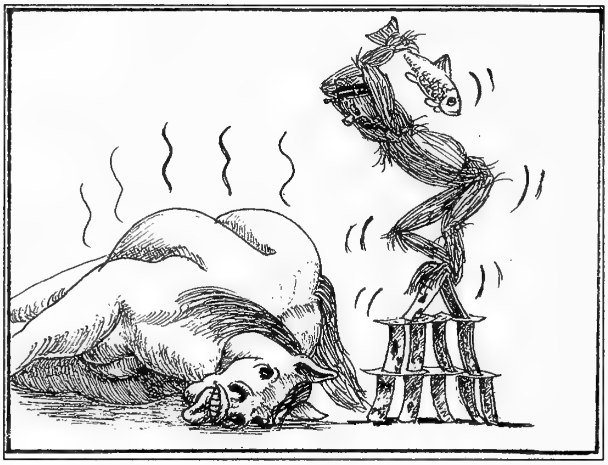


FIG. 7. Straw man on house of cards beating a dead horse with a red herring.

As your run-of-the-mill taxonomist, even I make a contribution to the study of tortricid moths from time to time. And once in a while some of our contributions are recognized by others in our field and they name a species after you. And here it is, my very own patronym—*Phtheochroa johnibrowni* Razowski, 1991—solid gold! This species was named after me by Josef Razowski—a *Polish* tortricid worker, wouldn't you know it. Actually, this is a pretty goofy-looking species name. Remember, you add an "i" to the end of a man's name, so with a last name like Brown, you shouldn't expect too many patronyms, if you get my drift.

Well, if you're one of those scientists who make **lots** of significant contributions, several people may name species after you. So for example, here's some of the Lepidoptera species named for Jerry Powell (Table 1), who is in our audience this evening. There are geometrids, and pyralids, and tortricids and all sorts of things. Well, if you're one of those scientists who makes lots of significant contributions and you're also really dead, there's virtually no end to the number of patronyms you may receive. Here's (Table 2) just the tortricid species named for Alex Diakonoff, a Dutch microlepidopterist whose work spanned the period from about 1940 to about 1990; he published over 250 papers on Lepidoptera, and he has a ton of things named after him.

Actually, I'll bet there are 15–20 folks here tonight with species named after them. I know there's one or more *leuschneri* (for Ron Leuschner), and we saw there are lots of *powelli*, and there's an *epsteini* and a *poguei*, but I think they're names of biting flies (ceratapogonids) rather than Lepidoptera, and there's a *millerorum* for Lee and Jackie Miller, and a *burnsorum* for John and Sarah Burns, and probably a whole bunch more that I don't know about. Okay, so we've got the concept of patronym nailed. So let's move on. But first, here's our first quiz. This quiz is for those young ladies in the audience 16 years or younger. Who is this devilishly handsome young lad? [Slide of Leonardo DiCaprio] [The voice of Astrid Caldas shouts out from the back of the room—Leonardo DiCaprio]. Okay. Any idea of his Latin binomen? How about *Homo sapiens*? Good.

TABLE 1. A few of the many Lepidoptera patronyms for Jerry Powell.

Coptodisca powellella Opler (Heliozelidae)
Gyros powelli Munroe (Pyralidae)
Stegea powelli Munroe (Pyralidae)
Pterotaea powelli Rindge (Geometridae)
Dorithia powellana Brown (Tortricidae)
Clepsis powelli Razowski (Tortricidae)
Henricus powelli Razowski (Tortricidae)

WHAT IS SYNONYMY?

When a species of animal has been described or named more than once, the names are said to be synonyms—that is, both (or all) names refer to the same species. This can happen in a variety of ways. For example, it can happen when different scientists name the same species because they are unaware of each other's work. But it also can happen when the same scientist names a species more than once from different specimens because he doesn't recognize that they represent the same species. And this typically happens when species are real variable, that is, no two individuals look alike, or when they exhibit strong sexual dimorphism, that is, males and females look different. Most of you are probably familiar with the California dog face butterfly—the male has been called the "flying pansy" and the female is a plain yellow butterfly, so they are remarkably distinct. Remember, a lot of us work on dead, pinned bugs in a museum, so we seldom get the chance to see interaction between the sexes (the Lepidoptera sexes, that is).

One of our greatest authors of synonyms in Lepidoptera was Francis Walker. And this is obviously a very dubious honor. Walker was paid by the British Museum to catalogue their Lepidoptera collection, and when he came across species that he did not recognize, to describe them. Actually, he was paid by the species. Well, apparently Walker did not have that great of an eye for species because he described many of them multiple times. For example, Mike Pogue tells me that in the noctuid genus *Spodoptera*, an ugly bunch of cutworms, Walker described 48 different species, placing them in 10 different genera. Of these

TABLE 2. The Tortricidae patronyms for Alex Diakonoff.

Bactra diakonoffi Amsel
Eucosma diakonoffi Gibeaux
Metaselena diakonoffi Horak & Sauter
Sycacantha diakonoffi Kawabe
Penthostola diakonoffi Kawabe
Statherotis diakonoffi Kuznetsov
Eboda diakonoffi Razowski
Tortricibaltia diakonoffi Skalski
Diakonoffiana Koçak
Diakonoffiana Kuznetsov

48 species, only 8 are recognized as valid today, so Walker is responsible for creating 40 synonyms in *Spodoptera* alone! Another example of Walker's keen eye is the species *Epiphyas postvittata* (Walker), the light brown apple moth, a leafrolling pest in many parts of the world. Granted, its pretty darn variable, and males look different from females. Walker described this species 9 times in three different genera—8 times in the same catalogue! All these names refer to the same species. And since a species can have only one unique name, only one is the correct name and the rest are synonyms, extra names that clutter the literature and cause confusion.

Now for a slightly more twisted example of synonymy, I'd like to tell you a little story about Edward Meyrick and William Kearfott. We'll start with Kearfott. William Kearfott was a physician who worked on American Tortricidae around the turn of the 20th century. And the names he proposed for new species are among those that are, well, shall I say, less than scholarly. Actually, Kearfott's names stand as a tribute to whimsy, whether intentionally or not. When faced with a large number of new species, most of us soon exhaust our imagination for names, leaning on old standard prefixes such as pro-, neo-, pseudo-, eu-, and so forth. Not Kearfott. Kearfott approached his new names in a very orderly fashion, apparently leaning heavily on his very thorough knowledge of the alphabet (you know, a, b, c, d . . .) and his keen ear for a good rhyme. Here are some real Kearfott species names (see Table 3): *bobana, cocana, dodana, fofana, gogana, hohana* . . .—stop me when you see a pattern. Well, for this set of names, Kearfott started a species name with every letter of the alphabet, except vowels, j, q, w, and x. So he got a lot of mileage from this one pattern—16 names. Here are more Kearfott names (Table 3): *fandana, gandana, handana, kandana* . . .; and who could forget the concise, euphonious, and memorable (Table 3) *gomonana, tomonana, vomonana, womonana, zomonana,* or *baracana, caracana, daracana, faracana, haracana, maracana, naracana, raracana,* and *yaracana.*

TABLE 3. A few of the many tortricid species names proposed by William Kearfott.

bobana	*dandana*	*baracana*	*gomonana*	*dana*
cocana	*fandana*	*caracana*	*tomonana*	*fana*
dodana	*gandana*	*daracana*	*vomonana*	*kana*
fofana	*handana*	*faracana*	*womonana*	*lana*
gogana	*kandana*	*haracana*	*zomonana*	*mana*
hohana	*landana*	*maracana*		*tana*
kokana	*mandana*	*naracana*		*vana*
lolana	*nandana*	*yaracana*		*wana*
momana	*pandana*			*zana*
nonana	*randana*			
popana	*sandana*			
rorana	*tandana*			
sosana	*vandana*			
totana	*wandana*			
vovana				
zozana				

Because Kearfott's (1904, 1907a, b, c) names were published in widely distributed scientific journals and his species were adequately described and diagnosed, his names are as valid as anyone's. Well I like Kearfott's names. Actually, they remind me of that song from the 1960's, by Shirley Ellis. [The voice of Don Harvey shouts out from the side of the room: "The Name Game."] Yes, exactly! And If I remember correctly, the first verse went something like: Shirley, Shirley, bope-early, banana, fana, fope-early, me, my, moe, merly, Shirley . . . or something like that. [Don nods in agreement.]

Well in contrast to Kearfott was Edward Meyrick, a no-nonsense, British school master that was a contemporary of Kearfott. Meyrick was quite the Latin scholar and probably the most prolific describer of microlepidoptera ever, describing over 14,000 species (Clarke 1955), all with well formed Latin binomials. You can just imagine his outrage and incredulity upon seeing the Kearfott names in a published journal. He surely must have thought that these unwashed, godless heathens in the colonies have no right naming new species if they can't do it correctly. Well, Meyrick responded to Kearfott's work with a paper called "On some impossible scientific names in Micro-Lepidoptera," published in 1912. In this paper Meyrick (1912a) described the Kearfott names as ". . . openly and obviously based on a barbarous and unmeaning gibberish." I like that. It kind of reminds me of something I've seen in reviews of my papers . . . .and at least one of those anonymous reviewers is probably in this room this evening. Meyrick totally rejected Kearfott's names and proposed new "appropriate" Latin names to replace them. Unfortunately, because the Kearfott names are valid, Meyrick did nothing more than create a ton of synonyms—new names for species that already have names. For Meyrick (1912b) the concept of priority,

TABLE 4. Names on final examination.

Eubetia Brown, 1999—valid
Eubetia bigaulae Brown, 1999—valid
Eubetia raz Brown—rejected
Eubetia boop Brown, 1999—valid
Phryganidia Packard, 1864—valid
Phryganidia steinbrenneri Miller—rejected
Polywana Brown—rejected
Polywana krakar Brown—rejected
Jerapowellia Miller, 1995—valid
Jerapowellia burnsorum Miller, 1995—valid
Dyaria Neumoegen, 1893—valid
Cephise nuspesez Burns, 1996—valid
Doa Neumoegen & Dyar, 1894—valid

that is, recognition of the oldest name as the valid name, was nothing more than a fetish of certain taxonomists of the time. So instead of saving nomenclature from the gibberish of Kearfott, Meyrick only cluttered it with useless names of his own. Okay. So that's the deal with synonymy. Time for a quick quiz. I'm going to show you the life history of a lepidopteran; and you'd better bask in it because they're the only photographs of Leps in the entire talk. As soon as you know the family, the genus, or the species, shout it out. Here's the egg; the first instar; the fifth instar; the pupa; and here's the adult. Oh, no....wrong adult! Here's the real adult. Everybody got *Papilio thoas?* Okay, our next and last topic.

WHAT IS AN INAPPROPRIATE NAME? WHAT IS TAUTONOMY?

Per the *Code,* inappropriate names are those that convey false information about a species or genus; for example, something like the name *gigantea* for the smallest member of the genus. Article 18 states: "The availability of a name is not affected by inappropriateness or tautonymy." So, here you can see that the *Code* does not dismiss these names just because they are stupid. Here's a few examples that sort of portray this concept.

Philotes sonorensis (Felder & Felder), the Sonoran blue butterfly. You might suspect that this butterfly is from Sonora. Nope—California. Well maybe it occupies the Sonoran Zone. Nope—it ranges from the coast to the mountains. How about *Ethmia arctostaphelella* (Walsingham). You might suspect that the larva of this feeds on *Arctostaphylos.* Nope—*Eriodictyon. Simmondsia chinensis* (Link) C. K. Schneid. This is the scientific name of jojoba, the plant that provides that fancy oil used in gucchi shampoos, which I use, of course (I thought it would be okay to use one plant name). From the name *chinensis,* you might suspect that it is from China. Nope—its native to Chile and California, not China. And *Decodes fragariana* (Busck). *Fragaria* is this genus of strawberry, so maybe this thing is a strawberry pest. Nope—its larvæ feed on oaks.

So how about tautonymy. Well, that's when the genus and species both have the same name. Its like if there was a man with the last name of William and he named his son William—he'd be William William, but I guess you could call him Bill, so that's a little different. Well here are a few tautonomous names: *Ozotuncus ozotuncus,* a tortricid moth described by the same Polish tortricid worker mentioned before. *Apus apus,* I haven't a clue what this is, but its always used as an example in the Code. *Rattus rattus* is one of those pesky European rats. And here's my favorite—*Bison bison bison* (three names; no its not a butterfly). It's not just a binomial tautonomy, it's a trinomial because there is a subspecies of bison in Europe. I really like this name because I can just image the first mammal taxonomist out there on the American prairie, creeping along on his hands and knees, peeking over a ridge and seeing this endless sea of American buffalo, and thinking to himself, BISON! BISON! BISON!

CONCLUSION

Well, there's just a few more sections of the *Code* that we haven't talked about, but I'll bet you now know plenty to take the test. And this is an oral examine, so you don't need a paper and pencil. Here's what I'm going to do. I'm going to present a bunch of proposed names, some of which are published and valid, and others of which have been rejected by manuscript reviewers for one reason or another. And you need to tell me which are which (See Table 4 for answers).

Here's our first question: the genus *Eubetia.* The Latin derivation is obvious, the "eu" means true or real, the "bet", Latin for wager or gamble, and the "ia" just for good measure. Anybody see a problem with this genus? Of course not, it's a fine generic name. So here are three potential species names in this genus: How about *Eubetia bigaulae?* Yes, this is a valid name. How about *Eubetia raz?* A sort of half-baked (i.e., one-cheek) or abbreviated patronym for the Polish tortricid worker Josef Razowski. No, offensive according to an anonymous reviewer . . . who happens to be in this room. How about *Eubetia boop?* Sure; although *boop* is not Latin, we can merely say that it is an arbitrary combination of letters; its short, euphonious, etc., and valid.

Now the next question: *Phryganidia.* I just love this one; it reminds me of something you might hear some taxi driver in New York shouting at you as you cross the street in front of him—"Hey, get outta da way, ya *Phryganidia!*" Anybody got a problem with *Phryganidia* as a valid name? Reasonable? Sure, its valid. So what if an avid baseball fan in New York wants to describe a patronym for George Steinbrenner and names it *Phryganidia steinbrenneri?* Would that be okay? No, I'm afraid this one was found unacceptable by a reviewer.

How about the genus *Polywana?* This name was proposed for a new genus in the tortricid tribe Polyorthini, a group that exhibits a Gondwanan distribution. Get it, Poly(orthini) (Gond)wana? However, the new genus would be represented by the single species *Polywana krakar.* Acceptable? No, both names were found unacceptable by a co-author with no sense of humor.

How about this genus: *Jerapowellia.* Here the author of the new genus has used both the first and last name of the honoree to make sure that no other Jerry or no other Powell can think that he is the person honored by the name. Actually, the animal is a nondescript little orange moth that nobody would want their name associated with anyway. Is this an acceptable genus name? Sure. How about if you add the species name *burnsorum?* How cow, now there's a frightening combination: *Jerapowellia burnsorum*—two Berkeley graduates united for perpetuity in the name of a tortricid moth. Acceptable? Yes, but in very poor taste (depending on your taste).

How about a new genus honoring the work of Harrison Dyar . . . . *Dyaria?* But what if it was intended to be pronounced "diarrhea"? Sure. Good name.

Well say you've got a new species of skipper butterfly, and all the good names in the genus already are used up. Could you name the new species "*nuspesez*"? Yes, and the culprit who perpetrated this atrocity also is in the audience this evening.

How about the genus D-O-A (*Doa*)? Sounds like every moth in my collection. [The voice of Ron Leuschner could be heard chiming in—"That's also a good name for a family."] Yes, this is a valid genus and actually the type genus for the family Doidae.

Well, I hope you've seen from this exercise that concepts like concise, euphonius, memorable, and offensive are really pretty subjective. And sometimes it seems as though the *Code* merely provides reviewers and editors with a justification to reject names that they don't like personally. And my interpretation is that some rules of the code are like this (see Fig. 7) . . . and this is called "Straw man on a house of cards beating a dead horse with a red herring." Well, there's little doubt that our *Code* will continue to evolve over time, let's just hope it evolves faster than the species for which it is intended to provide stable nomenclature. Thank you.

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INFLUENCE OF MOSQUITO CONTROL CHEMICALS ON BUTTERFLIES (NYMPHALIDAE, LYCAENIDAE, HESPERIIDAE) OF THE LOWER FLORIDA KEYS

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ABSTRACT. A 14-month survey was conducted in the rock pinelands of south Florida (Long Pine Key) and the Lower Florida Keys (Big Pine Key) to determine the status of three potentially threatened butterfly species. Populations of the Florida leafwing, *Anaea troglodyta floridalis* F. Johnson & Comstock, and Bartram's hairstreak, *Strymon acis bartrami* (Comstock & Huntington), were monitored in areas that receive year-round chemical applications for mosquito control and in those without such treatment. *Anaea troglodyta floridalis* maintained significantly higher adult densities during both years of the survey on transects where chemical applications were restricted. No significant differences were found in *A. troglodyta floridalis* larval densities among transects in either year; however, the overall larval density was significantly higher in the 1998 sampling period. *Strymon acis bartrami* showed consistently high adult and larval densities at all Big Pine Key transects, but was not observed in Long Pine Key. A third species, the rock-land grass skipper *Hesperia meskei* (W. H. Edwards), was not found on any of the survey transects despite a high density of its host grass, *Aristida purpurascens* Poir. (Poaceae). Experiments to test the potential toxicity of mosquito control chemicals on various surrogates of the above species showed naled and permethrin to be most toxic, with lethal dosage (LD_{50}) values of 1.0 µg or less of AI per gram of body weight for the species and stages tested. LD_{50} values of 48.1 µg or less AI per gram of body weight were found for surrogates treated with malathion. Given the susceptibility of these butterflies in all their life stages to the mosquito control insecticides presently in use, these chemicals should be considered a major factor in the populational declines and fluctuations of the butterflies studied.

Additional key words: *Anaea*, chemical pesticides, non-target arthropods, *Strymon*, *Hesperia*.

Human activity in south Florida and the Florida Keys has increased dramatically in recent decades. With year-round mild climate and scenic beauty, the area became an appealing place to live and visit. It was only a matter of time until this region's unique flora and fauna would feel the effect of human population growth. Among the first to be negatively influenced were the native butterflies. Although normally more appreciated for their aesthetic appeal, butterflies are also an extremely good indicator of an ecosystem's stability (Erhardt 1985, Longley & Sotherton 1997). *Anaea troglodyta floridalis,* the Florida leafwing F. (Johnson & Comstock) (Nymphalidae), *Strymon acis bartrami,* the Bartram's hairstreak (Comstock & Huntington) (Lycaenidae) and the rock-land grass skipper, *Hesperia meskei* (W. H. Edwards) (Hesperiidae) have enjoyed relatively large historic ranges, occupying the pinelands that once covered most of southern Florida and the Lower Keys (Minno & Emmel 1993, Smith et al. 1994). Their rapid demise in recent decades (Baggett 1982, Schwartz 1987, Hennessey & Habeck 1991, Schwarz et al. 1995, Salvato 1999) is representative of many species in the region and can be attributed in large part to habitat loss and mismanagement.

Another possible contributor to the decline of these butterflies is the use of chemical pesticides meant to control mosquitoes but with collateral effects on non-target arthropod species. The lethal effect of second-generation organophosphate pesticides, such as naled and fenthion, on non-target Lepidoptera was particularly well noted initially in south Florida and the Keys, with the demise of the Schaus' Swallowtail, *Papilio aristodemus ponceanus* Schaus (Emmel & Tucker 1991, Eliazar 1992). This species' dramatic decline in the early 1970s coincided with the expanded use of chemical pesticides by the Monroe County Mosquito Control District (MCMCD) on the northern Keys. When spraying was halted during two periods (1987 and 1989–1992), the species began to recover. Its immediate decline when applications resumed clearly suggested the adverse effect that chemical pesticides were having on non-target species. Baggett (1982) suggested that the rapid decline in *A. troglodyta floridalis* and *S. acis bartrami* populations on the Lower Keys was directly attributable to mosquito control insecticide applications.

Studies conducted by Hennessey et al. (1991, 1992) illustrated the presence of spray residue long after application in the habitat of the Schaus' Swallowtail and several other threatened butterflies, including *A. troglodyta floridalis* and *S. acis bartrami.* This research followed a joint agreement between U.S. Fish & Wildlife and MCMCD in 1987 on areas which were to be designated "no-spray" zones. Dade County did not spray insecticides for mosquito control during that time period. Thus the only chance for chemical contact on the southern mainland for these butterfly species occurs in the residential areas east of Long Pine Key, in Everglades National Park, where resmethrin is sprayed occasionally. As of 1989 the following areas in the Florida Keys were designated no-spray zones by agreement between U.S. Fish & Wildlife and MCMCD: in the north, a strip of land

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east of Crocodile Lake National Wildlife Refuge, Elliott Key, and several of the smaller keys of Biscayne National Park; and in the Lower Keys, the small outlying areas of the National Key Deer Wildlife Refuge. All of Big Pine Key except Watson's and eastern Cactus Hammocks is sprayed with the chemical pesticides naled, permethrin and *Bacillus thuringiensis* var. *israeliensis*.

However, no-spray does not mean a lack of chemical intrusion. These areas were established with the understanding that there was to be no use of insecticides, and any residues detected within them would be unacceptable. When these zones were created, pesticide drift downwind into them had not been documented. Hennessey et al. (1992) documented naled residues from the edge of Watson's Hammock on α-cellulose pads up to six hours after its application. The highest EEC recorded was $0.009 \pm 0.0001\ \mu g/cm^2$ as compared to $0.011 \pm 0.001\ \mu g/cm^2$ in the target area. Residues were detected 750 m into the no spray zone at Watson's Hammock, 150 m at Cactus Hammock and 30 m into the Schaus' hardwood hammock habitat on Key Largo's Crocodile Lake. Truck-applied ultra-low-volume (ULV) fenthion, sprayed primarily in residential areas, did not appear to drift into non-target areas. This study indicated that naled remained in the habitat well into midday, posing risk to diurnally active non-targets such as the Florida leafwing, rock-land grass skipper and Bartram's hairstreak.

Eliazar (1992) conducted intensive testing on the effects of the chemical pesticides naled and fenthion on several south Florida non-target nymphalid and papilionid species. His results indicated that chemical pesticides and their field application rates, particularly those of naled, were indeed extremely toxic to non-target Lepidoptera, and were being administered in the field at levels above the dosage required to kill target *Aedes* mosquitoes. Eliazar's naled experiments included several butterfly species likely to be found in the Lower Keys, including nymphalid species similar to the Florida leafwing. Among these were the gulf fritillary, *Agraulis vanillae* Michener, and the zebra longwing, *Heliconius charitonius* Comstock & Brown.

The potential influence of the pyrethroids, such as permethrin, which are currently used in the Lower Keys has only been evaluated for two butterfly species previously, *Papilio cresphontes* Cramer (Papilionidae) and *Vanessa caudui* L. (Nymphalidae) (Eliazar 1991, 1992). Furthermore, toxicity tests have never been performed to determine the effect of any chemical pesticide upon lycaenids, such as Bartram's hairstreak, or on hesperiids such as the rock-land grass skipper. Part of any recovery plan for these species must include evaluation of pesticide effects on populations. I conducted experiments on various life stages of non-threatened butterflies (congeneric to the three focal species here), to obtain lethal toxicity levels for exposure to naled, malathion and permethrin. Furthermore, I monitored populations of Florida leafwing, rock-land grass skipper and Bartram's hairstreak in the field, and examined the possible impact of chemicals being sprayed for control of adult mosquitoes in the Lower Keys.

MATERIALS AND METHODS

Population survey. A 14-month survey was conducted in south Florida and the Lower Florida Keys from July 1997 to August 1998. Line transects (N = 9) were established on Big Pine Key to monitor populations of *Anaea troglodyta floridalis, Strymon acis bartrami* and *Hesperia meskei.* The survey employed a combination of several butterfly count methods (Pollard 1977, Gall 1995). These were adapted to accommodate the sparse populations of butterflies associated with a consistently occurring host on Big Pine Key. Each transect was 400 m in length × 5 m in width (area 0.2 ha) (437 × 6 yards, or 0.5 acres); each had evenly distributed amounts of *Croton linearis* Jacq., the sole host plant for both *A. troglodyta floridalis* and *S. acis bartrami. Croton linearis* (N = 100) of varying sizes were randomly chosen within each transect and marked with flagging tape for larval inspection. These plants were surveyed at every visit during the course of the study. When plants died, new ones were included. Larvae and adults viewed at the fringes of designated transects were noted but not included in transect counts. *Aristida purpurascens,* the only known host plant for *H. meskei,* was inspected for larval activity. Transects were visited twice daily during late spring to early fall (April–August 1998, July–September 1997), and once daily the rest of the year (October–December 1997, January–March 1998) when daylight was more limited. This procedure allowed mainland and key transects to be visited on the same sampling dates. One transect was established at Gate 4 of Long Pine Key within Everglades National Park; it had the same dimensions as described above, but it was interrupted by a clear-cut area from historical logging times which mimicked grass savannah at its midpoint, and this clear-cut area was not considered part of the transect proper. Gate 4 at LPK was chosen because its pineland habitat is extremely similar to that of Big Pine Key. These two areas historically have maintained the largest populations of *A. troglodyta floridalis* and *S. acis bartrami* as well as moderate levels of *H. meskei.* The pinelands of Everglades National Park are not sprayed with chemical pesticides.

Anaea troglodyta floridalis and *S. acis bartrami* adults were captured by net and marked with the 1-2-4-7 numbering system (Ehrlich & Davidson 1960). *Hesperia meskei* was not observed within the transects at any point during the survey despite high density of its host. Plants which contained earlier stages were marked with field tape for later inspection; however, this technique was replaced by use of natural field markers whenever possible.

Adult and larval densities were transformed to the square root of (X + 0.5) and analyzed by ANOVA: Single Factor analysis in a completely randomized block design with all sampling dates and sites as sources of variance. Data from 1997 and 1998 were analyzed separately. All treatment areas were compared against controls (Watson's Hammock and Long Pine Key, the areas where insecticide applications are restricted). Where significant F values were found, Tukey's test was used to separate means.

Lethal dosage experiments. To help determine if mosquito control chemicals have a toxic effect on the various life stages of these potentially threatened butterfly species, lethal dosage levels were determined for similar, non-threatened butterfly species. The chemical insecticides used were malathion (O, O-dimethyl phosphorodithioate of diethyl mercaposuccinate; molecular weight = 330.4), naled (dimethyl-1, 2-dibromo-2, 2-dichloroethyl phosphate; molecular weight = 381) and permethrin ([3-Phenoxyphenyl] methyl-[+]-cis-trans-3-[2, 2-dichloroethenyl]-2, 2-dimethylcycopropane carboxylate; molecular weight = 391.3). Malathion and naled donated by the Division of Plant Industry (DPI) in Gainesville and DPI in Winter Haven, Florida, respectively. Permethrin was purchased from Chemserve (West Chester, Pennsylvania).

The Monroe County Mosquito Control District (MCMCD) applies naled, a second-generation organophosphate insecticide, by aircraft (DC-3 and helicopter) throughout the Florida Keys. Planes/helicopters fly at an altitude of 50 m (165 ft) with swath widths of 61 m (200 ft) (Hennessey et al. 1992). The field level of naled application by MCMCD is 0.08 kg (AI)/ha as a 4% mixture with No. 2 diesel fuel (vol/vol). Likewise, diesel fuel is frequently used by MCMCD in their ground based ULV fog mixtures of another organophosphate insecticide malathion and a pyethriod insecticide permethrin, so this substance was used as the control whenever possible to best simulate actual application conditions. Acetone was used as an alternate control when No. 2 diesel proved to be toxic to a test species. No. 2 diesel fuel was obtained from various gasoline stations and acetone was purchased from K-mart, both in Alachua County.

Test butterfly species and test procedure. The gulf fritillary, *Agraulis vanillae,* and the zebra longwing, *Heliconius charitonius,* were used as the experimental nymphalid butterflies to evaluate toxicity to topically applied mosquito control insecticides. Both species share similar habitat with *A. troglodyta floridalis* throughout south Florida. Larvae of both species were reared from eggs obtained at the Sanibel-Captiva Conservation Foundation (SCCF) in Sanibel, Florida, and from females reared at the Boender Endangered Species Laboratory in Gainesville, Florida. Developing larvae were fed a daily diet of *Passiflora* spp. leaves. Specimens were reared in plastic cups. Fifth instars and adults of both species were tested for toxicity of malathion and permethrin. Larvae were tested with treatment levels in logarithmic steps by applying one microliter (μl) of malathion or permethrin solution to the dorsum of the thorax with a Hamilton dispenser (PB600-1) fitted with a 25-μl syringe. Upon application, treatment groups were returned to their respective containers, provided fresh food, and monitored for 24 hours. Adult treatments were given in the same way. Adults were marked on the wing with colored ink to indicate the dosage used and released into a screen-enclosed flight cage at the Boender Endangered Species Laboratory or SCCF. These adults were provided with live flowering plants as a nectar source.

The Atala hairstreak, *Eumaeus atala* Rober, was used as a surrogate lycaenid butterfly in tests with mosquito control chemicals. Although *E. atala* is classified as a threatened species, large populations of the butterfly exist in parts of Dade County. One such area is Fairchild Tropical Gardens in Coral Gables. Here the larvae are considered a major pest of ornamental cycads, especially *Zamia pumila.* Early instars were obtained with permission on several occasions and reared to 5th instar for testing with naled and permethrin with the same techniques as those for the nymphalids. After treatment, adults were placed in small indoor cages for the test period, with each treatment in a different, labeled cage. Experimental survivors were brought to the SCCF for use in their butterfly enclosure exhibit.

The long-tailed skipper, *Proteus urbanus* (L.), and the tropical checkered skipper, *Pygrus oileus* (L.), are two hesperid species common throughout the pinelands of southern Florida and the Lower Keys. These species were tested as surrogates to determine the potential toxicity of naled and malathion toward *Hesperia meskei.* Larvae and adults of *P. urbanus* were collected from areas throughout Gainesville, Florida, where its host, beggar's tick, *Desmodium* spp., occurs. Additional *P. urbanus* specimens were collected in

TABLE 1. Comparison of mean adult *Anaea troglodyta floridalis* & *Strymon acis bartrami* densities per hectare at all transects for 1997 (29 sampling dates)–1998 (34 samples).

	A. troglodyta floridalis		*S. acis bartrami*	
Transect	1997	1998	1997	1998
Nature Conservancy	0.5	1.0	6.2	6.9
Lytton's Way	0.0	0.2	2.6	2.6
Watson's Blvd.	0.0	0.2	4.8	2.3
Blue Hole	0.0	0.2	3.6	2.4
Watson's Hammock	2.2	5.0	1.7	2.5
Key Deer Refuge North	0.3	0.6	5.0	4.6
Key Deer Refuge South	0.3	0.9	8.6	5.0
Coconut Palm	0.0	1.9	5.2	3.7
Ixora Drive	0.5	1.5	1.7	8.4
Long Pine Key, Gate 4	2.4	2.9	0.0	0.0

Alva, Florida at sites along State Route 78. *Pygrus oileus* larvae and adults were obtained from hollyhock in July and August 1998 from northeastern Newberry, Florida. The larvae of both species roll a silken tent on the leaves of their respective hosts, making them easily located. Larvae were tested by the above procedures. As with the lycaenids, adult hesperids were placed in individual cages after treatments.

Lethal dosage analysis. Determination of lethal dosage values for various surrogate species and stages of south Florida Lepidoptera were derived using an innovative experimental design created by Peter J. Eliazar (Department of Entomology and Nematology, University of Florida) (Eliazar 1992, Eliazar in press). Prior to each test, replicate larvae/adults were weighed to obtain an average instar/imago weight for each species before treatment. Mortality data were pooled for each species and stage tested, to provide a larger sample for analysis. Experimental LD_{50} values were then determined with a probit analysis program run through an Apple Macintosh Microsoft Excel Spreadsheet. This probit analysis program, created by Dr. James L. Nation (Department of Entomology and Nematology, University of Florida), was derived from the equations and discussion found in Finney (1964). Table values were taken from Busvine (1971). LD_{50} values of each species were divided by the average instar or adult weight of that species to derive an "LD_{50} per gram of body weight" value. For direct comparison of lethal dosages between larvae and adults, and for comparison of LD_{50} values for other lepidopteran species, the "percent volume-to-volume concentration per gram of body weight" value was converted into "micrograms of active ingredient per gram of body weight" (µg/g). The levels of active ingredient (AI) are 1510, 1186 and 26.9 micrograms per microliter of concentrate for naled, malathion and permethrin, respectively. See Eliazar (1992) and Salvato (1999) for a more detailed description of the testing protocol used in these experiments.

RESULTS

Adult survey results. A total of 131 adult *Anaea troglodyta floridalis* was marked and released during the survey period. Means per hectare at each of the ten transects for the 1997 portion ranged from 0.0 at four Big Pine locations (Lytton's Way, Watson's Blvd., residential sites, Blue Hole and Coconut Palm within the refuge) to 2.4 within the Everglades. The Watson's Hammock site maintained the highest density on Big Pine with 2.2 per hectare (Table 1). There was no significant difference (F-test, p = 0.05) in *A. troglodyta floridalis* density between the control sites. There were significant differences, however, between both these control sites and four treatment areas for 1997 (Tukey's test, p = 0.05), with lower butterfly density in these sprayed locations.

A total of 97 adult *A. troglodyta floridalis* was recorded on dates between 18 January and 29 August 1998 (Table 1). Means during this period ranged from 0.2 individuals per hectare at Lytton's Way to 5.0 at Watson's Hammock (Table 1). There was no significant difference between control transects (F-test, p = 0.05); however, there were differences between both controls and three of the treatment sites in 1998 (Tukey's test, p = 0.05).

A total of 407 *Strymon acis bartrami* adults was marked and released, 232 during the 1997 and 175 in the 1998 sampling periods. During the sampling dates of July and August 1997, far more individuals were observed than could be marked by a single surveyor; this combined with the few recaptures illustrates the large density of *S. acis bartrami* present. The 1997 sampling period revealed per-hectare population means ranging from 0.0 (at Long Pine Key) to 8.6 on the southern Key Deer Refuge transect (Table 1). This low *S. acis bartrami* density at Long Pine was significantly different from the Watson's Hammock transect (Tukey's-test, p = 0.05). Two other sites (Nature Conservancy and southern Key Deer Refuge, both are insecticide treated areas) were also shown to have a significant difference with both control transects, in these cases, however, butterfly density was much higher on the insecticide treated spots than controls.

Again in 1998, the low population for *S. acis bartrami* was at Long Pine Key where no *S. acis bartrami* were recorded, thus being significantly different from Big Pine Key control site at Watson's Hammock (Table 1). Ixora Drive had the highest density on Big Pine at 8.4; this site, as well as the Nature Conservancy site, were both significantly different in hairstreak density (higher) than either control.

TABLE 2. Comparison of mean larval *Anaea troglodyta floridalis* and *Strymon acis bartrami* densities per hectare at all transects for 1997 (29 sampling dates)–1998 (34 samples).

	A. troglodyta floridalis		*S. acis bartrami*	
Transect	1997	1998	1997	1998
Nature Conservancy	0.5	1.6	0.0	0.2
Lytton's Way	0.3	1.5	2.1	0.6
Watson's Blvd	0.0	0.3	0.7	0.2
Blue Hole	0.2	4.9	1.0	0.9
Watson's Hammock	0.0	3.7	0.5	2.2
Key Deer Refuge North	0.2	1.3	0.0	0.2
Key Deer Refuge South	0.7	1.3	0.5	0.3
Coconut Palm	0.7	4.1	1.2	1.0
Ixora Drive	0.2	3.1	0.4	1.2
Long Pine Key, Gate 4	0.0	1.9	0.0	0.0

Adult *Hesperia meskei* were observed during the course of this study, but not within the transects. These sightings, first reported by Dr. Thomas C. Emmel on Big Pine, represent the first documented observations of the rock-land grass skipper in more than twenty years. A female specimen was taken by Dr. Jaret C. Daniels and the author on Big Pine on 2 June 1998.

Larval survey results. *Anaea troglodyta floridalis* larvae became increasingly more common at all transects as the survey progressed. A total of 168 larvae of various stages were marked in the field, 145 of these on Big Pine Key. Sixteen were marked in 1997 (July–December), all at Big Pine locations (Table 2). Per hectare mean estimates for this sampling period ranged from 0.0 at three locations (Watson's Blvd., Watson's Hammock and Long Pine) to 0.7 at both the southern Key Deer Refuge and Coconut Palm transects (Table 2). The remaining 152 larvae were marked in 1998 (January–August). Densities ranged from 0.3/ha on the residential Watson's Blvd. to 4.9/ha at Blue Hole (Table 2). The highest larval density occurred on 18 May 1998 at Blue Hole, where 18 larvae were marked. As with the adults, larvae of the Bartram's hairstreak were plentiful on Big Pine during the summer of 1997, with a total of 37 larvae marked from July to December (Table 2). Lytton's Way maintained the highest per hectare density at 2.1, while Nature Conservancy, north Key Deer Refuge and Long Pine had none. However, in keeping with the decrease in adult density to mid-1998, the number of larvae also declined slightly to 31 for the 1998 portion of the census. Four locations supported no larval activity (Watson's Blvd., north–south Key Deer Refuge and Long Pine). The un-sprayed Watson's Hammock had the highest density for 1998 with 2.2/ha. No *S. acis bartrami* larvae were found at Long Pine Key.

There were no significant differences found in larval density between transects for *S. acis bartrami* larvae in either survey year. However, there were significant differences in 1998 for larvae of the Florida leafwing on four transects, with these higher densities on areas that are normally treated with chemicals. Extremely dry conditions dominated the final two thirds of 1998, this alleviated the need for insecticide applications.

LD_{50} results. Following the experimental design of Eliazar (1992), LD_{50} values obtained using probit analysis (Salvato 1999) were divided by the average weight for the instar/imago of each species to give a percent volume-to-volume concentration per gram of body weight value. These values were then multiplied by micrograms of active ingredient (AI) per microliter of liquid concentrate to give an LD_{50} value expressed as µg/AI per gram of body weight (Table 4). These treatments showed naled and permethrin to be the most toxic, with LD_{50} values of 1.0 g or less of AI per gram of body weight for the surrogate species tested. LD_{50} values of 48.1 g or less of AI per gram of body weight were found for surrogates treated with malathion.

DISCUSSION

Adverse effects of pesticides on non-target organisms depend not only on the concentration of chemicals applied, but also on the pesticides' persistence and availability to susceptible life stages of the organisms (Pierce et al. 1989). During these surveys, transects were established on Big Pine to assess not only potential differences in butterfly density between treated and untreated areas, but also to measure and correlate the potential differences between the impact of drift and contact from aerial and/or ground ultra-low-volume applications. If indeed upwards of 70–80% of aerially delivered insecticides are lost in the canopy, then the nature of that canopy, the needles of slash pine or the herbaceous layer itself; as a landing site for the spray droplets needed to be considered (Fairchild et al. 1987).

Although these butterfly species are multivoltine, their numbers experience their largest increase at the same time as the seasonal increase in the insecticide applications. The largest adult densities for *A. troglodyta floridalis* were in Watson's Hammock, the no-spray area, both years. Similarly, 2.7/ha was the mean density for *A. troglodyta floridalis* in the Everglades. Chemical insecticide applications, which had formerly involved resmethrin by airplane, have not been performed at this location in 30 years. Thus these sites were considered control areas for comparison with those on Big Pine that are currently treated. These remaining insecticide treated transects (N = 8) were further divided by the insecticide applications

TABLE 3. Type of mosquito control application with influence to each transect and mean adult densities (per hectare) for *A. troglodyta floridalis, S. acis bartrami* and *H. meskei* over 63 sampling dates during 1997–98 on Big Pine Key and Everglades National Park.

Transect	Aerial spray	Ground spray	*A. troglodyta floridalis*	*S. acis bartrami*	*H. meskei*
Nature Conservancy	X	—	0.8	6.6	0.0
Lytton's Way	X	X	0.1	2.6	0.0
Watson's Blvd.	—	X	0.1	3.5	0.0
Blue Hole	X	X	0.1	2.9	0.0
Watson's Hammock	—	—	3.7	2.1	0.0
NKDWR (N)	—	X	0.5	4.8	0.0
NKDWR (S)	—	X	0.6	6.7	0.0
Coconut-Palm	X	X	1.0	4.4	0.0
Ixora Drive	—	X	1.0	5.3	0.0
Gate 4 at LPK	—	—	2.7	0.0	0.0

that might impinge upon them (aerial swath of ultra-low-volume or thermal naled fog, ultra-low-volume spray of truck applied thermal permethrin fog, or both). A comparison of all three treatment scenarios revealed no significant difference in adult butterfly mean densities over the survey period as a result of application type (Table 3). In all cases, *A. troglodyta floridalis* density failed to exceed 1.9/ha (Coconut Palm transect 1998) during this study, on chemically treated transects. *Anaea troglodyta floridalis* would appear at greater risk overall from both types of application, due to the fact that it flies at all levels of the canopy, including perching high atop the slash pines.

All surrogate nymphalid species tested proved very sensitive to chemical insecticides applied for mosquito control. *Heliconius charitonius* was found to possess a high sensitivity towards permethrin with LD_{50} values of 0.002 and 0.0004 µg of AI per gram of body weight for the fifth-instar and adult, respectively (Table 4). This species appeared less sensitive to malathion. It must be noted that all values provided for *H. charitonius* indicate the species toxicity solely towards the insecticide. These studies, as with those of Eliazar (1992) found a 100% mortality rate for *H. charitonius* towards the No. 2 diesel fuel. Because of this toxicity to No. 2 diesel fuel, acetone was used as the control substance for treatments using this species. However, No. 2 diesel fuel appeared to have a less dramatic effect on the other nymphalid tested, *Agraulis vanillae*. When tested with malathion, *A. vanillae* indicated LD_{50} values of 6.7 and 8.5 µg of AI per gram of body weight for fifth instar and adult, respectively (Table 4). These malathion values, while not as low as those recorded for this species towards naled (from Eliazar 1992) and permethrin, can still be classified as extremely toxic.

Immature and adult Atala hairstreaks were found to be equally susceptible to truck applied ULV permethrin as well as the aerially applied naled. Given the extreme sensitivity of this lycaenid to both pyrethroid and organophosphate insecticides, it is likely that threatened species, such as *Strymon acis bartrami*, are at grave risk to these applications. Due to the fact that this species commonly aggregates on the low-lying shrubs along disturbed roadsides, areas frequently targeted by ULV truck spraying, this butterfly would appear most at risk to insecticide applications of this type. If this is truly the case, then the potential *S. acis bartrami* densities indicated in this survey, especially during the summer 1997 sampling dates, are only a fraction of what might have been attained.

TABLE 4. LD_{50} values (in micrograms of active ingredient per gram of body weight) for all surrogate test species.

Species/Stage	Naled (acetone)	Naled (diesel)	Malathion	Permethrin
Proteus urbanus				
3rd instar	0.0699	—	0.2603	—
4th instar	0.0439	—	8.912	—
5th instar	0.0296	0.0889	0.3045	—
adult	0.1892	0.3632	13.458	—
Pygrus oileus				
4th instar	1.021	—	—	—
5th instar	0.304	—	—	—
adult	0.0823	—	—	—
Eumaeus atala				
5th instar	—	0.0009	—	0.0009
adult	—	0.0012	—	0.0036
Agraulis vanillae				
5th instar	—	—	6.572	—
adult	—	—	8.515	—
Heliconius charitonius				
5th instar	—	—	8.127	0.0015
adult	—	—	48.087	0.0004

The lower density of *S. acis bartrami* within the non-chemically treated areas appears to be in response to an inconsistent burn agenda and a negative effect on host density due to this fire restriction. Bartram's hairstreak larvae are dependent upon fresh host growth for development, *Croton linearis* is the single host both for this butterfly and *A. troglodyta floridalis*. The adult hairstreaks appear to require consistently occurring host for larger densities and successful dispersal (Salvato 1999, in press). Neither of these requirements seems to be met within the areas of Watson's Hammock or Long Pine Key used for this study.

Hesperiid species maintain populations in virtually every ecosystem type found throughout the keys. Both hesperiid species tested showed the greatest susceptibility to naled, followed by the ULV malathion. Large densities of *Aristida purpurascens* are also located where they are directly threatened by ULV truck applications, and other large populations of the plant exist across the open grass savannah areas of Big Pine within the Refuge. These large clumps of *A. purpuras-*

cens have allowed *H. meskei* to be perhaps the most exposed butterfly of the three rock-pineland occurring species discussed here to the full array of insecticides used for mosquito control. *Proteus urbanus* was found to be extremely sensitive to naled, in both juvenile and adult stages. The area in which *Hesperia meskei* were located during this survey was one not frequented by ULV trucks, but one that was still likely exposed to the aerial applications. The drier conditions on Big Pine during the last eight months of 1998 resulted in fewer mosquito control insecticide applications. The new observations of adult *H. meskei* and the enormous increases in *A. troglodyta floridalis* larval and adult activity in normally treated areas could likely be the result of this reduction in chemical spraying. Contrarily, the dry conditions had a negative impact on *Croton linearis* blooms and density, which directly affected *S. acis bartrami,* over a time frame apparently so favorable to the other two butterflies (Salvato 1999, in press).

The toxicity of permethrin to *E. atala* and *H. charitonius* indicated in this study may be underestimates. Permethrin was prepared in an non-synergized form. Further studies with this insecticide and these butterflies will need to include piperonyl butoxide (PBO), the synergist added to most pyrethroid insecticides to increase the potency and residual effects and thus likely their toxicity to non-target organisms.

According to Matsumura (1990), an insecticide that produces an LD_{50} value that is less than 1 μg/g of body weight is commonly classified as extremely toxic; 1–50 μg/g is highly toxic; 50–500 μg/g is considered moderately toxic and a value between 500–5000 μg/g is only slightly toxic. Beyond this last level, the chemical is considered practically nontoxic to relatively harmless. In regard to the Florida leafwing, Bartram's hairstreak, and rock-land grass skipper, the chemicals currently being applied for mosquito control in the Lower Florida Keys can be considered extremely to highly toxic, depending on the surrogate species and stage tested. Given the results of the Hennessey et al. (1991, 1992), insecticide drift experiments in Watson's Hammock, it is likely that chemical applications play an important role in affecting the population size and behavior of these species.

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BIODIVERSITY OF PYRRHOPYGINE SKIPPER BUTTERFLIES (HESPERIIDAE) IN THE AREA DE CONSERVACIÓN GUANACASTE, COSTA RICA

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ABSTRACT. Twenty-two years of rearing 2192 pyrrhopygine caterpillars (and collecting far fewer adults) show that the Area de Conservación Guanacaste (ACG) supports at least 15 species, or some 60% of the Costa Rican pyrrhopygine fauna: 3 in (lowest elevation) dry forest—*Elbella scylla* (Ménétriés) [of which *E. dulcinea* (Plötz) is a **synonym**], *Mysoria ambigua* (Mabille & Boullet), and *Myscelus amystis hages* Godman & Salvin; 4 in (highest elevation) cloud forest—*Pyrrhopyge creon* H. Druce, *P. aesculapus* Staudinger, *P. cosyra* H. Druce, and *Passova gellias* (Godman & Salvin); and 10 in (middle elevation) rainforest—*Pyrrhopyge zenodorus* Godman & Salvin, *P. crida* (Hewitson), *P. cosyra*, *P. erythrosticta* (Godman & Salvin) [**lectotype** designated], *Parelbella macleannani* (Godman & Salvin), *Jemadia pseudognetus* (Mabille) [**reinstated status**], another *Jemadia* belonging to a *J. hewitsonii* species complex, *Myscelus belti* Godman & Salvin, *M. perissodora* Dyar [**reinstated status**], and *Passova gellias.* No species spans all three ecosystems, and none occurs in both dry forest and rainforest. The caterpillars are mostly 0.1–3 m above the ground, even when individuals of their foodplants rise 20–40 m. Except for *Myscelus* and *Passova*, the caterpillars are showy because they are ringed, barred, or spotted (with a row of large round dots) in contrasting colors. Pyrrhopygine caterpillars and pupae differ sharply from those of all other hesperiids in being long-haired.

ACG pyrrhopygines are strongly host specific, like other dicot-eating skippers (pyrgines) and certain butterfly and moth families in the ACG. (However, pyrrhopygines are more ecosystem-specialized than pyrgines.) Although ACG pyrrhopygine foodplants are dotted across the botanical taxonomic landscape (in the families Lauraceae, Clusiaceae, Flacourtiaceae, Cunoniaceae, Myrtaceae, Combretaceae, Meliaceae, Malpighiaceae, and Araliaceae), some patterns emerge. The three species of *Myscelus* plus *Passova gellias*, which are morphologically similar, all focus on Meliaceae (mainly *Guarea glabra* Vahl). Two-thirds of the reared species currently in the large genus *Pyrrhopyge* are monophagous to oligophagous on members of the Clusiaceae. At the same time, ACG pyrrhopygine caterpillars are specialists at levels far below that of the plant family: for each species of caterpillar, there are many ACG species of plants within the plant family fed upon that are not used. Moreover, within an oligophagous species, percentages of records among its few foodplants do not reflect the relative abundances of those plants. Host specificity seems to be geographically conservative: relatives of half of the ACG pyrrhopygine species were reared by Moss (1949) in Pará, Brazil, on plants that are usually in the same genera, and always in the same families, as those of their Costa Rican counterparts. The only pyrrhopygine to enter the USA, *Pyrrhopyge arizonae* Godman & Salvin [**reinstated status**], has an unusually drab adult but a gaudily ringed caterpillar, whose foodplant (*Quercus*) is in yet another unrelated family (Fagaceae).

Though attacked at times by ichneumonids, braconids, and tachinids, ACG pyrrhopygines are remarkably free of parasitoids. Despite slow larval growth rates (among the longest within the ACG hesperiids), pyrrhopygines are at the low end of the spread of larval parasitization frequencies—not just among skippers but among ACG macrolepidoptera generally: only 7.1% of all wild-caught pyrrhopygine caterpillars were parasitized. Most notably, not one of 295 caterpillars in the closely related genera *Myscelus* and *Passova* (the Meliaceae eaters) has yielded parasitoids.

Additional key words: caterpillars, foodplants, pupae, parasitoids, ecology, taxonomy.

Not once upon a time, but every day, a protected tropical wildland such as the Area de Conservación Guanacaste (ACG) in northwestern Costa Rica (Fig. 1) becomes more of an ecological island in an agrarian sea. Its biodiversity, derived mostly from what was there before the advent of European agriculture, keeps dwindling to a new equilibrium density of species. Some additional species may immigrate to the ACG or—given enough time—even evolve in situ, owing to the increasing insularization of the site. An inventory of its present biodiversity offers a baseline against which these changes can be measured.

Skipper butterflies (Hesperiidae)—along with the moth families Saturniidae, Sphingidae, and Notodontidae—have had special attention in the early years of the macrocaterpillar inventory of the ACG (Janzen & Hallwachs 2001). Here we treat the distinctive skipper subfamily Pyrrhopyginae, after rearing 2192 pyrrhopygine caterpillars of 15 species found over a 22-year period in ACG dry forest, cloud forest, and rainforest. Though the inventory will not have turned up every last pyrrhopygine species in the ACG, we think it has almost all of them by now.

Pyrrhopygines, whatever their taxonomic rank, are a monophyletic group (Ackery et al. 1999) of basically neotropical Hesperiidae ranging from the southwestern USA (southeastern Arizona and adjacent southwestern New Mexico, plus the Big Bend area of Texas) to northern Argentina (especially Misiones, but also Salta, Formosa, Chaco, Tucumán, La Rioja, Corrientes, Entre Ríos, and Buenos Aires [Hayward 1948]). While only one species extends northward to the USA,

TABLE 1. Foodplants and parasitization frequency of wild-caught pyrrhopygine caterpillars in the Area de Conservación Guanacaste (data source: Janzen & Hallwachs 2001).

Caterpillar species Plant family *Plant species*	Rearing records		% caterpillars attacked by			Total % parasitized
	n	%	Ichneumonidae	Braconidae	Tachinidae	
Pyrrhopyge zenodorus	541		0	3.7	3.0	6.7
Clusiaceae						
Vismia baccifera		99				
Vismia ferruginea		1				
Pyrrhopyge crida	14		0	0	0	0
Clusiaceae						
Vismia billbergiana		100				
Pyrrhopyge creon (1 found as pupa, 2 found as larvae not reared out but presumed to belong to this species)	3		0	0	0	0
Araliaceae						
Dendropanax gonatopodus		50				
Dendropanax querceti		50				
Pyrrhopyge aesculapus	4		0	0	0	0
Cunoniaceae						
Weinmannia wercklei		100				
Pyrrhopyge cosyra	353		12.1	0.2	5.4	17.7
Clusiaceae						
Chrysochlamys glauca		81				
Chrysochlamys psychotriifolia		1				
Clusia cylindrica		2				
Clusia minor		9				
Clusia rosea		1				
Clusia 13877		1				
Clusia 14104		5				
Pyrrhopyge erythrosticta	3		0	0	0	0
Clusiaceae						
Marila laxiflora		100				
Elbella scylla	137		0	8.0	0	8.0
Malpighiaceae						
Banisteriopsis muricata		7				
Byrsonima crassifolia		66				
Heteropterys laurifolia		2				
Hiraea reclinata		13				
Combretaceae						
Combretum farinosum		12				
Terminalia catappa		1				
Parelbella macleannani	59		0	0	2.0	2.0
Myrtaceae						
Eugenia basilaris		29				
Eugenia aff. *basilaris*		1				
Eugenia 13782		1				
Eugenia 14017		69				
Jemadia pseudognetus	31		0	0	0	0
Lauraceae						
Nectandra hihua		45				
Nectandra aff. *latifolia*		16				
Nectandra membranacea		16				
Ocotea cernua		7				
Ocotea insularis		3				
Persea povedae		13				
Jemadia sp. X	16		0	0	0	0
Flacourtiaceae						
Casearia arborea		100				
Mysoria ambigua	736		0	0.3	5.4	5.7
Flacourtiaceae						
Casearia arguta		4				
Casearia corymbosa		67				
Casearia sylvestris		11				
Zuelania guidonia		18				

TABLE 1. (continued).

Caterpillar species Plant family *Plant species*	Rearing records n	Rearing records %	% caterpillars attacked by Ichneumonidae	Braconidae	Tachinidae	Total % parasitized
Myscelus amystis hages	54		0	0	0	0
Meliaceae						
Trichilia americana		91				
Trichilia glabra		1				
Trichilia trifolia		8				
Myscelus belti	106		0	0	0	0
Meliaceae						
Guarea bullata		2				
Guarea glabra		37				
Guarea rhopalocarpa		14				
Guarea 14097		47				
Myscelus perissodora	1		0	0	0	0
Meliaceae						
Guarea glabra		100				
Passova gellias	134		0	0	0	0
Meliaceae						
Guarea glabra		88				
Guarea rhopalocarpa		1				
Guarea 13856		2				
Guarea 13860		1				
Guarea 14097		7				
Guarea 14137		1				

many extend southward into Argentina. Pyrrhopygines occur from sea level to upper elevation forests. Owing to their diurnal flight, flower visitation, large size, and showy patterns, plus the puddling and hilltopping behaviors of males, adult pyrrhopygines have been rather extensively collected; but their early stages are poorly known. Adults of these robust skippers are distinctive in having most to all of the antennal club reflexed. Both their dicot-eating caterpillars and the resulting pupae are the hippies of the skipper world; they are well endowed with long hairs—not just on the head but over the body as well (Figs. 2–28). We hope that this exposure of the pyrrhopygine caterpillars of the ACG, and this demonstration of their foodplant specificity, will stimulate further rearing in other areas.

MATERIALS AND METHODS

The inventory site. The macrocaterpillar inventory of the ACG (Janzen 1988a, 1993, in press; Janzen & Hallwachs 2001) began in the dry forest in 1978 and has gradually intensified and spread to adjacent rainforest and cloud forest (and all intergrades) (Fig. 1). ACG dry forest (about 60,000 ha) ranges from sea level to about 600 m across the Pacific coastal plain on volcanic, marine alluvial, and serpentine soils, and receives about 1.5 m of rain during the May–December 6-month rainy season, but essentially none during the dry season. It is a fine-scale mosaic of different successional stages (5–400 years of age) and scattered bits of old-growth forest (Janzen 1988b, http://www.acguanacaste.ac.cr). The cloud forest (about 10,000 ha) ranges from about 800 to 2000 m on three recent volcanos (Orosí, Cacao, Rincón de la Vieja) and receives 3–5 m of rain and frequent ground-level clouds, with distinct seasonality. It is mostly old-growth forest with some abandoned farms, ranches, and logging sites on both the Pacific and Caribbean sides of the volcanos. The rainforest (about 40,000 ha) ranges from about 400 to 800 m on the eastern and northern foothills of the three volcanos, even extending in a narrow band at about 800 to 1000 m around the western sides of the volcanos, and receives 3–4 m of rain, with a 1- to 3-month semi-dry season (February–May). It is a large-scale mosaic of old-growth forest, lightly logged forest, secondary succession, and abandoned farms and ranches (see http://janzen.sas.upenn.edu/caterpillars/RR/rincon_rainforest.htm for photographs of the cloud forest and rainforest).

Collection and rearing process. We report records through 1999 (along with a few critical recent records) from this ongoing inventory. Many methods of haphazard and patterned search by highly experienced resident paraecologists and parataxonomists have been used to locate caterpillars in all ACG habitats and ecosystems. The 2192 pyrrhopygine rearing records summarized here are part of some 120,000 wild-caught caterpillar rearings. Except in a few recent cases, pyrrhopygines were not explicitly sought but were found through general search for all macrocaterpillars on all species of plants. Wild-caught caterpillars were brought to rearing barns and reared individually, in foliage-filled plastic bags, at ambient temperatures (see photographs in Janzen & Hallwachs 2001). Pyrrhopygines were segregated for this analysis after completion of the rearing process. Each caterpillar rearing was recorded, and each species of caterpillar was usually photographed when first encountered (as well as later). These individual rearing records and some of these photographs are in the web site database (Janzen & Hallwachs 2001).

Parasitoid frequency (Table 1) comes from rearing wild-caught pyrrhopygine caterpillars of any instar in captivity. It is an underestimate of what occurs in nature because, once caterpillars are captured, they are protected from parasitoids. Parasitoids that oviposit in eggs or pupae are not considered here.

Adult pyrrhopygines were identified by Burns, who studied and compared genitalia of both sexes. This involved not only our reared individuals but also other museum material of the same species as well as similar, related taxa. Arriving at the best names for reared Costa Rican species sometimes required taxonomic minirevision. Caterpillars that failed to produce adults were identified by Janzen and an experienced team of 13 resident paraecologists and parataxonomists. In each case the identifier is specified in the database (Janzen & Hallwachs 2001). Species of ACG pyrrhopygines reared to date can be identified from their larvae and pupae (Figs. 2–25).

Series of conspecific adults reared by the macrocaterpillar inventory are pinned and spread, and many of the Hesperiidae are deposited as voucher specimens in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC, USA. Representative series are also being deposited in INBio (Instituto Nacional de Biodiversidad), Santo Domingo de Heredia, Costa Rica, and elsewhere.

Adult hesperiids were rather thoroughly but haphazardly collected throughout the ACG by Janzen and W. Hallwachs from 1978 to the present and, in a total of about 20 person-years of effort, by INBio and ACG parataxonomists from 1989 to the present. Furthermore, adult skippers were intensively collected by Dan L. Lindsley in 1998 and by Paul A. Opler and Evi Buckner in 2000. All this collecting has yielded no pyrrhopygine species that we have not reared. On the other hand, six of our 15 reared pyrrhopygine species have yet to be found as wild adults in the ACG.

PYRRHOPYGINE CATERPILLARS

Feeding behavior and growth rate. Pyrrhopygine eggs are laid singly near the margins of mature leaves, on the upper sides. If the foodplant grows in a sun/shade mix, the leaves chosen are usually fully insolated.

The first instar cuts a 5–7 mm diameter disc nearly all the way out of the leaf interior, or in from the margin, and silks the disc initially so as to fold it over on its hinge, and then so as to form a shallow cup tightly pressed to the leaf surface. As the caterpillar grows, it builds and abandons successive nests (or shelters), each larger than the last.

All instars live solitarily in their leaf/silk nests, venturing out at night to feed. In later instars the nest varies from a couple of overlapping leaves to several leaves silked together. The leaf nests of pyrrhopygines are among the most heavily silked of all ACG hesperiids. Of the ACG pyrrhopygines examined, *Pyrrhopyge cosyra* H. Druce and *Passova gellias* (Godman & Salvin) make the strongest and densest nests.

Pupation occurs in a leaf/silk nest, which is usually on the host plant and is usually the nest of the last instar. Occasionally a caterpillar makes its feeding and/or pupation nest with the foliage of a plant other than its host, generally when the foliage of the two plant species is interleaved.

Each species of ACG pyrrhopygine caterpillar is monophagous to oligophagous within a single plant family—or, in one case, two plant families (Table 1). (No laboratory trials were conducted to determine if the caterpillars can feed and develop on species other than those on which they are found in nature.) Because the ACG inventory of macrocaterpillars searches all species of foodplants and has been going on for 22 years, further search probably will not expand the plant lists for the caterpillar species in Table 1 except to add a few more closely related species within the genera or families already listed.

Pyrrhopyginae caterpillars are among the slowest growing of the ACG Hesperiidae (Table 2). As a group, they are conspicuously slower than Pyrginae and Hesperiinae. Their prepupal stage lasts 3–5 days, also among the longest in the ACG Hesperiidae. In no instance has a reared pyrrhopygine prepupa become quiescent or dormant in response to the dry season or some other inimical time of year (other large ACG hesperiids, such as the pyrgines *Epargyreus* and *Typhedanus ampyx* [Godman & Salvin], do so as one of their behaviors for passing part of the dry season). Once pupation has occurred, their rate of development (Table 2) is about the same as that of other hesperiids of similar body weight. In no instance has a pyrrhopygine pupa become seasonally dormant, though there are several cases where the pupal stage has lasted a few weeks more than expected. The cooler

TABLE 2. Life table traits for wild-caught pyrrhopygine caterpillars reared at ambient temperatures on the species of foodplants on which they were found, Area de Conservación Guanacaste (data source: Janzen & Hallwachs 2001). The prepupal stage lasts about 3 days, but the prepupa is not always located on its first day. A close approximation to pupal duration may be obtained by subtracting two days from the mean number of days between prepupa and eclosion. Extreme values are not included in the means.

	First instar to prepupa (days)			Prepupa to eclosion (days)			
Species	Mean	Range	n	Mean	Range	n	Extremes
Pyrrhopyge zenodorus	78	61–93	13	20.8	15–33	106	none
Pyrrhopyge crida	n/a	n/a	n/a	23.5	23–24	2	none
Pyrrhopyge aesculapus	n/a	n/a	n/a	33.7	31–36	3	none
Pyrrhopyge cosyra							
in Sector Cacao	104	92–137	21	31.1	24–37	91	52 (n = 1)
in Sector San Cristobal	125	106–160	8	23.9	19–27	59	none
Pyrrhopyge erythrosticta	n/a	n/a	n/a	18.0	18.0	1	none
Elbella scylla	89	82–96	2	19.1	17–22	35	none
Parelbella macleannani	141	139–144	3	20.4	17–28	21	none
Jemadia pseudognetus	133	127–139	2	25.4	22–28	11	none
Mysoria ambigua	45	41–47	3	19.7	17–28	129	34–48 (n = 4)
Myscelus amystis hages	51	51	1	16.6	15–21	5	none
Myscelus belti	81	64–117	5	22.9	16–26	67	35–51 (n = 3)
Myscelus perissodora	n/a	n/a	n/a	24.0	24.0	1	none
Passova gellias	68	51–95	10	21.1	15–34	50	none

the weather, the longer the pupal duration, as evidenced by *Pyrrhopyge cosyra* (Table 2).

Color pattern and hairiness. ACG pyrrhopygine caterpillars have one of two color patterns. The first is basically dark with strongly contrasting yellow to orange-yellow "rings" that are ventrally incomplete (Figs. 2, 3, 7, 8, 9, 12) or lateral, vertical bars (Figs. 5, 6, 10, 11) or, in one case, large, orange lateral discs (Fig. 4)—sometimes with red on the head and rump (Figs. 2, 3, 8, 9) and ventrally as well (Fig. 12). These pyrrhopygine caterpillars are thus part of an array of presumably aposematic, mimetic ACG caterpillars that involves hundreds of species, scores of genera, and virtually all families (see photographs in Janzen & Hallwachs 2001). The second pattern is dull green/pink with black to brown/red heads (Figs. 13–15), a seemingly cryptic color pattern shared with hundreds of other species of ACG macrocaterpillars. In contrast to many other ACG hesperiids (see Janzen & Hallwachs 2001), none of the pyrrhopygine caterpillars has false eye markings on the head.

All ACG pyrrhopygines in all instars have notably long hairs on both the body and the head. They are the only ACG skippers with long head hairs—except for the pyrgine *Astraptes fulgerator azul* (Reakirt) whose polymorphic caterpillars include one morph that superficially resembles the yellow-ringed pyrrhopygine caterpillars figured here (but *A. f. azul* lacks long body hairs). Pyrrhopygine pupae are hairy over much of the body and are often brightly colored (Figs. 16–25). Unlike the caterpillars, the pupae of several pyrrhopygines have conspicuous false eye markings, which will be treated in a future study of this phenomenon across all Hesperiidae (see Janzen & Hallwachs 2001).

SPECIES COMMENTARY ON PYRRHOPYGINES OF THE ACG

In the course of reviewing the skipper fauna of the world using the matchless holdings of the British Museum (Natural History), Evans became overly enamored of the polytypic species concept and applied it far too freely. In the brief introduction to his treatment of the skippers of Europe, Asia, and Australia, Evans (1949:xi) observed that

> In accordance with modern ideas, as expressed in books such as Mayr's [1942] *Systematics and the Origin of Species*, as wide a view as is possible has been taken of a species. Whenever a form in one area can be considered as replacing a form in another area, the two are presumed to be conspecific, even though the differences in facies, structure and genitalia appear considerable. The bringing together of subspecies in this manner presents no great difficulty through the Malay Archipelago and the South Sea islands; for instance, the variations of *Tagiades japetus* [(Stoll)] can be traced all the way from Ceylon to the Solomons and compared with those of other similar species flying with it. In continental areas, such as China and Malaya, it is not always easy to decide whether two forms flying together are species or overlapping sub-species of the same species. There are difficulties also in the islands. For instance, in Borneo there seem to be unduly numerous forms of the genus *Telicota*, due perhaps to migrations or infiltration from Java, Timor or the Philippines, and it is difficult to decide whether a particular series, differing slightly in genitalia and facies from another series, represents a species or a sub-species or perhaps a migration, which will become submerged in due course by the dominant form in the island.

Evans used the same philosophy in his subsequent treatments of pyrrhopygines (Evans 1951) and the rest of the New World skippers. Although Evans's distributional data were incomparably rich, they were incomplete. Because of this, because of his cavalier tolerance of sympatry between subspecies, and because he pushed to finish cataloging all the skippers on earth before he died, he frequently lumped separate species as subspecies of a single species. On finer analysis, his polytypic species often turn out to comprise one or more superspecies (e.g., Burns 1964) or species groups—or even a distinct genus (Mielke 1995). We know that allopatry, parapatry, or slight sympatry of closely related species is frequent. What Evans called subspecies are sometimes nothing more; but, for the reasons given above, they should be reexamined whenever possible.

Pyrrhopyge zenodorus Godman & Salvin

According to Evans (1951), *Pyrrhopyge zenodorus* is one of 10 subspecies of *P. phidias* (Linnaeus). However, especially on the basis of genitalic comparison (Godman & Salvin 1893:pl. 73, fig. 3, Bell 1931:fig. 10, Evans 1951:fig. A.1.2), *P. zenodorus* is a species in its own right, ranging from central Mexico to Costa Rica, at least.

While the caterpillars of *P. zenodorus* are moderately common in the ACG rainforest, neither caterpillars nor adults have been found in the dry forest, even though patches of the food plant, *Vismia baccifera* (L.) Triana & Planch. (Clusiaceae), are scattered through it in moist places. This apparent absence from dry forest is supported by the fact that the conspicuous caterpillar nests have not been found there either. A *V. baccifera* leaf is dark green above and bright rusty beige below so that, when the caterpillar cuts a section and folds it up and over, the resulting nest is a bold fingerprint that lasts for many months. Even where caterpillars are found, adults are not usually seen. They rarely have been encountered visiting flowers of *Stachytarpheta jamaicensis* (L.) Vahl (Verbenaceae) at the intersection of ACG dry forest and rainforest (in the Río Gongora region).

The adult of *Pyrrhopyge zenodorus* (Fig. 2), which is blue-black, white-fringed, and red-orange on both its head and rump, looks enough like the unrelated *Passova gellias* (Fig. 15) to be indistinguishable from it in flight (unless one can detect the marginal pale blue on the dorsal hindwing of *P. gellias*). In flight, *Pyrrhopyge zenodorus* superficially resembles one other ACG rainforest skipper, the pyrgine *Phocides palemon lilea* (Reakirt) (which, however, has a small red bar at mid-costa of the forewing both above and below and lacks the red-orange rump that gives *Pyrrhopyge* its name).

The caterpillar of *P. zenodorus,* which is ringed brightly with orange-yellow (Fig. 2), superficially resembles those of at least 12 other ACG rainforest skippers (Janzen & Hallwachs 2001), but none of these feeds on *Vismia baccifera: Pyrrhopyge crida* (Hewitson) (Fig. 3), *P. cosyra* (Fig. 6), *P. erythrosticta* (Godman & Salvin) (Fig. 7), *Parelbella macleannani* (Godman & Salvin) (Fig. 9), *Jemadia pseudognetus* (Mabille) (Fig. 10), another *Jemadia* belonging to a *J. hewitsonii* species complex (Fig. 11), *Phocides palemon lilea* (penultimate instar), *Polythrix caunus* (Herrich-Schäffer), *Astraptes fulgerator azul, Nascus broteas* (Cramer), one of two species currently going under the one name *Nascus phocus* (Cramer), and *Achlyodes busirus heros* Ehrmann. The highly similar caterpillars of *Pyrrhopyge zenodorus* and *P. crida* are most readily distinguished by knowing what they were found on (*Vismia baccifera* and the foodplant of *P. crida, V. billbergiana* Beurl., grow within a few meters of each other, with the former in the sun and the latter more on the forest edge). Then, too, the purplish-red hairs on the head and body of the caterpillar are not as brilliant in *P. zenodorus* (Fig. 2) as they are in *P. crida* (Fig. 3).

Caterpillars of *P. zenodorus* are oligophagous on mature leaves of the shrubby treelets *V. baccifera* and *V. ferruginea* Kunth (Table 1). *Vismia baccifera* is widespread and common in the early successional stages of old ACG rainforest pastures returning to forest. When the area was entirely old-growth forest, *V. baccifera* was probably a much rarer plant restricted to the early stages of tree-fall succession and continually disturbed sites such as watercourse edges and landslides. A few hours' search can usually produce at least a few old nests of *P. zenodorus* caterpillars on *V. baccifera,* and currently this plant supports the vast bulk of the population. *Vismia ferruginea* is very rare, occurring just in the interface between dry forest and rainforest (Estación Biológica Maritza area). Despite intensive search, only five caterpillars have been found on it.

Moss (1949:33) reared other members of the *Pyrrhopyge phidias* species complex (to which *P. zenodorus* belongs) without knowing exactly what they were: "Amongst the commonest of the *Pyrrhopyge* in Pará [Brazil], were a number of species closely resembling in their underside coloration [*P. phidias hyperici* (Hübner)]. Unfortunately I took them for one single species and in consequence did not make detailed observations on their separate larvae and pupae. Their tent-like shelters are found on the upper side of the leaves of *Lacre* bushes (*Vismia guianensis* (Aubl.) Choisy., [Clusiaceae]). They also frequently occur[r]ed on *Guava* and *Aracá* (*Myrtaceae*)."

In later instars, *P. zenodorus,* like *P. crida* and *P. aesculapus* Staudinger, only lightly silks a pair of leaves to-

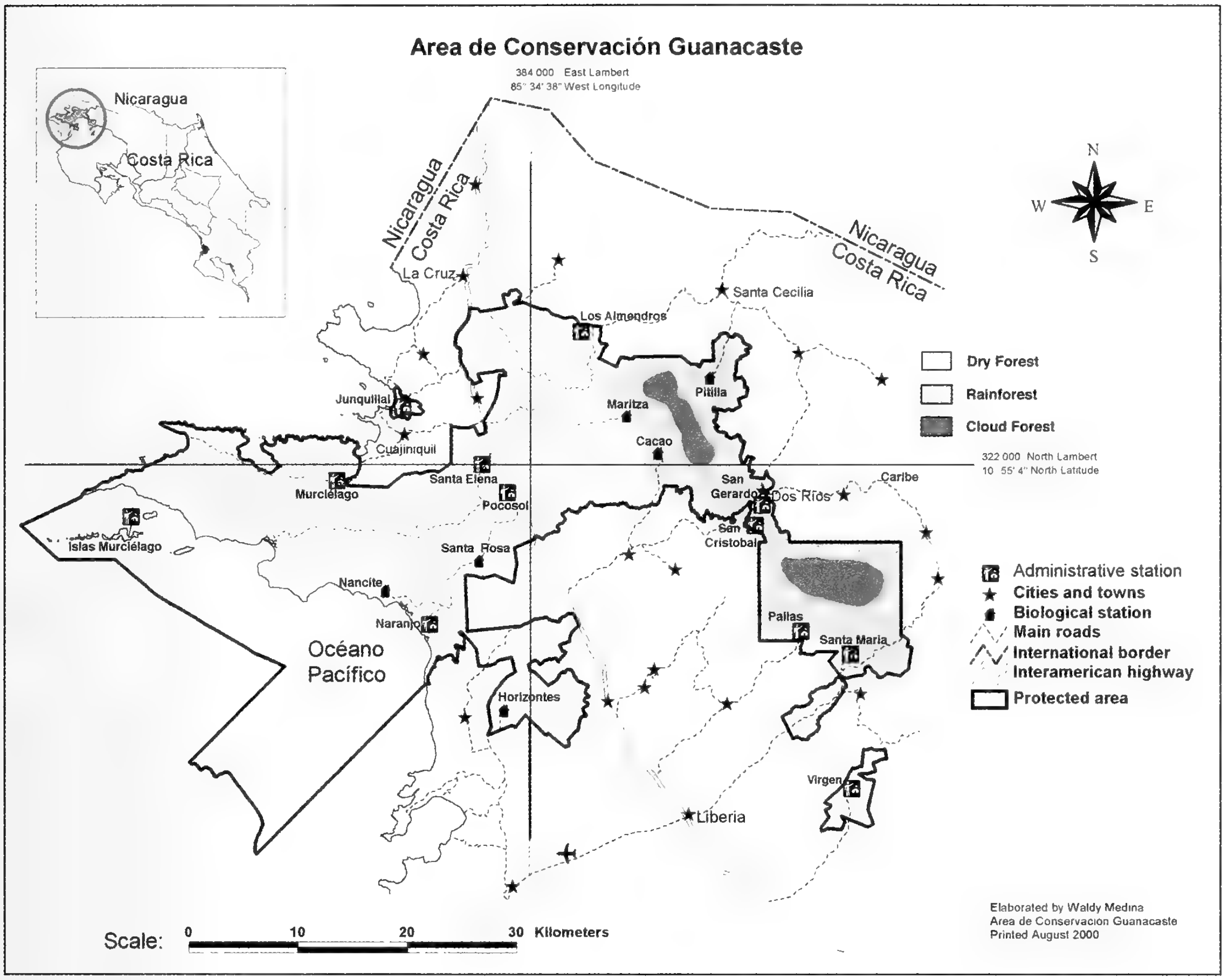


FIG. 1. Area de Conservación Guanacaste (ACG) in northwestern Costa Rica and the locations of its three major ecosystems.

gether to make its nest, in striking contrast to the other pyrrhopygines, most of which make nests with much more extensive and dense silk linings.

Pyrrhopyge zenodorus is one of the three pyrrhopygine caterpillars with more or less host-specific tachinid fly parasites. Eleven of the records of *Houghia* sp. 9 are from this skipper (the other record is from *Phocides nigrescens* Bell); and all three records of *Pseudosturmia* sp. 1 are from *Pyrrhopyge zenodorus*. The distinctive *Apanteles* wasp (Braconidae) that attacks *P. zenodorus* (n = 20) may also turn out to be host-specific.

Pyrrhopyge crida (Hewitson)

Superficially, the adult of *Pyrrhopyge crida* (Fig. 3) does not closely resemble other pyrrhopygines or other ACG hesperiids. The combination of uniform black (both dorsally and ventrally) with an oblique, wide, bright white, hyaline slash tapering across the forewing from below the mid-costa to above the tornus—along with a narrow, off-white fringe on the hindwing and an orange head and rump—is unique (though a number of ACG pyrgines are very dark with a row of white hyaline spots angling across the forewing).

Pyrrhopyge crida is a rainforest skipper in the ACG. Knowledge of its presence comes from 14 rearings, and the capture of a single wild female, by P. Ríos and C. Moraga, parataxonomists at Estación Biológica Pitilla in the northeastern ACG. Though clearly a wide-ranging species, *P. crida* is rare in collections. For example, there are only 8 specimens in the BMNH (from Nicaragua, Colombia, and Ecuador) and 5 in the USNM (from Costa Rica, Panama, and Colombia). It extends north to southern Mexico (Hoffmann 1941).

The caterpillar of *P. crida*, unlike that of *P. zeno-*

dorus (which occurs throughout the rainforest on the widespread *Vismia baccifera*), is apparently restricted to *V. billbergiana* (Table 1), found to date only in the understory of old secondary successional rainforest at about 600 m along the entrance road to Estación Biológica Pitilla. The caterpillar of *P. crida* (Fig. 3) looks very like that of *P. zenodorus* (Fig. 2). However, the hairs on the head and the shorter hairs on the body of *P. crida* are more brilliantly purplish-red than they are in *P. zenodorus*.

Although Evans (1951) included *P. zenodorus* in his second species of *Pyrrhopyge* and treated *P. crida* as his thirty-fifth species (five species groups removed from *P. zenodorus*), the two seem closer. This is suggested by similarities not only in the caterpillars, their foodplants, and how lightly they silk leaves of those plants together when making a nest, but also in basic genitalic form of the adults (Godman & Salvin 1893:pl. 73, fig. 3 & pl. 74, fig. 3, Evans 1951:figs. A.1.2 & A.1.35).

Pyrrhopyge creon H. Druce

The wings of this stunning skipper are iridescent blue, with black edges and fringes and a red-orange spot above the tornus of the hindwing (in space 1c); this prominent spot is expressed on both surfaces, but is a little smaller dorsally than ventrally. Evans (1951) treated *Pyrrhopyge creon* as a monotypic species, represented in the BMNH by specimens from Costa Rica and Panama (plus a pair from Colombia). Much later, Nicolay and Small (1969, 1981) described two subspecies—superficially quite distinct from each other and from *P. creon creon*—from cloud forest on isolated mountains of Panama and Costa Rica, respectively: *Pyrrhopyge creon lilliana,* in which the red-orange subtornal spot of the hindwing is not only enlarged but also expanded into a series of three to five submarginal spots (in spaces 1b to 4); and *P. c. taylori,* in which the iridescent blue of both pairs of wings is replaced by iridescent purple, while the subtornal spot remains unchanged.

Pyrrhopyge c. creon ranges along the continental divide from Guanacaste, Costa Rica, to Coclé, Panama; because it was never found farther east in suitable Panamanian habitat, despite intensive efforts, records from Colombia seem doubtful (Nicolay & Small 1981). Both *P. c. taylori* (at 1150 m in the Fila Cruces, Puntarenas, Costa Rica) and *P. c. lilliana* (at 800 m at Cerro Campana and La Mesa in a disjunct massif in the provinces of Panamá and Coclé, Panama) are separated from typical *P. c. creon* by relatively low-elevation gaps of just 30–40 km. Since intergrades are unknown, these skippers, though strong fliers, are presumably sedentary (Nicolay & Small 1981).

Male genitalia, which are moderately asymmetric in the distal part of the valvae (Godman & Salvin 1893:pl. 73, fig. 11, Bell 1931:fig. 45), are identical in all three subspecies (Nicolay & Small 1969:fig. 3, 1981:fig. 2). In comparing the genitalia of 14 ♂ and 3 ♀ that represent these taxa, we, too, found no significant differences.

Pyrrhopyge c. creon is the epitome of cloud forest hesperiids. Adults are occasionally seen flying and perching on leaves 2–10 m above the ground in the upper parts of tree falls on sunny/warm to foggy/cool days on the peak of Volcán Cacao (1200–1500 m). Their presence in this elevated habitat mirrors their presence at 1600–2000 m—flying even in heavy fog—on Volcán Barba and Volcán Poás, further south in Costa Rica. *Pyrrhopyge c. creon* flies in fog so heavy that its wings may be covered with fine beads of moisture. No other diurnal ACG butterflies have been seen on the wing under these conditions.

In flight in the ACG cloud forest, this large blue-black skipper can be confounded with *P. aesculapus.* When *P. c. creon* perches, the red-orange subtornal spot of the hindwing sets it apart.

A pupa found at 1550 m, on the summit of Volcán Cacao, produced our only reared adult of *P. c. creon.* However, two pyrrhopygine caterpillars whose dark bodies sported large orange dots (Fig. 4)—instead of bars or rings—were found somewhat lower (at about 1200 and 1000 m) on *Dendropanax querceti* Donn. Sm. and *D. gonatopodus* (Donn. Sm.) A. C. Sm. (Araliaceae). The first died of apparent disease in the penultimate instar while the second pupated, only to sprout a mass of white fungus. Though we have yet to rear the adult we need for positive identification of these odd caterpillars, we strongly suspect—from their elevation and habitat—that they are those of *P. c. creon.* But, because we cannot be certain, we have deliberately omitted photographs of the presumed adult from Fig. 4.

Pyrrhopyge aesculapus Staudinger

Pyrrhopyge aesculapus presents no taxonomic problems at the species level. The adult has iridescent purplish-blue wings with a wide, strongly contrasting, orange fringe on the hindwing but not on the forewing (Fig. 5) (except for traces in space 1b in some individuals). The hindwing is purpler and darker, whereas the forewing is bluer. The body is dull because it lacks the orange or red hot tail for which many pyrrhopygines are famous; nor is it "hotheaded." One feature of the distinctive male genitalia—the elongate caudal projection comprising the distal half of the valva—can be exposed relatively easily with dry dissection. In lateral view, this projection looks peculiar because it is almost uniformly wide, marginally dentate, terminally blunt, and evenly curved upward from its horizontal beginning to its vertical end (Godman & Salvin 1893:pl. 73, fig. 9, Bell 1931:fig. 43, Evans 1951:fig. A.1.46). Known mainly from Costa Rica and Panama, *P. aesculapus* apparently ranges south to Colombia and Ecuador.

In flight in the ACG cloud forest, the large blue-black *P. aesculapus* resembles only *P. c. creon.* At rest, these species are readily distinguished by their hindwings: orange-fringed in the former (Fig. 5), spotted red-orange above the tornus in the latter.

In this cloud-forest habitat, the caterpillar of *P. aesculapus,* with bright yellow, lateral, vertical bars on a black background (Fig. 5), resembles the barred caterpillar of *P. cosyra* (Fig. 6) and, to a lesser extent, the ringed caterpillars of *Ridens mephitis* (Hewitson), *Astraptes fulgerator azul,* and a species of *Venada.* However, none of these caterpillars feeds on *Weinmannia wercklei* Standl. (Cunoniaceae), the sole known foodplant of *P. aesculapus* (Table 1). *Weinmannia wercklei* is a shrubby treelet characteristic of high elevations in Costa Rica. *Pyrrhopyge aesculapus* spins its nest lightly and conspicuously among the thin, flimsy leaves of this plant. Tearing at the nest easily exposes the boldly patterned caterpillar which does not try to stay hidden in the nest but actively crawls away, as if to flaunt its colors.

Too few examples of *P. aesculapus* have been reared to draw conclusions about its lack of parasitoids (Table 1). In the habitat, and at the elevations, where *P. aesculapus* occurs, caterpillars of *P. cosyra* are attacked by a host-specific tachinid fly.

Pyrrhopyge cosyra H. Druce

Of the many species currently in *Pyrrhopyge,* this is one of at least 15 in which the valvae of the male genitalia are asymmetric (Godman & Salvin 1893:pl. 74, fig. 2, Evans 1951:fig. A.1.55) (others include *P. creon* and members of the *P. maculosa* species complex). Superficially, *P. cosyra* is extremely distinct: both pairs of wings are iridescent dark blue, but dorsally they sport a huge, bold, proximal, orange splotch; the forewing has three distal bands that are white and hyaline (hence ventral as well as dorsal); and the body, except for the dorsally orange thorax, is banded black and white (Fig. 6). In the only other pyrrhopygine that resembles it—a South American species, *P. spatiosa* (Hewitson)—the splotch is a redder orange. *Pyrrhopyge erythrosticta* (whose ground color is black instead of iridescent dark blue) presents a color pattern basically like that of *P. cosyra,* except that the huge, central, orange splotch is ventral instead of dorsal (Fig. 7). *Pyrrhopyge cosyra* ranges from Guatemala through Central America to Colombia and Ecuador.

In Costa Rica *P. cosyra* occurs from lowland rainforest (sea level on the Osa Peninsula in the southwest) to ACG rainforest at 400–800 m and extends up into cloud forest at 1400 m. Neither adults nor caterpillars have been found in ACG dry forest, even though one of its foodplants, *Clusia rosea* Jacq. (Clusiaceae), is sporadic in wet sites there. In ACG cloud forest and rainforest, adults have been seen only when they descended from the tree canopy for brief exploration of potential foodplants. The relatively common caterpillars of *P. cosyra* are found less than 3 m above the ground.

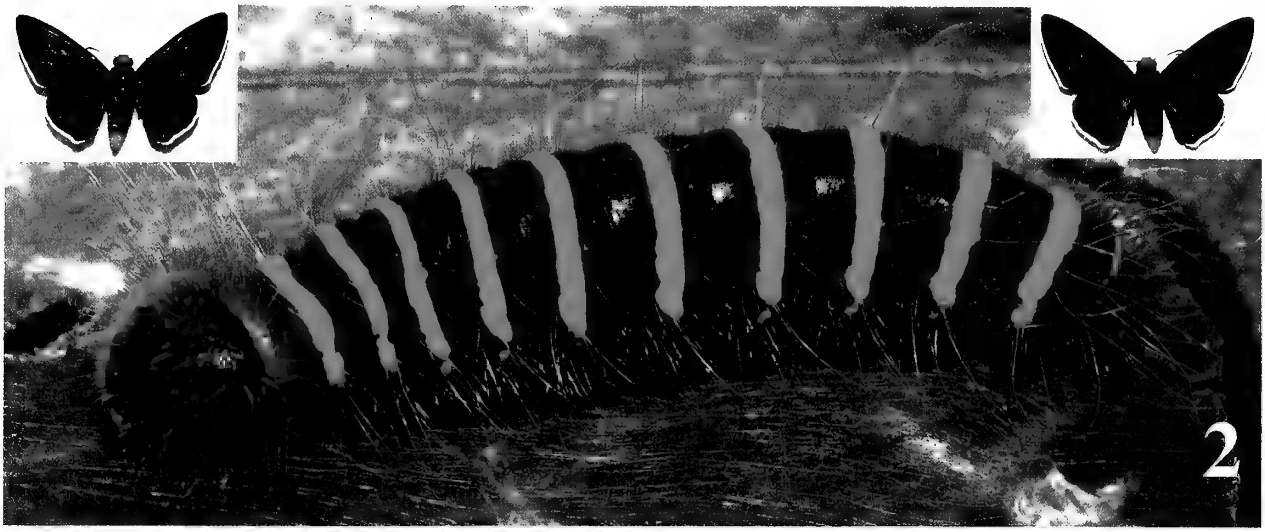
The caterpillar of *P. cosyra,* which is black with orange-yellow, lateral, vertical bars (Fig. 6), looks superficially a lot like the larvae of both *Jemadia* species (Figs. 10, 11) and much like those of *Pyrrhopyge zenodorus* (Fig. 2) and several other rainforest skippers listed in our account of that pyrrhopygine. However, none of these species feeds on *Chrysochlamys* (=*Tovomitopsis*) or *Clusia,* the only foodplants of *P. cosyra* (Table 1).

On small-leaved plants such as *Chrysochlamys* and *Clusia minor* L., the caterpillar of *P. cosyra* spins an extraordinarily tough and baglike silk nest. It is hard to tear open; and when one does, the caterpillar retreats inside in an apparent effort to stay out of sight. When feeding on the other species of *Clusia* with their massive thick leaves, the caterpillar silks a couple of leaves very tightly together into an equally strong nest.

Pyrrhopyge cosyra is the most heavily parasitized of all the pyrrhopygines reared, and the only one attacked by Tachinidae, Ichneumonidae, and Braconidae (Table 1). The tachinid *Chlorohystricia* sp. 1 appears to use it almost exclusively (18 records on *P. cosyra* plus one on *Venada* sp. in the same habitat) and occurs throughout the caterpillar's range in the ACG (400–1400 m). *Pyrrhopyge cosyra* is the sole known host for the ichneumonid genus "MCAM" sp. 1 (n = 10); and it is heavily used by *Casinaria* sp. 9, an ichneumonid wasp that also attacks a few species of pyrgines. The lone braconid individual reared from this skipper has yet to be placed to genus.

Pyrrhopyge erythrosticta (Godman & Salvin)

For their original description of *Pyrrhopyge erythrosticta,* Godman and Salvin (1879) used very few words, no illustrations, and an unspecified number of specimens (from Chontales, Nicaragua, and Veragua [part of central Panama]) without designating a type. Even in the Biologia Centrali-Americana, Godman and Salvin (1893) did not picture an adult; but they did



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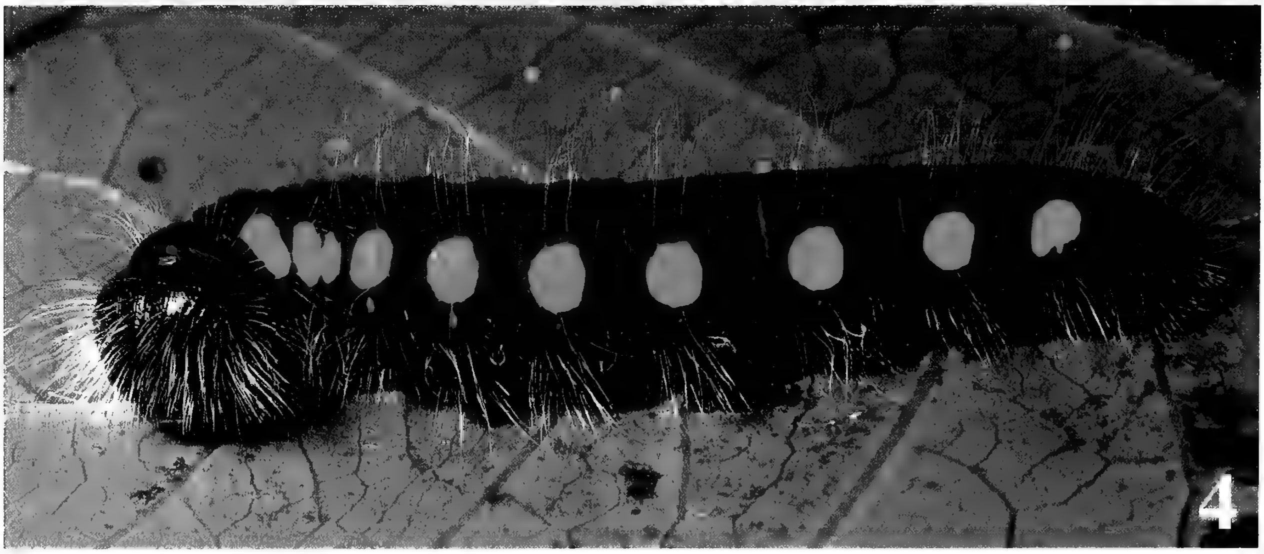

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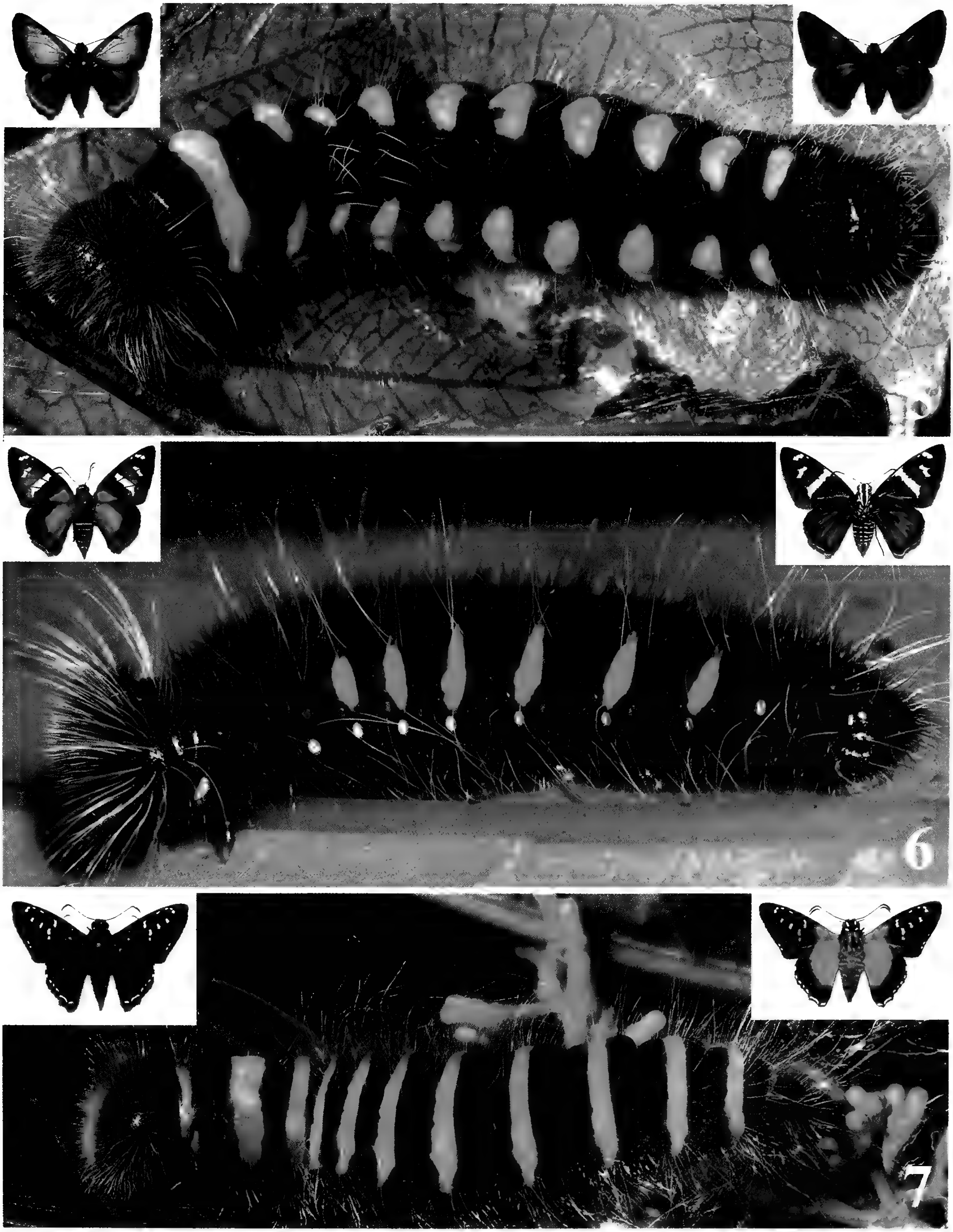
FIGS. 2–4. Last instars, plus adults in dorsal (L) and ventral (R) view, of ACG pyrrhopygines. **2,** *Pyrrhopyge zenodorus* (rainforest) 94-SRNP-707, L/R ♀ 94-SRNP-6631. **3,** *Pyrrhopyge crida* (rainforest) 97-Rios-491, L/R ♀ 97-Cali-188. **4,** *Pyrrhopyge creon* presumably (cloud forest) 00-SRNP-20314.



FIGS. 5–7. Last instars, plus adults in dorsal (L) and ventral (R) view, of ACG pyrrhopygines. **5,** *Pyrrhopyge aesculapus* (cloud forest) 97-SRNP-513, L/R ♂ 97-SRNP-514. **6,** *Pyrrhopyge cosyra* (rainforest to cloud forest) 98-SRNP-2767, L ♀ 97-SRNP-1805, R ♀ 97-SRNP-6531. **7,** *Pyrrhopyge erythrosticta* (rainforest) 00-SRNP-15831, L/R ♂ 00-SRNP-15831.

what was much better in the end by clearly figuring (vol. 3, pl. 73, fig. 13) and verbally describing (vol. 2, p. 252) the "very peculiar" male genitalia of *P. erythrosticta.* Having found that their type series includes more than one genitalically divergent species, Burns hereby chooses as lectotype (BMNH) the male whose genitalia were shown. This action fixes the taxonomic concept of the name and ensures its future consistent interpretation. The lectotype bears a distinctive Godman-Salvin miniature genitalia slide (numbered 369) plus three labels: (1) Chontales, / Nicaragua. / T.Belt. (2) B.C.A. Lep. Rhop. / Pyrrhopyge / erythrosticta, / G. & S. (3) Godman-Salvin / Coll.1912.–23. Its left wings have been bleached for study of venation. This is the species that we have reared in the ACG. At present we know it only from Nicaragua and Costa Rica. The more wide-ranging entity that has been confused with it will be described separately, in the context of the entire *P. maculosa* complex.

While we were writing the paper you hold, ACG parataxonomists Petrona Ríos and Calixto Moraga reported that twice in 1996 they had seen yellow-ringed, black pyrrhopygine caterpillars on *Marila laxiflora* Rusby (Clusiaceae) at Estación Biológica Pitilla (in rainforest at 700 m on the northeast side of Volcán Orosí) but had been unable to rear them. Asked now to try for more, Ríos found a single last instar (Fig. 7) in its nest on a non-host plant—i.e., a plant that the caterpillar was not eating in the field and would not eat in captivity. It fed normally on *M. laxiflora* until pupation (Fig. 19) and produced our lone reared adult (Fig. 7). Two wild adults of *P. erythrosticta* have been caught in the rainforest at 600–800 m in the pass between Volcán Cacao and Volcán Rincón de la Vieja. This species has not been seen anywhere else in the ACG.

Pyrrhopyge erythrosticta gets its specific name from the small, dull red spot near the base of the dorsal forewing between veins 1 and 2 (Fig. 7); but the forewing also bears nine, more conspicuous, small, white hyaline spots in fixed positions. It is important that in true *P. erythrosticta,* the lowest hyaline spot, which is in space 1b, is directly under the spot in space 2 (Fig. 7). The spot in space 1b is likewise under the spot in space 2 in a more northern species, *P. hoffmanni* Freeman, to which *P. erythrosticta* is also genitalically related. However, *P. hoffmanni* is much more closely related to the still more northern *P. mulleri* (Bell): this pair has essentially the same genitalia in both sexes (for males, cf. Bell 1934:fig. 5 and Freeman 1977:fig. 17), but *P. mulleri* has lost all hyaline spots. The members of the *P. mulleri-P. hoffmanni* / *P. erythrosticta* trio appear to replace each other geographically. Their apparent parapatry independently supports their grouping on morphological grounds. On the other hand, both *P. hoffmanni* and *P. erythrosticta* coexist with the species that is currently confounded with the latter. In this unnamed species, the spot in space 1b is not under the spot in space 2 but, instead, displaced outward so that the spots in spaces 1b, 2, and the cell form a straight line—as they also do in its more southern (and closer) relative, *P. maculosa* Hewitson.

Elbella scylla (Ménétriés)

Elbella scylla amounts to much more than the latest taxonomic revision implies. Mielke (1995) treats *E. dulcinea* (Plötz) as a different species, occurring in Mexico with *E. scylla* and extending farther south than *E. scylla* into northern South America (see map plotting both in Mielke 1995:fig. 44); but all this is one species ranging from central Mexico to Colombia, Venezuela, and Ecuador. Its genitalia (Godman & Salvin 1893:pl. 73, fig. 6, Bell 1931:fig. 35, Evans 1951:fig. A.2.1, Mielke 1995:figs. 15, 16) look the same (within normal limits of individual variation) everywhere (41 closely compared KOH-dissections: Mexico 3 ♂, Guatemala 1 ♂ 1 ♀, Honduras 1 ♂ 1 ♀, Costa Rica 14 ♂ 14 ♀, and Panama 3 ♂ 3 ♀). *Elbella scylla* (described in 1855 from Nicaragua) and *E. dulcinea* (described in 1879 from the part of Colombia that, in 1903, became Panama) were considered synonymous in the 1940s. However, Evans (1951) called *dulcinea* a subspecies of *scylla;* and Freeman (1966:227)—who claimed, without specifics, that the two "differ somewhat genitalically and morphologically" and "occur together in the same areas of Veracruz," Mexico—raised *dulcinea* back to the level of species (for complete references, see Mielke 1995:460).

The main color character that "distinguishes" *dulcinea* from *scylla*—i.e., inward expansion of white from the white hindwing fringe into the outer margin of the black hindwing proper—is variably expressed by most of the ACG specimens of *E. scylla.* Since this "white expansion" is more pronounced and more uniformly expressed in specimens from Panama, and since it is still more pronounced in Venezuela (see Mielke 1995:fig. 87), it is apparently a clinally varying trait in southern portions of *E. scylla*'s range. (The "white expansion" is better expressed ventrally than dorsally in every individual showing it; furthermore, it is sexually dimorphic and better expressed by females than by coexisting males.) Geographic variation in fringe-whitening, and in the extent to which white invades the dark hindwing itself, has been well documented in the pyrgine genus *Erynnis* in which a white fringe has evolved eight times independently, always in those populations occurring in the southwestern USA and Mexico plus points south (Burns 1964). In *Elbella scylla* a color character of the tegulae—whether their longitudinal stripe is yellowish, reddish-orange, or bluish-white (it is occasionally unexpressed)—also varies geographically, but not in concordance with the clinal variation noted above. In ACG material the stripe is reddish-orange.

Adults of *E. scylla* are occasionally encountered visiting flowers (e.g., *Trigonia rugosa* Benth. [Trigoniaceae], *Cordia* spp. [Boraginaceae]) in the ACG dry forest and on the dry side of the intergrades between dry forest on the one hand and rainforests and cloud forests on the other in the eastern ACG. Neither adults nor caterpillars have ever been encountered in rainforest or cloud forest.

Although the adult of *E. scylla* does not closely resemble adults of other ACG dry-forest hesperiids, it can—in flight—be confused with two other large and generally black skippers, *Mysoria ambigua* (Mabille & Boullet) and *Phocides palemon lilea.* The former species has yellow and magenta along the outer and costal margins, respectively, of the underside of the hindwing (Fig. 12), while the latter species has a small red bar at mid-costa of the forewing both above and below.

The brightly yellow-ringed caterpillar of *E. scylla* (Fig. 8) superficially resembles those of at least 13 other ACG dry-forest skippers (Janzen & Hallwachs 2001): *Mysoria ambigua* (Fig. 12), *Phocides palemon lilea, Drephalys alcmon* (Cramer) and *D. kidonoi* Burns (see Burns & Janzen 2000:figs. 21–25), *Polythrix caunus, Chrysoplectrum pervivax* (Hübner), *Ridens mephitis, Astraptes fulgerator azul, Nascus solon corilla* Evans, two species currently going under the one name *Nascus phocus, Pellicia dimidiata* Herrich-Schäffer, and *Achlyodes busirus heros,* all of which appear to be involved in an as yet undescribed, multi-familial, aposematic, caterpillar mimicry complex.

Caterpillars of *E. scylla* are oligophagous on mature leaves of a small subset of the species of ACG Malpighiaceae plus two species of Combretaceae (Table 1). Most caterpillars eat *Byrsonima crassifolia* (L.) Kunth (Malpighiaceae), a shrubby tree that is common in the old and frequently burned pastures cut out of ACG dry forest, but that also persists in many kinds of old-growth forest ranging from exposed sea cliffs to deep soils on the volcanic foothills. The other three malpighiaceous foodplants are woody perennial vines occurring commonly on forest edges and in understory of secondary succession. All four of these foodplants probably will be rarer and more locally distributed when the ACG dry forest has returned to full old-growth status. Other common dry-forest Malpighiaceae (*Heteropterys obovata* [Small] Cuatrec. & Croat, *Gaudichaudia hexandra* Chodat, *Stigmaphyllon ellipticum* A. Juss., *S. lindenianum* A. Juss., *Mascagnia sinemariensis* Griseb., *Bunchosia biocellata* Schlecht., *Malpighia glabra* L., *Banisteriopsis cornifolia* C. B. Rob.), which occur both on edges and in heavily-shaded understory of deep forest, have never yielded *E. scylla* caterpillars. Neither have any of the other five or so species of malpighiaceous treelets and shrubs (e.g., *Tetrapterys discolor* G. Mey., *Hiraea* sp., *Bunchosia* sp.) in the wetter portions of the ACG produced these caterpillars, despite intensive search.

Combretum farinosum H. B. & K. is an occasional woody vine and scandent shrub that grows along ravines and watercourses, and *E. scylla* apparently eats its semi-evergreen foliage primarily in the dry season. This is the only native species of Combretaceae in the ACG dry forest. The others are in the mangroves or in local riparian wet sites, and we do not know whether they, too, would be acceptable. *Terminalia catappa* L. is an introduced beach-edge and garden evergreen combretaceous tree that is very rarely used by *E. scylla.* Inclusion of Combretaceae in the diet of a malpig-eater is mirrored by the pyrgine genus *Cephise:* caterpillars of the tailless species *Cephise nuspesez* Burns as well as the tailed species *C. auginulus* (Godman & Salvin)—which now is considered a synonym of *C. aelius* (Plötz) (Austin & Mielke 2000)—feed heavily on Malpighiaceae and also use Combretaceae (Burns 1996, Janzen & Hallwachs 2001). There is no hint that *E. scylla* caterpillars feed on any plants in the ACG besides the four Malpighiaceae and the two Combretaceae in Table 1.

For *E. dulcinea*—which is synonymous with *E. scylla*—Mielke (1995) reported that, in Maracay, Aragua, Venezuela, the caterpillar was reared by F. F. Yépez on *Terminalia catappa.* This Asian introduction was recorded once as a foodplant in the ACG.

In Pará, Brazil, Moss (1949) reared larvae of *E. intersecta* (Herrich-Schäffer) on at least three unspecified species of Malpighiaceae. *Elbella scylla* and *E. intersecta* are very closely related and, since the latter is primarily South American in distribution, mostly allopatric. For *E. intersecta intersecta,* Mielke (1995) stated that larvae are very common on *Vismia guianensis* (Clusiaceae) in Imperatriz, Pará; and for *E. i. peter* Evans, he simply listed *Vismia guianensis* and *Banisteria mossii* Morton (Malpighiaceae) as foodplants.

Elbella scylla appears to be attacked by only one species of parasitoid, a microgastrine braconid (*Cotesia*) (Table 1). A single individual was found with tachi-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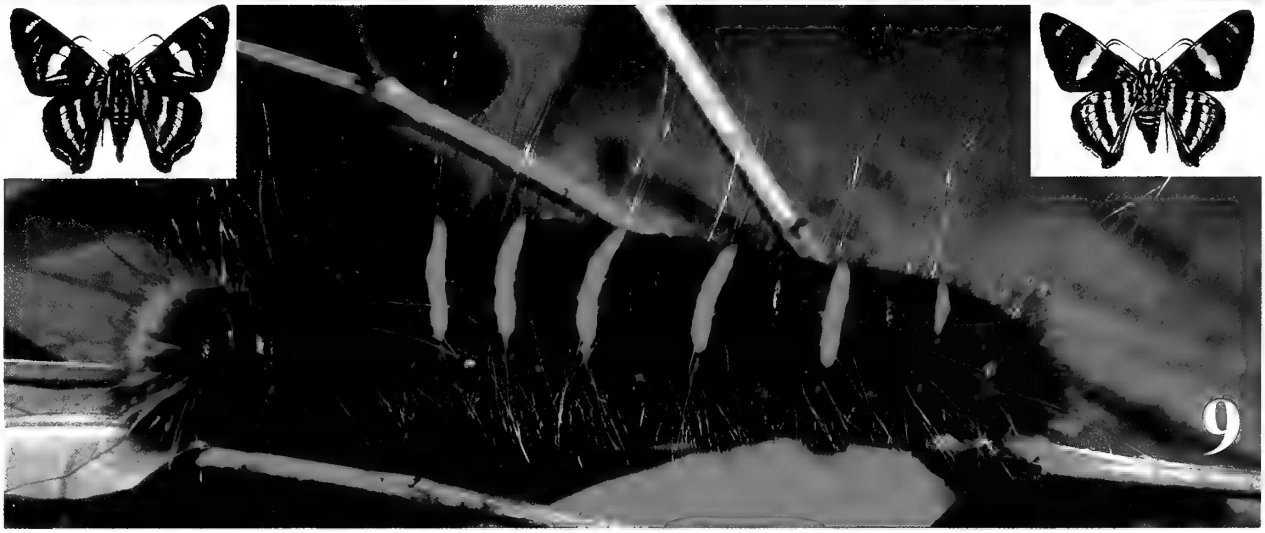
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FIGS. 8–10. Last instars, plus adults in dorsal (L) and ventral (R) view, of ACG pyrrhopygines. **8,** *Elbella scylla* (dry forest) 96-SRNP-224, L/R ♀ 93-SRNP-6852. **9,** *Parelbella macleannani* (rainforest) 01-SRNP-113, L/R ♀ 98-SRNP-6468. **10,** *Jemadia pseudognetus* (rainforest) 00-SRNP-21908, L/R ♂ 98-SRNP-6196.

FIGS. 11–13. Last instars, plus adults in dorsal (L) and ventral (R) view, of ACG pyrrhopygines. **11,** *Jemadia* sp. X of a *J. hewitsonii* species complex (rainforest) 01-SRNP-9029, L/R ♂ 00-SRNP-4482. **12,** *Mysoria ambigua* (dry forest) 80-SRNP-272, L ♀ 87-SRNP-1162, R ♂ 95-SRNP-8409. **13,** *Myscelus amystis hages* (dry forest) 93-SRNP-8387, L ♂ 96-SRNP-12399, R ♀ 96-SRNP-365.

nid eggs glued on the front of the head, but neither flies nor caterpillar survived the rearing process.

Parelbella macleannani (Godman & Salvin)

Evans (1951) grouped five subspecies in his polytypic species *Elbella polyzona* (Latreille). Mielke (1995) regards this assemblage as a new genus, *Parelbella;* treats four of the subspecies as three distinct species (one that is polytypic includes not only two of those four subspecies but also the fifth as a synonym); and adds a new species. One of *Parelbella*'s four species extends north of South America.

Parelbella macleannani ranges from northern Ecuador (Imbabura) to southern Mexico (Veracruz, Oaxaca), with intervening records from Colombia, Panama, Costa Rica (ours), Nicaragua, and Guatemala (Mielke 1995:fig. 51, 561-562). In the ACG, its caterpillars have been found only in the rainforest from 400–800 m—never in the dry forest—and free-flying adults have not been seen or collected.

Parelbella and *Jemadia* (the genus we consider next) are among those distinctive pyrrhopygines in which adults with a more or less black ground color are striped and banded pastel blue over the body and on both pairs of wings and, in addition, are banded hyaline white on the forewings (Figs. 9–11). (Some species of the pyrgine genus *Phocides* have independently evolved this striking color pattern; but their stout antennal club—in sharp contrast to that of pyrrhopygines—ends in a long, delicate, reflexed apiculus. Nevertheless, in life these pyrgines fold the apiculus back so tightly against the body of the club that even the club suggests that of a pyrrhopygine.)

Though at first glance *Parelbella macleannani* and ACG species of *Jemadia* look much the same, they do differ—not just in major genitalic ways (cf. Mielke 1995:figs. 32–36 and Evans 1951:figs. A.5.1–A.5.7) but in wing pattern and shape (cf. Figs. 9–11). In *P. macleannani* the slender hyaline spots in spaces 3 and 4 of the forewing (which, at times, are barely or not expressed) are widely disjunct, whereas in *Jemadia* these two spots are in contact and aligned. *Parelbella macleannani* has a fine blue line (expressed much better ventrally than dorsally) at the distal end of the forewing cell, but *Jemadia* does not. In *P. macleannani* the inner (basal) blue band on the dorsal hindwing is single; in *Jemadia* it is double. The submarginal blue band on the ventral hindwing of *P. macleannani* (which is not as well-developed as the three more proximal blue bands) is lacking in *Jemadia.* And there is a small lobe at the hindwing tornus in *P. macleannani* but not in *Jemadia.*

Caterpillars of *P. macleannani* are monophagous to oligophagous on mature leaves of one to three species (some determinations pending) of *Eugenia* (Table 1). These Myrtaceae are forest-understory-to-edge scandent shrubs, on which the caterpillars were all found within 2 m of the ground. Given that there are more than 30 species of Myrtaceae in the ACG and that *P. macleannani* has been found on only one to three congeneric species, it may eat just it or those. On the other hand, the caterpillar of this skipper occurs at such low density that, with more years of search, its list of myrtaceous foodplants may increase.

In Pará, Brazil, Moss (1949) found caterpillars of what Mielke (1995) treats as *Parelbella ahira ahira* (Hewitson) on an undetermined species of *Eugenia* (and once also on *Virola sebifera* Aubl. [Myristicaceae]). He described both larvae and pupae as strongly crimson and indicated that the larvae have transverse yellow belts.

The caterpillar of *Parelbella macleannani* is reddish-black with orange-yellow rings (Fig. 9). This color pattern basically resembles those of various other ACG rainforest skippers such as *Pyrrhopyge zenodorus,* as listed in the account of that species. Except for the pyrgine *Phocides palemon lilea,* these other skippers do not feed on Myrtaceae.

Our only parasitized caterpillar of *Parelbella macleannani* (Table 1) was attacked by *Hyphantrophaga virilis* (Aldrich & Webber), which is the most extreme generalist of all ACG tachinids reared.

Jemadia pseudognetus (Mabille), **reinstated status**

Evans's (1951:50) polytypic species *Jemadia hospita,* ranging from Guatemala to Peru, Bolivia, and Brazil, includes four subspecies. The two subspecies that are widely distributed are also the first to have been described (originally as species): *Jemadia hospita hospita* (Butler, 1877) and *J. hospita pseudognetus* (Mabille, 1878). Repeated comparison of the genitalia of 20 ♂ shows that these two taxa are indeed separate species, with *J. pseudognetus* ranging from southern Mexico to Colombia, at least, and with *J. hospita* strictly South American (like the other taxa in this complex). The characters given by Evans (1951:50–51) for superficially distinguishing between *pseudognetus* and *hospita* are good. Differences in the male genitalia (not noted by Evans) are subtle and involve a narrow, pointed, finely dentate projection that sweeps anterodorsally from the posterior half of the valva: this projection is shorter and a little less dentate in *J. pseudognetus* (Godman & Salvin 1893:pl. 74, fig. 6) than it is in *J. hospita* (Bell 1933:fig. 24, Evans 1951:fig. A.5.1).

Caterpillars of *J. pseudognetus* have been found only in the rainforest from 400–800 m, and free-flying adults have never been seen or collected in the ACG. Since no caterpillars have been found in the dry forest, *J. pseudognetus* is clearly a rainforest skipper within the ACG.

Several differences in external appearance between adults of ACG species of *Jemadia* and those of *Parelbella macleannani* are listed under the latter species. But *J. pseudognetus* specifically differs from *P. macleannani* in another respect: the dorsal hindwing has only two pastel blue bands (inner and outer), instead of three (inner, central, and outer) as in *P. macleannani*.

Caterpillars of *J. pseudognetus* are oligophagous on mature leaves of Lauraceae (Table 1). Although there are more than 30 species of Lauraceae in the ACG, *J. pseudognetus* has been found on only six and may be limited to them. But, because the density of caterpillars is low, the list of lauraceous foodplants may, in time, increase. All known foodplants are forest-understory-to-edge saplings and treelets, and all caterpillars have been found within 2 m of the ground.

The caterpillar of *J. pseudognetus* is black with short, lateral, vertical bars of orange-yellow (Fig. 10). More or less similar barred color patterns occur in *Pyrrhopyge aesculapus* (Fig. 5), *P. cosyra* (Fig. 6), and another species of *Jemadia* (Fig. 11) to be treated next. However, each of these ACG wet-forest pyrrhopygines eats plants in a different family (Table 1).

New member of a *Jemadia hewitsonii* species complex

Evans's (1951:53) polytypic species *Jemadia hewitsonii,* which is essentially South American, contains five subspecies: *Jemadia h. pater* Evans, 1951, *J. h. ovid* Evans, 1951, *J. h. albescens* Röber, 1925, *J. h. hewitsonii* (Mabille, 1878), and *J. h. brevipennis* Schaus, 1902. Consideration of the color-pattern characters used by Evans to distinguish among these taxa, coupled with comparison of their genitalia (from a total of 30 ♂—including the holotype of *J. brevipennis*—in the USNM), suggests that several closely related species, rather than subspecies, comprise a *J. hewitsonii* species complex. Genitalic differences among these taxa are modest: for example, the dorsally dentate distal portion of the valva is relatively long, finely dentate, and lower distally than proximally in *J. hewitsonii* (Bell 1933:fig. 27) but relatively short, coarsely dentate, and fully as high distally as proximally in *J. pater,* **new status** (Godman & Salvin 1893:pl. 74, fig. 9). Genitalic study further shows that *J. brevipennis* is not what Evans had in mind but, instead, a species well-removed from the rest and closely allied with *J. gnetus* (Fabricius).

Although Evans recorded *J. pater* from Venezuela (3 ♂ 2 ♀), Colombia (65 ♂ 1 ♀), and Panama (1 ♂ 1 ♀), it is not the northernmost member of the *J. hewitsonii* species complex. What is, is something deep in the rainforest of the ACG known from 16 caterpillars found eating *Casearia arborea* Urb. (Flacourtiaceae) (Table 1) and from the three adults (1 ♂ 2 ♀) they produced. More adults (especially males) are desired before formal description of this apparent differentiate. Here we simply call it *Jemadia* sp. X. Its caterpillar is black with short, lateral, vertical bars of bright, clear yellow (Fig. 11). These short, lateral bars are orange-yellow in *J. pseudognetus* (Fig. 10).

At both Óbidos and Santarém, Pará, Brazil, Moss (1949) found caterpillars of *J. gnetus* feeding on a different flacourtiaceous plant, *Laetia corymbulosa* Spruce.

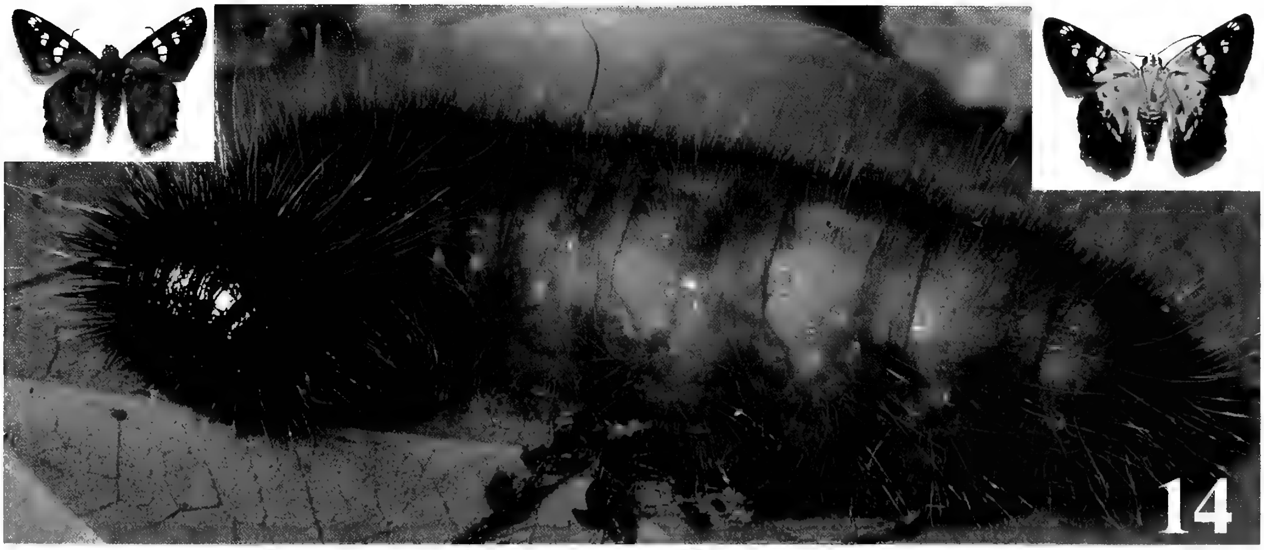
Adults of *Jemadia* sp. X look like those of its ACG congener, except that, on the dorsal hindwing, between the inner and outer pastel blue bands, there is a short, blue, central band (running only from veins 3 to 7), which is absent in *J. pseudognetus* (cf. Figs. 10 and 11).

Mysoria ambigua (Mabille & Boullet)

Although Evans (1951) saw *Mysoria ambigua* as the most northern of six subspecies comprising polytypic species *M. barcastus* (Sepp), comparative study—particularly of genitalia (note major valval differences depicted in Evans 1951:fig. A.12.1)—shows that *M. ambigua* is a separate species, occurring from Mexico to Costa Rica.

In the ACG, *M. ambigua* frequents dry forest and the dry side of the intergrades between dry forest and wetter forests to the east. Neither adults nor caterpillars have ever been encountered in rainforest or cloud forest itself. When flying in the ACG dry forest, *M. ambigua* can be confused with two other large and generally black skippers, *Elbella scylla* and *Phocides palemon lilea*—but neither of them has a yellow outer margin and purplish-red costal margin on the ventral hindwing (Fig. 12).

In the ACG, the caterpillars of *M. ambigua* (Fig. 12) are oligophagous on mature leaves of a subset of the resident species of Flacourtiaceae (Table 1). *Casearia corymbosa* Kunth, which is unambiguously the foodplant for the great majority of the caterpillars, is a common forest-edge treelet in secondary succession (both anthropogenic and naturally occurring). *Casearia sylvestris* Sw., though an equally common forest-understory treelet, is rarely used by *M. ambigua* caterpillars. *Casearia arguta* Kunth is a somewhat scarcer secondary successional treelet that likewise is rarely used. *Zuelania guidonia* Britton & Millsp.,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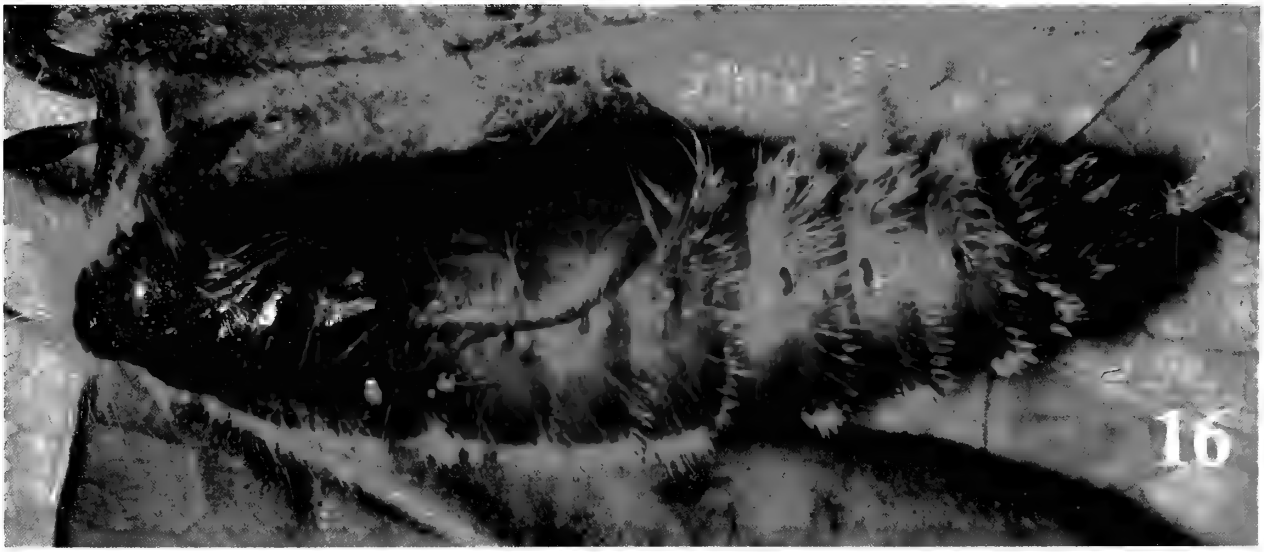
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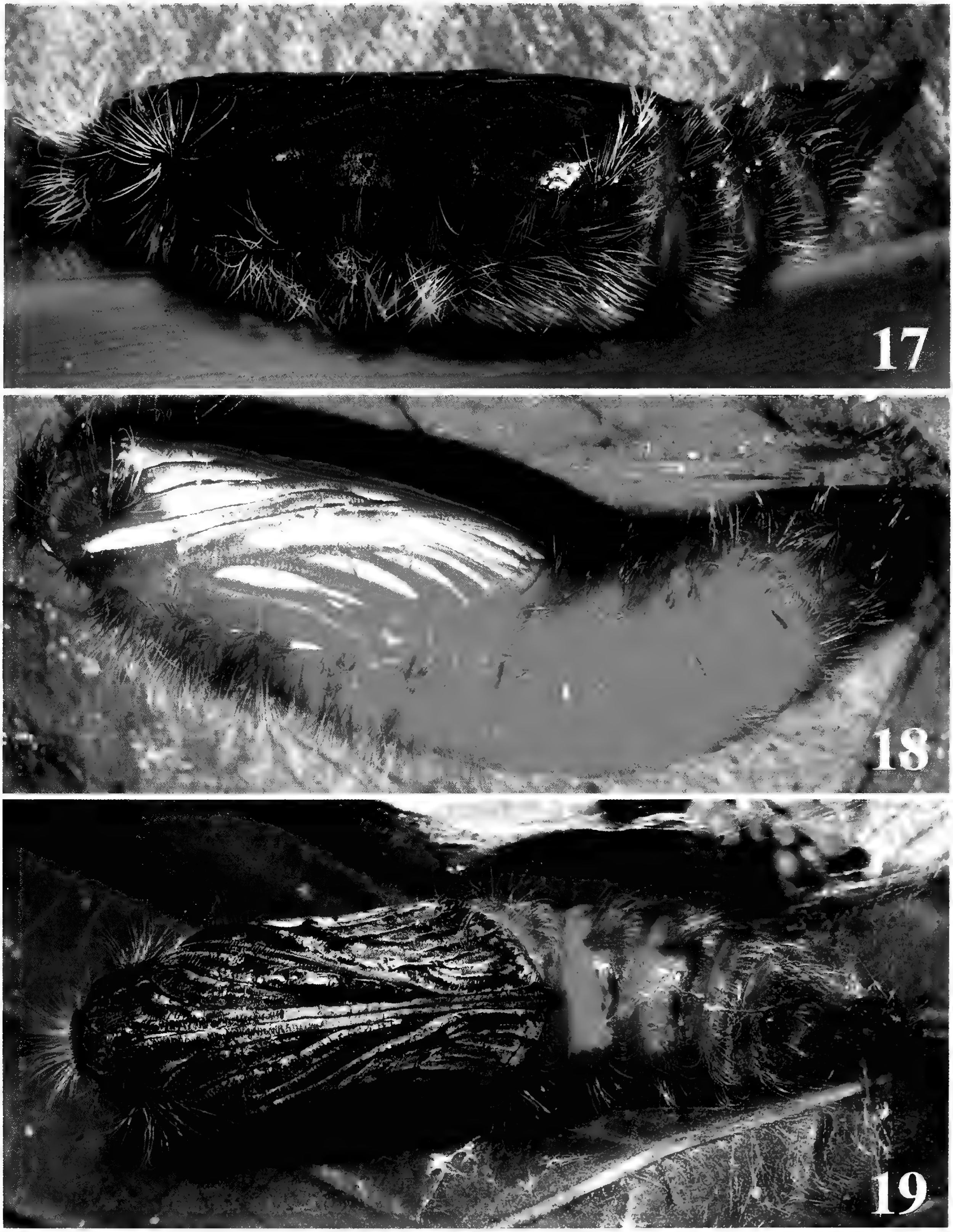
FIGS. 14–16. Last instars, plus adults in dorsal (L) and ventral (R) view, and pupa of ACG pyrrhopygines. **14,** *Myscelus belti* (rainforest) 95-SRNP-8435, L ♀ 99-SRNP-12882, R ♀ 99-SRNP-12671. **15,** *Passova gellias* (rainforest to cloud forest) 95-SRNP-8758, L ♀ 99-SRNP-8542, R ♂ 99-SRNP-4972. **16,** *Pyrrhopyge crida* (rainforest) 00-Cali-013.



FIGS. 17–19. Pupae of ACG pyrrhopygines. **17,** *Pyrrhopyge aesculapus* (cloud forest) 97-SRNP-513. **18,** *Pyrrhopyge cosyra* (rainforest to cloud forest) 95-SRNP-539. **19,** *Pyrrhopyge erythrosticta* (rainforest) 00-SRNP-15831.

though a common tree, is not commonly used (and caterpillars occur only on the foliage of saplings, 1–3 m from the ground). The other four species of ACG dry forest Flacourtiaceae—*Casearia tremula* Griseb. and *C. praecox* Griseb. (both locally common, but with very small distributions) and *Xylosma horrida* Rose and *X. flexuosa* (Kunth) Hemsl.—have never yielded caterpillars of *M. ambigua;* nor have any of the other 10+ species of flacourtiaceous treelets and shrubs in the wetter portions of the ACG, despite intensive search.

At Santarém, Pará, Brazil, Moss (1949) found caterpillars (described as mauve, belted with lemon-yellow) of the *M. barcastus* species complex on small bushes of *Casearia.*

The yellow-ringed caterpillar of *M. ambigua* is superficially similar to at least 13 other ACG dry forest hesperiid caterpillars: *Elbella scylla* plus the 12 pyrgine species listed in our account of that pyrrhopygine. The caterpillar of *M. ambigua* (Fig. 12) has twice as many rings as does that of *E. scylla* (Fig. 8), and they are narrower.

Parasitization frequency of *M. ambigua* caterpillars is very low (Table 1). *Mysoria ambigua* is used by three generalist tachinids—*Hyphantrophaga virilis* (Aldrich & Webber), *Chaetogena scutellaris* (Wulp), and *Lespesia aletiae* (Riley)—as well as by two still unidentified species of *Winthemia,* both of which will probably turn out to be essentially specialists on this pyrrhopygine. The only two cases of parasitization by Hymenoptera (microgastrine braconids) appear to be by species that attack a number of skipper species.

Myscelus amystis hages Godman & Salvin

This taxon ranges from about the Tropic of Cancer in Mexico to Panama (and probably also Colombia). In the ACG dry forest, and on the dry side of the intergrades between dry forest and wetter forests to the east, adults of *Myscelus amystis hages* are very rarely seen visiting flowers such as *Trigonia rugosa* (Trigoniaceae) and *Cordia* spp. (Boraginaceae). Neither adults nor caterpillars have ever been found in ACG rainforest or cloud forest.

Myscelus amystis hages, which looks like no other skipper in the ACG dry forest, most resembles its rust-red congeners *M. belti* Godman & Salvin (Fig. 14) and *M. perissodora* Dyar of the ACG rainforest. Owing to the pronounced sexual dimorphism in color pattern in *M. a. hages,* which is not expressed in the other two species, the females of *M. a. hages* (Fig. 13) approach those species in general appearance, while the more yellow-orange males (Fig. 13) do not.

In the ACG, the caterpillars of *M. a. hages* are apparently oligophagous on mature leaves of three species of *Trichilia* (Meliaceae) and nothing else (Table 1). (*Trichilia* is rarely eaten by other caterpillars of any kind.) *Trichilia americana* (Sessé & Moc.) T. D. Penn., the heavily favored foodplant, is a common forest-edge medium-sized tree in all kinds of secondary succession; the caterpillars (and newly laid eggs) are most often encountered on branches with fully insolated mature leaves. The other four species of ACG dry forest Meliaceae—*Trichilia martiana* C. DC., *Swietenia macrophylla* King, *Cedrela odorata* L., and *Guarea excelsa* H. B. & K.—have never produced these caterpillars; and neither have any of the other five or so species of meliaceous trees in the wetter portions of the ACG, despite intensive search.

The pink/dull green, shaggy caterpillar of *M. a. hages* (Fig. 13) does not resemble any other species of ACG dry-forest hesperiid caterpillar. But it strongly resembles the dull green, shaggy caterpillars of *M. belti* (Fig. 14) and *M. perissodora* and the pink/dull green, shaggy caterpillar of *Passova gellias* (Fig. 15), all found in the wetter forests on the eastern side of the ACG. It can easily be distinguished from *M. belti* and *P. gellias* by the reddish long hairs on its head (which, itself, becomes red posteriorly instead of remaining black).

Myscelus belti Godman & Salvin

Although *Myscelus belti,* like *M. a. hages,* ranges from Mexico to Panama (and perhaps also Venezuela), *M. belti* is a rainforest skipper instead of a dry-forest one. While the caterpillars of *M. belti* are found in the ACG rainforest and in intergrades with dry forest from 400–700 m, no caterpillars have ever been found in dry forest or cloud forest (and free-flying adults have not been seen or collected anywhere).

Myscelus belti, with its brick-red dorsal surface and bright yellow central splotch ventrally (Fig. 14), can be confused with only one ACG rainforest skipper—*M. perissodora.* However, *M. belti* has a small hyaline spot in the cell of the hindwing and, ventrally, a small black spot on the hindwing costa at the angle near its base, both of which *M. perissodora* lacks. Moreover, the three hyaline spots (in spaces 1b, 2, and the cell) that form the innermost band on the forewing are less well aligned and less even along their proximal margin in *M. belti* than they are in *M. perissodora.* The dark, diffuse discal band of the dorsal hindwing is a little less continuous, but at the same time a little darker in spaces 5 and 6, in the former than in the latter. Finally, the dorsal ground color of both wings is a bit redder in *M. belti* than it is in *M. perissodora.*

In the ACG, the caterpillars of *M. belti* are oligophagous on mature leaves of three species of

Guarea (Meliaceae)—*G. glabra* Vahl, *G. rhopalocarpa* Radlk., and *G. bullata* Radlk.—the first of which is also eaten by both *M. perissodora* and *Passova gellias,* and the second, by *P. gellias* (Table 1). *Guarea glabra,* which is certainly the principal foodplant, is a common forest understory and edge treelet in all sorts of secondary succession. Our efforts notwithstanding, *M. belti* caterpillars have never been found feeding on any of some 15 other species of ACG Meliaceae: *Trichilia* spp., *Swietenia macrophylla, Cedrela odorata, Guarea* spp., and various other rainforest Meliaceae.

The dull green, shaggy caterpillar of *M. belti* (Fig. 14) does not resemble any species of ACG dry forest hesperiid caterpillar except the pink/dull green, shaggy caterpillar of *M. a. hages* (Fig. 13) which, however, has reddish hairs on its head. But in the ACG rainforest and cloud forest, it strongly resembles the pink/dull green, shaggy caterpillar of *Passova gellias* (Fig. 15), with which it is easily confused because they feed on the same plants in the same place, and because *P. gellias* varies from pink (usual) to dull green. We know it must also closely resemble the caterpillar of *M. perissodora* (of which we have no photo) because our only reared adult of that species was mistaken, as a caterpillar, for *M. belti.*

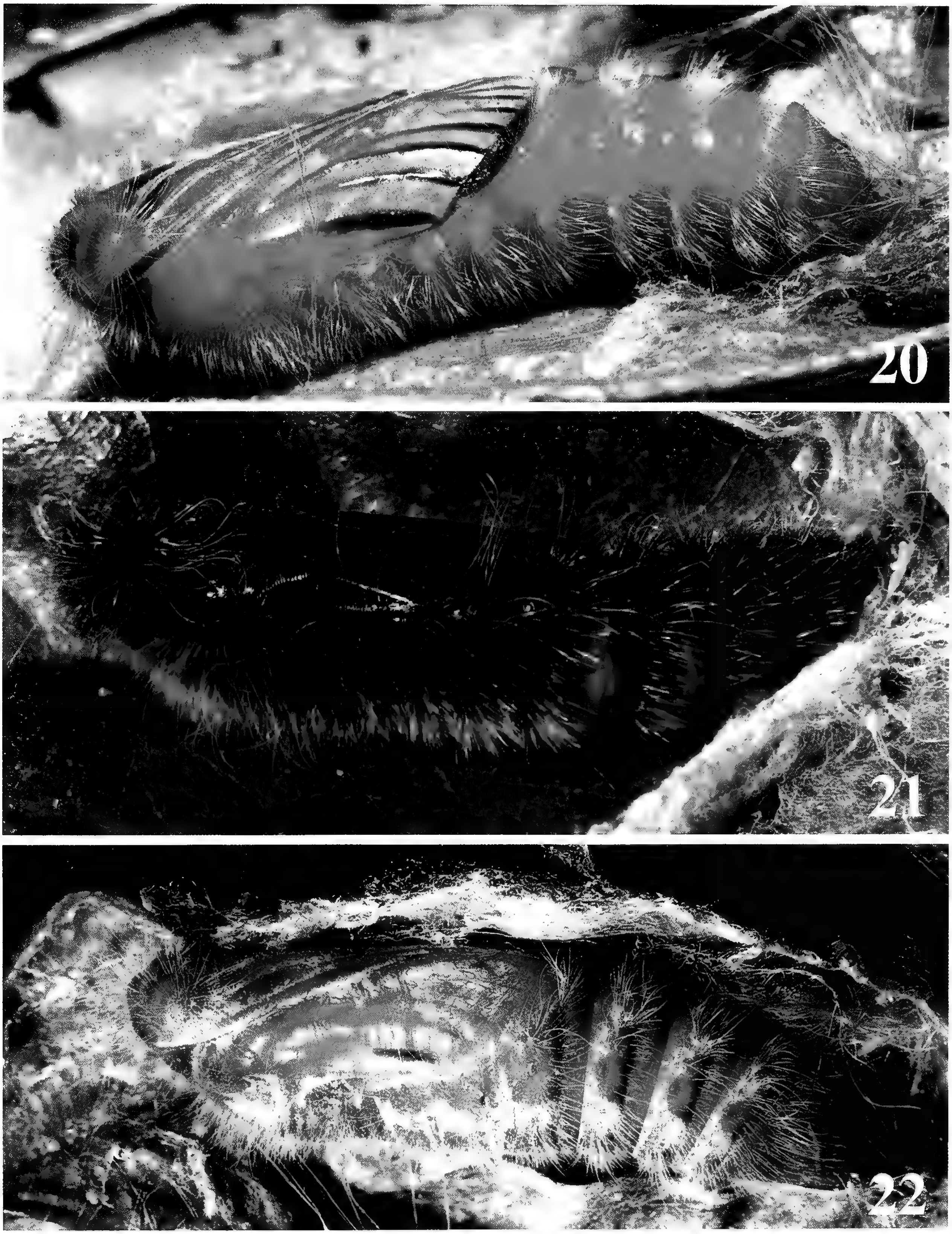
In Pará, Brazil, Moss (1949) reared three species that soon (Evans 1951) came to be called *Myscelus pardalina guarea* Evans, *Passova gazera* (Hewitson), and *Passova passova gortyna* (Hewitson), all on *Guarea trichilioides* L.; in addition, he found nests of the *Myscelus* on a second species of *Guarea.* Moss (1949:34) noted not only that the larvae of these three skipper species "are scarcely distinguishable" from one another but also that they are very distinct from those of other pyrrhopygines he had reared because "they do not possess belts or patches of lighter colour. The general tone is olive brown to greenish, ventrally pink with pinkish extremities and the head is warm brown . . . ." Although Evans (1951) viewed *Myscelus* and his new genus *Passova* as separate genera, they are closely related. For those two genera, Evans (1951:72, 79) explicitly stated that "All males have dense brushes on the inside of the femora and tibiae of the hind legs"; and he had already pointed out (Evans 1951:5) that this is "the only secondary sexual character in the subfamily" Pyrrhopyginae. Close similarities in the male genitalia of *Myscelus* and *Passova* are evident in plates 8 and 9 of Evans (1951).

Myscelus perissodora Dyar, **reinstated status**

Evans (1951)—whose material (except from the Colombian department of Cauca) was both limited and variable—treated *Myscelus pegasus* as a polytypic species comprising a pair of subspecies: *Myscelus p. perissodora* ranging from Mexico to Colombia and *Myscelus p. pegasus* Mabille occurring in Venezuela, French Guiana, and Ecuador. Although we lacked males of the latter, we had enough females of both taxa to allow critical comparison, which led to the conclusion that they represent different species. We studied 5 ♀ of *M. perissodora* (1 from Mexico [holotype, USNM], 2 Costa Rica, 2 Panama) and 4 ♀ of *M. pegasus* (Venezuela). Evans (1951) saw even fewer females: 4 ♀ of the former (1 Costa Rica, 1 Panama, 2 Colombia) and 2 ♀ of the latter (1 Venezuela, 1 Ecuador).

Comparison of KOH-dissected genitalia of the holotype, 3 other ♀ of *M. perissodora,* and 2 ♀ of *M. pegasus* showed nothing but slight individual variation on a single theme. However, absence of genitalic differentiation in a group whose genitalia are generally conservative does not argue strongly for conspecificity.

What is more important here is that species of *Myscelus* are also conservative in superficial appearance and that a number of independent superficial features distinguish our females of the taxa in question. The three large, white hyaline spots (in spaces 1b, 2, and the cell) that form the innermost band on the forewing are much smaller in *M. perissodora* than they are in *M. pegasus* and, moreover, they are broadly, rather than narrowly, edged in black. With respect to the four contiguous, subapical hyaline spots on the forewing, which run from the upper part of space 5 through space 8, the spot in space 6 is half again to twice as high as those in spaces 7 and 8 in *M. perissodora,* but only slightly higher than those in spaces 7 and 8 in *M. pegasus;* the subapical spots are not as elongate in *M. perissodora* as they are in *M. pegasus;* and the spot in the top of space 5 is only a point in *M. perissodora* but a short dash in *M. pegasus.* The dark, diffuse discal band of the dorsal hindwing is offset distad at vein 4 more conspicuously in *M. pegasus* than it is in *M. perissodora.* The lobe in the outer margin of the hindwing at the end of vein 4 is a little more pronounced in *M. pegasus* than it is in *M. perissodora.* The rusty-red ground color of the wings dorsally looks slightly paler in *M. pegasus* than it does in *M. perissodora.* The dark central band in the proximal yellow area of the ventral hindwing extends to vein 7 in *M. pegasus* but limits itself to a dash in space 1c in *M. perissodora.* The dark discal band (which extends at least to vein 6 or, more often, to vein 7, with sometimes a detached spot in space 7) is separated from the dark distal half of the ventral hindwing by a strip of yellow in *M. perissodora* (except in the type where just traces of



FIGS. 20–22. Pupae of ACG pyrrhopygines. **20,** *Elbella scylla* (dry forest) 94-SRNP-192. **21,** *Parelbella macleannani* (rainforest) 99-SRNP-13509. **22,** *Mysoria ambigua* (dry forest) 85-SRNP-80.

FIGS. 23–25. Pupae of ACG pyrrhopygines. **23,** *Myscelus amystis hages* (dry forest) 93-SRNP-8387. **24, 25,** *Passova gellias* (rainforest to cloud forest) 94-SRNP-7815.

yellow remain) but is fused with the dark distal half in *M. pegasus.*

Because the caterpillar that produced our lone adult of *M. perissodora* was identified in the field by its finder as *M. belti,* the larvae of these two skippers must look about the same. The look-alike *M. perissodora* caterpillar was likewise feeding on *Guarea glabra,* the usual foodplant of *M. belti.* However, the caterpillar came from the upper Río Mena (700 m) in the intergrade between dry forest and rainforest on the north slope of Volcán Orosí. No examples of *M. belti* have been reared from there, although the habitat looks similar to that on the southeast side of the Volcán Orosí-Volcán Cacao complex where caterpillars of *M. belti* have commonly been found.

Passova gellias (Godman & Salvin)

Passova gellias (Fig. 15) is definitely known from Honduras, Costa Rica, and Panama. While its caterpillars are found in the ACG rainforest, cloud forest, and intergrades with dry forest from 400–700 m, they have not been found in the dry forest proper; and no free-flying adults have been seen or collected in the ACG.

In the wetter forests of the ACG, the caterpillars of *P. gellias* (Fig. 15) are oligophagous on mature leaves of two of the three species of *Guarea* (Meliaceae) that *Myscelus belti* eats (one of which is also eaten by *M. perissodora*); and *G. glabra* is almost always the foodplant of choice (Table 1). See the account of *M. belti* for (1) a list of some 15 other ACG rainforest species of Meliaceae that, despite repeated search, have never yielded caterpillars of *M. belti, M. perissodora,* or *P. gellias* and (2) comments on basic similarities not only in the foodplants and the caterpillars but also in certain critical morphological features of the adults of the genera *Myscelus* and *Passova.*

THE ONLY PYRRHOPYGINE THAT ENTERS THE USA

Pyrrhopyge arizonae Godman & Salvin, **reinstated status**

Because this taxon has been considered a northern subspecies of the Mexican *Pyrrhopyge araxes* (Hewitson), it has generally been called either *Pyrrhopyge araxes arizonae* (also, for a time, *Apyrrothrix araxes arizonae*) or—by those who have chosen to downplay subspecies—simply *P. araxes.* Godman and Salvin's (1893:253) original description of *P. arizonae* was both minimal (because this Arizonan skipper was outside the fauna that they were treating) and incidental to their account of *P. araxes* (which belonged to that fauna):

> Hewitson's description of this species [*P. araxes*] was based upon a Mexican specimen now in the British Museum. Our Mexican series of examples agrees generally with the type, though there is a considerable amount of variation as regards the definition of the markings of the underside of the secondaries. In Arizona specimens these marks are evanescent, and the dark outer border is not clearly defined on its inner edge. The difference is sufficient to constitute a distinct race. Plötz also recognized two forms, but unfortunately gave a new name, *cyrillus,* to the true *araxes,* the Arizona form being his *araxes.* To rectify this we propose to call the northern insect *Pyrrhopyge arizonae,* specimens of both sexes being in our collection, sent us by Morrison from the neighbourhood of Fort Grant [which almost certainly means from the Pinaleño Mountains].

It is worth noting that, even though they wrote "*Pyrrhopyge arizonae,*" Godman and Salvin used the term "race" rather than "species" in referring to it. Apparently, they themselves saw this taxon as equivalent to a subspecies.

But *P. arizonae* and *P. araxes* are separate (albeit extremely close) species. Superficially—besides the pair of differences noted by Godman and Salvin—the brown ground color of *P. arizonae* is not nearly so dark as that of *P. araxes;* the white wing fringes of *P. arizonae* are more prominent and more heavily checkered than those of its sister; and, ventrally, the proximal yellow of the (mainly hind-) wings is not as intense, not as orangy, in *P. arizonae* as in *P. araxes.* On an average, *P. arizonae* is a little smaller than *P. araxes.*

Genitalically, in males, there are several subtle differences which are not evident when comparing published genitalia figures of *P. araxes* (Godman & Salvin 1893:pl. 73, fig. 16, Bell 1931:fig. 51, Evans 1951:fig. A.1.58) and *P. arizonae* (Skinner & Williams 1922:fig. 1, reprinted in Lindsey et al. 1931:pl. 2, fig. 1). These differences are described here in strict lateral view. Immediately anterior to the uncus, at the posterodorsolateral corners of the tegumen (where in many pyrrhopygines paired, long, caudally-projecting prongs originate), there are very short, dorsally-projecting lobes in *P. araxes* but not in *P. arizonae.* The proximal (massive) portion of the valva is longer in *P. araxes* than it is in *P. arizonae;* and its dorsal edge, as it changes (anterior to posterior) from roughly horizontal to nearly vertical, is somewhat angled in *P. araxes* but more evenly curved in *P. arizonae.* Although the dentate, distal projections of the valvae are variable (and slightly asymmetric) in both species, the ventral ones are wider in *P. araxes* than they are in *P. arizonae.* In the female genitalia of both species, the posteriormost end of the ductus bursae is closely surrounded by heavy sclerotization that forms a long, caudally-extending tube which brings the ostium bursae far back beneath the proximal ends of the ovipositor lobes. Originating from the posterior end of the sclerotized

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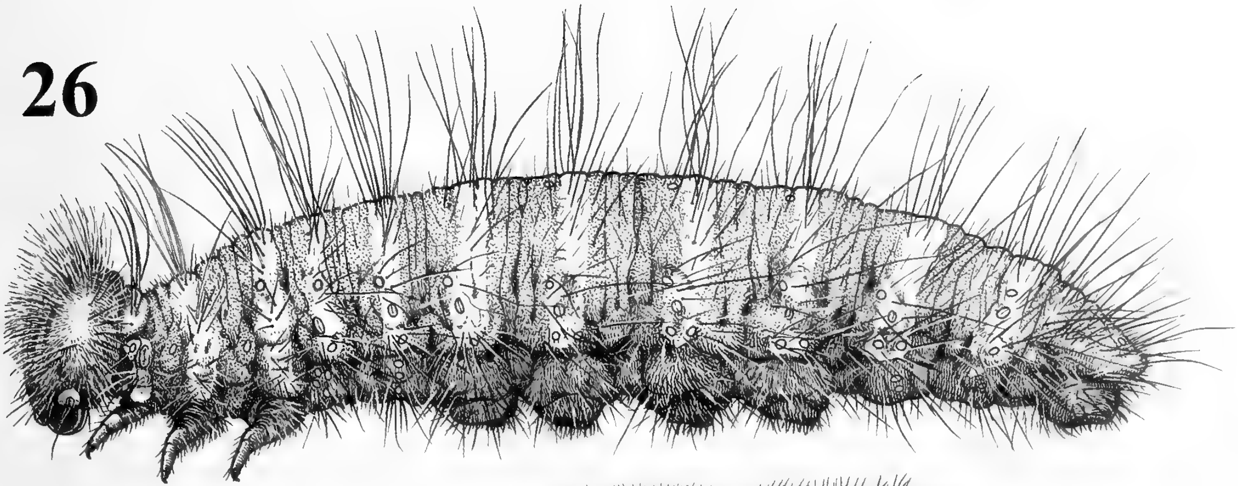

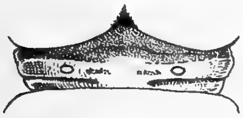

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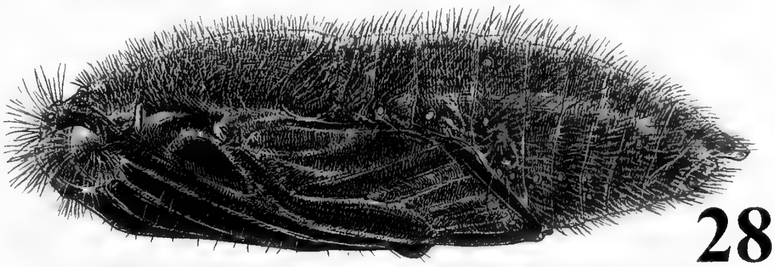

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FIGS. 26–28. Last instar and pupa of *Pyrrhopyge arizonae* (oak eater) in summer 1959; collected as larvae along the Swift Trail, 1615 m, Pinaleño Mountains, Graham County, Arizona, USA, on 5 June 1959. **26,** Larva in left lateral view. **27,** Prothoracic segment (enlarged) in dorsal view. **28,** Pupa in left lateral view.

tube (i.e., at the ostium bursae), a midventral, long, narrow, delicate, terminally-pointed prong and a mid-dorsal, equally long, but wide (and progressively widening) projection, which, in its distal half, is mid-dorsally divided so as to suggest a pair of terminally-blunt paddles, all extend back to the level of the distal ends of the ovipositor lobes. Compared genitalic dissections include 7 ♂ 4 ♀ of *P. arizonae* from the Chiricahua and Huachuca mountains, Cochise Co., plus Peña Blanca Lake, Santa Cruz Co., Arizona, USA, and 30 mi (48 km) N of Mante, Tamaulipas, Mexico; and 4 ♂ 3 ♀ of *P. araxes* from Mexico City, Cuernavaca, and Tizapán, Mexico.

Pyrrhopyge arizonae occurs in the southwestern USA (in the montane oak belt of southeastern Arizona, adjacent southwestern New Mexico, and also the Big Bend region of Texas) and in northern Mexico (from Sonora, Chihuahua, and Tamaulipas southward to uncertain limits). *Pyrrhopyge araxes* occurs in central and southern Mexico (at least from Jalisco through the Distrito Federal and Morelos to Veracruz, south to at least Guerrero and Oaxaca).

In southeastern Arizona (Cochise and Graham counties), Comstock (1956) collected a single caterpillar of *P. arizonae* on oak at 1860 m in Miller Canyon, Huachuca Mountains, on 27 July 1955; and Burns (1964:109, unpubl.) collected three caterpillars on *Quercus arizonica* Sarg. and another on *Quercus* sp. at 1615 m in the South Fork of Cave Creek Canyon, Chiricahua Mountains, on 22, 23, 24 April 1959, plus two, on *Q. arizonica* and *Q. emoryi* Torr., respectively, at 1615 m along the Swift Trail, Pinaleño Mountains, on 5 June 1959 (*Quercus* is in the Fagaceae). After further growth, these last two specimens posed for Figs. 26 to 28. This skipper has also been reported on *Q. oblongifolia* Torr. (Bailowitz & Brock 1991).

Although the adult of *P. arizonae* is a classic "skipper-brown"—with the "usual" hyaline spots on the forewing—and is in no way a flashy pyrrhopygine, the caterpillar (Fig. 26) ranks with the best of them. Its head is black (clypeus tan), densely clothed with (for the most part, relatively short) white hairs—paired ventrolateral patches of which are rusty-orange; and its body is a rich, deep maroon crossed by brilliant yellow bands (one per segment), with long white hairs springing mainly from the yellow bands, but also from a pale, creamy-yellow prothoracic shield. This pale shield bears a very thin, black band dorsolaterally (but not medially) about two-thirds of the way from its anterior to its posterior margin (Fig. 25).

The pupa (Fig. 26) is dark and heavily clothed with hairs, which are mostly white, but brilliant orange-yellow on the prothorax. The wing covers, the thorax dorsally, plus the proboscis, legs, antennae, the greater part of the eyes, and a few other head plates are all a dark (purplish) black with a whitish blue-gray bloom. The thoracic spiracles, part of the eyes, the anterior head region, and the paired plates anterior to the prothorax are all a rich chestnut-brown. The abdomen looks dirty yellowish-brown, with alternating yellower and browner zones, the latter coated with blue-gray bloom. The terminal segment is mostly brown and blackish-brown, and the cremaster is brown. Although descriptions of the last instar and pupa provided by Comstock (1956) variously supplement, support, and depart from those above, both his and our pupal descriptions clearly fit the subfamily mold (Figs. 16–25).

DISCUSSION

Ecology. Twenty-two years of rearing 2192 pyrrhopygine caterpillars and collecting far fewer adults show that the ACG supports at least 15 species of pyrrhopygine hesperiids: 3 in (lowest elevation) dry forest (*Elbella scylla*, *Mysoria ambigua*, and *Myscelus amystis hages*); 4 in (highest elevation) cloud forest (*Pyrrhopyge creon*, *P. aesculapus*, *P. cosyra*, and *Passova gellias*); and 10 in (middle elevation) rainforest (*Pyrrhopyge zenodorus*, *P. crida*, *P. cosyra*, *P. erythrosticta*, *Parelbella macleannani*, *Jemadia pseudognetus*, *Jemadia* sp. X (an unnamed *Jemadia* belonging to a *J. hewitsonii* species complex), *Myscelus belti*, *M. perissodora*, and *Passova gellias*). Although caterpillars of some of these species are occasionally found in the intergrades between their "usual" ecosystem and an adjacent one, no pyrrhopygine species spans all three ecosystems; and none occurs in both dry forest and rainforest. Only two range from rainforest to cloud forest: *Pyrrhopyge cosyra*, which occurs from hot lowland rainforest to high, cold cloud forest; and *Passova gellias*, which generally goes less far up into the cloud forest.

ACG pyrrhopygines seem not to migrate seasonally between major ecosystems. Even in the dry season, sexually dormant adults of the three dry-forest species appear in local moist areas of the dry forest rather than in the adjacent rainforest. (Note that these adults do not break reproductive dormancy and oviposit on their respective foodplants when those plants—responding to, say, the clearing of right-of-ways and firebreaks—produce new, leafy, sucker shoots from fresh stumps in the middle of the dry season.)

Ecosystem-level specificity of ACG pyrrhopygines does not stem entirely from the ecology of their foodplants. On the one hand, dry-forest pyrrhopygine foodplants do not occur in rainforest and cloud forest (although congeners do). On the other hand, some wet-forest pyrrhopygine foodplants do occur in dry forest as well (along with congeners), while the pyrrhopygines that eat them do not. For example, *Vismia baccifera* and *Clusia rosea* occur in both ACG dry forest and rainforest; but *Pyrrhopyge zenodorus* and *P. cosyra*, their respective grazers, stick to the wetter forest. However, many other ACG skipper species do occur in both dry forest and rainforest. The plant families Lauraceae, Flacourtiaceae, Myrtaceae, Combretaceae, and Malpighiaceae—which are used by ecosystem-specialist pyrrhopygines—all contain species that occur in both dry forest and rainforest where they support larval pyrgines that likewise range across both ecosystems.

Costa Rica has about 25 species of pyrrhopygines, or about one-eighth of our estimated total of all pyrrhopygine species. This estimate of 200 may still be too low, but it far exceeds the number ("almost 150") offered by Ackery et al. (1999). Since we now have reared 15 species (and anticipate only one to three more), the ACG is home to at least 60% of the Costa Rican pyrrhopygine fauna. Though an ecological island, the ACG seems to offer enough habitat, with abundant foodplants, to sustain these skippers. However, substantial global warming, with a concomitant rise in the elevation of the cloud layer (e.g., Pounds et al. 1999), could seriously reduce the area of cloud-forest habitat for *Pyrrhopyge creon* and *P. aesculapus*. Moreover, the gradual return of large areas of ACG secondary successional forest to old-growth forest over the coming centuries will substantially reduce the sizes and ubiquity of populations of important rainforest foodplants such as *Vismia baccifera* and dry-forest foodplants such as *Byrsonima crassifolia* and *Casearia corymbosa*.

Pyrrhopygine caterpillars, like those of other ACG skippers that feed on broadleaf plants, are concentrated primarily in the zone between 10 cm and 3 m above the ground, even when individuals of their foodplants rise as much as 20–40 m. Although further inventory exploration of the ACG canopy may turn up exceptions, they are not yet evident. While adult skippers can be seen visiting flowers in the crowns of the tallest trees, they do not seem to be ovipositing at these heights.

Foodplants. ACG pyrrhopygine larvae have exclusive tastes. The caterpillars of *Myscelus belti*, *M. perissodora*, and *Passova gellias* are the only ones that share their foodplants with other pyrrhopygines—in these cases, each other (Table 1). The caterpillars of *Elbella scylla, Parelbella macleannani,* and *Jemadia pseudognetus* are the only ones that share their foodplants with non-pyrrhopygine hesperiid larvae.

The strong host specificity shown by pyrrhopygine caterpillars is frequent among ACG butterflies and certain families of moths (e.g., host records in Janzen & Hallwachs 2001), and especially among dicot-eating skippers. Even though the foodplant records for our pyrrhopygines (Table 1) are dotted across the botanical taxonomic landscape (i.e., in the families Lauraceae, Clusiaceae, Flacourtiaceae, Cunoniaceae, Myrtaceae, Combretaceae, Meliaceae, Malpighiaceae, and Araliaceae), some patterns emerge. *Myscelus amystis hages, M. belti, M. perissodora,* and *Passova gellias,* which (aside from their adult color patterns) are similar, all focus on Meliaceae—mainly *Guarea glabra.* Several species currently in the large genus *Pyrrhopyge* (*P. zenodorus, P. crida, P. cosyra,* and *P. erythrosticta*) are monophagous to oligophagous on members of the Clusiaceae. A female of another Costa Rican species of *Pyrrhopyge, P. haemon* Godman & Salvin, was found and reared (in 1995 at 1600 m in Tapantí National Park by R. Delgado) on a clusiaceous plant in the genus *Vismia,* species of which are the foodplants of *P. zenodorus* and *P. crida.*

In this connection, it is also clear that ACG pyrrhopygine caterpillars are specialists at levels far below that of the plant family. For each species of caterpillar, there are many ACG species of plants within the plant family fed upon that are not used. It is particularly striking, for example, that *Pyrrhopyge zenodorus* eats the common *Vismia baccifera* (occurring from dry forest to rainforest) and the rare *V. ferruginea,* while *P. crida* eats neither, restricting its diet to the low density and local rainforest *V. billbergiana.*

Within an oligophagous species, percentages of caterpillar records among its small set of foodplants (Table 1) do not reflect the relative abundances of those plants. For example, *Mysoria ambigua* uses *Casearia corymbosa* most of the time, even though its other three foodplants are common in the same dry-forest habitats.

More or less close relatives of half of the pyrrhopygine species that we have reared in the ACG were reared previously in Pará, Brazil, by Moss (1949). The plants he found them eating are usually in the same genera as the foodplants of their Costa Rican counterparts, and are always in the same families. Not surprisingly, the strong host specificity shown by ACG pyrrhopygine caterpillars seems to be geographically conservative.

In also rearing a few pyrrhopygines most of which were well removed from the species we have reared, Moss (1949) recorded foodplants in some other families: Annonaceae, Myristicaceae, Sterculiaceae, and Sapindaceae (although he questioned the accuracy of the identification of the last). In revising both *Elbella* and its near relatives (most of whose diets remain unknown), Mielke (1995) added one foodplant genus (*Quiina* and *Miconia*) from each of the families Quiinaceae and Melastomataceae. While the total taxonomic spread of pyrrhopygine foodplant families becomes a little wider, there is also a little clustering. The Annonaceae may relate to the Myristicaceae; the Quiinaceae, to the Clusiaceae; and the Melastomataceae, to the Combretaceae or Myrtaceae (Heywood 1993).

The only pyrrhopygine to enter the USA, *Pyrrhopyge arizonae,* puts another isolated genus and family (*Quercus,* Fagaceae) on the list of disparate foodplants.

Biogeography. To judge from current distributions, the Pyrrhopyginae (a strictly New World group) probably arose in tropical South America. Most of the existing species are there. Nearly half of the ACG pyrrhopygines we have reared (*Pyrrhopyge zenodorus, Elbella scylla, Parelbella macleannani, Jemadia pseudognetus, Jemadia* sp. X, *Mysoria ambigua,* and *Myscelus amystis hages*) appear to be northern extensions of species complexes that are better represented and more widely distributed in South America. Four more (*Pyrrhopyge crida, P. aesculapus, P. cosyra,* and *Myscelus perissodora*) are species with significant South American ranges (usually Colombia and Ecuador) as well as Middle American ones. Only four (*Pyrrhopyge creon, P. erythrosticta, Myscelus belti,* and *Passova gellias*) seem to be confined to Middle America. There are no pyrrhopygines in the West Indies.

Parasitoids. ACG pyrrhopygines are notably free of parasitoids. Despite their slow larval growth rates (among the longest within the ACG hesperiids), pyrrhopygines are at the low end of the spread of larval parasitization frequencies—and not just among skippers but among ACG macrolepidoptera generally. Only 7.1% of the total wild-caught pyrrhopygine caterpillars were parasitized. Ten of the 15 species reared from wild-caught caterpillars produced no parasitoids whatsoever, even when samples were large (Table 1). It is especially noteworthy that none of our many caterpillars (n = 295) belonging to the closely related genera *Myscelus* and *Passova* has yielded parasitoids (Table 1).

Ichneumonids have been reared only from *Pyrrhopyge cosyra* caterpillars. However, *Casinaria* sp. 9, which frequently attacks *P. cosyra* (31 records), also attacks the pyrgines *Phocides nigrescens* (2 records) as well as *Achlyodes thraso* (Hübner) (1 record), *A. selva* Evans (2 records), and *A. busirus heros* (6 records) in the same habitat (but has not yet been found to attack tens of other hesperiid species in this habitat). To date, the ichneumonid genus "MCAM" sp. 1 (10 records) has been found parasitizing only *Pyrrhopyge cosyra.* Only *Elbella scylla* is attacked by a braconid with enough frequency to suggest that the relationship might be host-specific. Parasitization by tachinid flies is light, and only four of the 15 species reared from wild-caught caterpillars had any at all. Whether the slow growth rate of pyrrhopygine caterpillars is evolutionarily "permitted" by the low parasitization frequency, or the low parasitization frequency stems from traits of the caterpillars, will be the subject of family-wide analysis at a later time.

Taxonomy. It is hardly surprising that most of the parasitoids attacking ACG pyrrhopygines are undescribed whereas their large and ostentatious hosts are not. Nevertheless, when it came to identifying these Costa Rican skipper butterflies (which led to examining them in a much broader geographic and taxonomic context), fully half of them posed biological questions. The recurring one involved the status of an ACG entity vis-à-vis its nearest relative: Are those perceptible (but closely similar) differentiates species or subspecies? In general, taxa that Evans (1951) treated as subspecies are here granted species rank. Other biological problems bearing on accurate application of names involved (1) something currently passing as a single species that actually comprises a pair of sympatric species, (2) the reverse of this—a supposed pair of sympatric species that actually are one and the same thing, and (3) an entity that belongs to an essentially South American species complex not previously recorded from Costa Rica. Pyrrhopygines are a flashy tip of a taxonomic iceberg. If some of *their* identities were this uncertain, what about those of all the rest of the ACG skipper butterflies (which reflect the world's uniquely rich neotropical hesperiid fauna)? And then, by extension, what about the placement of all the rest of ACG invertebrate biodiversity? Taxonomists and time are of the essence.

ACKNOWLEDGMENTS

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BOOK REVIEWS

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A Contribution to Riodinid Systematics (Lepidoptera: Riodinidae), by Jason P. W. Hall with Keith R. Willmott & Donald J. Harvey, Contributors. 1998. Tropical Lepidoptera. Volume 9, Supplement 11. 42 pp., 7 color plates. Published by The Association for Tropical Lepidoptera (www.troplep.org), P.O. Box 141210, Gainesville, Florida, USA. ISSN 1048-8138, available from the publisher.

A Revision of the Genus *Theope*, its Systematics and Biology (Lepidoptera: Riodinidae: Nymphidiini), by Jason P. W. Hall. 1999. Published by Flora & Fauna Books (www.ffbooks.org), Gainesville. 127 pp., 9 color plates. Paperback, 8.5 × 11 in., glossy paper, ISBN 0-945417-95-0, available from the publisher.

As an amateur rather than a professional entomologist, it is easy to wax enthusiastic about these two publications. Those of us interested in riodinid butterflies have seen a steady increase in the quantity and quality of publications regarding this group. Supplement 1 to Volume 9 of Tropical Lepidoptera consists of four papers authored or co-authored by Jason P. W. Hall. The co-authored papers describe a total of 13 new riodinid species from Ecuador. The longer paper is a systematic revision of *Sarota*, including 5 species and 2 subspecies previously not described. A particularly helpful key is provided which will prove invaluable for the worker trying to differentiate these rather small butterflies.

The second publication, "A Revision of the Genus *Theope*," carries the process to an even higher level. For this 125 page tome, the author has personally examined 4253 *Theope* specimens in 23 major collections on three continents, including all but three of the extant primary types. Most *Theope* are rare in collections (with a few notable exceptions), and half the described species are known from 20 or fewer specimens. Nevertheless the paper contains dorsal and ventral photographs of all the recognized species with genitalia illustrations of 70% of the females and all the males save *Theope villai*. Terminal abdominal tergite drawings are also included, which show a remarkable diversity of sizes and shapes. To avoid confusion by future researchers, the author has extensively documented the material examined and figured, including the location for each figured specimen and genitalia dissection. Many lectotypes are also designated.

This revision identifies 68 *Theope* taxa. A binomial key for identification of males is provided, but not females, since many are unknown, especially in the "*foliorum* group." The author has included corrected identifications for specimens figured by Seitz, Godman and Salvin, Barcant, D'Abrera, DeVries, and others, updating all these works to conform with this revision.

Most interesting is the discussion of *Theope* as an indicator of species diversity in Upper Amazonian areas. The extensive range maps are most helpful and the tables listing perching times for 34 species of *Theope* will provide a basis for correlation of further field observations. I believe this publication could serve as a template for any doctoral thesis in this field, much less any taxonomic revision. To have this much valuable information, so concisely compiled, is an unexpected pleasure.

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The Western Palearctic Zygaenidae (Lepidoptera), by C. M. Naumann, G. M. Tarmann and W. G. Tremewan, 1999. Published by Apollo Books, Kirkeby Sand 19, DK-5771 Stenstrup, Denmark. 304 pp., 178 line drawings and black and white photographs, 12 color plates. Hardback, 24 × 17 cm, ISBN: 87-88757-15-3. Available from Apollo Books, Price DK 6000.00 (about $80.00 US) excluding postage, available from the publisher.

Three eminent specialists have combined their expertise to create a book on one of the most striking groups of day-flying moths, the Zygaenidae. In addition, they have compiled the results of many studies by other workers, amateur or professional, over the last 100 years. The foreword by Miriam Rothschild, written in her typical entertaining style, introduces the reader to this book in the context of her own interests such as their extensive variation, complex diapause patterns, behavior, conservation, and toxicity. The purpose of the book, as explained in the authors' foreword, is to provide an up-to-date summary of past and current biochemical, physiological, behavioral, and ecological studies, and to present an overview of the distribution, ecology, and systematics of the zygaenid moths of the western Palaearctic. They have certainly succeeded in achieving these aims.

The book is divided in two parts. In the "General Part" the systematics and phylogeny of the Zygaenidae are briefly discussed, followed by a description of life cycles and their peculiarities. The morphology of the immature and imaginal stages, with frequent references to their phylogenetic implications, is briefly, but comprehensively, described and illustrated in the section "Structures and functions" that includes a discussion on "Senses and orientation" and "Nutrition." "Genetics and individual variation" deals with wing patterns and coloration, including color mutants and other aberrations, of some *Zygaena* species. In "Zoogeography" the geographical variation in *Zygaena* moths, hybrid belts, littoral and montane melanism, and geographical variation in color and size of larvae is discussed. The distribution patterns in the western Palaearctic are assigned to a Mediterranean, Syro-Anatolian, Iranian, Transcaucasian or Euro-Siberian type, which but for the latter, reflect and include Pleistocene refugia and survivors of the last glaciation. Fossil zygaenids are briefly mentioned. "Ecology and behavior" deals extensively with their diverse habitat preferences. A discussion on the food plants leads to a highly informative section on cyanogenensis, cuticular secretion of defensive compounds by larvae and imagoes as a defensive strategy. The strong attraction of adults to certain flowers is ascribed to compounds related to sex attractants of some *Zygaena* species. Two independent mate-locating systems, the early morning (optical cue) strategy and the pheromone induced matings, are described. The toxicity and aposematic coloration of zygaenids is related to mimicry, behavior, and predation. Diapause in these insects reveal complex patterns which regulate phases of growth and dormancy. Parasites of larvae and pupae include wasps and tachinid flies. In "Zygaenids as indicator species" their importance as such is emphasized. Conservation should concentrate on the protection of habitats. "Breeding" and "Collecting techniques" is followed by an "History of research on the Zygaenidae" highlighting the contributions made in taxonomy, collecting expeditions, biology, genetics, biochemistry, ecology and behavior, reproductive biology, and bibliography by past and present researchers and naturalists. The first part ends with a list of vernacular names as used in the western Palaearctic. "Selected references" introduces the reader to more details of zygaenid biology and systematics.

The "Systematic Part" starts with a check list of the 116 species found in the western Palaearctic. This list is divided into the three subfamilies, the Procridinae, Chalcosiinae and Zygaeninae, each with their constituent taxa and currently accepted names. The diagnosis of the family is followed by a dichotomous key to the three subfamilies of the western palaearctic Zygaenidae. Under Procridinae there is a list of the constituent genera and characters that separate the procridines from other subfamilies; these general characters and their variation are then described in more detail. A dichotomous key to the genera of the Procridinae is presented. Each genus and subgenus, where applicable, is described in terms of diagnostic characters, followed by a detailed standardized description of the constituent species. The pertinent details of each species include a reference to the imago by referring to plate number, length of fore wing, brief description of both sexes, including descriptions and drawings of their genitalia, similar species, individual geographical and ecological variation, and its distribution, including a range map for every species. Where known, details of the immature stages, including food plants, are also given. Every species is illustrated in color. Dichotomous keys to species, sometimes between sexes, are presented. The treatment of Chalcosiinae is as for Procridinae. The Zygaeninae are introduced by a diagnostic overview of the subfamily and the genus *Zygaena,* followed by a dichotomous key to the species of the western Palaearctic. Descriptions of the various species are then presented. An "Appendix" provides information on the recently described *Jordanita (J.) fazekasi.* A comprehensive "Index" concludes the text.

The overall design of the book is excellent. The book is well bound with a quality decorative cover. The text, text figures, and photographs are on glossy paper and provide excellent detail. The text is in an easy, well-organized reading style. The 178 text figures consist of an array of diagrams, drawings and photographs; for every species a distribution map is also given. The color reproduction of the plates is of the highest quality, accurate, and shadow-free. Plates 1–6 illustrate 318 set specimens, often more than one exemplar of a species, at life size with facing pages giving the species or subspecies, sex, locality and reference page number. Plates 7–8 show imagoes resting, *in copula* or feeding; various aspects of behavior are shown on plate 9. Plate 10 is devoted to larvae. Plates 11–12, depicting various habitats, will put shame to any tourist brochure! The book has been well proofed and I could spot only smaller errors (misspelling of Somabrachyidae (p. 14), alkaloids (p. 15) and food plants (p. 16)). The only distraction is that the entry for the last species ends in mid-sentence (p. 262), interrupted by the plates, to continue on p. 288; the plates could have been bound following p. 290.

This book is beautifully produced and reasonably priced. Its comprehensive treatment resulting from the combination of authoritative authorship and editorial care guarantee that this work will be the standard reference on the zygaenid fauna of the western Palaearctic for many decades to come. This book should not only be on the bookshelf of lepidopterists, but it will also be of interest to students of biogeography and evolutionary history of Lepidoptera and other insects from a highly interesting faunistic region. I recommend this book enthusiastically.

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FORESTER MOTHS, by K. A. Efetov and G. M. Tarmann. 1999. Apollo Books, 192 pp., 12 color plates with 241 illustrations, 174 line drawings, 24 × 17 cm. Available from Apollo Books, price: 460 Danish Kroner, excl. postage (hardback).

As a worker on the other half of the superfamily Zygaenoidea (i.e., the limacodid group), the publication of two books on Zygaenidae at roughly the same time is like meeting your lost relatives. For those of us that have large quantities of unsorted palaearctic zygaenids, this is a welcome event indeed. It is also a major benefit for those interested in the biologies and life histories of these beautiful diurnal creatures and makes literature more accessible to the English-speaking lepidopterist.

The scope of the two books on western palaearctic Zygaenidae overlap in part, which at first glance is a bit confusing. "Forester Moths" by Efetov & Tarmann is solely about the subfamily Procridinae (also known as foresters), and its four genera and 63 species from the western palaearctic. "The Western Palearctic Zygaenidae" (1999, C. M. Naumann, G. M. Tarmann and W. G. Tremewan, Apollo Books) covers the same 4 genera, but only 44 species of Procridinae, in addition to the Zygaeninae and Chalcosiinae. In fact, one might question why the two books could not have been combined because of the overlap of the Procridinae and in genitalia drawings, checklist, and keys.

"Forester Moths" by Efetov & Tarmann, perhaps the last book of the two to be published in 1999, mentions the other as a complementary text in its introduction. Indeed the focus on the Procridinae by Efetov & Tarmann provides more detailed information about this subfamily, including citations of misspelling and all known synonymies and homonymies. It should be noted that there is a lack of agreement between the checklists of the Procridinae regarding format and inclusion of taxa. Efetov & Tarmann separate the subgenera into species groups and have subspecies, whereas Naumann et al. does not. The discrepancy between the procridine species included (63 in Efetov & Tarmann and 44 in Naumann et al.) between the two books is in part due to the covered region and primarily concerns the genus *Adscita* Retzius. Naumann et al. only contains species from the Iberian Peninsula and North Africa to the Urals, including Turkey, Transcaucasia and Caucasus, but Efetov & Tarmann, in addition, include species from northern Iran and some countries east of the Caspian Sea of "the western and central parts of Asia (i.e., the western and central Palaearctis)."

"Forester Moths" begins with a concise introduction and definition of the Procridinae. This is followed by an intriguing chapter (III) on the characters of the subfamily including a chart and associated illustrations that review the broad variation of dorsal and subdorsal setae on the first abdominal segment in first instar larvae. This is reminiscent of the broad variation found within the entire limacodid group (Epstein, M. E. 1996. Revision and phylogeny of the limacodid-group families, with evolutionary studies on slug caterpillars (Lepidoptera: Zygaenoidea), Smithsonian Contributions to Zooology, 582). Next is a review of the chromosomal numbers in the subgenera. The final part Chapter III includes a novel character combination diagram and table, which divides the forester genera or subgenera into groups based on shared characters of adult and immature stages. These include biological (e.g., host plants, diapause stage) and chromosomal information, in addition to morphological data. There is also a similar table for genera and host plant families. These tables serve as a concise way to organize information on these genera, although do not necessarily reflect the relationships between the forester moths. Chapter IV on phylogenetic relationships, while centering on the palaearctic genera of Procridinae, provides a useful review for future workers on the worldwide fauna.

Chapter V is a checklist where each species is numbered and corresponds to the species numbers in the next chapter, the systematic catalogue. The text is very telegraphic in the catalogue, but there is detailed information on the types (localities and place of deposition) and host plants. I applaud the authors who took care of nomenclatural business by designating 17 lectotypes. Distributional information is provided, but according to the authors, maps are forthcoming in an atlas which will complement the text. Two new subgenera, *Tremewania* and *Procrita*, are also described.

In the next chapter (VII), the authors have chosen to replace the usual descriptions of taxa with keys to genera and species, and provide large numbers of illustrations of key taxonomic characters, especially of the genitalia in Chapter VIII. These two chapters might have been more logically placed before the systematic catalogue, but this is only a minor inconvenience. Sadly, these excellent illustrations will be the last by V. V. Kislovsky who died during a heart operation at age 24, shortly before the book was published.

The penultimate chapter is on the immature stages and life histories of six species in the genera *Jordanita* Verity and *Adscita*. These include observations of the adults and biotype where the species occur, along with detailed life history information on the immature stages, with color photographs of each in the back of the book. The final chapter presents a table of new parasitic records based on host identification by the authors and parasitic information by specialists for each group.

The book is made up of rag type paper, which has the disadvantage of having somewhat dull images for the color plates and taking up more space on your shelf than glossy paper for the same number of pages. In the back of the book are seven plates. The first five plates contain 130 paintings by N. V. Dyadenko of all included forester species shown at 2× natural size. This is followed by a plate with photographs of 16 of the 17 lectotypes designated in this book along with early stages and adults in natural settings of *Theresiminia* Strand, *Rhagades,* and *Jordanita*. The figure of the lectotype of *Ino paupera* Christoph would have benefited from a lighter background. The next two plates correspond to the life history information of *Jordanita* and *Adscita*, mentioned above. These are followed by a plate of beautiful zygaenid host plant photographs and three plates of scenic photographs illustrating the diverse biotypes of foresters of the western palaearctic.

I recommend both books on western palaearctic Zygaenidae for serious study, because it is clear that you would be missing a great deal of useful information on this group by owning just one of them.

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In taxonomic manuscripts, **taxon names** can be used both as headings and subheadings. They should be centered, italicized, and followed by the author's name in roman type. Year of publication is optional; if provided, it should be separated from author's name by a comma. Indicate new taxa and change in status of a taxon in English, spelled fully, and in boldface (e.g., new species, new combination, new synonym). New taxa with author and status appear entirely in boldface. When needed, authors' initials may be added to elucidate their identity. In the examples below, the genus name appears as a section heading, and species names are subheadings; new status is assigned to one species, and one is being described as new:

Mylon Godman & Salvin, 1894
Mylon orsa Evans, 1953
Mylon exstincta Mabille & Boullet, 1917, **new status**
***Mylon simplex* Austin, new species**

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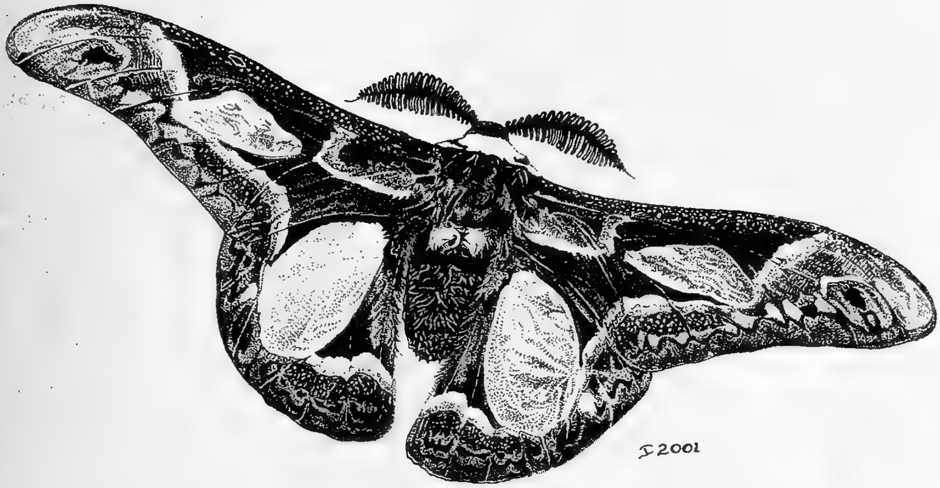

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SPECIES' COMPOSITION OF MOTHS CAPTURED IN TRAPS BAITED WITH ACETIC ACID AND 3-METHYL-1-BUTANOL, IN YAKIMA COUNTY, WASHINGTON

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ABSTRACT. Moths were captured in traps baited with acetic acid and 3-methyl-1-butanol at four sites in Yakima County, Washington, from March to October, 1999. Nine hundred and ninety-one moths captured were identified to 60 species. Three families of Lepidoptera were represented: Noctuidae, Thyatiridae, and Pyralidae. The majority of species (90%) and individuals (90%) were noctuids. These included many non-pest species and numbers of several pest species: the forage looper *Caenurgina erechtea* Cramer, glassy cutworm *Apamea devastator* Brace, bertha armyworm *Mamestra configurata* Walker, true armyworm *Pseudaletia unipuncta* Haworth, and spotted cutworm *Xestia c-nigrum* (L.). Noctuids collected included representatives of the subfamilies Catocolinae, Cuculliinae, Hadeninae, Amphipyrinae, and Noctuinae. The majority of moths trapped were captured during August and September.

Additional key words: trapping, attractant, survey, biodiversity, sampling.

Many insect species, including Lepidoptera, are attracted to baits containing fermenting sugar solutions or other sweet materials (Norris 1935). Such baits have long been used by moth and butterfly collectors (e.g., Holland 1903, Sargent 1976) and have been employed or investigated by applied entomologists attempting to monitor or control pest species of moths (Ditman & Cory 1933, Eyer 1931, Frost 1926, Landolt 1995, Landolt & Mitchell 1996). Recently, Yamazaki (1998) used sweet baits in traps as a means of sampling moths for survey and ecological work.

The identification of attractive chemical odorants from fermented sugar baits provides opportunities to develop useful insect lures. Three pest species of Noctuidae, *Lacanobia subjuncta* (Grote & Robinson), the bertha armyworm *Mamestra configurata* Walker, and the spotted cutworm *Xestia c-nigrum* (L.), are attracted to a combination of acetic acid and 3-methyl-1-butanol (Landolt 2000). Acetic acid and 3-methyl-1-butanol are found in fermented sweet baits and some microbial cultures (DeMilo et al. 1996, Utrio & Eriksson 1977). These compounds are thought to be feeding attractants for those moths (Landolt 2000) and are being developed as lures for monitoring and controlling pest species of Noctuidae (Landolt & Alfaro 2001, Landolt & Higbee 2002).

The purpose of this study was to determine what types of moths are attracted to acetic acid and 3-methyl-1-butanol more thoroughly than in previous surveys. In a study that documented attraction of *L. subjuncta*, *M. configurata*, and *X. c-nigrum* to these chemicals (Landolt 2000), other moths were captured but were not identified. We sought to determine if other pest species of Lepidoptera are attracted to this lure. A secondary objective was to document responses of non-target species in order to assess the complexity of using the lure to monitor pests. Knowledge of the types of insects responding to this lure may suggest additional uses of the attractant in survey and sampling studies, such as that of Yamazaki (1998).

MATERIALS AND METHODS

Moths were trapped with Butterfly Bait Traps (BioQuip Products, Santa Monica, California). These cage

TABLE 1. Species of moths captured in traps in Yakima County, 1999.

					Total	
Species	Orchard	Parker	Moxee	Ahtanum	♀	♂
Thyatiridae						
Euthyatira semicircularis (Grote)	0	0	0	1	1	0
Habrosyne scripta (Gosse)	0	1	0	0	1	0
Pseudothyatira cymatopheroides (Guenée)	0	0	1	0	1	0
Noctuidae						
Catocolinae						
Caenurgina erechtea (Cramer)	0	1	8	1	8	2
Catocala stretchi Behr	0	0	2	0	2	0
Catocala briseis Edwards	0	0	0	2	2	0
Zale lunata (Drury)	0	3	1	1	5	0
Plusiinae						
Autographa californica (Speyer)	0	0	2	0	2	0
Amphipyrinae						
Protagrotis obscura (Barnes & MacDunnough)	0	0	0	1	0	1
Apamea (Agroperina) dubitans (Walker)	0	1	1	2	1	3
Apamea amputatrix (Fitch)	0	1	0	1	2	0
Apamea (Crymodes) devastator (Brace)	0	5	77	58	54	89
Apamea occidens (Grote)	0	0	1	0	1	0
Aseptis characta (Grote)	0	0	18	0	9	9
Caradrina meralis (Morrison)	0	1	9	0	4	6
Caradrina morpheus (Hufnagel)	0	0	1	0	0	1
Chytonix divesta (Grote)	0	1	0	0	0	1
Oligia indirecta (Grote)	0	0	0	3	1	2
Oligia tonsa (Grote)	0	1	9	0	5	5
Athetis mindara (Barnes & MacDunnough)	0	0	1	0	1	0
Spodoptera praefica (Grote)	0	0	2	0	0	2
Cuculliinae						
Epidemas cinerea Smith	0	0	8	0	4	4
Hadeninae						
Aletia oxygala (Grote)	0	7	18	91	63	53
Leucania farcta (Grote)	0	1	0	1	1	1
Discestra oregonica (Grote)	0	0	0	1	1	0
Discestra mutata (Dod)	0	0	0	1	1	0
Dargida procinta (Grote)	1	3	130	4	67	71
Lacanobia subjuncta (Grote & Robinson)	1	0	0	0	1	0
Lacinipolia stricta (Walker)	0	3	0	14	10	7
Lacinipolia vicina (Grote)	0	0	8	0	4	4
Lygephila victoria (Grote)	0	0	1	0	1	0
Mamestra configurata (Walker)	0	0	21	3	12	12
Protorthodes curtica (Smith)	0	4	17	24	27	18
Anhimella contrahens (Walker)	0	0	2	0	0	2
Pseudaletia unipuncta (Haworth)	0	26	15	3	20	24
Noctuinae						
Abagrotis negascia (Smith)	0	2	1	1	4	0
Agrotis ipsilon (Hufnagel)	1	0	0	0	1	0
Agrotis venerabilis (Walker)	0	0	2	0	2	0
Agrotis vetusta (Walker)	0	2	2	4	5	3
Diarsia rosaria (Grote)	1	1	0	3	4	1
Euxoa albipennis (Grote)	0	0	1	1	2	0
Euxoa atomaris (Smith)	1	0	1	0	1	1
Euxoa auxiliaris (Grote)	0	0	1	0	1	0
Euxoa choris (Harvey)	0	0	1	0	1	0
Euxoa declarata (Walker)	0	0	1	0	0	1
Euxoa idahoensis (Grote)	1	0	1	1	3	0
Euxoa infausta (Walker)	1	0	0	0	1	0
Euxoa septentrionalis (Walker)	1	8	135	9	101	52
Feltia jaculifera (Guenée)	0	0	33	1	17	17

TABLE 1. Continued

Species	Orchard	Parker	Moxee	Ahtanum	Total	
					♀	♂
Peridroma saucia (Hübner)	0	0	1	0	0	1
Rhynchagrotis formalis (Grote)	0	0	6	0	6	0
Spaelotis bicava LaFontaine	0	0	1	0	1	0
Spaelotis clandestina (Harris)	0	0	2	0	2	0
Xestia c-nigrum (L.)	1	5	12	8	15	11
Xestia (Anomogyna) infimatis (Grote)	0	0	2	1	3	0
Xestia plebeia (Smith)	0	0	1	4	5	0
Xestia xanthographa (Denis & Schiffermüller)	0	0	1	0	1	0
Pyralidae						
Hypsopygia costalis (Fabr.)	0	0	0	93	38	55
Udea profundalis (Packard)	0	0	1	0	0	1
Pyralis farinalis L.	2	2	3	1	7	1

traps are fiberglass screen cylinders (90 cm high and 38 cm wide) hung vertically about 3 cm above a 40 cm wide wooden platform (figured in Covell 1984:16). The trap entrance is a screen cone at the bottom of the screen cylinder and above the wooden platform. The lure was a 30 ml polypropylene vial containing 15 ml of a 1:1 mixture of glacial acetic acid (Baker Chemical, Pittsburgh, Pennsylvania) and 3-methyl-1-butanol (Aldrich Chemical, Milwaukee, Wisconsin) on cotton. Release of the chemicals from the vial was through a 6.4 mm diameter hole in the vial lid. The vial was positioned on the wooden platform directly beneath the center of the trap opening, held in place by three corks glued to the platform. Our objective was to obtain relatively undamaged specimens that are identifiable; large numbers of insects captured in the butterfly bait trap can perch relatively undisturbed on the screening of the trap after capture.

Four cage traps were set up on 12 March 1999, each at a different site with somewhat different habitats in Yakima County, Washington. All traps were hung from tree branches. The first trap was placed within a commercial apple orchard near the town of Donald, 11 km southeast of Union Gap. This site received multiple applications of conventional pesticides for control of insect pests. The second trap was placed along the edge of a forested riparian habitat along the Yakima River, 7 km southeast of Union Gap, and adjacent to an apple orchard. The third trap was placed in a windbreak of Douglas Fir trees, at the Moxee Experimental Farm, 20 km east of Moxee. This trap was near mixed irrigated agriculture and native dryland or steppe plant community. The fourth trap was placed along a riparian habitat, along Ahtanum Creek, 10 km west of Union Gap, and adjacent to small farms and pasture. Traps were checked once or twice per week, depending on the amount of moth activity, and lures were replaced every 2 weeks. Traps were maintained until 1 October 1999.

To assess the relative effectiveness of the butterfly bait trap in comparison to methods used in previous studies (Landolt & Alfaro 2001) we compared four butterfly bait traps to four Universal moth traps (UniTrap). Universal moth traps have been used in previous experiments for trapping *L. subjuncta* (Landolt & Alfaro 2001). All traps were baited with 30 ml polypropylene vials with a 6 mm hole in the lid. Vials were loaded with 15 ml of a 1:1 mixture of acetic acid and 3-methyl-1-butanol. The eight traps were placed in one row of an apple orchard, with butterfly bait traps and UniTraps alternated in the row. All traps were positioned so that the bait was at a 2 m height and traps were 20 m apart. Treatment (trap design) positions were switched each time that traps were checked. Traps were checked twice per week from 4 to 17 May 2000. Treatment means for pooled male and female trap catch data were compared using Student's *t*-test, with separate analyses for *L. subjuncta*, *M. configurata,* and *X. c-nigrum* trap catch data.

Voucher specimens are deposited in the collection of the Department of Entomology, Washington State University, Pullman, Washington.

RESULTS

A total of 991 moths were collected in the 4 butterfly bait traps maintained from 12 March to 1 October 1999. Sixty species were recovered (Table 1). Some specimens (<10%) in several late summer samples were not identifiable because of severe loss of wing scales. Noctuids constituted 90% of specimens and 91% of species (56 of 62) of moths captured in traps. The remaining species were in the families Thyatiridae (3 species) and Pyralidae (3 species) (Table 1). A rela-

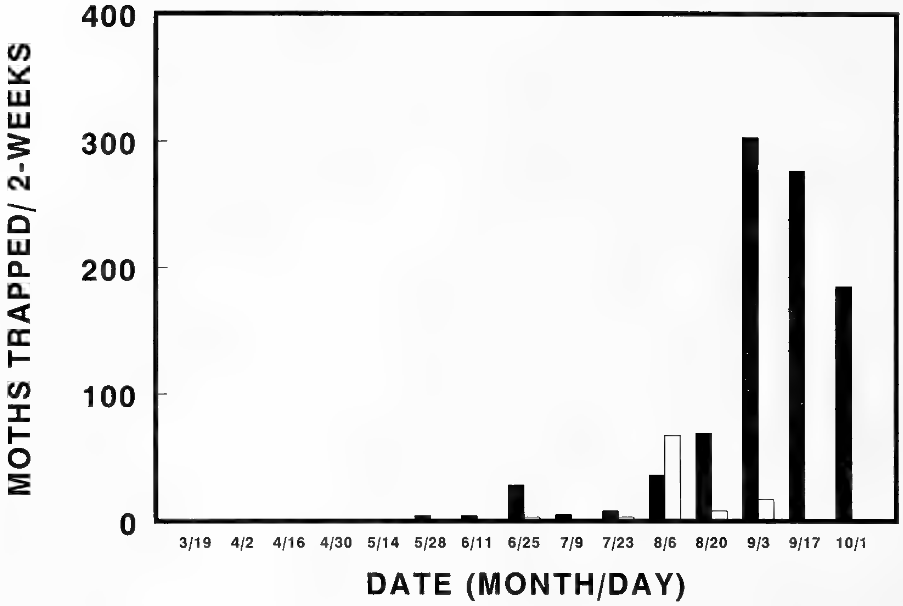

FIG. 1. Numbers of Noctuidae (black bars) and Pyralidae (white bars) captured in 4 cage traps baited with acetic acid and 3-methyl-1-butanol lures, at 2 week intervals through the season. Yakima County, Washington State, 1999.

tively small number of species constituted a large percentage of the moths captured. The four noctuid species *Apamea devastator* Brace, *Dargida procincta* Grote, *Aletia oxygala* (Grote), and *Euxoa septentrionalis* Walker and the pyralid *Hypsopygia costalis* (Fab.) together constituted 65% of the moths trapped and identified. For most species of noctuids trapped, both sexes were caught (Table 1).

During the seasonal study there were relatively few types of other insects (non-Lepidoptera) captured in the traps. Of note, no butterflies and no bees (Apoidea) were caught. However, eight *Sceliphron caementarium* (Drury) mud dauber wasps (Sphecidae) were captured at the Ahtanum Creek site and the yellow jackets *Vespula germanica* (Fabr.) and *Vespula pensylvanica* (Saussure) (Vespidae) were captured fairly consistently in late summer at all sites. Very few moths were captured in traps before August, with most moths captured from late August through late September (Fig. 1).

TABLE 2. Means (±SE) numbers of 3 pest species of Noctuidae captured in Universal moth traps (Unitrap) and in butterfly bait traps (cage) baited with acetic acid and 3-methyl-1-butanol, in apple orchards in Yakima County, Washington. May 2000.

Moth species	Unitrap	Cage trap	t value	p
Lacanobia subjuncta	3.7 ± 0.9	2.5 ± 0.6	1.40	0.09
Mamestra configurata	1.1 ± 0.4	0.6 ± 0.2	2.24	0.02
Xestia c-nigrum	3.6 ± 1.1	3.2 ± 0.9	0.49	0.31

In the comparison of butterfly bait traps and UniTraps, significantly more *M. configurata* moths were captured in UniTraps (Table 2). However, numbers of the other 2 species of pest moths targeted in this study, *L. subjuncta* and *X. c-nigrum*, were not significantly different between trap types (Table 2).

DISCUSSION

Landolt (2000) found that the combination of acetic acid and 3-methyl-1-butanol is attractive to both sexes of 3 noctuid pests that are common in Washington state apple orchards; *L. subjuncta*, *M. configurata*, and *X. c-nigrum*. The results of this study confirm that this lure attracts a variety of moths, predominantly of the family Noctuidae (Table 1). The capture of several other pest species, including the glassy cutworm *A. devastator*, the true armyworm *Pseudaletia unipuncta* (Haworth), and the forage looper *Caenurgina erechtea* (Cramer) (Table 1) indicates that this chemical attractant may have broad application for use in monitoring and control of noctuid pests of agricultural crops. These and other species captured (Table 1) indicate a taxonomically diverse response within the family Noctuidae, with 5 of the noctuid subfamilies represented in the sampling. This lure in a suitable trap may prove useful also as a means of sampling moth biodiversity, as was attempted by Yamazaki (1998) using fermented sugar solutions.

It is interesting that numbers of these 3 moth species were captured consistently in apple orchards during the comparison of the two trap designs and were only infrequently trapped at the 3 non-agricultural sites used for the season-long study (Table 1), while only one female *L. subjuncta* was captured in the season-long study in a different apple orchard. Populations of these moths are expected to vary with the season (Hitchcox 2000) and appear to vary greatly between orchards, depending on prior history and management practices (unpublished data).

The reasons for the pronounced seasonal pattern in captures of moths are not known but may include a relative abundance of some species of moths at trapping sites late in the season compared to early summer. For example, the cutworm *Euxoa septentrionalis* (Walker) (135 captured) is univoltine and flies from late August into October (Lafontaine 1987). There are other species of moths known to be attracted to acetic acid and 3-methyl-1-butanol which are bivoltine and are present earlier in the season, such as *M. configurata* and *L. subjuncta,* (Landolt 2000). Perhaps they were simply not present at the trapping sites used in this study but have been common in other apple orchards.

There was a near absence of species in the noctuid subfamily Cuculliinae in traps (Table 1). In contrast to our study, Yamazaki (1998) captured 15 species of cuculliine moths during spring with fermented sugar solutions. Their general absence in our traps (excepting *Epidemas cinerea* Smith) may be due to an absence of host plants at the sites sampled. Moreover, Yamazaki (1998) worked in a secondary forest, which was not a habitat type included in this study. It is also possible that some moths attracted to fermented sweet baits may be attracted by different blends of chemicals, and not to the combination of acetic acid and 3-methyl-1-butanol.

It is not known if the lack of captures for other groups of insects, such as butterflies, relates to low or nonexistent populations or to low or non-existent responsiveness of those insects to acetic acid and 3-methyl-1-butanol. It is suspected that yellow jacket wasps may have been visually attracted into traps by the presence of prey items (captured insects). However, both *V. germanica* and *V. pensylvanica* are weakly attracted to some degree by the combination of acetic acid and 3-methyl-1-butanol (Landolt et al. 2000).

Based on the results of the trap comparison test, we do not think that many species of moths were missed due to the use of the cage trap, rather than the Uni-Trap, which has been used extensively in studies to develop the lure for pest species (Landolt & Alfaro 2001). However, some species of moths attracted to acetic acid and 3-methyl-1-butanol likely are better captured with different designs of traps.

In summary, this study indicates broad attractiveness of acetic acid with 3-methyl-1-butanol to a diversity of moth species, predominantly Noctuidae, with a number of agricultural species included. This lure, in an appropriate trap, may then be useful as a means of sampling moth populations in ecological or environmental studies, for general collecting of moths, and for monitoring of pest populations in agricultural crops. The general attractiveness of the lure to noctuids is of some concern for lure use in monitoring specific agricultural pests, because the monitoring of targeted species will be complicated by the trapping of non-target species, requiring time spent sorting specimens.

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A NEW AGONOXENINE MOTH FROM THE GALÁPAGOS ISLANDS (GELECHIOIDEA: ELACHISTIDAE)

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ABSTRACT. The only member of the Elachistidae, Agonoxeninae so far encountered in the Galápagos Islands is described as a new species: ***Haplochrois galapagosalis*, new species.**

RESUMEN. Se describe la unica especie de Elachistidae, Agonoxeninae de las islas Galápagos ***Haplochrois galapagosalis*, sp. n.**

Additional key words: Ecuador, South America, *Croton* sp., Euphorbiaceae.

The Agonoxeninae moths of the world are poorly known. Hodges (1997) reviewed the classification of their Neotropical members, and Sinev (1999) synonymized *Tetanocentria* Rebel (1902) with *Haplochrois* Meyrick (1897), the genus to which the only Galápagos agonoxenine species belongs. This is the first record of Agonoxeninae for the famous Ecuadorian archipelago.

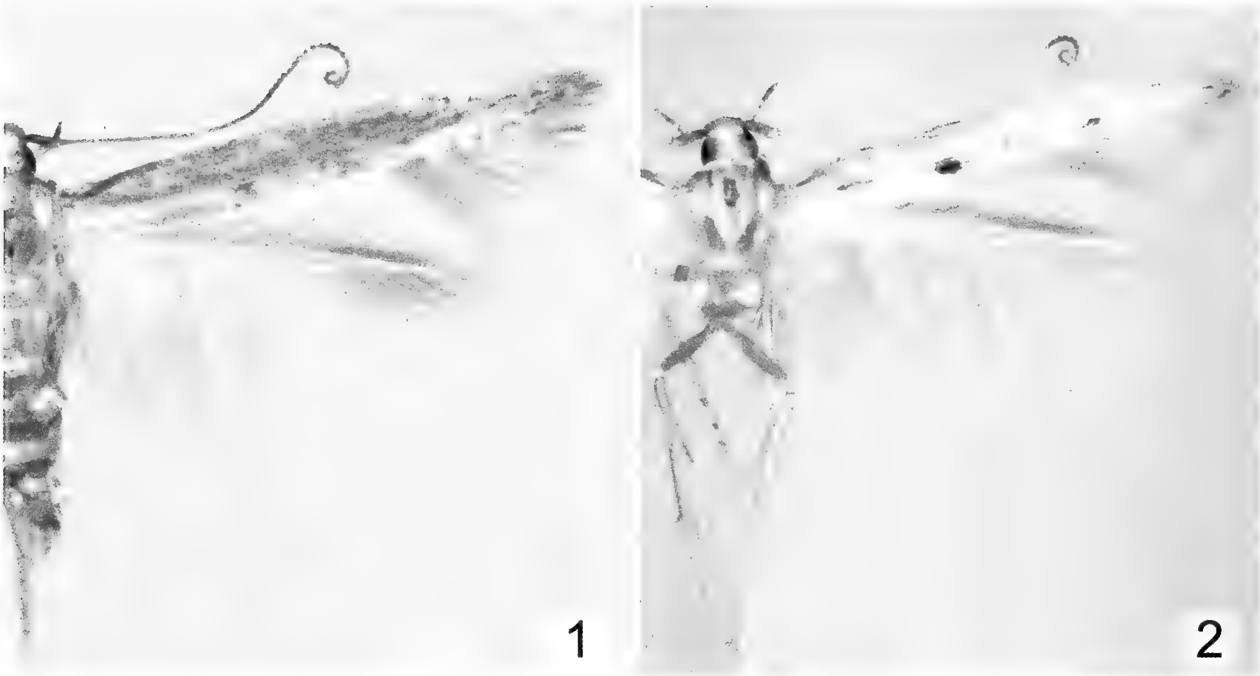
The original description of *Haplochrois* (Meyrick 1897; type-species *H. chromatella* Meyrick 1897) is brief, but Bottimer (1926), Clarke (1965), and Riedl (1969) provide more information on adult and larval morphology of congeneric species. Based on Hodges (1983, 1997), Sinev (1999), and the new species recorded here, *Haplochrois* includes 30 described species distributed in tropical and subtropical regions of the world. The genus is diagnosed by characters of the male genitalia; i.e., the elongate and narrow tegumen and saccus, paired setose gnathos, and soft-lobed valvae (Sinev 1999). The available information on host plant comes from Kusnezov (1916), who described *H. theae* from larvae reared from the tea bush (*Camellia sinensis* (L.) O. Kuntze, Theaceae) in Transcaucasia, and from Bottimer (1926), who reported *H. bipunctella* (Chambers) larvae from leaf petiole galls and seeds of *Croton engelmannii* Ferguson (=*C. capitatus* Michaux, Euphorbiaceae) in Texas.

According to Hodges (1997), *Tetanocentria* (now *Haplochrois*) includes seven Neotropical species; six described by E. Meyrick and one by A. Busck. I examined the holotype (or a paratype in one case) of each of these species, as well as specimens of the North American species, *H. bipunctella*, to conclude that the Galápagos taxon is new.

Haplochrois galapagosalis B. Landry, new species
(Figs. 1–9)

Diagnosis. The long and narrow forewing and hindwing, the upturned labial palpus, the scaled haustellum, and the simple wing pattern will separate this species from all other Galápagos moths. Two species of Gracillariidae may appear somewhat similar in color and size, but their forewing patterns are different and they don't have the haustellum scaled. *Pyroderces rileyi* (Walsingham), a Cosmopterigidae, also appears superficially similar to *H. galapagosalis*, but its forewing is mostly dark brown with an oblique paler line subterminally, and its antennae are annulate black and white (see Landry 2001).

Description. Male (n = 17). **Head** beige along median line with brown to dark-brown scales laterally. Haustellum beige. Labial palpus beige medially on segment II and at base and apex of segment III, brown laterally on segment II, dark brown on most of segment III. Antenna beige to dark brown, slightly paler on scape and first few flagellomeres; pecten made of about 25 long and thin scales; flagellomeres simple, with short setae and two sets of scales, the second erect. **Thorax** beige with three longitudinal dark-brown lines apically, or dark brown, but "greasy" in all specimens and consequently hard to characterize. **Foreleg** coxa dark brown with beige scales at base; femur dark brown, some specimens with scales bicolored beige basally and dark brown distally; tibia mostly dark brown with beige scaling at 1/3, 2/3, and terminally; tarsomeres I and II mostly dark brown with scales bicolored beige basally and dark brown distally, with beige spot subterminally; tarsomere III mostly beige, with dark-brown scales at base and apex; tarsomere IV dark brown; tarsomere V beige with dark brown at base. **Midleg** coxa and femur dark brown; tibia dark brown with scales bicolored beige basally and dark brown distally, darker brown toward apex, with short and thin projecting scales dorsally at base, middle, and apex; tarsomeres dark brown with scales bicolored beige basally and dark brown distally, with darker brown scales apically on tarsomeres I–IV. **Hindleg** coxa with a mixture of beige and brown to dark-brown scales; femur dark brown; tibia dark brown with scales bicolored beige basally and dark brown distally, with darker brown spots at base, middle, and apex, and with projecting long and thin pale-brown scales on entire dorsal margin and on ventral margin as a patch posterior to anterior pair of spurs; tarsomeres I–III with beige to dark-brown scales bicolored beige basally and dark brown distally, with darker brown scales apically; tarsomeres IV–V uniformly pale grayish brown; tarsomere I also with darker brown spot at middle and with patch of thin and long projecting scales dorsoapically; tarsomere II also with a few long and thin pale-brown scales projecting at apex dorsally. **Forewing** (Figs. 1, 2) length: 4–6 mm; ground color beige to dark grayish brown; pale specimens sometimes with slightly paler dorsal half and with most conspicuous dark-brown markings consisting of a small dot above middle subbasally, a short streak subbasally on cubital fold, a spot on cubital fold submedially (usually the most conspicuous, and sometimes only, marking), a smaller spot above end of cubital fold, some specimens with dark-brown scales dispersed between latter spot and costa, and three or four small subapical and apical spots on dorsal margin; fringe mostly dark brown at apex, pale brown to beige on dorsal margin. **Hindwing** uniformly grayish brown; fringe pale brown to beige. Frenulum simple. Retinaculum with frenulum hook. **Abdomen** usually appearing uniformly beige to beige brown, some specimens with brown scales laterally and ventrally, available specimens greasy and consequently difficult to characterize in color. **Male genitalia** (n = 5)



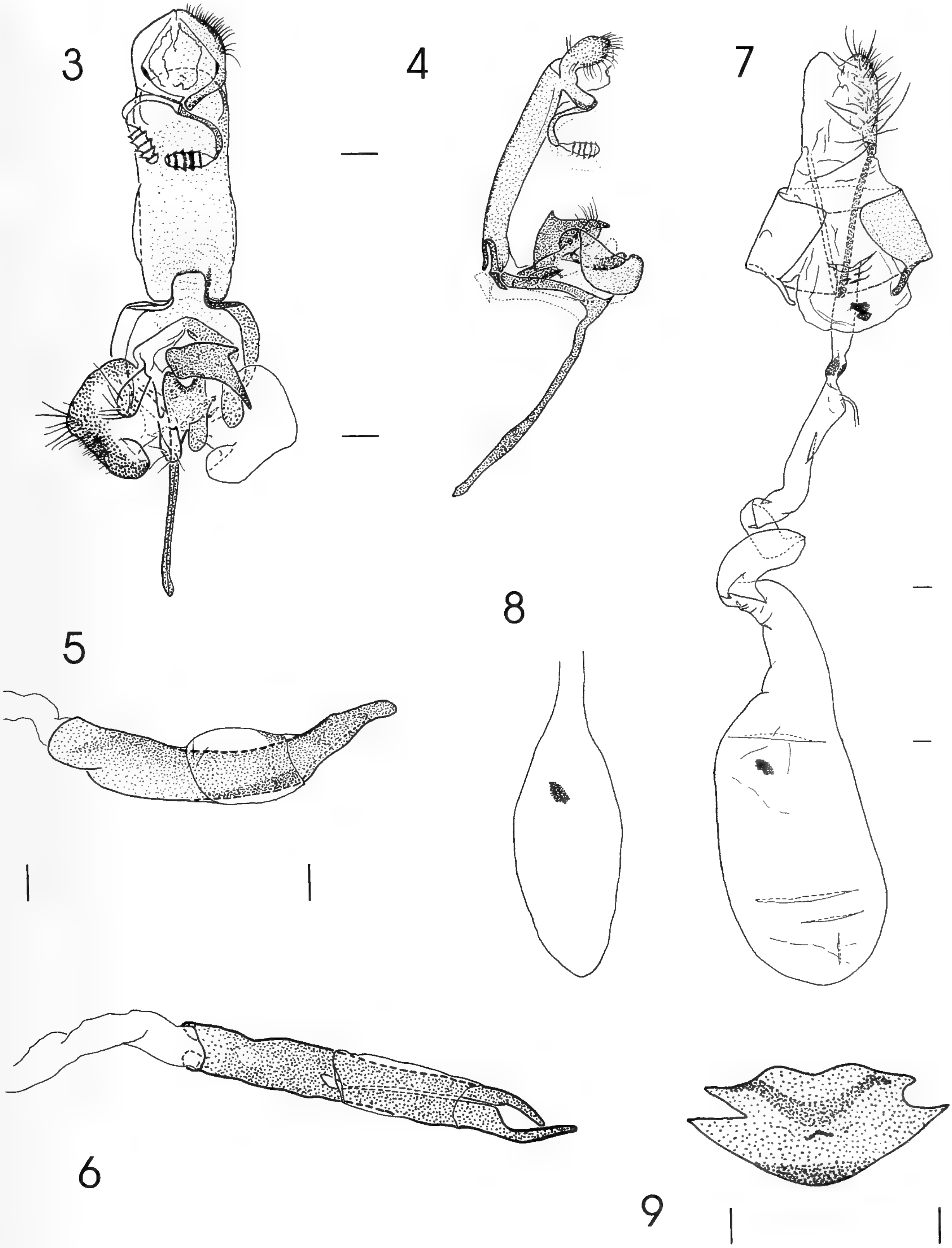
FIGS. 1–2. Adults of *Haplochrois galapagosalis*. 1. Female from Isabela (Volcan Darwin, 1000 m elev.). 2. Female from Isabela (±15 km N Puerto Villamil).

(Figs. 3–6). Uncus rounded, flattened dorsoventrally but bulged and shortly setose along apical and lateral margins, about 1/4th length of tegumen. Gnathos with thin arms broadly curved, constricted before apical elongate club bearing series of long, narrow, and curved spinules in five transverse rows forming incomplete rings, except for the most apical row. Tegumen rectangular, with parallel margins, elongate, fused dorsally and ventrally for most of length (basal arms very short), dorsal surface scaled, ventral surface spiculate, connecting with vinculum by an elongate and subtriangular projection originating dorsomedially on each short arm. Transtilla narrow, well sclerotized, straight, with lateral partially articulated setose knobs projecting posteriorly to apex of valva. Anellus forming a median, crescent-shaped, and crested structure projected posteriorly. Juxta narrow and poorly sclerotized, U-shaped to accommodate anellus, with a few setae ventrally, with two short and sparsely setose arms projecting posteroventrally. Valva short, flat, roughly semicircular, somewhat angular, curved backward, with minute setae on most of surface, dorsal and lateral margins with longer setae and long thin scales forming a lateral fan on undissected specimens. Vinculum very narrow, ventrally with long and thin saccus reaching middle of segment VII. Aedeagus of medium length, broadly curved in lateral view, apex directed dorsally, without coecum penis, distal half dorsally with longitudinal separation between two lateral halves, apically asymmetrical with only the lateral margins well sclerotized into narrow laterally flattened and apically rounded projections; the left projection longer, broader and coming out on the left side of the anellus; manica surrounding aedeagus at median third, with short sclerotized section apicodorsally; vesica without cornuti.

Female (n = 30). Forewing length: 5–7 mm. Antennal flagellomeres simple, without noticeable setae, with erect scales on last third of flagellum only. Frenulum with two acanthae. Retinaculum with evenly spaced thin scales on $Sc+R_1$ and Radial stem. **Female genitalia** (n = 4) (Figs. 7–9). Papillae anales laterally flattened, narrowing slightly toward rounded apex, with setae of medium length on lateral surface and very long setae around base; dorsal margin straight; ventral margin convex. Posterior apophyses narrow, straight, reaching anterior margin of segment VIII. Segment VIII about as wide as preceding segment, unsclerotized medioventrally. Anterior apophyses short and narrow, directed medially at half right angle. Ostium bursae in fold in middle of ventral membranous section of segment VIII, without sclerotization. Middle of intersegmental membrane VII–VIII with two small subtriangular plates variable in width and degree of sclerotization between them. Ductus bursae long, narrow, slightly variable in width and length, coiled twice, with pair of very short sclerotized plates laterally at about 1/5th of length, posterior to inception of ductus seminalis. Corpus bursae elongate, about 1/3rd length of ductus bursae, without scobination, reaching apical margin of abdominal segment II; single small signum a very short inwardly directed spine on a small irregularly shaped plate.

Holotype ♂ (CNC # 22679): 1—"ECU[ADOR]., GALAPAGOS/ Santiago, Central/ 700 m elev[ation]., 9.iv.1992/ M[ercury] V[apor] L[amp], leg. B. Landry" [white, rectangular, printed in black ink]. 2—"HOLOTYPE/ Haplochrois/ galapagosalis B. Landry/ CNC #22679" [red, rectangular, hand written in black ink].

Paratypes: 16 ♂, 30 ♀ ECUADOR, Galápagos, MVL, leg. B. Landry. **Floreana:** Las Cuevas, 23.iv.1992 (1 ♂, slide BL 1254). Punta Cormoran, 21.iv.1992 (1 ♀). **Genovesa:** Bahía Darwin, 10.iii.1992 (3 ♀, slide BL 1256); 26.iii.1992 (1 ♂, 1 ♀). **Isabela:** Puerto Villamil (8.5 km N), 11.iii.1989 (1 ♀); (ca. 15 km N), 25.v.1992 (2 ♀, slide BL 1228). Tagus Cove, 13.v.1992 (1 ♂, slide BL 1253). Volcán Darwin, 300 m elev., 15.v.1992 (1 ♀); 630 m elev., 16.v.1992 (1 ♀); 1000 m elev., 18.v.1992 (2 ♀); 1240 m elev., 19.v.1992 (3 ♀). **Marchena:** 12.iii.1992 (1 ♂, 3 ♀ slide BL 1258); 23.iii.1992 (1 ♀). **Pinta:** arid zone, 15.iii.1992 (1 ♀, slide BL 1255); 200 m elev., 16.iii.1992 (1 ♀); 400 m elev., 18.iii.1992 (1 ♂, 2 ♀). **San Cristóbal:** 4 km SE Puerto Baquerizo, 12.ii.1989 (1 ♂, CNC slide MIC 4677). Base of Cerro Pelado, 22.ii.1989 (1 ♀). **Santa Cruz:** Charles Darwin Research Station, arid zone, 19.i.1989 (1 ♂, slide JFL 604). 4 km N Puerto Ayora, 20.i.1989 (1 ♂). Los Gemelos, 31.i.1989 (1 ♀); 27 May 1992 (1 ♂). Tortuga Reserve (W Santa Rosa), 6.ii.1989 (4 ♂, 1 ♀). Finca S. Devine, 17.iii.1989 (1 ♀); Finca Vilema (2 km W Bella Vista), 1.iv.1992 (1 ♀). **Santiago:** Bahí Espumilla, 4.iv.1992 (1 ♂ slide



FIGS. 3–9. Genitalia of *Haplochrois galapagosalis*. 3–6. Males (scales = 0.5 mm). 3. Apical view, valvae flattened, aedeagus removed [slide BL 1257]. 4. Lateral view of whole genitalia except aedeagus [slide BL 1254]. 5. Aedeagus in lateral view [slide BL 1257]. 6. Aedeagus in dorsal view [slide 1254]. 7–9. Females. 7. Ventral view [from slides BL 1228, 1256, 1258] (scale = 0.5 mm). 8. Bursa in ventral view [slide BL 1228]. 9. Plates on membrane below ostium bursae [slide BL 1258] (scale = 0.0625 mm).

BL 1257, 1 ♀). 200 m elev., 5.iv.1992 (1 ♀). Aguacate, 520 m elev., 12.iv.1992 (1 ♂, 1 ♀).

The material collected in 1989 belongs to the Canadian National Collection of Insects, Ottawa, Ontario, Canada (CNC). The material collected in 1992 will be distributed among the Muséum d'histoire naturelle, Geneva, Switzerland (MHNG), The Natural History Museum, London, England (BMNH), the CNC (holotype), the Charles Darwin Research Station, Santa Cruz Island, Galápagos, Ecuador (ECCD), and the National Museum of Natural History, Washington, D.C., U.S.A. (USNM).

Remarks. The type locality, Central, is a campsite, and so is Aguacate on Santiago. The nomenclature used for the description of the male genitalia structures surrounding the aedeagus (the transtilla, anellus and juxta) is tentative. No recent or older species descriptions in this genus treat these structures in detail. Sinev (1999) mentions that the lobes of the gnathos bear setae, but I was not able to see any evidence of sockets and so I have called these projections spinules, in concordance with Hodges (1999). The two original specimens of one of Meyrick's species, *H. catholica*, are without abdomen and superficially similar to the Galápagos species. Resemblance in color pattern is common in *Haplochrois* and it is possible that the two taxa are conspecific. However, the type locality of *H. catholica* is Mallali, Guyana, where non endemic Galapagos species are not typically encountered, unless they have a broad Neotropical distribution.

Etymology. This species is named for the Ecuadorian archipelago where it was collected.

Distribution and biology. The species was found on the Galápagos Islands of Floreana, Genovesa, Isabela, Marchena, Pinta, San Cristóbal, Santa Cruz, and Santiago. I suspect that it may be distributed also on the other larger islands of the archipelago. Moths were collected between January 19 and May 25. They were attracted to light and found from sea level to 1240 m elevation on Volcán Darwin. The host plant is unknown.

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I express my sincere gratitude to the authorities of the Galápagos National Park and those of the Charles Darwin Research Station for allowing fieldwork and for logistical support in 1989 and 1992. The fieldwork and other costs were partially supported by an operating grant to Stewart B. Peck, Carleton University, Ottawa, from the Natural Sciences and Engineering Research Council of Canada, for field research on arthropod evolution. Without the following companions, some of my work in the Galápagos would have been impossible, or at least much less pleasant, and I thank them sincerely: Joyce Cook, Moraima Inca, Ricardo Palma, S. B. Peck, Bradley J. Sinclair, and Eduardo Vilema. I thank curators Kevin Tuck (BMNH), David Adamski (USNM), and Richard Hoebeke, Cornell University Insect Collection, Ithaca, New York, U.S.A., for their help in the examination of critical specimens. I am grateful to Ronald W. Hodges (formerly at USNM) for a preliminary determination of the insect described herein. David Adamski and Ronald Hodges also provided useful comments on the manuscript. Finally, I am greatly indebted to Jean-François Landry, Agriculture and Agrifood Canada, Ottawa, for facilitating lab work, for his help in processing the images, and for mentioning critical literature.

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MORTALITY OF LEPIDOPTERA ALONG ROADWAYS IN CENTRAL ILLINOIS

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ABSTRACT. We conducted this study to investigate the magnitude of roadway mortality of Lepidoptera in central Illinois. To quantify the number and kinds of Lepidoptera killed along roadways, dead adult Lepidoptera were collected, identified, and counted from along 13 roadside transects in the vicinity of Champaign/Urbana, Illinois, with collections occurring weekly on each transect for six weeks. During the six weeks of this study, 1824 presumably road-killed Lepidoptera were collected. At traffic rates of 1000, 13,500, and 19,700 vehicles per day, more Lepidoptera were collected per 100 m than at other traffic rates. A peak in monarch butterfly mortality may coincide with the timing of their annual migration through the area. Based on these data, the number of Lepidoptera killed along roadways for the entire state of Illinois during one week was estimated at more than 20,000,000 individuals. The number of monarch butterflies killed may have exceeded 500,000 individuals. Our results suggest that increases in traffic rate and speed limit may to a certain extent increase mortality.

Additional key words: Butterflies, *Danaus plexippus*, traffic.

Although roadway traffic is known to affect population densities of amphibians (Fahrig et al. 1995), snakes (Bernardino & Dalrymple 1992), koalas (Canfield 1991), wolves (Mech 1989), turkeys (Holbrook & Vaughan 1985), badgers (Davies et al. 1987), and other vertebrates (Lalo 1987, Putman 1997), practically nothing is known about the impact that roadways have on invertebrates (Seibert & Conover 1991). In fact, a recent book on butterfly conservation (New 1997) makes no mention of the subject, and roads are mentioned only briefly in two other recent books on insect conservation, as barriers to butterfly movement (Samways 1994, Pullin 1995). Samways (1994) states "Roads are line corridors that can cause high mortality where traffic volume is high. In 1989, 100 m of Tennessee roadside was a graveyard for over 120 traffic-killed butterflies" (Samways 1994:117). Other than these sources, the best information on road mortality of butterflies is by Munguira and Thomas (1992) in England. They found that roads were not a serious barrier to butterfly movement, but that vehicles killed up to 7% of adult butterflies from some populations.

Illinois has 2050 miles of interstate, 276 miles of toll road, 14,892 miles of highway, and 120,782 miles of county, municipal, and other roads (Illinois Department of Transportation pers. com. 1998). Although this comprises the third largest state highway system in the United States, nothing is known about the magnitude of lepidopteran mortality along Illinois roadways.

This study was conducted to investigate the magnitude of roadway mortality of Lepidoptera in central Illinois. To quantify the number and kinds of Lepidoptera killed, dead adult Lepidoptera were collected, counted, and identified from along 13 roadside transects in the vicinity of Champaign/Urbana 40°2′N, 88°17′W, Champaign Co., Illinois, with collections occurring weekly on each transect for six weeks. This study is the first to document systematically the magnitude of roadway mortality of Lepidoptera anywhere in the United States.

MATERIALS AND METHODS

Eleven roadside transects were chosen at the outset of this study to represent different rates of traffic and different roadway types (Table 1). Traffic rates ranged from 0–26,000 vehicles per 24 hour period (Illinois Department of Transportation (IDOT) pers. com.). To facilitate comparisons, traffic rates above 500 vehicles per day were rounded to the nearest 100. Each roadside transect fit into one of the following general plant community types: remnant prairie, agriculture, or woodland. Roadways were classified into four types:

TABLE 1. Transect Characteristics.

Transect number	Transect name	Roadway type	Roadside community type*	Transect length (m)	Speed limit (mph)	Vehicles/24 hours ** (#Vehicles)
1	Highway 150 #1	Highway	Prairie/Ag	150	55	1,000
2	Highway 150 #2	Highway	Prairie/Ag	250	55	1,000
3	Highway 150 #3	Highway	Prairie/Ag	180	55	1,000
4	Cunningham #1	Divided Highway	Ag	180	55	13,500
5	Cunningham #2	Divided Highway	Ag	250	55	13,500
6	Cunningham #3	Divided Highway	Ag	180	55	13,500
7	I-74	Interstate	Ag	200	65	26,000
8	M-57	Interstate	Ag	200	65	19,700
9	Trelease Woods	Country Road	Old Field/Woodland	160	35	150
10	Brownfield Woods	Country Road	Woodland	200	0–35***	1000
11	Airport Grass Control	N/A (Mowed Airfield)	Mowed Grass	100	N/A	0
12	Country Road Control	Country Road	Ag	200	0–45***	150
13	Highway 150	Paved Country Road	Prairie/Ag	600	45	50

*Ag = Agriculture.

**The number of vehicles per day (24 hour period) was obtained through the Illinois Division of Highways.

***The range of speeds given are those typically observed for vehicles accelerating from the stop signs at the beginning of these transects.

paved country road, highway, divided highway, and interstate. One additional transect was chosen to control for the effects of roadside mowing. A second additional transect was chosen to quantify the baseline mortality in mowed grass, a habitat resembling the mowed roadsides of all transects.

Two transects were abandoned one week into the study due to road construction. These transects were replaced with two new transects, and two interstate transects were also added, for a total of 13 transects (Table 1). The nine original transects were first sampled on 25 August 1998. The two replacement transects were first collected on 2 September 1998, and the two interstate transects were first collected on 9 September 1998. We collected along transects weekly until 19 October 1998. Over the two weeks after that date, no dead Lepidoptera were found and the sampling was terminated.

Once every seven days each transect was walked and road-killed Lepidoptera were collected into a plastic bag. All 13 transects were collected over a two-day period each week. Transects with a median were searched on all sides of the road, including both sides of the median. As a safety precaution, the medians of interstate transects were not sampled. Both sides of the road were walked against the flow of traffic. Lepidoptera were collected that lay dead within two meters of the edge of the road. This usually included the shoulder and about one meter of "ditch". Lepidoptera lying on the roadway itself were not collected, but fewer than 10 such individuals were noticed throughout the entire study.

Transect length varied from 100 to 610 m, with a mean of 219 m and standard deviation of 121 m (Table 1). A total of 2850 m of transect was sampled during weeks when all 13 transects were sampled. The Thomasboro, Illinois office of the Illinois Division of Highways reported that transect locations received similar roadside maintenance, but on different days. Typical maintenance included mowing and trash removal.

After collection, the Lepidoptera were sorted by species or species-group and were counted. They were sorted into six taxonomic groups:

1. Hesperiidae, mostly *Epargyreus clarus* (silver-spotted skipper).
2. Lycaenidae, which were not identified below the family level.
3. Moths, mostly Arctiidae and Noctuidae, grouped together because too few individuals from most families were collected to warrant separate treatment.
4. Nymphalidae, including *Danaus plexippus* (monarch), *Euptoieta claudia* (variegated fritillary), *Libytheana carineta* (American snout butterfly), *Limenitis archippus* (viceroy), *Limenitis arthemis astyanax* (red-spotted purple), *Phyciodes tharos* (pearl crescent), *Polygonia interrogationis* (question mark), *Junonia coenia* (common buckeye), and *Vanessa cardui* (painted lady).
5. Papilionidae, represented in the roadside transects only by *Papilio polyxenes* (black swallowtail).
6. Pieridae, including *Colias eurytheme* (yellow sulfur) and *Colias philodice* (clouded sulfur), which due to hybridization and difficulty in separation into species were grouped together and called the *C. eurytheme/C. philodice* hybrid complex. Pieridae also included *Eurema lisa* (little yellow) and *Pieris rapae* (cabbage white).

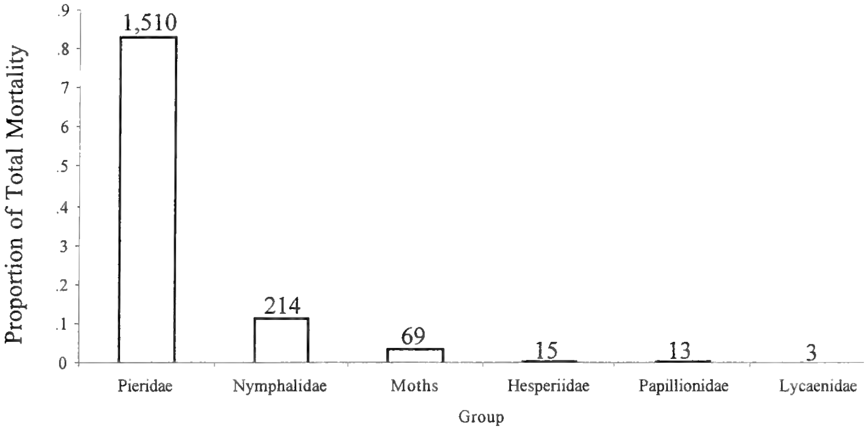

FIG. 1. Proportion of total mortality for each group of Lepidoptera studied. The total number of individuals collected from each group is given above each column. N = 1824.

Data were analyzed using analysis of variance (ANOVA) techniques. Weeks one and two were excluded from the analyses because they included data for only a subset of the 13 transects. Results were considered significant at $p \leq .05$.

Calculations of theoretical statewide mortality were made by multiplying the number of meters of roadway in Illinois of each of the roadway "types" (see above) by the number of butterflies killed per meter of roadside transect for each roadway type during the week of 9 September 1998 (IDOT pers. com.).

RESULTS

During the six weeks of this study, 1824 Lepidoptera were collected from along the 13 roadside transects, including 1510 Pieridae, 214 Nymphalidae, 69 moths, 15 Hesperiidae, 13 Papilionidae, and 3 Lycaenidae (Fig. 1). Insects belonging to orders other than Lepidoptera were only infrequently encountered and are not reported here. The greatest number of Lepidoptera killed per 100 m of transect occurred during week 1 (Fig. 2). Mortality decreased thereafter, except for a slight increase at week 4. Not included in the figures are the last two weeks of transect samples during which no dead Lepidoptera were found.

The first week of collection resulted in the two highest mortality rates per 100 m recorded for any of the traffic rates during the study (Table 2). At 1000, and 13,500 vehicles per day, 51.28 and 49.34 individuals

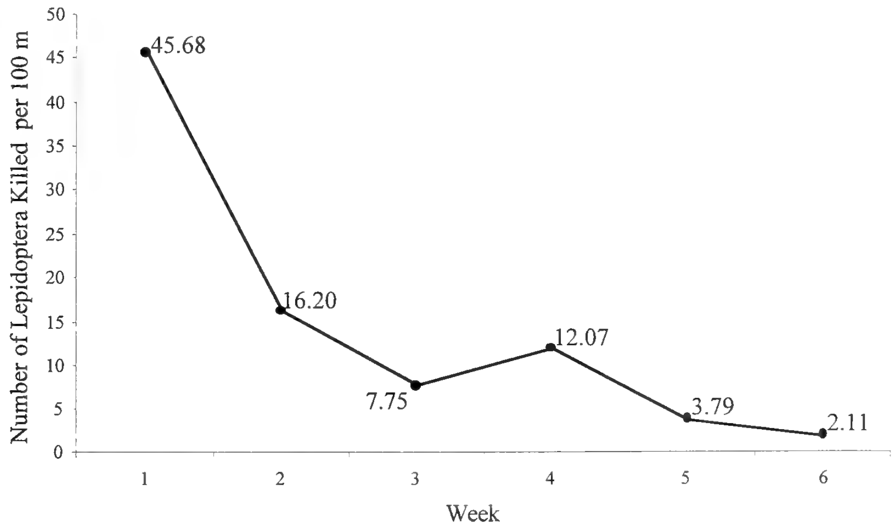

FIG. 2. Number of Lepidoptera sampled per 100 m during the six-week study.

TABLE 2. Lepidoptera sampled (number/100 m) over six weeks at each of nine traffic rates (number of vehicles/day). An "X" indicates that no data were collected.

	Vehicles/Day						
Week	0	50	150	1000	13,500	19,700	26,000
1	0	0.17	0	51.30	49.30	X	X
2	0	0	6.40	25.0	19.50	X	X
3	0	0	3.60	4.50	27.70	25.50	1.50
4	0	0	2.80	14.70	27.90	23.0	1.50
5	0	0	0.280	1.90	10.50	13.50	.50
6	0	0	0	1.30	3.30	8.50	2.50

respectively, were collected per 100 m of transect. At a traffic rate of 13,500 vehicles per day, more Lepidoptera were routinely sampled each week per 100 m than at any other traffic rate (Table 2). The lowest numbers were consistently recorded from transects with traffic rates of 150 vehicles per day and at the highest traffic rate, 26,000 vehicles per day. The number of Lepidoptera collected per 100 m of roadway increased from 0.03 at 50 vehicles per day to 23.03 at 13,500 vehicles per day (Fig. 3). At 19,700 vehicles per day 17.63 individuals were sampled per 100 m of transect, and at 26,000 vehicles per day only 1.5 individuals were sampled per 100 m of transect. Thus, at a rate of 13,500 vehicles per day, observed mortality was greatest, and at the highest traffic rate mortality was much lower. The mean number of butterflies collected per 100 m along transects with a traffic rate of 26,000 vehicles per day was not significantly different from that along transects with traffic rates of 19,700 ($p = 0.13$), 1,000 ($p = 0.67$), and 150 ($p = 0.19$) vehicles per day. At a traffic rate of 13,500 vehicles per day, significantly more Lepidoptera were collected per 100 m than at 26,000 vehicles per day ($p = 0.01$).

The *C. eurytheme/C. philodice* hybrid complex was most frequently collected. Over the course of the study, 1492 individuals were found dead along transects. Monarch butterflies, *D. plexippus*, were the next most abundant species found dead on transects; 99 were collected, including 55 males, 31 females, and 13 that were not identified to sex due to damaged or detached wings and abdomens. The number of monarchs collected varied greatly from transect to transect, and less so from week to week (Table 3 and Fig. 4). From 0.013 to 0.119 monarch butterflies were killed per 100 m of transect each week. The most monarch butterflies collected per 100 m from a transect was 6.5 at a traffic rate of 19,700 vehicles per day during week four. The second and third greatest mortality, 2.13 and 1.64 individuals per 100 m respectively, were observed at a traffic rate of 13,500 vehicles per day, also during week four. The mean number of monarch butterflies collected per 100 m during week four was significantly greater than during weeks three, five, and six ($p = 0.02$). Relatively few individuals of other species of Lepidoptera were collected.

The red-spotted purple, *L. arthemis*, and viceroy, *L. archippus*, were found only along transects with woodland or prairie roadsides. The little yellow *E. lisa* was found only along transects with prairie roadsides. Here, larvae were observed feeding on *Cassia* (a legume). We collected both day-flying and night-flying moths. No rare Lepidoptera were collected.

Using the roadway types and mortality statistics of the study transects to estimate rates of mortality for different roadway types in Illinois, we estimated the potential number of Lepidoptera killed for the entire state during the seven days prior to transect collection on week three; 9 September 1999. According to our

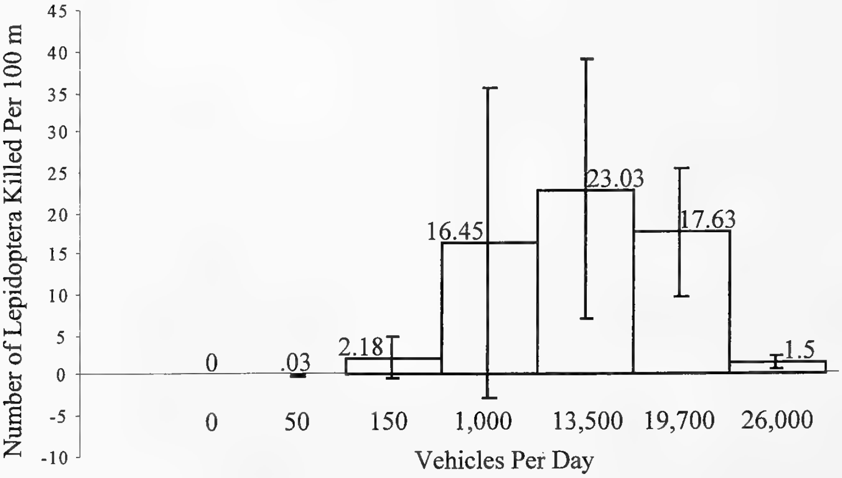

FIG. 3. Number of Lepidoptera sampled per 100 m at each traffic rate. Bars indicate standard deviations.

TABLE 3. Monarch butterflies killed (number/100 m) over six weeks at each of seven traffic rates (number of vehicles/day). An "X" indicates that no data was collected.

Week	Mowed grass	50	Traffic rate 150	1000	13,500	19,700	26,000
1	0	0	0.56	0.90	1.64	X	X
2	0	0	0.83	1.28	0.82	X	X
3	0	0	0	0.38	1.15	1.00	1.00
4	0	0	0	0.90	2.13	6.50	0.50
5	0	0	0	0.77	0.33	1.50	0
6	0	0	0	0.77	0	0.50	1.00

estimates, the number of Lepidoptera killed along interstates in Illinois during this week could have been more than 500,000, the number killed along highways could have been more than 5,000,000, and the number of Lepidoptera killed along other roads could have been more than 15,000,000. In total, the number of Lepidoptera killed by automobiles was estimated at more than 20,000,000 individuals in this seven–day period.

Using similar methods, we estimated the potential number of monarch butterflies killed during one week. According to our estimates, the number of monarchs killed along interstates in Illinois in one week during this study may have been more than 500,000.

DISCUSSION

Quantifying definitively the impact of automobile traffic on Lepidoptera is operationally challenging for many reasons. The small number of Lycaenidae in the samples for example, may result from the timing of our study. The collection methods used may have also resulted in a significant undercount of dark-colored and small moths, as they were difficult to see lying on the ground. Moreover, small Lepidoptera of all kinds may stay attached to the automobile that hits them (DDM pers. obs.). As well, ants and other insects, birds, and rodents were observed removing the remains of small dead insects from the transect roadsides. Weathering and mowing were observed to disintegrate a few Lepidoptera specimens before they could be counted. Thus, the numbers we report here should be considered a minimum estimate of mortality for the area studied; more precise measurements of mortality await further studies.

The numbers of individuals killed per 100 m on the first sample date in Table 2, Fig. 2, and Fig. 4, are not likely to reflect accurately actual mortality along the transects during the week prior to collection because these samples include all dead Lepidoptera that had accumulated and persisted along the transects prior to initiation of the study.

Somewhat surprising is the result that, at highest traffic rates, mortality declines. There are several possible explanations for this finding. At speeds around 55 mph or greater, Lepidoptera were seen to be caught in a "wind current" going over the roof of the car, with the result that they were "catapulted" over the car instead of colliding into it. It is not clear if this catapult effect may have resulted in fewer dead butterflies at sites with the highest traffic rates and speed limits compared to sites with lower traffic rates and speed limits. A further complication is the lack of collections from expressway medians. The length of expressway transects and the mortality data do not incorporate this sampling anomaly. The number of lanes of traffic may also be an important factor. An alternative explanation is that the observed decrease in numbers of dead Lep-

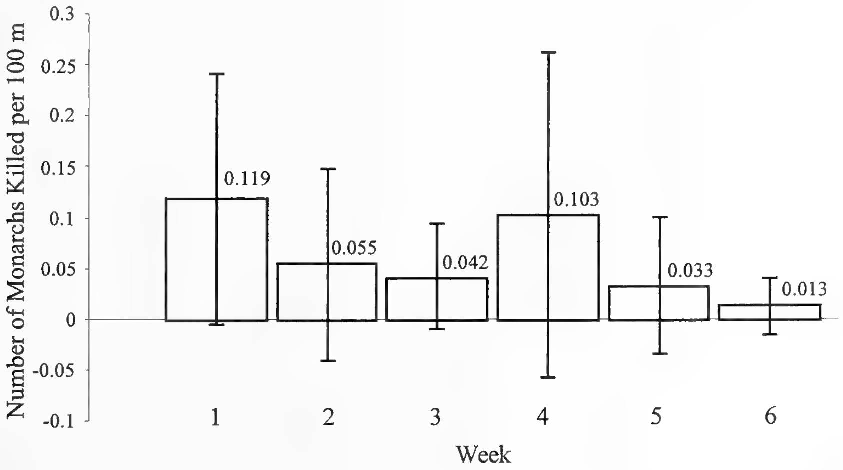

FIG. 4. Mean number of monarch butterflies sampled per 100 m during the six-week study. Bars indicate standard deviations. Week one collections were started on September 25.

idoptera when traffic volume and speed limit were relatively high (Table 2 and Fig. 3) may be due to a relatively high per capita morality rate at these sites resulting in decreased population density and the observation of fewer dead Lepidoptera. While we did not test this hypothesis, it is an interesting possibility because it suggests population-level effects of roadway mortality.

The peak in mortality of monarch butterflies observed on or about week 4 (September 16) may have been due to their southward migration (Fig. 2). Migrating monarchs usually fly high enough to avoid collision with vehicles, but during mid-morning, they generally fly lower to the ground (Orley Taylor pers. comm.). They also fly low to the ground during windy weather such as that which prevailed during the study period (DDM pers. obs.).

Many more male monarchs were found in the samples than females. Along Highway 150, where four transects were located, male monarchs were observed chasing other butterflies for distances of up to 100 m, often across the roadway. This behavior may account for the apparent overrepresentation of males in the samples.

More black swallowtails than monarchs were observed flying at highway sites, but more monarchs were found dead. Along most highway and expressway transects, considerable numbers of stems of whorled milkweed (*Asclepias verticillata*, Asclepiadaceae) were observed within two m of the roadway edge. These plants were observed to be an important larval host plant and source of nectar for adult monarch butterflies at these sites. Black swallowtails were observed to use whorled milkweed as a nectar plant, but were chased away from the extensive clonal growths of whorled milkweed along roadsides by monarch butterflies. Black swallowtails generally frequented areas further removed from the roadside than monarch butterflies where nectar plants for adults such as thistles and clovers (*Cirsium* spp., Asteraceae and *Trifolium* spp., Fabaceae) and larval host plants such as wild parsnip (*Pastinaca sativa*, Apiaceae) and Queen Anne's lace (*Daucus carota*, Apiaceae) were most abundant (DDM pers. obs.). These behavioral differences may account for the observation of fewer dead black swallowtails.

Regardless of the practicality of making estimates of statewide mortality from this small data set, it is apparent from this study that roadways kill significant numbers of adult Lepidoptera in central Illinois. Unfortunately, estimates of adult lepidopteran mortality caused by other factors in this region are generally lacking. The implications of roadways, roadsides, and traffic rates for lepidopteran mortality and populations are unclear, but evidence suggests that increases in traffic rate and speed limit may increase mortality to a certain extent and may have a detrimental effect on some populations. Future studies should explicitly address these questions. Studies are also needed from other regions and throughout the season in order to determine overall impacts of traffic on Lepidoptera and as well to provide baseline information that may be helpful in designing programs for reducing this mortality as it affects threatened or endangered species.

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ONTOGENY OF DEFENSE AND ADAPTIVE COLORATION IN LARVAE OF THE COMMA BUTTERFLY, *POLYGONIA C-ALBUM* (NYMPHALIDAE)

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ABSTRACT. In many butterfly species early and late larval instars differ in coloration. The first three larval instars in the comma butterfly, *Polygonia c-album*, have coloration that, to the human eye, appears to be disruptively cryptic. The last two instars, which are defended by strong branching spines, are instead strikingly colored in white, black, and orange. It has been suggested that this coloration is also cryptic, mimicking bird droppings. We test the idea that this coloration is instead (or simultaneously) aposematic, using young chickens as models of bird predators. Some chicks readily ate third-instar larvae, both initially and after having tasted them, suggesting that no chemical defense is present in comma larvae. The chicks also ate dead fifth-instar larvae from which the spines had been removed. Chicks initially attacked fifth-instar larvae with intact spines, but learned to avoid them already after the first attack. This suggests an aposematic function of the coloration, which can have evolved by individual selection in this and many other nymphalid species with spiny larvae, because larvae were not harmed during the learning process. The evolutionary causes of the ontogenetic shift in defense tactics are discussed.

Additional key words: aposematism, mimicry, life history, predation, adaptive function.

Adaptive coloration in animals has been a very active research field in evolutionary biology over the years (e.g., Poulton 1890, Cott 1940, Kettlewell 1973, Sillén-Tullberg 1988, Malcolm 1990), and one in which the Lepidoptera have always featured prominently as model species. Adaptive coloration includes crypsis (helping to avoid detection by other animals), signalling, and thermoregulation. Crypsis can be achieved by having colors similar to the background, or by having mosaic patterns of spots or stripes that break up the contour and surface area of the animal (called "disruptive crypsis"; Cott 1940, Edmunds 1990). Signals can be of several types, including "aposematism," defined as conspicuous colors advertising unprofitability to predators (Guilford 1990a, b). A phenomenon that may include aspects of both signalling and crypsis is "mimicry," a term used for organisms that adaptively resemble another species, as in the cases of Müllerian and Batesian mimicry (Malcolm 1990). In the former case, unpalatable aposematic organisms mimic each other. In the latter case, a palatable organism mimics an aposematic one, capitalizing on its defenses. Sometimes the term mimicry is extended to cases when organisms mimic the shape and colors of objects or immobile organisms for the purpose of crypsis, for example as in stick insects (Edmunds 1990). Finally, variation in coloration can be due to different requirements for thermoregulation rather than predator avoidance (e.g., Shapiro 1976, Kingsolver & Watt 1983). For all of these types of (presumably) adaptive coloration, it is probably fair to say that the function is often assumed, but seldom tested.

The coloration of the first three larval instars in the comma butterfly, *Polygonia c-album* L. (Nymphalidae), appears to the human eye to be disruptively cryptic (Fig. 1A), at least when seen against a naturally variegated background of light and shadow. The last two instars, which are defended by strong branching spines, are much more strikingly colored in white, black and orange (Fig. 1B). The same type of coloration is present in the probable sister species to *P. c-album*, the Nearctic *P. faunus* (Scudder 1889, Scott 1986). It has been suggested that this type of coloration is also cryptic, the large continuous white area supposedly mimicking bird droppings (Thomas 1986). Resemblance to bird droppings is seen in many butterfly larvae, e.g., in *Limenitis* and *Papilio* (Scott 1986), although to our knowledge the function has never been tested.

Late instar larvae of other *Polygonia* species (e.g., *P. interrogationis, P. comma, P. satyrus*, and *P. c-aureum)* and the related *Kaniska canace* are similarly colored in conspicuous white, black and orange, but with no continuous white areas (Scott 1986, Teshirogi 1990). This suggests the possibility that the coloration is aposematic in these species, and then perhaps in *P. c-album* and *P. faunus* as well. Here, we study the function of the coloration of late instar larvae of *P. c-album* using young chickens as models of bird predators. For comparison and as a control for effects of novel food, we also tested the chicks with third-instar larvae.

MATERIALS AND METHODS

Females of *P. c-album* were captured near Akersberga, north of Stockholm, Sweden. Eggs were obtained in flight cages where the host plant *Urtica dioica* (Urticaceae) was present. Larvae were reared on this plant in the laboratory. Several asynchronous rearings

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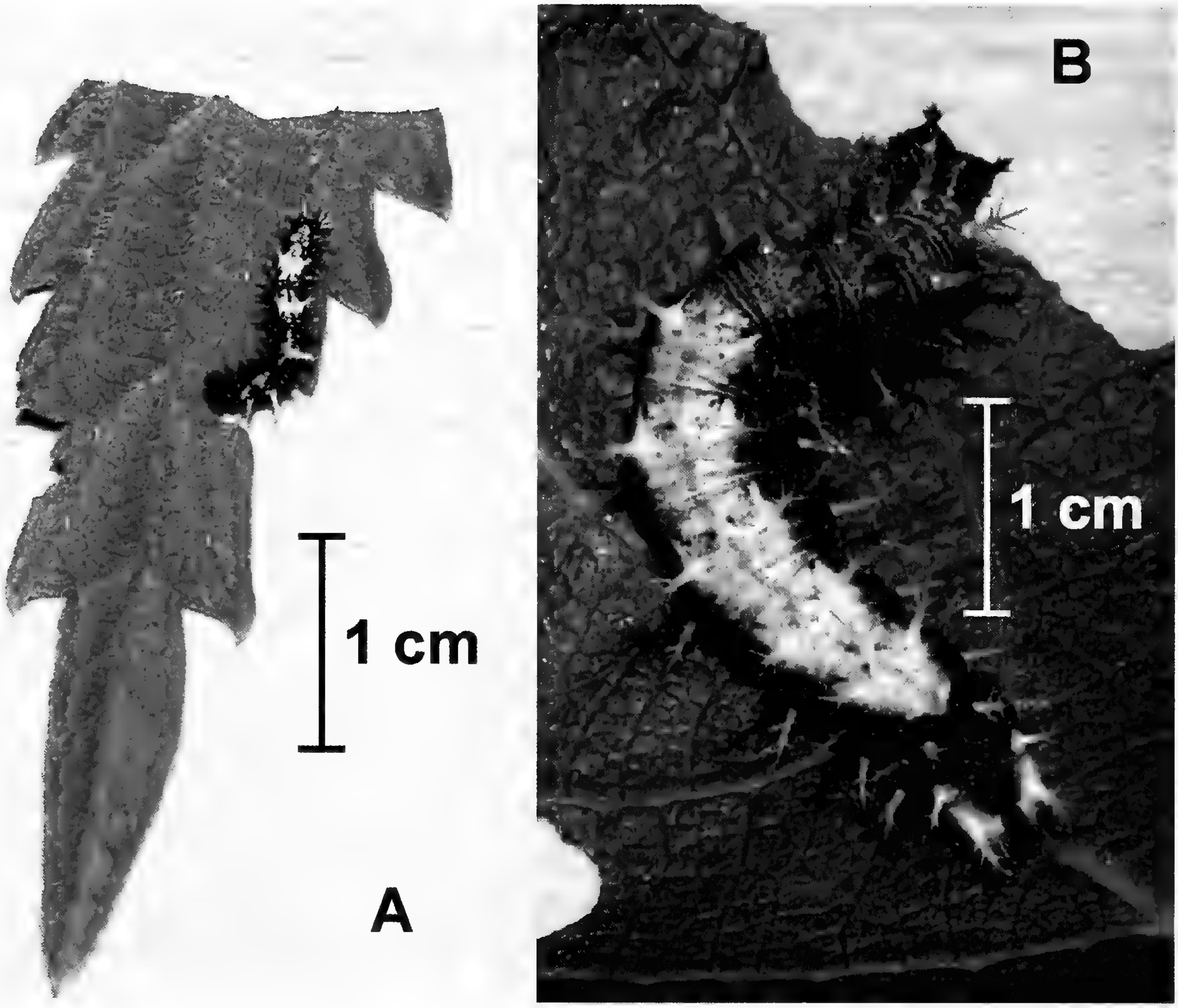

FIG. 1. Larvae of *Polygonia c-album* on leaves of *Urtica dioica*. **A.** Third-instar larva. **B.** Fifth-instar larva.

were made, so that third- and fifth-instar larvae were available for trial simultaneously.

Third-instar larvae. In this instar, the larvae lack large areas of any color except for the background color, black. Small spines are present, and towards the end of this instar the spines have a yellowish color on the foremost part of the body and a whitish color towards the rear (as seen in Fig. 1A). The impression to the human eye is not that of a striking coloration but rather a pattern that could function disruptively against a variegated background.

Fifth-instar larvae. In this instar, the foremost part of the body is colored orange, and the rear part is continuously colored white. The rest of the body is black with orange markings (Fig. 1B). Large, chitinous, branching spines are present on the back and sides of the body, and they are colored orange, white or black, according to position. Larvae are several centimeters in length (Figs. 1A and B are approximately to scale).

Chicks. We used domestic chicks (*Gallus gallus domesticus*) as predators. The chicks had not eaten when they arrived from the hatchery at an age of less than 20 h. Batches of 30–40 chicks were housed in cages (100 cm × 55 cm × 20 cm) with wooden sides, steel-net floor, and a roof made partly of wood and partly of chicken wire. The cages were heated with 60 W carbon light bulbs and the floors were covered with sawdust. Chicks were fed chick starter crumbs and water, and at least from their second day on they were also fed live mealworms (*Tenebrio molitor*).

Experiments. The experiments took place in an arena of the same kind of cage in which chicks were housed. Part of the cage was screened off, leaving a testing floor of 30 cm × 55 cm. Experiments took place when the chicks were about three days old. The chicks

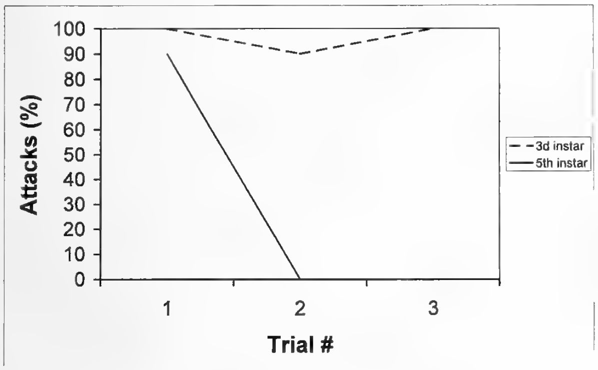

FIG. 2. Results from trials with domestic chicks presented with third-instar (dashed line) or fifth-instar (solid line) larvae of *Polygonia c-album.* The same pair of chicks was tested on several occasions during one experimental day (subsequent trials from left to right). Both young and old larvae were attacked in initial trials, but fifth-instar larvae were avoided in the next trial. N = 10 pairs of chicks in trial #1 and 2 for both larval instars, N = 7 pairs of chicks in trial #3 with young larvae (see text).

were tested in pairs, because single chicks become distressed and do not feed normally (Gamberale & Tullberg 1996, and references therein). One of the chicks was fed as many mealworms as it would eat before a trial, which made it satiated and uninterested in feeding during the trial. This chick was used as a companion to the experimental chick. We used the same companion chick in all trials.

Prey was presented in a petri dish with transparent bottom, i.e., chicks saw the prey against a background of sawdust. Before each trial, the chicks were presented two mealworms in the petri dish. This was done to show the place where prey was displayed, and as a check before each trial that the chicks were in fact interested in insect prey. The chicks were then presented one mealworm and one larva of *P. c-album.* We collected data concerning chick attack behavior and the mortality of the attacked insects. Chicks were exposed to the prey throughout the trial and allowed to make as many attacks as they wished. A trial was ended when the *P. c-album* larva had been eaten, or after 60 seconds if the chick did not peck on the *P. c-album* larva at all. If it did, we waited another 60 seconds to see if the larva was eaten.

Twenty chicks (other than the companion chick) were used in total, originating from two separate batches. Half of them were tested with third-instar larvae and the other half with fifth-instar larvae, using chicks from both batches in both types of experiments. All chicks were tested twice with the same type of larva. In addition, to test for the presence of any aversion learning against third-instar larvae, seven chicks (of the same batch) were also tested with such larvae a third time. Finally, four of these chicks, that had eaten or attacked third-instar larvae on all three occasions, were tested a fourth time. All trial runs were performed consecutively on the same day, within five hours. We used Fisher's exact test for statistical comparisons.

A follow-up experiment was performed next season, with new larval stock and a new batch of chicks, this time they were one week old. Five pairs of chicks were presented with a spineless fifth-instar larva together with a mealworm in a petri dish. The larvae had been killed by freezing and their spines had been cut off.

RESULTS

General observations. The two mealworms presented at the start of each trial were always eaten rapidly, demonstrating that the chicks were very interested in insect prey. In all trials the chicks were initially more interested in attacking the mealworms than the comma larvae when subsequently given a choice, not surprisingly since this was a food type with which they had previous experience. The third-instar *P. c-album* larvae might also have been somewhat hard to see against the variegated background of sawdust. However, the experimental chicks were curious and in 19 out of 20 initial trials (both age classes combined) eventually pecked at the comma larvae.

Third-instar larvae. In the initial trials all 10 experimental chicks attacked the third-instar comma larvae (Fig. 2). In five of these cases the larva was also eaten (after a time span of, respectively, 19, 30, 35, 45, and 45 seconds). In the next trial the same chicks attacked in nine out of ten cases (decrease in attack frequency not statistically significant: Fisher's exact test), and ate the larva in two cases (both after 45 seconds). Both of these cases involved chicks which had also eaten the comma larva in the previous experiment.

As explained in Materials and Methods one group of chicks was tested a third time, with attacks by all seven experimental chicks (Fig. 2) and the larvae being eaten by the same two chicks (after 25 and 120 seconds). When the two chicks that had eaten the larva on all three occasions were tested anew they did so again, this time within 20 seconds after exposure. When two chicks that had attacked but not eaten (on all three occasions) were tested again they repeated this behavior. The last trials with this group took place 2 hours and 40 minutes after the start of the experiment.

In all cases when the larva was not eaten it was still alive after the experiment (despite having been pecked at), but on one occasion it was visibly damaged, and for this reason it was killed by us.

Fifth-instar larvae. The older larvae were never eaten by the chicks. In the initial trials attacks took place in nine out of ten cases (Fig. 2). They were in the form of pecks, in three cases followed by the chicks lifting the larva and dropping it. In the next trial, which took place less than an hour after the first, the chicks behaved very differently. There were no attacks in the form of pecks (Fig. 2). The decrease in attack frequency between trials is statistically significant (Fisher's exact test: two-tailed $p < 0.05$, one-tailed $p < 0.01$). In all cases except one ($N = 10$) the experimental chick inspected the comma larvae closely, sometimes for periods up to 15 seconds. In two cases attacks were initiated but terminated before contact. Larvae were alive and apparently undamaged after all experiments, and they were returned to their host plants where they soon continued to feed.

Fifth-instar larvae without spines. In this experiment larvae from which the spines had been removed were presented to the chicks. The first pair of chicks did not eat the larva, but they showed no aversion and handled the larva throughout the experiment. This larva was presented also to the next pair of chicks, and it was then eaten within 10 seconds. The three additional pairs of chicks also ate the spineless larvae within seconds.

DISCUSSION

Five out of ten chicks in initial trials ate third-instar larvae, but only two chicks continued to eat them in subsequent trials. This suggests that they are not highly palatable to birds; possibly the small spines confer them a limited defense. On the other hand, chicks showed no other signs of beginning to avoid third-instar larvae after having experienced them. They were almost always attacked (even though the previous experience was less than an hour earlier), and two chicks did eat them in all four trials within a time span of less than three hours. Evidently no chemical defense effective against birds is present in the comma butterfly. This conclusion is also supported by the fact that the adults of the species are highly cryptic and also very palatable to great tits (*Parus major*) in laboratory experiments (SN & BST unpubl.). However, this evidence is not conclusive, since butterfly larvae can be unpalatable even when adults are palatable (Bowers & Farley 1990, Dyer & Bowers 1996).

The chicks showed no initial aversion to the older comma larvae, but very rapidly learned to avoid them. It seems highly improbable that a chemical defense should be present in old larvae but not in young larvae or adults. More probably, the strong and sharp spines are what defend older larvae, as demonstrated by the result of removing the spines. In any case, the rapid aversion learning suggests the possibility of an aposematic function of the striking coloration. In the absence of color manipulations we cannot, however, rule out the possibility that aversion was in fact to the sight of the spines themselves, independently of color. Interestingly enough, the spines are colored in such a way that might make them more conspicuous (Fig. 1B), so these two possibilities may be hard to separate. A dual function is also possible, so that the coloration indeed mimics bird droppings, as previously suggested (Thomas 1986) but has an aposematic function once the larva has been discovered. This would be useful if some predators are not deterred by the spines, or if larvae are often damaged by naive predators.

In this context it is, however, interesting to note that the fifth-instar larvae were not damaged by the attacks in the initial trials, when the chicks learned to avoid them. This is in line with previous results from chemically defended aposematic insects (Boyden 1976, Järvi et al. 1981, Wiklund & Järvi 1982, Wiklund & Sillén-Tullberg 1985) but has not often been investigated in mechanically defended prey (but see Carrick (1936) for results from the related butterfly *Aglais urticae*). The importance of such observations is that they demonstrate that individual selection for aposematic coloration is possible. In other words it is not necessary to invoke kin selection or other types of indirect selection, as would be the case if some individuals must be sacrificed before predators can learn aversion (Fisher 1930, Benson 1971). Individual selection is a more parsimonious explanation of aposematic coloration when direct benefits to the individual are present, because for indirect selection additional assumptions of starting conditions are necessary regarding prey family groupings and the movements and memory of predators. Indeed, even aposematic butterflies often have cryptic pupae, and this is the stage of the life cycle that is most likely to be killed by inspecting predators (Wiklund & Sillén-Tullberg 1985). Conversely, strong spines, which (as demonstrated here) should give direct benefits to the individual, are found very commonly in nymphalid larvae, often together with contrasting, bright colors or a jet-black color that should provide little crypsis against green leaves (e.g., in other Nymphalini and in the Kallimini and Argynniti). Spines are absent in some chemically defended groups such as the Danainae, with aposematic larvae, and also in groups such as the Satyrinae and Apaturinae, which have clearly cryptic larvae. In many cases, however, the patterns are far less clear and the function of the coloration uncertain (for instance, *Ladoga* larvae in the Limenitidini have spines but cryptic coloration; Teshirogi 1990).

The ontogenetic shift in defense tactics in *P. c-album*, from cryptic coloration to aposematic coloration and mechanical defense (seen also in *A. urticae;* Carrick 1936), is understandable in terms of the general increase in size during larval growth, for several reasons. First, it may not be possible for a small larva to have spines large enough to deter birds and other vertebrate predators. Second, small larvae may be more vulnerable to attacks by vertebrate predators. If predators need to learn aversion, small larvae may not survive this process, and as a consequence it may not be a profitable strategy to advertise a degree of unpalatability (Gamberale & Tullberg 1996). Third, the increase in size during growth of butterfly larvae has been found to be coupled with a shift from predominantly predation by invertebrates to predominantly predation by vertebrates, such as birds (Kristensen 1994). Hence, the need for defense against vertebrate predators should be largest in the last larval instars. Fourth, it may be difficult to evolve a pattern that is effectively aposematic given a very small size of the colored areas. In tests with aposematic bugs (Lygaeidae), chicks more readily learned aversion towards to the larger late instars, even though the coloration is the same (Gamberale & Tullberg 1996).

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SEXUAL DIMORPHISM IN EYE MORPHOLOGY IN *EUCHEIRA SOCIALIS* (PIERIDAE)

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ABSTRACT. We examined the magnitude of sexual dimorphism in the eyes of madrone butterflies, *Eucheira socialis* (Pieridae). Via microscopic examination of the cornea, we determined the eye surface area, facet number, and facet diameter in 5 eye regions for males and females. Our analysis, which controlled for body size (forewing length), showed that in this species, as in most Lepidoptera, males have a significantly larger eye surface area and more facets than females. Facet diameters vary with eye region but in an unusual way for the Lepidoptera: the largest facets we observed were in the dorsal region of the male eye. While the results reveal interesting patterns of sexual dimorphism in eye structure in *E. socialis* there is insufficient information about adult behavior to understand the behavioral and ecological implications and causes of these patterns, especially those in facet diameter.

Additional key words: sexual dimorphism, eye structure, eye size, facet diameter.

Sexual dimorphism in eye structure is common in the Lepidoptera (Yagi & Koyama 1963). Males usually have eyes that are larger and have more and larger facets than those of females. In response to a presentation on sexual dimorphism in butterfly eyes by one of us (RLR) at the 1999 meeting of the Lepidopterists' Society, Dr. Arthur Shapiro suggested that sexual dimorphism in eye structure was particularly pronounced in the madrone butterfly, *Eucheira socialis* Westwood (Pieridae). We investigated this claim by examining corneal structure in males and females of this species.

Little has been reported about the behavior of *E. socialis* adults that bears on the question of selection pressures that might have shaped eye structure. Previous studies of *E. socialis* have focused on the social behavior of the larvae and the relationship between this butterfly and madrone trees (*Arbutus* spp., Ericaceae) on which the larvae feed (Kevan & Bye 1991, Underwood 1992, 1994). The adults live for approximately one week and are apparently unable to feed because the two halves of the proboscis do not anneal correctly. Within 3 h of eclosion adult females generally travel about 15–18 m to oviposit. A female lays her eggs in a single large mass (20 to over 350 eggs) on the ventral side of one madrone leaf (Underwood 1992). Males fly around madrones and other trees in the vicinity only when there is bright sunlight (D. Underwood pers. comm.). The mating behavior of males and females is essentially unknown.

MATERIALS AND METHODS

The *E. socialis* specimens used in this study were obtained from Art Shapiro (University of California, Davis) and Dessie Underwood (California State University, Long Beach) and reported to have been reared in April 1991 from larvae found in two nests in the Sierra Madre Occidental, Durango, Mexico. We received them as papered specimens. We processed each of 5 males and 5 females in the following way. We measured the forewing length (FWL) to the nearest 0.1 mm using dial calipers. Then the head was removed, bisected, and immersed in 10% NaOH solution until the soft tissue could be gently removed from each cornea, approximately 5 minutes. Non-corneal cuticle was trimmed away from the eye. Radial cuts—two starting close together dorsally, one starting ventrally, and some starting both anteriorly and posteriorly from the edges of the cornea—were made toward the center of the cornea (Fig. 1). These permitted the cornea to lie flat on a microscope slide and provided references for identification of eye regions. To improve the visibility of the cornea for handling, we applied acid fuchsia stain for a few minutes to the cornea. Finally, the cornea was mounted in glycerol and covered with a coverslip, the edges of which we sealed with Cytosol 60 mounting medium (Stephen Scientific).

Digitized images of each cornea were obtained by video microscopy with a Nikon inverted microscope. Approximately 15 images of each cornea made with a 10× objective were required to capture the entire cornea. A composite image of each complete cornea (for example, see Fig. 1) was created using Adobe Photoshop (Adobe Systems Incorporated). For a size reference a micrometer scale at 10× was photographed.

The numbers of facets in the cornea were manually counted from the composite images. However, we used image analysis software (Scion Image) to measure facet diameters and eye surface area (ESA) from the composite images. The micrometer scale on each image was used to calibrate the software. To obtain the ESA of each image an outline tool was used. Two ESA measurements taken by this method were averaged to control for error in tracing the image; if the two measurements differed by more than 5%, then a third measurement was included in the average. Facet di-

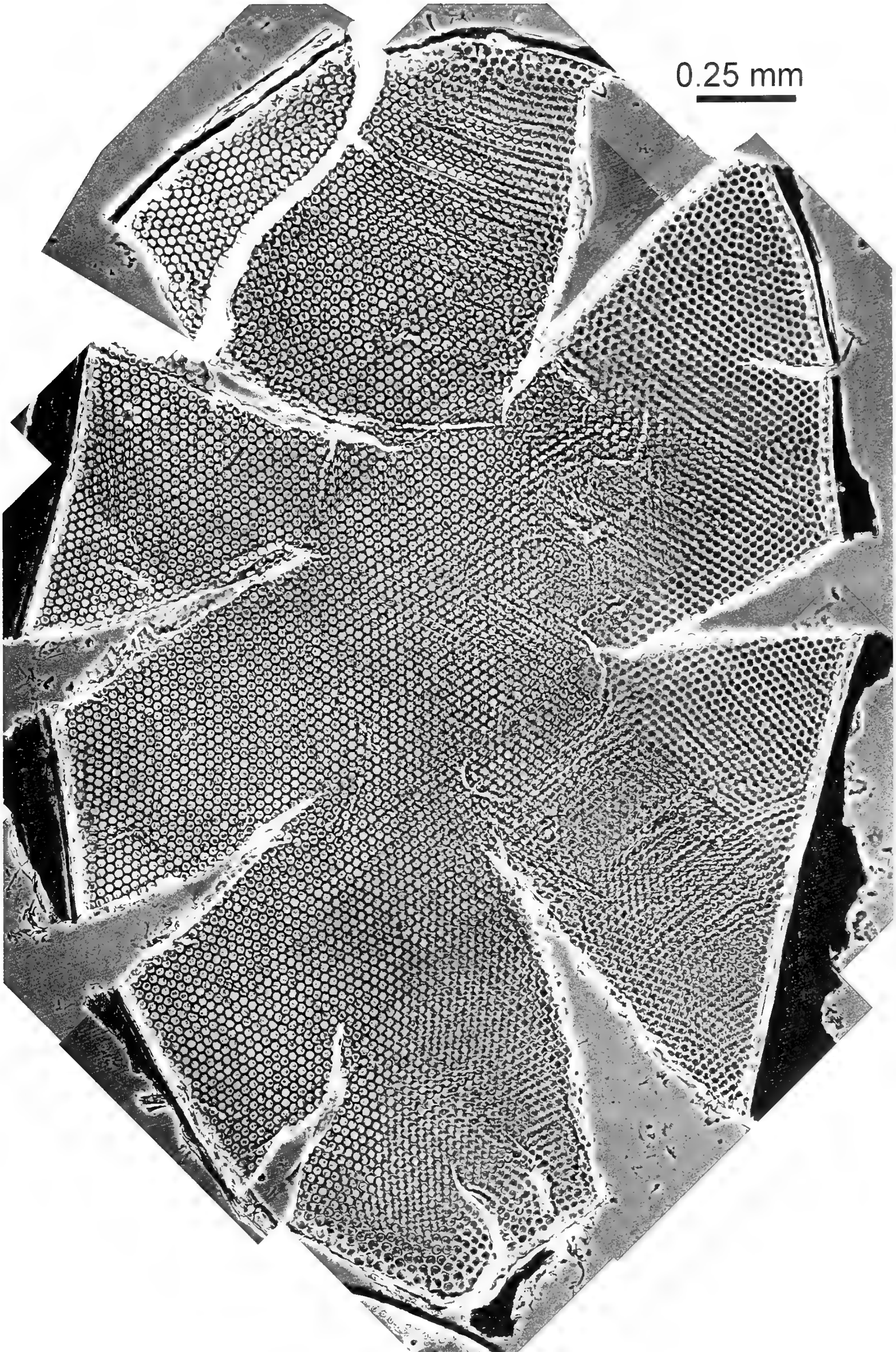

FIG. 1. A micrograph of a representative cornea from the eye of a male *E. socialis* made from multiple images. Dorsal is toward the top and anterior to the left in this image. Scale line = 0.25 mm.

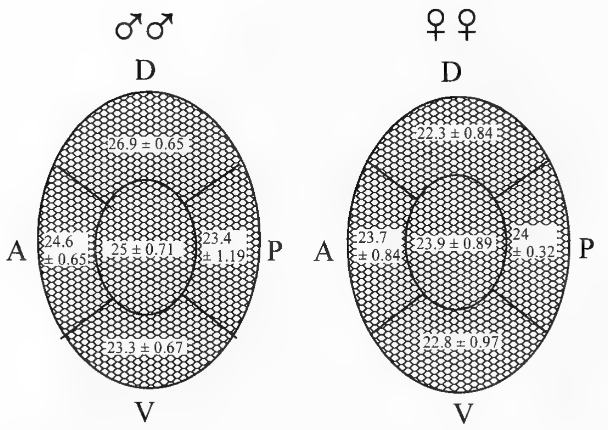

FIG. 2. Schematic of the cornea of *E. socialis* showing the facet diameters (in mm; mean ± standard deviation) measured for both males and females in each of five regions of the cornea. Abbreviations: A, anterior; D, dorsal; P, posterior; V, ventral.

ameters were calculated by dividing the length of a row of 10 facets by 10. Two measurements were taken in each of the 5 eye regions (anterior, posterior, dorsal, ventral, center), then averaged. If the two measurements differed by more than 8%, then a third measurement was included in the average. The measurement points within each eye region were chosen based on the clarity of the facet images within that region (i.e. no wrinkles or tears in the cornea). All statistical analyses were done on SYSTAT 9.0 (SYSTAT, Inc.).

RESULTS

The males in our sample were significantly smaller than the females as measured by forewing length (males: 25.7 ± 1.22 mm; females: 31.2 ± 1.43 mm; t = 6.58, 8 df, $p < 0.0002$). Despite their smaller body size, males have a significantly larger ESA than females (males: 4.45 ± 0.15 mm^2; females: 3.20 ± 0.15 mm^2; ANCOVA, with forewing length as covariate, $p < 0.0001$). ESA is not correlated with forewing length within either sex ($p = 0.135$), although sample sizes were small.

A larger ESA in males could mean that compared to females they have more facets, larger facets, or both. Males have significantly more facets (7781 ± 85) than females (6648 ± 357: ANCOVA, with forewing length as covariate, $p = 0.011$), but within the sexes there was no significant correlation between facet number and ESA ($p = 0.117$).

The mean facet diameters for each of the five eye regions in males and females are illustrated in Fig. 2. A two-way repeated measures ANOVA with facet diameter as the dependent variable and region as the repeated measure showed that the effects of region, sex, and the interaction between sex and eye region were all significant ($p < 0.001$ for each). Therefore, variation in facet diameters is explained by both sex and eye region, but there are significant differences between sexes in the pattern of variation among regions. Facet diameters of males were generally larger than those of females but especially in the dorsal region. In fact, only in the dorsal eye region was the difference in facet diameter between males and females significant (t = 8.69, 8 df, $p < 0.0001$). Facet diameters did not differ significantly between males and females in any other eye regions (anterior, t = 1.9, posterior, t = 0.368, ventral, t = 0.376; center, t = 2.157; all: 8 df, $p > 0.05$). Another clear trend in the eyes of both males and females was that facets in the ventral region tended to be smaller than those in the anterior, central, and posterior regions along the equator of the eye.

DISCUSSION

Compared with conspecific females who are on average larger in body size, *E. socialis* males have eyes that are 1.39 times larger in surface area, have 1.17 times more facets, and have, at least dorsally, larger facet lenses. Contrary to Dr. Shapiro's initial impression, this sexual dimorphism in eye morphology is similar in direction and magnitude to that seen in butterflies and other Lepidoptera (Rutowski 2000). For comparison, Yagi and Koyama (1963) report male : female eye surface area ratios of 1.37 and 1.33 and facet number ratios of 1.1 and 1.18 for two pierids, *Colias erate* and *Pieris rapae*, respectively. Eyes in males that are larger and have more ommatidia relative to body size than those in females are generally interpreted as indicating that acute vision in males is more important to reproductive success than in females (Rutowski 2000, and in press).

In spite of this general similarity in eye structure, the pattern of variation in facet diameters is quite different from that reported for another butterfly, *Asterocampa leilia*. In *A. leilia* the largest facets are found in the frontal and dorsofrontal regions of the eye regions with facets in the dorsal region being smaller (Ziemba & Rutowski 2000). Large facets indicate eye regions of high resolution and sensitivity and imply that those regions of the eye are frequently used in specific tasks requiring high resolution or sensitivity such as when males track females during rapid pursuit flights (Land 1989, 1997). The large facets in the dorsal part of the male eye in *E. socialis* suggest that dorsal vision is better than in other parts of the visual field. Little is known about the behavior of adult madrone butterflies so the possible functions of this dorsal region of high acuity are not clear, but it might be important in sexual interactions. In some insects, acute dorsal vision produced by large facets is important in males for detecting females against the sky (Land 1997). Some pierids have been observed engaging in ascending flights during courtship attempts. During an ascending flight a male-female pair flies up together until one of them, usually the male, terminates pursuit and drops rapidly toward the ground (Rutowski 1978a, b). When Dessie Underwood threw *E. socialis* females up in the air in an attempt to pair them, she noted that *E. socialis* males would only chase the female if she flew well (D. Underwood pers. com.). If ascending flights are a common occurrence in *E. socialis* courtship, then the male's dorsal acute zone may be used for tracking the female's movements in this context.

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GENERAL NOTES

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OBSERVATIONS OF ADULT AND LARVAL BEHAVIOR IN THE WINTER SPHINGID, *ARCTONOTUS LUCIDUS* (SPHINGIDAE)

Additional key words: phenology, hostplants, circadian habits, mate location, Bear sphinx moth.

Arctonotus lucidus (Boisduval), the Bear Sphinx, is a poorly known, small green sphingid that occurs along the Pacific coast of the United States and Canada. Part of the reason for the Bear Sphinx's anonymity is its very early season flight, ranging from December in southern California to April in Washington state and British Columbia, when little else is flying. After its description by Boisduval (1852), it was 90 years before Comstock and Henne (1942) described the larva and adult phenology. Those descriptions were based upon specimens reared from eggs on *Oenothera dentata* Jepson. Osborne's (2000) report of larvae on *Clarkia breweri* (A. Gray) E. Greene and *C. modesta* (Jepson) represents the first confirmed record of larvae found on hostplants in nature.

Female specimens are rare in collections: there are only 7 of 285 (2.5%) field collected specimens in the Essig Museum (U.C. Berkeley), the Bohart Museum (U.C. Davis), the Los Angeles County Museum, and the San Diego County Museum combined. The rarity of captured females and larvae explains why so little is known about the species' natural history. The purpose of this note is to describe poorly known aspects of adult behavior including circadian habits (flight times), mating, oviposition, and some larval behavior.

On 2 February 1997 J. Kruse and I captured 30 males (no females) using mercury vapor and UV traps near Chinese Camp, Tuolumne Co., California. On 7 February 1997 we were unsuccessful in attracting any *Arctonotus* to the same traps at the same localities. However, that same evening we took two females and one male at residential lights in the same general area.

Captured females were caged outdoors in Berkeley, Alameda Co., California. Feeding was attempted by forcibly unrolling the proboscis into sugar water (a technique that works with many Lepidoptera). I found that the proboscis was vestigial, flaccid and not capable of reaching the substrate on which the moth was perched. Captive females became active at dusk (1745–1800 h PST) and laid eggs singly or in pairs after brief flights around the enclosure. The two females lived 5 days and laid a combined total of 380 eggs. Approximately half the eggs were maintained out of doors (4–21°C), and the rest were brought indoors (16–21°C). Indoors the eggs turned from pale green to yellow in 7 days and hatched 9 days following deposition. The eggs maintained outside hatched in 19 days, 10 days after those maintained indoors. Larvae were fed *Fuschia thymefolia* Kunth, *Clarkia unguiculata* Lindley, *C. amoena* Lehm., and *Oenothera* species (all Onagraceae). Osborne (in press) provides an excellent description of larval biology, to which I only add the observation that large (5 cm) 5th instar larvae regularly hide at the base of the hostplant during non-feeding periods; mature larvae fed mostly in the morning and late afternoon. The larvae range from nearly all green with yellow spiracles to pink and black to all black and this habit occurred regardless of color form.

FIG. 1. Female *Arctonotus lucidus* in 'calling' posture. Photo by Daniel Rubinoff.

Larvae began to burrow in soil in preparation for pupation 36–45 days after egg hatch. Mortality was high at this stage: of 45 larvae that burrowed, only 18 pupated. Larvae pupated under dead leaves and pieces of wood, just under the soil surface, and up to 16.5 cm underground in the rootball of senescing hostplants. Pupation usually occurred in firmly packed ovate cells. The cremaster possesses a bifurcate tip as depicted by Osborne (1995) for *Proserpinus clarkiae* (Boisduval) (Sphingidae).

The 18 pupae were maintained outside in a ventilated plastic tub in Berkeley until November when they were placed in a refrigerator at 1.7°C ± 1°C. No development was evident in the pupae until they had been moved from refrigeration to outside temperatures (between 8–20°C) for more than 45 days. J. Kruse (pers. com.) found that daily cycling of pupae removed from a refrigerator (3°C) to room temperature (18°C) for approximately 4–8 hours, also induced eclosion. The green coloration of the developing wings was visible through the pupal cuticle for two days before the moths emerged. The cuticle became very soft 24 hours before emergence.

Adults eclosed from 8–19 March 1998, usually between 1800 and 1900 h PST; they took 1–2 hours to dry their wings. Adults in cages were active only from 1800 to 1930 h PST, though mating occasionally lasted a few hours longer. Virgin females rested on the substrate, everting and pulsating the papillae anales to disperse pheromone (Fig. 1). When a male was placed in the same enclosure he rapidly approached the female and mated. If no male arrived by 2000 h PST, females stopped calling until the next sunset. One male fertilized three females; those females laid 369, 397, and 401 eggs respectively.

Arctonotus lucidus pupae apparently are able to develop when surface temperatures still regularly fall below freezing. Eggs hatch and larvae begin development when most apparent hostplants are less than 2 cm high, and night temperatures occasionally fall below 0°C.

Hodges (1971) stated that adults can be collected during the day while nectaring on flowers. I suspect this report to be in error since all collections throughout the range of the moth, that I have been able to document, were made at lights, and none of the moths I reared was active during the day. Moreover, the adults do not feed.

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EMERGENCE OF PARASITIC FLIES FROM ADULT *ACTINOTE DICEUS* (NYMPHALIDAE: ACRAEINAE) IN ECUADOR

Additional key words: parasitoid, adult Lepidoptera, neotropics, *Arachidomyia.*

A parasitoid is defined as 'an organism which develops on or in another single (host) organism, extracts nourishment from it, and kills it as a direct or indirect result of that development' (Eggleton & Gaston 1990). In contrast parasites rarely kill their hosts and predators always consume more than one host. In addition, parasitoids possess a free-living adult stage (whereas many parasites do not), and do not reproduce inside the host (as do many parasites). Insects with parasitoid life cycles are known from many taxanomic groups including many families of Hymenoptera and Diptera (Eggleton & Belshaw 1992), yet knowledge of host specificity and parasitoid life-cycles remains patchy. Host relationships are known for only a small percentage of parasitoid taxa in the tropics (e.g., references in Hanson & Gauld 1995), and many parasitoid species remain undescribed due to their often small size and highly specialized lifestyles (Gaston 1991). The emergence of parasitoids from adult Lepidoptera is infrequently reported in the literature (e.g., Marshall 1896, Cockayne 1911, Edelsten 1933, DeVries 1979, Smith 1981, McCabe 1998). The following record of sarcophagid flies emerging from adult butterflies in Ecuador represents the first record of this in several years, and only the second record involving Sarcophagidae.

On 8 December 1996 three female *Actinote diceus* Latreille were collected at Cabañas San Isidro, located at around 2000 meters elevation in north-eastern Ecuador. All were flying normally along a road cut through disturbed cloud forest and cattle pasture. At the time of collection all three butterflies were killed by a quick pinch to the thorax, as described by DeVries (1987), placed together inside a glassine envelope, and marked with the date and locality. The specimens were then placed together in a plastic tub with other specimens collected that day and returned to the lab. Upon arrival at the lab and inspection of the specimens, two fly pupal exuviae were found inside the envelope with the three *Actinote* females. Two adult sarcophagid flies were also present inside the envelope. These adults were identified using Shewell (1987) as belonging to the genus *Arachidomyia* Townsend. Due to eclosion inside the glassine envelope, both specimens were badly damaged and could not be identified to species. Another empty puparium was found in an envelope containing a fourth individual female *A. diceus* collected on the same date, but no adult fly was recovered. Lepidopteran specimens were retained in the collection of the senior author and the dipteran specimens were deposited in the Tulane University collection.

Sarcophagid flies develop on a wide variety of food resources and range in habit from detritivores to predators and parasitoids of invertebrate and vertebrate hosts (Clausen 1940). The parasitoid habit appears to have evolved on many separate occasions, and about half of the described species can be considered parasitoids or cleptoparasitoids. Of these, approximately 750 species can be considered true internal parasitoids (Eggleton & Belshaw 1992). Parasitoid Sarcophagidae are known to develop inside adult hosts of a variety of insects and vertebrates including Orthoptera, spiders, gastropods, and lizards (Shewell 1987, Allen & Pape 1996, Dial & Roughgarden 1996, Danyk et al. 2000, Pape et al. 2000). A number of Sarcophagidae, including *Arachidomyia*, have been reared from lepidopteran pupae (Clausen 1940, Shewell 1987, Parry 1995) and McCabe (1998) reported *Sarcophaga* (=*Arachidomyia*) *aldrichi* Parker emerging from adult moths, but large scale larval lepidopteran rearing projects have found very few instances of parasitism by sarcophagids (Janzen & Hallwachs 1999, Dyer & Gentry 2001, Stireman & Singer unpublished data). In our area, little is known of the life history of *Actinote diceus*. Adults and larvae are present year-round and found in association with their larval food plant, *Erato polymnioides* DC (Asteraceae) (Greeney et al. 2001). While their adult lifespan is unknown adult females live only a few days in captivity (HFG unpublished data). McCabe (1998) argued that attack by *Arachidomyia* occurred during the adult stage of the host, however in the present case this is unlikely due to the "fresh" appearance of the adult butterflies and the rapidity with which the adult flies appeared. We suspect that the parasitized individuals were attacked as pupae.

Knowledge of parasitoid/host associations is necessary for understanding the structure and function of ecological communities, developing theories of parasite/host population dynamics, and establishing of sound biological control programs (Godfray 1994, Hawkins 1994, Hawkins & Sheehan 1994, Jervis & Kidd 1996, VanDriesche & Bellows 1996). Reports of parasitism of adult Lepidoptera are rare, but extensive rearing programs, especially in poorly studied tropical ecosystems, are needed to assess whether these relationships tend to be facultative or obligate and generalized or specialized. Such rearing data is also needed to determine how parasitism of adults is achieved (i.e., via immature stages or directly) and to assess the prevalence of this life history strategy and how it may effect host populations. We hope that this report encourages further research on tropical parasitoid-host relationships and the prevalence of adult parasitism in Lepidoptera.

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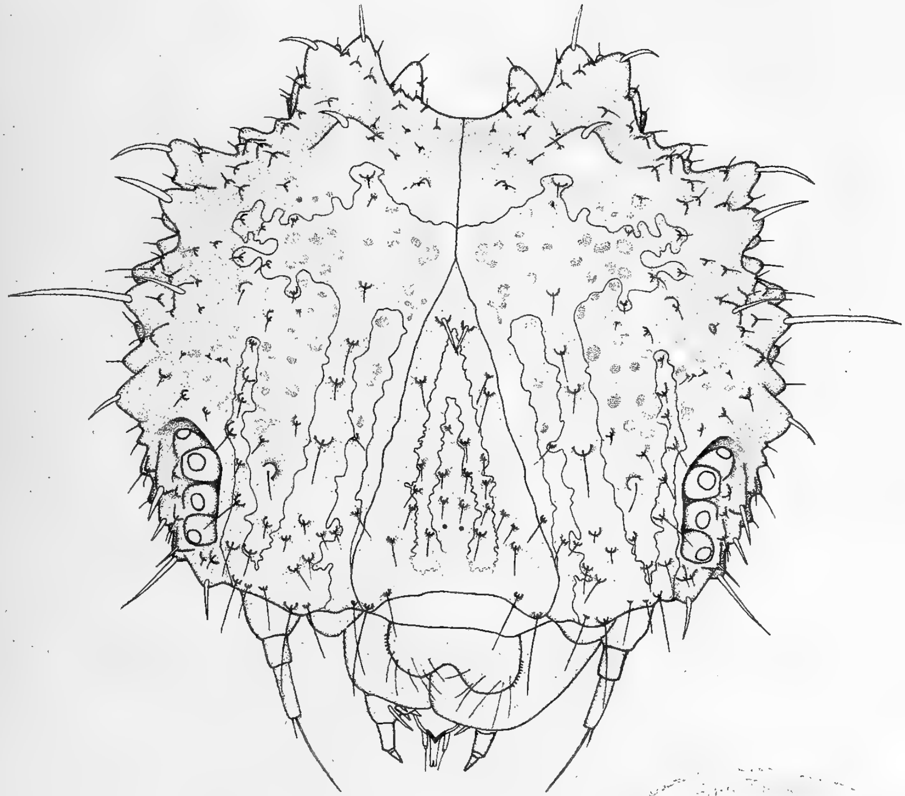

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Cover illustration: Head capsule of *Memphis* 5th instar caterpillar (Nymphalidae, Charaxinae), by C. M. Penz.

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A NEW SPECIES OF *EUCOSMOMORPHA* FROM NORTH AMERICA (TORTRICIDAE)

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ABSTRACT. ***Eucosmomorpha nearctica*, new species,** is described from 19 adult specimens, 18 male and 1 female. It previously was misidentified in North America as *E. albersana* (Hübner). It differs from *E. albersana* in its more mottled forewing, smaller body size, more prominent male hindwing anal pouch, and in details of female genital anatomy. *Eucosmomorpha nearctica* occurs widely, having been collected in Kentucky, Michigan, Mississippi, North Carolina, and Saskatchewan. Although *E. nearctica* was thought to be an immigrant in North America when reported as *E. albersana*, it now seems more likely that it is a native insect that escaped earlier recognition.

Additional key words: *E. albersana, E. a. ussuriana, E. nearctica,* Olethreutinae, Eucosmini.

Eucosmomorpha, up to now comprising four Palaearctic species, is a structurally distinct but poorly known genus tentatively included in the olethreutine tribe Eucosmini (Horak & Brown 1991). The new species described here already has a publication history in North America. I reported one male, captured in Michigan in 1961, as the Palaearctic *E. albersana* (Hübner) (Miller 1983). I noted that it might prove to be *E. albersana ussuriana* (Caradja); Caradja's (1916) description was insufficient to permit a more definite determination. Additional reports of the insect followed from Saskatchewan, Kentucky, and Michigan (Dang & Parker 1990, Gibson 1993). Because of recent unpublished finds in North America, as well as increased interest in immigrant insects, I undertook to resolve the insect's identity.

MATERIALS AND METHODS

Forewing length was measured under a binocular microscope at nominal 10× magnification to within 0.2 mm with an eyepiece micrometer. Wing venation was examined in reflected light under a binocular microscope after touching xylene to wings. Genitalia slides were prepared by standard methods, and genitalia double stained with chlorozole black E and saffranin. Specimens mentioned without genitalia slide number are undissected.

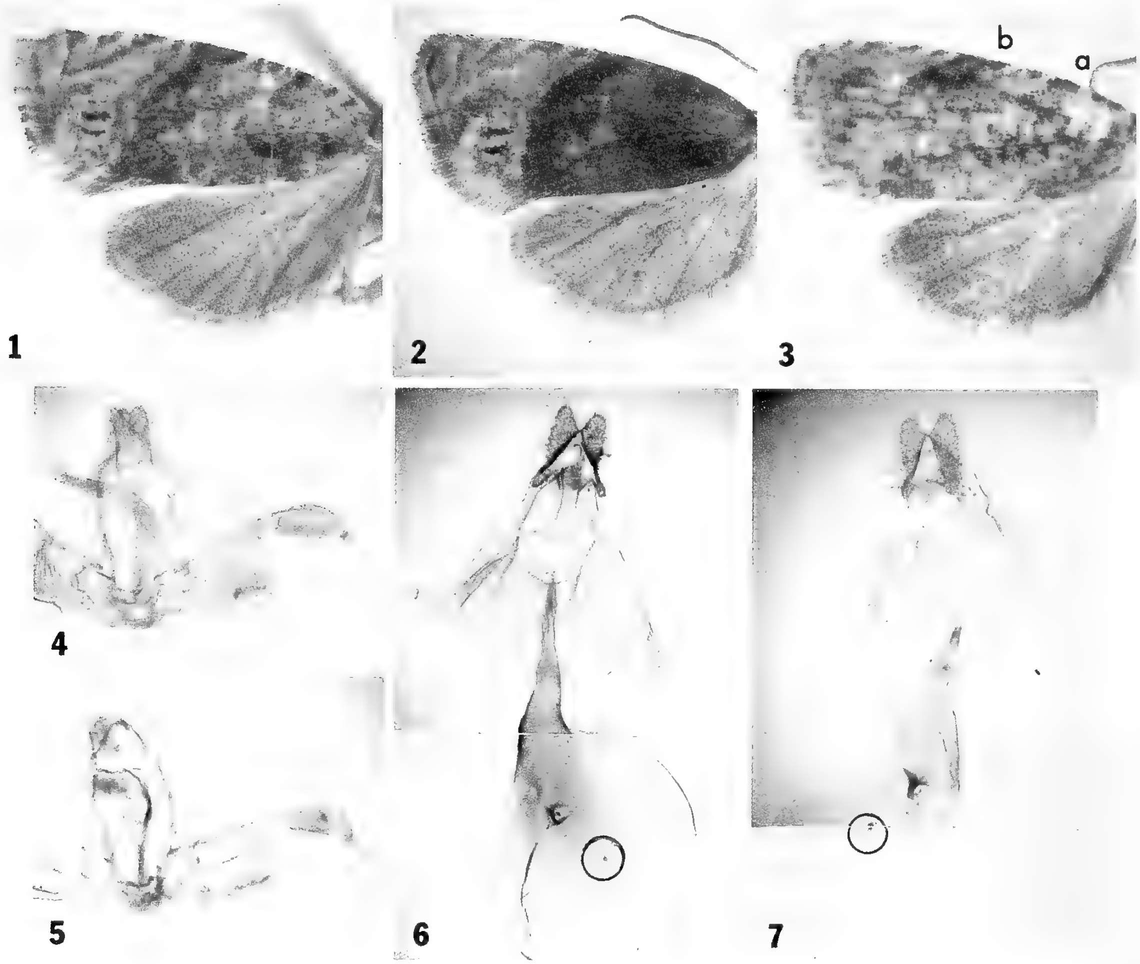
Character states are included in the description which place the new species in the genus *Eucosmomorpha* as defined by Obraztsov (1961).

Collection and museum abbreviations are as follows: JBS, J. B. Sullivan, Beaufort, North Carolina; LDG, L. D. Gibson, Florence, Kentucky; MEM, Mississippi Entomological Museum, Mississippi State, Mississippi; MGAB, Muzeul de Istorie Naturala "Grigore Antipa," Bucharest, Romania; MSU, Michigan State University, East Lansing, Michigan; UMSP, University of Minnesota Entomology Museum, St. Paul, Minnesota; USNM, National Museum of Natural History, Washington, DC.

IDENTITY OF *EUCOSMOMORPHA ALBERSANA USSURIANA*

As the identity of *E. a. ussuriana* was unclear from Caradja's (1916) description, I obtained the holotype for study. Examination showed that it did not differ structurally from typical *E. albersana*, and that its forewing scale pattern differed only trivially (Figs. 1, 2). Thus *E. a. ussuriana* seems to represent no more than individual or geographic variation. Moreover, Caradja (1916) mentioned a specimen intermediate in scale pattern between *E. a. ussuriana* and the typical form. These observations confirm the appropriateness of Kuznetsov's (1989) treatment of *E. a. ussuriana* as a synonym of *E. albersana*.

The early stages of what Caradja described as *E. a. ussuriana* are unknown, but *E. albersana* is univoltine, overwintering as a mature larva, the larva feeding on *Lonicera* and *Symphoricarpos* (both Caprifoliaceae) (Bentinck & Diakonoff 1968, Bradley et al. 1979, Hannemann 1961, Kuznetsov 1987, 1989, Razowski 1987).



FIGS. 1–7. Wings and genitalia of *Eucosmomorpha* species. **1,** Wings of *E. albersana ussuriana* holotype ♀. **2,** Wings of *E. albersana* ♀ from Potsdam, Germany. **3.** Wings of *E. nearctica* paratype ♂ from Franklin Co., Mississippi. a, subbasal fascia. b, medial fascia. **4,** Genitalia of *E. albersana* ♂ from "Geelskov" (genit. slide WEM 299993). **5,** Genitalia of *E. nearctica* paratype ♂ from Jones Co., North Carolina (genit. slide WEM 55995). The aedeagus appears shorter than actual because of angle of mounting. **6,** Genitalia of *E. a. ussuriana* holotype ♀. The smaller signum is circled. **7,** Genitalia of *E. nearctica* paratype ♀ from Boone Co., Kentucky (genit. slide WEM 1310991). The smaller signum is circled. The ductus bursae and corpus bursae became severed during dissection and are out of their natural positions.

Published forewing lengths, after conversion from spans by an empirically derived equation (Miller 1977), range 5–7 mm, averaging 6 mm (Bentinck & Diakonoff 1968, Bradley et al. 1979, Hannemann 1961, Kuznetsov 1987, Razowski 1987).

Specimens examined. *E. a. ussuriana:* Holotype ♀ [sex incorrectly given as ♂ in original description and on pin], Kasakewitch, Ussuri R., E. Siberia, Korb, 5729 Wlsm. 1908, *Grapholitha albersana* var. *ussuriana* Car., forewing length 6.0 mm, genit. slide WEM 289995 (MGAB); *E. a. albersana:* 1 ♂, "Geelskov," 4 May 1895, *P. albersana* Hb., V. Kuznetsov det., genit. slide WEM 299993 (MGAB); 1 ♀, Potsdam [Germany], Z. 18/388, *Lonicera,* Henneby, genit. slide WEM 289994 (MGAB); 1 ♂, 25.5.1882, Hamfelt Coll. [of known European origin], genit. slide WEM 299991 (USNM); 1 ♂, Kent [England], 6.1913, H. C. Hayward, genit. slide WEM 299992 (USNM). At other times I have examined additional specimens not recounted here.

OTHER *EUCOSMOMORPHA* SPECIES

Review of the literature reveals three other described species of *Eucosmomorpha* besides *E. albersana,* all Asian: *E. multicolor* Kuznetsov, *E. magnifica* Kuznetsov, and *E. figurana* Kuznetsov (Kuznetsov 1964, 1997). Nothing is known of these species beyond their taxonomic descriptions. However, it is evident from the published descriptions and illustrations that all differ in forewing scale pattern and genital anatomy from both *E. albersana* and the new species described here. For example, unlike the valvae of *E. albersana* and the new species, that of *E. multicolor* has a distinct pollex, that of *E. magnifica* is parallel sided, and that of *E. figurana* tapers gradually between the sacculus and cucullus (Kuznetsov 1964, 1997).

Eucosmomorpha nearctica W. E. Miller, new species

Eucosmomorpha albersana (not Hübner, 1822);
Miller (1983, 1987), Dang and Parker (1990),
Gibson (1993).

Male (n = 18). Head. Middle front and vertex brownish orange, lower front white with shorter scales, a band of brown scaling crossing vertex; antenna brownish dorsally, darker ventrally, flagellar scales no longer than flagellomere, pecten apparently absent; labial palpus white basally and ventrally, terminal segment short, ≈ 0.25 length of second segment, brown, second segment expanded distally, subequal in length to vertical eye diameter, scaled with patches of orange and brown, brown distally; proboscis subequal in length to labial palpus. Thorax. Mesonotum and tegulae brownish orange, sternum shining white, legs shining white between coxa and tibia, tibia and tarsi banded white and grayish brown, paler on inner sides. Forewing (Fig. 3). Costal fold absent; upper side mottled brown and orange; subbasal and median fasciae (a, b, respectively, in Fig. 3) brown, angling outwardly from costa, expressed mainly on costa, the median fascia distinct also on dorsum near tornus; 6 to 10 short white costal strigulae angling outwardly, separated in outer one-third of wing by sinuate orange striae; speculum consisting of three blackish brown longitudinal dashes; fringe brownish orange distally, paler basally; underside of wing grayish brown. Hindwing. Veins M_3 and Cu_1 connate, base of M_2 slightly closer to base of M_3, all three subparallel; upper and under sides grayish brown, fringe paler except for a grayish brown line near base; basal two-thirds of anal angle with wing edge thickened and bowed, forming a pouch that appears aligned with the hind tibia when the wing is spread. Abdomen. Shining brown dorsally, shining white ventrally. Genitalia (n = 7) (Fig. 5). Sacculus broad basally; a long, thick seta at apex of cucullus; uncus absent; socii pulvinate and directed upwards in an uncus position; aedeagus with two sinuous cornuti.

Female (n = 1). Exterior essentially as described for male, except for absence of the hindwing anal pouch. Genitalia (n = 1) (Fig. 7). Lamella antevaginalis absent; apophyses anteriores and posteriores subequal in length; ductus bursae short, encircled at the opening to the ductus seminalis by a sclerotized ring subequal in width to ductus bursae diameter; two unequal sized signa on corpus bursae, the larger one cone shaped.

Diagnosis. I found no consistent differences in male genitalia between *E. albersana* and *E. nearctica* (Figs. 4–5). The taxa are distinguishable by other characters detailed below. In brief, *E. nearctica* has a distinctive forewing scale pattern, is smaller in body size, the anal area of the male hindwing is more extensively modified, and the female genitalia differ in length of the ductus bursae and other structural details.

The forewing of *E. nearctica* is more or less mottled throughout (Fig. 3 here, and Fig. 1 in Miller 1983), whereas that of *E. albersana* is dark purplish on the basal two-thirds, and mostly pale orange or yellowish on the distal one-third, a combination that creates an overall bicolored appearance (Figs. 1, 2 here and illustrations in Bentinck & Diakonoff 1968, Bradley et al. 1979, Hannemann 1961, Razowski 1987).

Forewing length in *E. nearctica* of the combined sexes ranges 3.8–5.5 mm, averaging 4.6 mm (n = 19). The 4.6 average is three-fourths the corresponding 6 mm value derived from the literature for *E. albersana,* but translates into only one-half of the *E. albersana* body mass (Miller 1977).

The anal edge of the *E. nearctica* male hindwing is thicker and more bowed than that of *E. albersana,* thus creating a more prominent hindwing anal pouch in *E. nearctica*. The apparent difference between the taxa in aedeagus length in Figs. 4 and 5 is an artifact of slide mounting absent in other preparations.

The ductus bursae in *E. nearctica* is only half as long as that in *E. albersana,* is ringed with a sclerotized band at the opening to the ductus seminalis which *E. albersana* apparently lacks, and the smaller signum of *E. nearctica* is larger than that of *E. albersana* (Figs. 6, 7). The smaller signum of *E. albersana* is but a speck and is easily overlooked.

Types. Holotype ♂: Mississippi, Franklin Co., Trib. of McGehee Crk., T6N, R4E, Sec. 26 SW, 31 Aug. 1992, J. MacGown, T. Schiefer, forewing length 4.9 mm, genit. slide WEM 299995 (USNM). Paratypes: KENTUCKY: 1 ♀, Boone Co., Big Bone Lick State Park, 4 Aug. 1989, L. D. Gibson, genit. slide WEM 1310991 (LDG); 1 ♂, same data, except 9 July 1991, genit. slide LDG 102 (LDG). MICHIGAN: 1 ♂, Midland Co., 2 June 1961, R. R. Dreisbach, genit. slide PJ 163 (MSU); 1 ♂, Otsego Co., 13 June 1988, L. D. Gibson, genit. slide LDG 095 (LDG). MISSISSIPPI: 1 ♂, Scott Co., Bienville Natl. For., Caney Crk. Wildlife Mgt. Area, 2 mi [3.2 km] E. Pulaski, 10 June 1988, D. & M. Hildebrandt, genit. slide WEM 299994 (MEM); 1 ♂, same data as holotype (MEM). NORTH CAROLINA: 3 ♂, Jones Co., N. of Stella, Haywood Landing, Croatan Natl. For., hardwoods, 15-watt U-V trap, 18 July 1998, J. B. Sullivan (JBS, UMSP, USNM); 2 ♂, same data as preceding, except 2 Aug. 1997 (JBS, UMSP); 1 ♂, same data as preceding, except genit. slide WEM 59995 (JBS); 1 ♂, Jones Co., Island Walk, Croatan Natl. For., hardwoods, 15-watt UV trap, 17 June 1998, J. B. Sullivan (JBS); 1 ♂, same data as preceding, except 30 April 1997 (JBS); 1 ♂, Craven Co., Croatan Natl. For. Rd. 167, 21 June 1993, J. B. Sullivan, genit. in vial on pin (JBS); 1 ♂, same data as preceding, except Rd. 3046, Gum Branch Rd., 25 April 1998 (JBS); 1 ♂, Pender Co., Holly Shelter gamelands, 15-watt UV trap, pine savannah, 26 August 1997, J. B. Sullivan (USNM). SASKATCHEWAN: 1 ♂, Saskatoon, pheromone trap, 1984, Chisoholm (USNM).

DISCUSSION

Specimen and literature records of *E. nearctica* are widely distributed: Kentucky, Michigan, Mississippi, North Carolina, and Saskatchewan. Capture dates from combined localities range from 25 April to 31 August, suggesting one to two generations per year. Larval foodplants are unknown.

It is possible that *E. nearctica* is an immigrant in North America as supposed when it was reported as *E. albersana* (Miller 1983). However, a more straightforward interpretation of the information assembled here is that it is a native American species that escaped previous recognition because of low population densities, sparse collecting, and diminutive size. The species is not known anywhere else than in North America, and collection localities are inland, away from commercial ports where immigrants usually are detected first.

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AN OVERVIEW OF *STRYMON* HÜBNER (LYCAENIDAE: THECLINAE: EUMAEINI)

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ABSTRACT. North American *Strymon* Hübner was revised about 40 years ago, and the significantly larger Neotropical *Strymon* is now incorporated into this classification. *Strymon* is characterized by anteriorly directed teeth on the posterior dorsal surface of the valvae. These teeth were first noted by Clench and appear to be modifications of the sockets of setae that normally occur on eumaeine valvae. This characterization is most consistent with past usage and appears to represent the best evidence for monophyly. As characterized, *Strymon* contains 48 described species. Variation in morphology of the male genitalia, female genitalia, wings, and head is documented, and male behaviors and larval foodplant records are summarized. We tentatively divide *Strymon* into species groups, one of which is unusual in its use of Bromeliaceae as its sole larval foodplant.

One recently described genus, *Heoda* Johnson, L. Miller & Herrera 1992, and one recently resurrected genus, *Eiseliana* Toledo 1978, are made junior synonyms of *Strymon* Hübner 1818. Six names recently described in *Strymon* are transferred to other genera: *Strymon angulus* Le Crom & Johnson, 1997 to *Thereus* Hübner; *Strymon daplissus* Johnson & Salazar, 1993 to *Ministrymon* Clench 1961; *Strymon carmencitae* Le Crom & Johnson, 1997 and *Strymon cryptogramus* Johnson, Eisele & MacPherson, 1992 to *Nicolaea* Johnson; *Strymon nivnix* Johnson, Eisele & MacPherson, 1990 to *Calycopis* Scudder; and *Strymon additionalis* Le Crom & Johnson, 1997 to *Thecla* F. The hindwings of *Strymon nivnix* are designated a lectotype, and *Strymon anthracaetus* Salazar, Vélez, & Johnson, 1997 is regarded as a ***nomen dubium.***

Additional key words: Bromeliaceae, foodplants, territoriality, *Heoda, Eiseliana.*

Strymon Hübner is possibly the best-known New World hairstreak genus (Lycaenidae: Theclinae: Eumaeini). It occurs from Canada to the temperate parts of Chile and Argentina. Some *Strymon* are common and well-known, such as *S. melinus* (Gray Hairstreak), and some are pests on commercial pineapple, such as *S. ziba* (Hewitson), *S. megarus* (Godart), and relatives (Harris 1927, Carter 1934, Fonseca 1934, Zikán 1956, Guagliumi 1965, 1967, D'Araujo e Silva et al. 1967–1968, Beutelspacher 1972, Otero & Marigo 1990). The name *Strymon* has been widely used in North America; the first extensive list of North American *Strymon* species (Barnes & McDunnough 1917) contained about 40 taxa and was followed by similar listings (Barnes & Benjamin 1926, McDunnough 1938, Klots 1951, Dos Passos 1964). Although Ziegler (1960) and Clench (1961) rather drastically changed the characterization of *Strymon*, 14 of the 48 described *Strymon* species currently recognized (Appendix 1) are recorded from North America (Opler & Malikul 1992, Opler & Wright 1999).

"Modern" taxonomic usage of *Strymon* began when the genus was distinguished primarily by genitalic structures (Ziegler 1960, Clench 1961). With increased knowledge of the Neotropical eumaeine fauna, however, it became clear that these characters, as originally proposed, do not delimit *Strymon.* For example, *S. yojoa* (Reakirt) has small anteriorly directed teeth on the dorsal valva tips—a structure mentioned in Clench's generic diagnosis—but lacks a tightly convoluted spiral of the ductus bursae (Fig. 20)—a structure noted in Ziegler's generic characterization. Alternately, *S. serapio* (G. & S.) has the tightly-convoluted spiral (Fig. 25), but also has a double cornutus, not the single acuminate one described by Clench (1961) (Fig. 16). To complicate matters, the subsequently described genera *Eiseliana* Toledo and *Heoda* Johnson, Miller, & Herrera possess some genitalic structures that Ziegler and Clench used to characterize *Strymon.* Finally, six species described in *Strymon* since 1990 possess none of these characters.

The purposes of this paper are to characterize *Strymon*, so that it will be clear which species belong to *Strymon*, and to provide an overview of the comparative morphology and ecology of the genus. Specifically, this paper (1) outlines the nomenclatural history of *Strymon*, (2) suggests that the best structure for distinguishing *Strymon* is the unique morphology of the male genitalia valvae, which was first noted by Clench, (3) describes and illustrates morphological variation within the genus, (4) summarizes information on male behavior, larval foodplant specificity, and habitat, (5) preliminarily partitions *Strymon* species in nine species groups, and (6) transfers six names from *Strymon* to other genera. This work is intended to set the stage for a species revision, including the description of about five new species, mostly from the dry mountains of Peru and southern Ecuador.

MATERIALS AND METHODS

The results in the this paper were based upon a comparison of adult morphology using the 6,000+ specimens of *Strymon* in the National Museum of Natural History (Smithsonian Institution, Washington, DC, USA), of which 3,972 are Neotropical, plus many specimens borrowed from other museums. This comparison employed standard entomological techniques (Robbins 1991), including the examination of the male and female genitalia (449 dissections) of all species currently recognized in *Strymon* (Appendix 1), except that we relied on genitalic figures of two species. For those names that we could not identify from their original descriptions, we examined their types or pictures of the types. For only one species, *Strymon anthracaetus* Salazar, Vélez, & Johnson, could we not identify the name or find its type (explained below). In preparing a checklist of all Neotropical hairstreaks (Robbins in press), RKR examined the adult morphology of virtually all Neotropical species, although not in the same detail as with *Strymon*. All genitalic terms follow those in Klots (1970). All specific author names for *Strymon* are listed in Appendix 1 and thus are omitted from the following text.

Because relationships within the Eumaeini are still poorly known, such as the genera that are most closely related to *Strymon*, we characterize *Strymon* by a complex and conspicuous trait that is unique within the Eumaeini and that is phylogenetically consistent with other traits that are unique within the Eumaeini. We tentatively divide *Strymon* into species group on the basis of many characters, but evidence for their monophyly awaits formal phylogenetic analysis.

NOMENCLATURAL HISTORY

Hübner (1818) described *Strymon* and included two species, *S. melinus* and *Hesperia acaciae* Fabricius. (*Hesperia* currently belongs to the Hesperiidae.) A subsequent list of 13 *Strymon* species (Hübner 1819) caused considerable confusion in the eventual selection of a type species. Scudder (1872) selected *Hesperia titus* F. from the 1819 list as the type (the dates of Hübner's books were uncertain at the time), but Riley (1922) invalidated this selection and replaced it with *Strymon melinus*. Finally, the International Commission on Zoological Nomenclature (1959) placed *Strymon* on the Official List as Name No. 1332 with *Strymon melinus* as type. Hemming (1967) gives a more complete nomenclatural history.

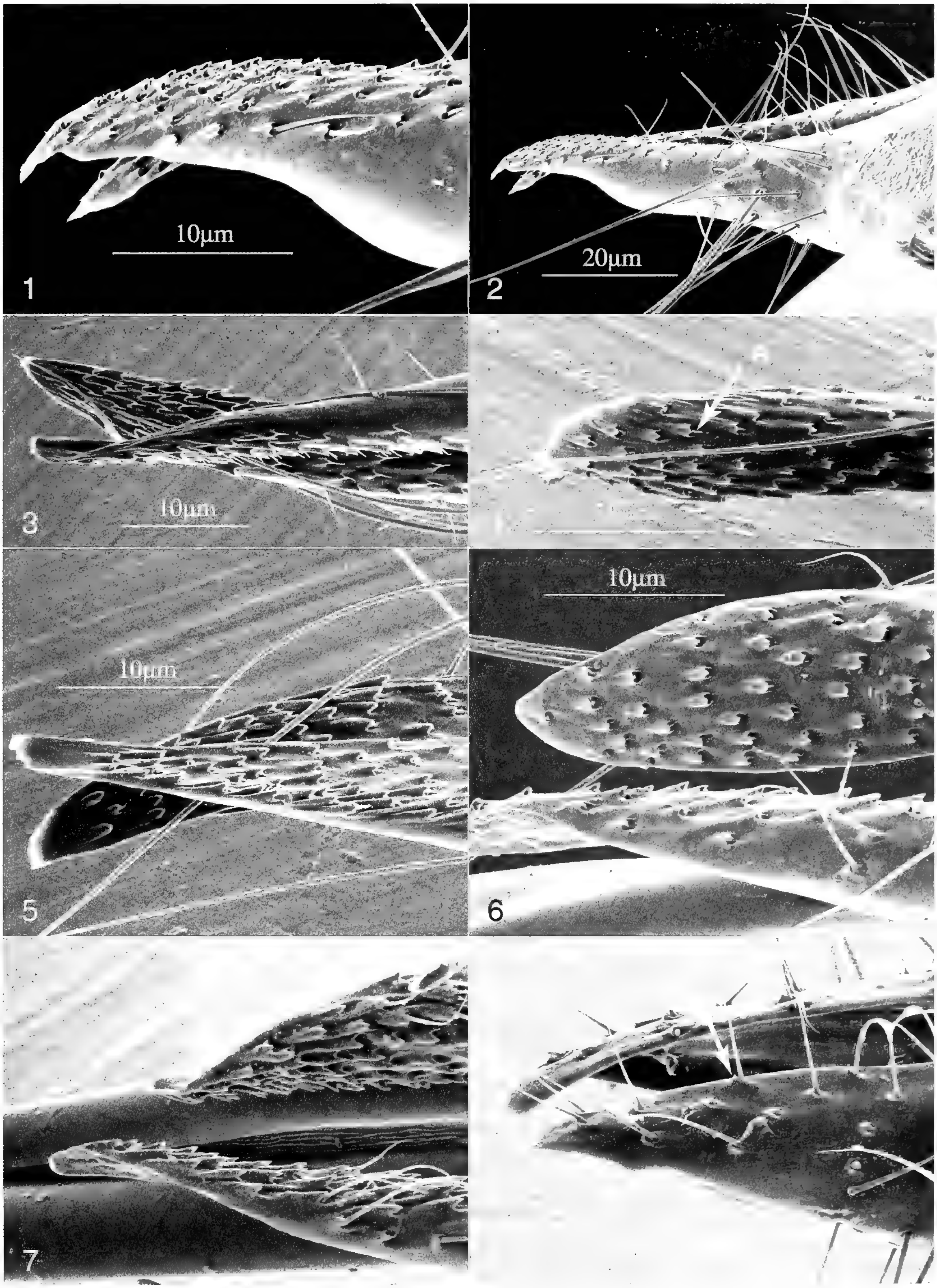
STRYMON HÜBNER

We characterize *Strymon* for the following discussion of comparative morphology by setae on the posterior dorsal surface of the valvae that are modified into anteriorly pointing "teeth" (Clench 1961) (Figs. 1–7). This structure is immediately recognizable; either a species has it or does not. The only exception is *S. ziba* (Fig. 8), whose valva morphology and systematic position are detailed below. Although the valva structure of *Strymon* is most easily illustrated using a scanning electron microscope (SEM), Clench discovered it using a light microscope. Almost all species that have been placed in *Strymon* since 1960 (e.g., Ziegler 1960, Clench 1961, 1964, Johnson et al. 1990, Johnson et al. 1992, Johnson & Kroenlein 1993, Johnson & Salazar 1993, Austin & Johnson 1997) have this valva structure. The only superficially similar valvae in the Eumaeini are those of *Allosmaitia* Clench, whose valvae are needle-like posteriorly, unlike *Strymon*, and covered with teeth that are not anteriorly directed (Clench 1964).

COMPARATIVE MORPHOLOGY

Male genitalia. The setae on the valvae of eumaeine hairstreaks are indistinguishable when viewed with an SEM from those specialized setae that were termed B-type trichoid sensilla (Ma & Schoonhoven 1973). In *Strymon*, these setae are modified. The anteriorly directed teeth on the posterior dorsal surface of the valvae appear to be modifications of the sockets of these setae. Supporting this interpretation, the setal flagellum is still present, but is short (usually less than 1 μm long) (Figs. 1–7). In *S. ziba*, some of the setal sockets on the posterior dorsal valva tips are slightly modified into anteriorly pointing teeth with a flagellum that is not reduced in length (Fig. 8). As discussed below, some evidence suggests that this structure is transitional between that in other eumaeines and in *Strymon* while other evidence suggests that it is a further modification of that which occurs in other *Strymon*.

We illustrate the male genitalia of nine *Strymon* species to show the range of morphological variation (Figs. 9–17). The tips of the gnathos in all *Strymon* species are subterminally expanded and then sharply tapered to a down-curved point (Figs. 9–17), but this structure does not appear to be sufficiently distinct from other eumaeines to distinguish the genus unequivocally. At least one cornutus is present within the shaft of the penis unless the vesica is partially everted (Figs. 12, 14, 15). If there is one cornutus, it is long and slender (slightly wider in *S. maritalis* and *S. christophei*) and sometimes barely sclerotized (*S. yojoa*, Fig. 11). If there are two cornuti, they are usually paired and about the same size (Fig. 16) (first noted and illustrated by Schwartz & Miller 1985). The primary exception is *S. ziba*, which has one cornutus con-



FIGS. 1–8. Scanning electron micrographs (SEMs) of male genitalia valva tips in lateral and dorsal aspects. **1,** *S. melinus* in lateral aspect; **2,** *S. melinus* at lower magnification; **3,** *S. acis*; **4,** *S. eurytulus* in dorsal aspect (Arrow **A** — setal flagellum); **5,** *S. bazochii*; **6,** *S. gabatha*; **7,** *S. megarus*; **8,** and *S. ziba* (Arrow **B** — slightly modified setal socket).

siderably larger than the other (Fig. 17). *Strymon* male genitalia are asymmetrical. For example, the penis is twisted and down turned (Clench 1961) except for *S. ziba* and *S. sylea* (Figs. 10, 17). The saccus is generally asymmetrical to the right (Figs. 9b, 12, 14, in ventral aspect, they are on the left side).

Strymon species have paired brush organs (sensu Eliot 1973) that lie on the dorsal vinculum, but we omit them in the figures for clarity. The vinculum is not modified in structure, as it is in some eumaeines (Robbins 1991), except for slight projections of the vinculum in some species, such as *S. tyleri* and *S. crambusa*. We are unable to distinguish the structure of the brush organs in *Strymon* from those that occur in *Lamprospilus* Hübner, *Electrostrymon* Clench, *Ziegleria* Johnson, and *Calycopis* Scudder. Males of *S. istapa* in one part of its range (Florida to Puerto Rico) may have or lack brush organs (Robbins & Nicolay 1999), and a similar dimorphism also appears to occur in *S. bicolor*.

Other than the variation outlined above, the male genitalia of *Strymon* seem to have few good structures for distinguishing species. For example, the male genitalia of *S. istapa, S. columella, S. limenia,* and *S. toussainti* are essentially indistinguishable except for small differences in size (Robbins & Nicolay 1999) — these species are distinguished by their wing pattern and female genitalia. Except for *S. ziba* and *S. sylea*, few *Strymon* species appear to be authoritatively identifiable solely on the basis of their male genitalic structures.

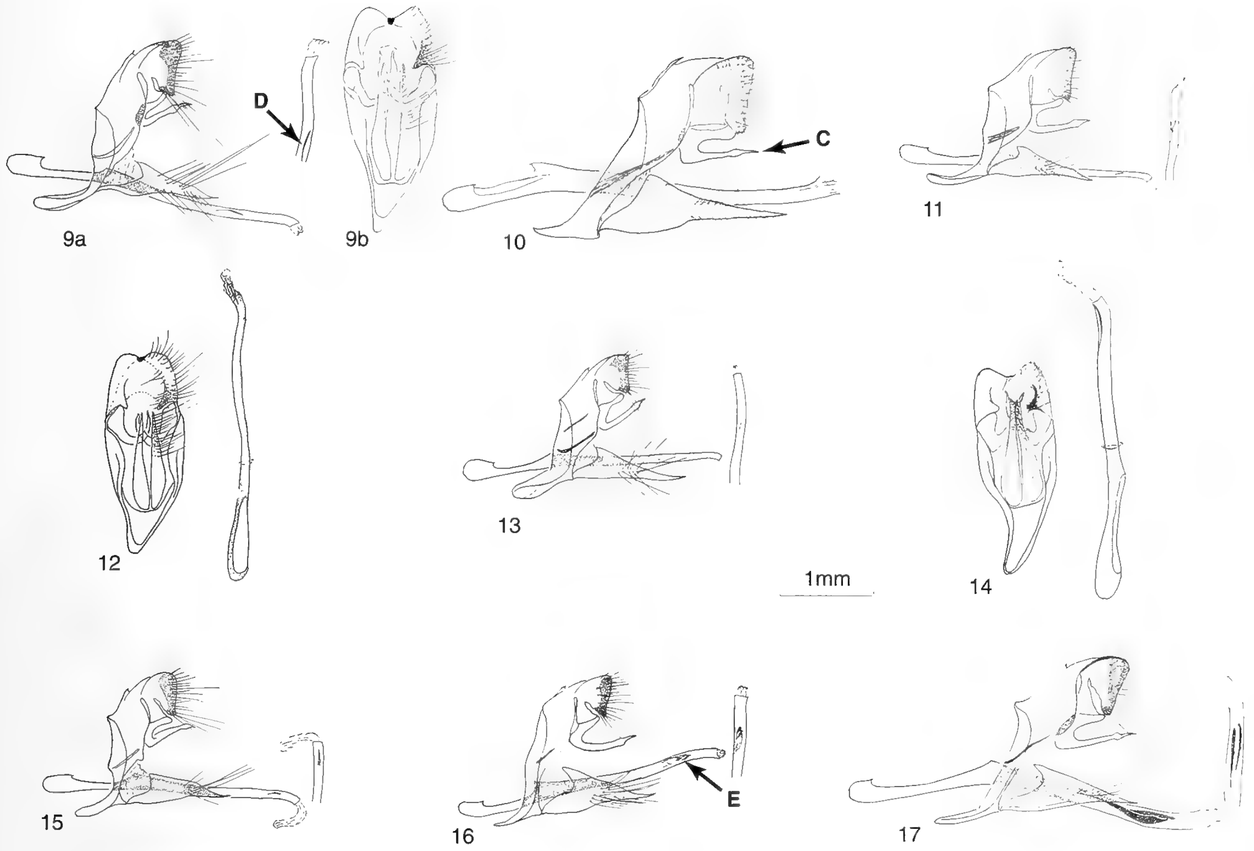
Female genitalia. The bursa copulatrix of *Strymon* is asymmetrical, and we illustrate the range of variation (Figs. 18–26). All eumaeines with a sclerotized, looped ductus bursae belong to *Strymon*, as first noted by Ziegler (1960), but the exact shape of the loop varies greatly interspecifically (Figs. 18–26). It is also highly variable intraspecifically, as in *S. cestri*, where some individuals lack the sclerotized loop of the ductus bursae, some have it, and others are intermediate between these extremes (Figs. 27–29). A few *Strymon* species appear to always lack the loop (*S. yojoa, S. tegea, S. ohausi, S. sylea,* and *S. ziba*), but the ductus bursae is twisted at the point where the loop would otherwise occur except in *S. sylea* (Figs. 19, 20, 23). The signa, which are "boat"-shaped, occur in all *Strymon* species, but may be small in some, such as *S. limenia* (Hewitson) (Fig. 24), and may lack the anterior pointing spine (*S. sylea*, Fig. 19). Similar signa are found on occasion in other eumaeines, such as *Trichonis* Hewitson (Robbins 1987). There are two small teeth inside the anterior ductus bursae (Fig. 18). Similar teeth occur in other eumaeines, such as those illustrated for *Rekoa palegon* (Cramer) (Robbins 1991).

The female 8th abdominal tergum of Eumaeini is sclerotized, the sternum is membranous, and two small circles lacking setae are also membranous (e.g., illustrated by Field 1941). Since spiracles on the 8th abdominal segment of the endoporian Ditrysia, including the butterflies, are absent or vestigial (Dugdale 1974), we presume that these membranous circles are vestigial spiracles. In female *Strymon*, there are two kinds of 8th abdominal segments. The first, of which *S. melinus* is an example (Fig. 30), is like many eumaeines with presumed vestigial spiracles at the juncture between the tergum and sternum. The second, of which *S. bicolor* is an example (Fig. 31), has the presumed vestigial spiracles located within the tergum, whose latero-posterior part has more furrows than the first kind. Johnson et al. (1992) first described the furrowed tergum as "rough" and used it as a distinguishing character of their new genus *Heoda.* However, this structure is difficult to discern and actually occurs in all members of the *S. istapa* group (except for *S. acis*, Appendix 1), including species that Johnson et al. (1992) placed in *Eiseliana* and *Strymon*.

When the ductus seminalis does not arise from the posterior tip of the corpus bursae in *Strymon*, such as *S. limenia*, the tip of the corpus bursae, posterior of the ductus seminalis, is lightly sclerotized (Fig. 24). All *Strymon* species with this structure are a subset of those whose females have an 8th tergum with the latero-posterior surface furrowed and with imbedded presumed vestigial spiracles. The posterior end of the corpus bursae of a few other species, such as *S. ziba, S. martialis*, and *S. christophei*, is also sclerotized (Figs. 23, 26), but this structure appears to be analogous with the structure in *S. limenia* and relatives because the ductus seminalis arises from the posterior tip of the corpus bursae in these species.

Wings. The wing venation of *Strymon* is typical of the Eumaeini with 10 forewing veins (Eliot 1973). A male scent patch (sensu Robbins 1991) occurs on the dorsal surface of the forewing in the distal part of the discal cell of most species, but is lacking in *S. melinus, S. avalona, S. sabinus, S. tyleri, S. rufofusca, S. cyanofusca, S. ohausi, S. christophei, S. oribata,* and *S. legota*. Because these species appear to belong to a number of different species groups, as determined below on the basis of many characters, we suspect multiple losses of the forewing scent patch in *Strymon*.

Wing pattern, shape, and size vary greatly among *Strymon* species (Figs. 34–53), and it is difficult to characterize *Strymon* on the basis of these traits. Generally, the pattern on the ventral wing surface is not sexually dimorphic, but males have more sharply produced forewing apices. Seasonal variation of the ven-



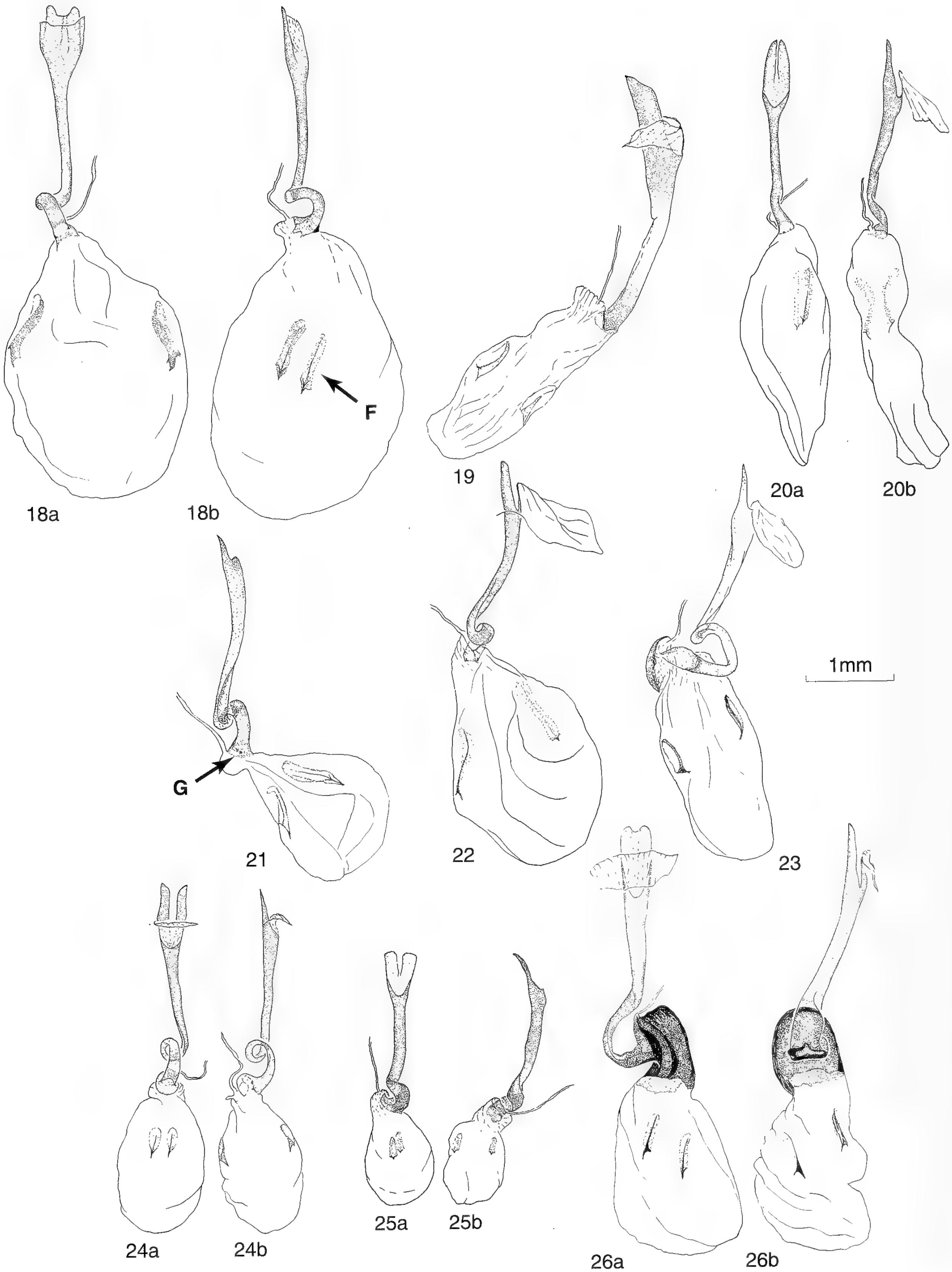
FIGS. 9–17. Male genitalia of *Strymon*; teeth on valvae are inconspicuous at this magnification. **9,** *S. melinus* in lateral (a) and ventral (b) aspects (Arrow **D** — acuminate cornutus); **10,** *S. sylea* (Arrow **C** — tip of gnathos); **11,** *S. yojoa*; **12,** *S. mulucha*; **13,** *S. albata*; **14,** *S. martialis*; **15,** *S. limenia*; **16,** *S. serapio* (Arrow **E** — paired cornuti); and **17,** *S. ziba*.

tral wing surface can be marked in some species, such as *S. melinus*, but virtually absent in others, such as *S. bazochii*. For example, individuals of *S. melinus* are smaller and darker on average in early spring in North America than they are in the middle of summer. The dorsal surface of the forewing of most female *Strymon* has a patch of black scales centered at the end of the discal cell, which is sometimes mistaken for androconia (Figs. 35, 40). Other eumaeines sometimes also have a similar appearing patch of dark scales, such as females of *Tmolus venustus* (Druce). Forewing length varies from more than 2 cm (*S. sylea, S. oreala*, and *S. gabatha*) to less than 0.8 cm (*S. ohausi, S. ochraceus*). And some species, such as *S. gabatha* and *S. serapio*, vary greatly in size intraspecifically, which is perhaps related to their bromeliad larval foodplants (flowers of *Aechmea* and *Tillandsia*, respectively).

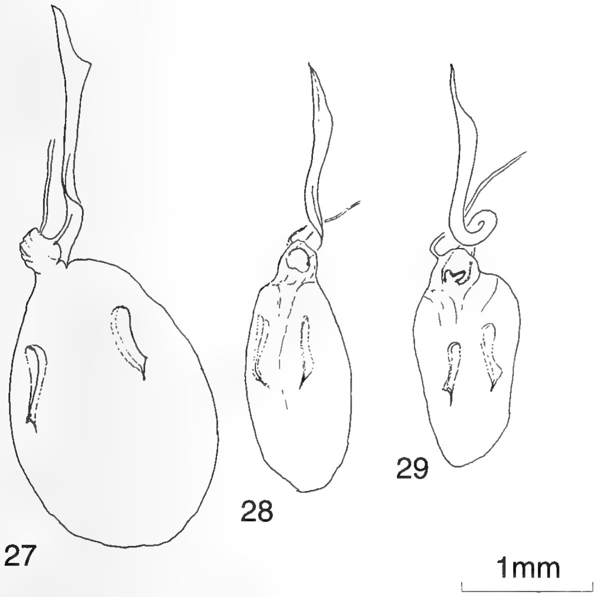
Head. The antennal club of Theclinae, including the Eumaeini, is generally cylindrical and incrassate, but those of most *Strymon* are abrupt and flattened, resembling those of Polyommatinae and Lycaeninae (Eliot 1973). An antenna with an abrupt and flattened club also occurs in a few other eumaeines, such as *Penaincisalia* Johnson. The frons of *S. melinus* is covered with white and orange scales, and there are also orange scales near the base of the antennae. Most other *Strymon* share this head coloration, but a few lack white or orange scales, such as *S. bazochii* (Godart). However, a hairstreak with orange scales near the base of the antennae, an orange-white frons, and an abrupt, flattened antennal club is almost definitely a *Strymon*, which allows field recognition of this genus in most cases.

BEHAVIOR AND ECOLOGY

Male behavior. Male *Strymon* occupy mating territories, usually on hilltops and along forest edges. The males perch in the "territory," fly at other butterflies that enter this area, and then return to a perch very close to the original one unless courtship has ensued (e.g., Powell 1968, Robbins 1978, Alcock 1983, Alcock & O'Neill 1986, 1987, Cordero & Soberón 1990). We



FIGS. 18–26. Female genitalia bursa copulatrix of *Strymon*. **18,** *S. melinus* in ventral (a) and lateral (b) aspects (Arrow **F** — signum); **19,** *S. sylea*; **20,** *S. yojoa* in ventral (a) and lateral (b) aspects; **21,** *S. mulucha* (Arrow **G** — teeth inside ductus bursae); **22,** *S. albata*; **23,** *S. martialis*; **24,** *S. limenia* in ventral (a) and lateral (b) aspects; **25,** *S. serapio* in ventral (a) and lateral (b) aspects; and **26,** *S. ziba* in ventral (a) and lateral (b) aspects.



FIGS. 27–29. Female genitalia variation of the bursa copulatrix of *S. cestri*. **27,** Peru; **28,** Costa Rica; **29,** Mexico.

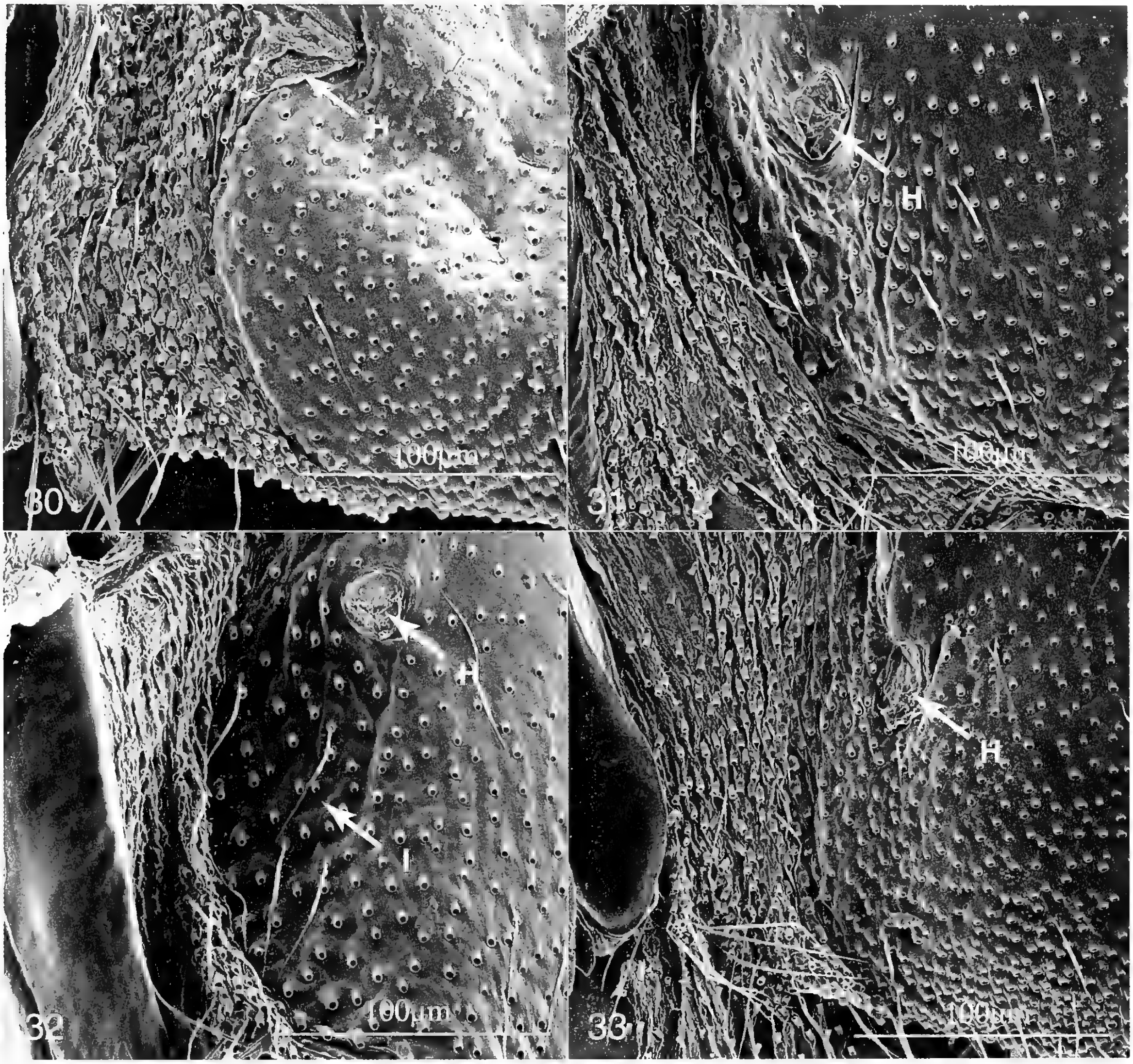
have observed this behavior in the United States, Panama, Venezuela, Ecuador, Peru, and Brazil for 15 *Strymon* species (RKR unpubl.). The males of most species occupy mating territories in the afternoon. A few species do so whenever the weather is favorable (i.e., *S. tyleri*, *S. davara*), and one species only in the early morning (males of *S. serapio* on hilltops in Panama and southern Brazil between 0730 and 1000 hours). The following discussion is based on our unpublished observations.

When male *Strymon* perch in a mating territory, they often open their wings 15–180 degrees, in addition to moving their hindwings back and forth as in all Theclinae (Robbins 1980). We have observed the unusual wing opening behavior (Figs. 54, 55) in *S. melinus, S. mulucha, S. yojoa, S. davara, S. cestri, S. bubastus, S. dindus, S. ochraceus, S. ziba, S. megarus, S. azuba,* and *S. gabatha*. Males of other hairstreak genera generally do not open their wings when perching, but we have observed this behavior in some species of *Tmolus* and *Chlorostrymon.* Another unusual male *Strymon* behavior is perching head downwards on tree-trunks, in addition to perching on leaves. This behavior has been recorded in *S. ziba, S. gabatha, S. ochraceus,* and *S. megarus*. Only once have we seen a male hairstreak of another genus perch on a tree-trunk (*Chalybs janias* [Cramer]).

Larval foodplants. The larvae of *Strymon* eat plants in more than 30 families, ranging from gymnosperms to monocots and dicots, including Alstroemeriaceae, Amaranthaceae, Begoniaceae, Boraginaceae, Bromeliaceae, Cactaceae, Cannabidaceae, Chenopodiaceae, Compositae, Convolvulaceae, Crassulaceae, Euphorbiaceae, Flacourtiaceae, Gesneriaceae, Gramineae, Guttiferae, Haemodoraceae, Juglandaceae, Labiatae, Leguminosae, Malvaceae, Melastomataceae, Musaceae, Orchidaceae, Pinaceae, Polygonaceae, Portulacaceae, Rosaceae, Sapindaceae, Sterculiaceae, Strelitziaceae, Surianaceae, Ulmaceae, and Verbenaceae (RKR unpubl., plant family names follow Willis 1973). Some individual *Strymon* species, such as *S. melinus*, are exceedingly polyphagous (Ehrlich & Raven 1965, Tietz 1972), eating plant reproductive structures in most of these families. Many of these *Strymon* species, though, most frequently feed on plants in the Leguminosae and Malvaceae, and some are recorded as pests of beans and cotton (Ehrlich & Raven 1965).

The only Eumaeini with larvae that eat plants in the Bromeliaceae belong to *Strymon* (RKR unpubl.). Some are serious pests of commercial pineapple (Harris 1927, Carter 1934, Fonseca 1934, Zikán 1956, Guagliumi 1965, 1967, D'Araujo e Silva et al. 1967–1968, Beutelspacher 1972, Otero & Marigo 1990), but the agricultural literature refers to lycaenid pineapple pests as either *Thecla echion* L. (a misidentification of *S. megarus* or *S. ziba*, cf. Honey & Scoble 2001) or *Thecla basalides* (Geyer), a misspelling of *Strymon basilides* (Geyer), which, in turn, is a junior synonym of *S. megarus* (Appendix 1). Consequently, it is unclear exactly how many *Strymon* species feed on pineapples, but there are records for at least four species. The larvae of *S. ziba*, unlike those of the others, eat plants in a number of monocot families in addition to those of the Bromeliaceae (e.g., Harris 1927, Robbins & Aiello 1982).

Habitat and range. Although *Strymon* occur in habitats ranging from tropical wet lowland rainforest to temperate climates, they are most diverse in xeric and seasonally very dry tropical areas, which includes most of the Pacific Coast of Mexico and Central America, northern Colombia and northern Venezuela, the mountains of Peru and southern Ecuador (where there are a number of undescribed species), the llanos of central Venezuela and surrounding countries, and eastern Brazil in the cerrado and caatinga life zones west to the Bolivian chaco. *Strymon melinus* is the only widespread *Strymon* in temperate North America while *S. bicolor* ranges from Peru in the Andes to Chile's temperate central valley (Santiago and surroundings), and *S. eurytulus* occurs from Bolivia and southern Brazil south into Patagonia (Argentina).

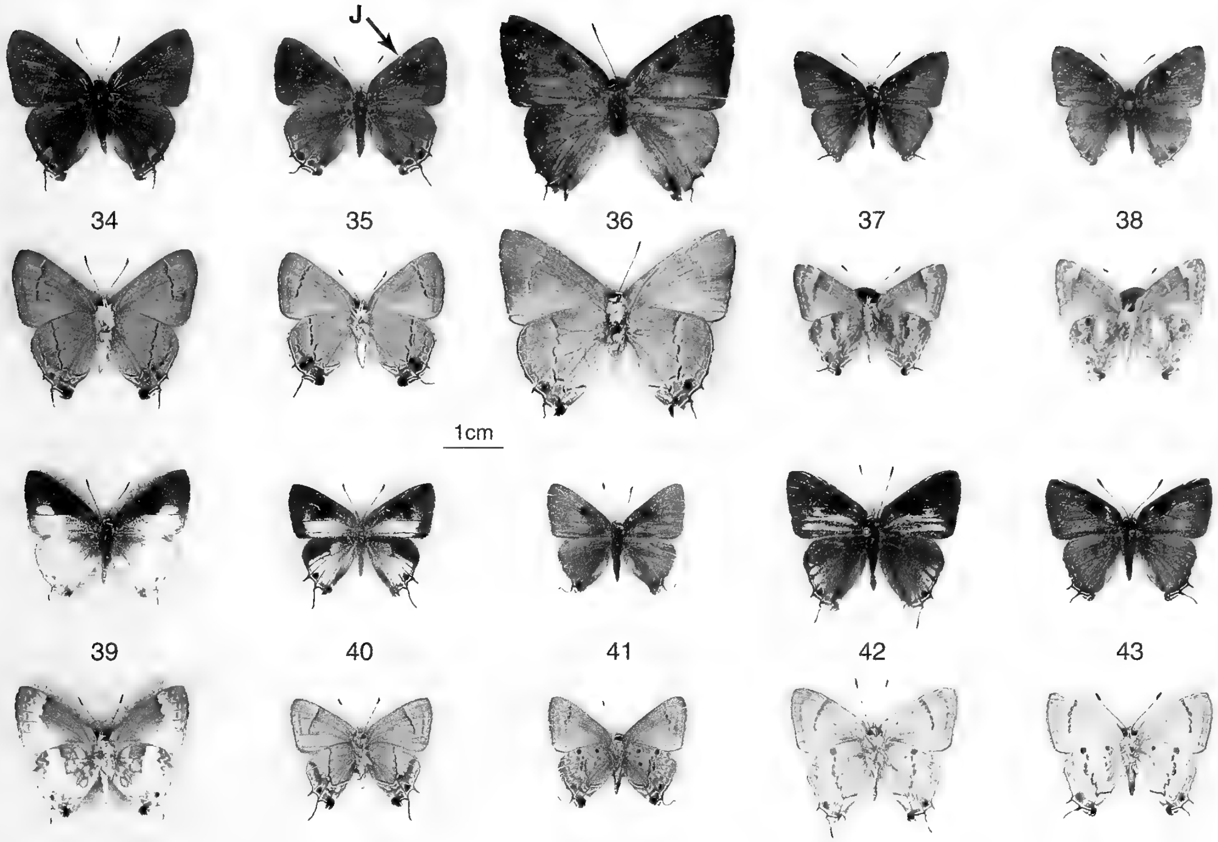


FIGS. 30–33. SEMs of female 8th abdominal tergum in dorso-lateral aspect. **30,** *S. melinus*; **31,** *S. bicolor*; **32,** *S. eurytulus* (Arrow **I** — furrow in tergum); **33,** *S. bazochii*. Arrows **H** — presumed vestigial spiracles.

STRYMON AND ITS SPECIES GROUPS

The monophyly of *Strymon*, as we have characterized it, is supported by a complex and conspicuous valva structure that is unique within the Eumaeini and whose presence or absence is unambiguous except for *S. ziba*. Other characters that are unique, or nearly so, within the Eumaeini are restricted to subsets of *Strymon*, adding further support to our characterization of *Strymon* as a monophyletic genus. All species with a scleortized looped ductus bursae belong to *Strymon*, as do all eumaeines with a ventro-lateral surface of the female 8th abdominal tergum that is furrowed with imbedded presumed vestigial spiracles. Behaviorally and ecologically, almost all eumaeine males that perch with their wings open 15–180° belong to *Strymon* (a behavior that may occur in all *Strymon*), as do all eumaeine males that perch on tree-trunks (one exception noted above), and all species whose larvae eat plants in the Bromeliaceae.

We have divided *Strymon* into nine species groups (listed in Appendix 1) on the basis of many characters, most of which were discussed above. Some of these groups, such as the *S. istapa* and *S. serapio* groups, are reasonably well-characterized while others, such as the *S. mulucha* and *S. albata* groups, lack clear-cut derived distinguishing traits. For example, some characters suggest that *S. cestri* belongs to the *S. yojoa* species group, and others that it belongs to the *S. mulucha* species group. In the following paragraphs we characterize the *S. istapa* and *S. serapio* species groups and discuss the systematic positions of *S. ziba* and *S. sylea*.



FIGS. 34–43. Dorsal and ventral wing surfaces. **34,** male *S. melinus* (New Jersey, USA) (Arrow **J** — patch of black scales on female dorsal forewing); **35,** female *S. melinus* (New Jersey, USA); **36,** male *S. sylea* (Loreto, Peru); **37,** male *S. yojoa* (Panama Prov., Panama); **38,** male *S. mulucha* (Canal Area, Panama); **39,** male *S. albata* (Canal Area, Panama); **40,** female *S. martialis* (Florida, USA); **41,** male *S. limenia* (Santiago, Cuba); **42,** male *S. serapio* (Santa Catarina, Brazil); and **43,** male *S. ziba* (Canal Area, Panama).

We characterize those species with paired cornuti that are about the same size as the *Strymon serapio* group (Appendix 1). All recorded larval foodplants in this group are plants in the Bromeliaceae. In fact, except for *S. ziba*, all neotropical lycaenid larvae that use Bromeliaceae, including all pests of commercial pineapple, belong to this group. Except for *S. ziba* and one observation of a male *Chalybs*, all males that are known to perch on tree-trunks belong to the *S. serapio* group.

We characterize the *Strymon istapa* group as those species with a female 8th abdominal tergum whose ventro-lateral surface is furrowed with imbedded presumed vestigial spiracles (Appendix 1). This tergum structure is otherwise unreported in the Eumaeini. Those species with a lightly sclerotized corpus bursae between the origin of the ductus seminalis and the posterior tip of the corpus bursae are a subset of this group. In all other *Strymon*, the ductus seminalis arises at the posterior tip of the corpus bursae. The inclusion of *S. acis* in this species group is provisional, as explained in Appendix 1.

The systematic position of *S. ziba* is unresolved because of conflicting evidence. On the one hand, *S. ziba* appears to belong to the *S. serapio* group. Both have two cornuti, larvae that eat plants in the Bromeliaceae, and males that perch on tree trunks. The ventral wing pattern and male behavior of *S. ziba* and *S. megarus* are nearly identical, suggesting that they are sisters. If this systematic position is correct, then the unique valva structure of *S. ziba* is a modification of the *Strymon* valva. On the other hand, *S. ziba* appears to be the sister to the remainder of *Strymon*. Evidence supporting this systematic position is that the valva structure of *S. ziba* appears to be intermediate between that of *Strymon* and other eumaeines. And unlike the *S. serapio* group, *S. ziba* has paired cornuti of unequal size, and its larvae eat plants in various monocot families, not just Bromeliaceae. This evidence suggests that *S. ziba* does not belong to the *S. serapio* group. Hanner and Robbins (in prep.) are trying to resolve this conflicting evidence using mitochondrial DNA sequences.

FIGS. 44–45. Males perching with their wings open. **54,** *S. melinus* (California, USA); **55,** *S. megarus* (Veracruz, Mexico).

The systematic position of *S. sylea* is tentative because its penis is upturned and its ductus bursae is straight, unlike virtually all other *Strymon* species. The male genitalia valvae of *S. sylea* possess the unusual basally directed teeth of *Strymon* when viewed with a light microscope. The tips of the gnathos, scent patch, and antennal club of *S. sylea* are consistent with *Strymon*, and we cannot place *S. sylea* in any other eumaeine genus. Because *S. sylea* is an exceedingly rare species in collections, we have not had the opportunity to examine its valvae using an SEM, which would definitively confirm that the valva teeth are indeed the *Strymon* type. The placement of *S. sylea* in *Strymon* appears to be the best option for now.

NOMENCLATURE

Generic synonymy. Using our characterization of *Strymon*, based largely on that of Clench (1961), there are five generic synonyms of *Strymon*, listed with their type species in parentheses. Citations to all original descriptions for this and the following list can be found in Lamas et al. (1995).

Strymon Hübner 1818 (*Rusticus melinus* Hübner)
Callipareus Scudder 1872 (*Strymon melinus* Hübner)
Callicista Grote 1873 (*Callicista ocellifera* Grote)
Uranotes Scudder 1876 (*Strymon melinus* Hübner)
Eiseliana Toledo 1978 (*Eiseliana koehleri* Toledo)
Heoda Johnson, L. Miller & Herrera 1992 (*Thecla heodes* Druce)

Our characterization of *Strymon* appears to be reasonable despite the uncertain systematic position of *S. ziba*. If *S. ziba* belongs to the *S. serapio* group, which is supported by some evidence, then *S. ziba* clearly belongs to *Strymon*. If, on the other hand, *S. ziba* is the sister to the remainder of *Strymon*, which is supported by other evidence, then placing *S. ziba* in *Strymon* avoids naming a monotypic genus for *S. ziba*.

The generic names *Callicista, Eiseliana,* and *Heoda* could be applied to the *S. istapa* species group, but we believe that our characterization of *Strymon* is more reasonable and stable. Recognizing *Callicista, Eiseliana,* or *Heoda* would leave the name *Strymon* for the remainder of species with anteriorly directed teeth on the dorsal valvae, but there is no evidence that this remaining group of species is monophyletic. And if a generic name were also proposed for the *S. serapio* group, there would still be no evidence for the monophyly of *Strymon*. Lastly, our characterization of *Strymon* is consistent with the way that *Strymon* has been used in North America for the last 40 years (Ziegler 1960, Clench 1961).

Species groups. We list the 183 names that belong to *Strymon* as we have characterized it, partitioned into species groups (Appendix 1). We list the characters for each species group, but many characters are homoplastic, and formal phylogenetic analysis is necessary to establish the monophyly of these groups. The original description of *Strymon anthracaetus* Salazar, Vélez, & Johnson, 1997 was too poor to identify this name or to determine whether it belongs to *Strymon*. In August 2000 G. Lamas could not find the type at the museum in Manizales, Colombia, where it was supposed to be deposited. Consequently, we regard *S. anthracaetus* as a ***nomen dubium***.

Names removed from *Strymon*. Many names that were described in *Strymon* do not belong to *Strymon* as we have characterized it. We confirm the previous transfer to other genera (Bridges 1988) of 23 names that were originally described in *Strymon* (Appendix 2).

We transfer the following six species, which were recently described in *Strymon*, to other genera and give brief reasons for the new generic placement. One is transferred to *"Thecla"* because it belongs to a genus that is yet undescribed.

1. *Strymon angulus* (Le Crom & Johnson, 1997) is transferred to *Thereus* Hübner, **new combination.** Robbins (1991, 2000) characterized *Thereus* by a pair of sclerotized invaginations on the membrane attached to the ventro-lateral sides of the papillae anales, a pair of ventro-lateral brush organs in addition to the pair of dorsal ones, and sexual dimorphism in the antennal club (>4 more nudum segments in the female than the male). Although these characters are not mentioned in the original description of *S. angulus*, the illustrated holotype is a male of *Thereus endera* Hewitson, which possesses the three synapomorphies of *Thereus* listed above (Robbins in press).

2. *Strymon daplissus* Johnson & Salazar, 1993 is transferred to *Ministrymon* Clench, **new combination.** The illustrated holotype of *S. daplissus* is a male of *Thecla clytie* Edwards, which Clench (1961) placed in *Ministrymon*.

3. and 4. *Strymon carmencitae* (Le Crom & Johnson, 1997) and *Strymon cryptogramus* (Johnson, Eisele & MacPherson, 1992) are transferred to *Nicolaea* Johnson, **new combinations.** We characterize *Nicolaea* by its male genitalia vinculum, which is strongly curved anteriorly in lateral aspect and which is flattened dorsally in anterior aspect. These characters cannot be seen in the original descriptions, but the illustrated holotypes of *Strymon carmencitae* and *Strymon cryptogramus* are specimens of *Nicolaea fabulla* (Hewitson, 1868) and *N. torris* (Druce, 1907), respectively, which possess the vinculum of *Nicolaea* as described (Robbins in press).

5. *Strymon nivnix* (Johnson, Eisele & MacPherson, 1990) is transferred to *Calycopis* Scudder, **new combination.** The forewings of the holotype of *S. nivnix* belong to a different genus than the hindwings (Robbins in press), which appear to be the slightly aberrant hindwings of *Calcyopis cecrops* F. We designate the hindwings as the lectotype, which is placed in *Calycopis* as characterized by Clench (1961) and Field (1967).

6. *Strymon additionalis* (Le Crom & Johnson, 1997) is transferred to *Thecla* F., **new combination.** The holotype is a male of *"Thecla" emessa* Hewitson, 1867, which is characterized by the form of its scent patch on the dorsal surface of the forewings, a white medial stripe on the frons, and a penis tip with its ventral surface flattened. Because the latter two characters were not illustrated in the original description, our identification is based upon the illustrated wing pattern and scent patch.

ACKNOWLEDGMENTS

We dedicate this paper to the memories of J. B. Ziegler and H. K. Clench, who together modernized the generic taxonomy of North American hairstreaks. For the loan or gift of *Strymon* specimens over the years, we are grateful to P. Ackery, C. Brévignon, C. Callaghan, M. Casagrande, J.-Y. Gallard, J. Glassberg, G. Lamas, J. MacDonald, L. Miller, Jacqueline Miller, James Miller, O. Mielke, J. Rawlins, B. Sullivan, R. Vane-Wright, and J. Weintraub. We thank J. Glassberg for allowing us to use his photographs of perching *Strymon* males. We are grateful to V. Malikul for help with photography, S. Braden with the SEM, and G. Venable with digitization and layout of the figures. For detailed comments on the manuscript, we thank J. Brown, J. Burns, P. Gentili-Poole, J. Glassberg, J. Hall, D. Harvey, G. Lamas, C. Penz, B. Sullivan, and the late B. Ziegler.

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APPENDIX 1. Species groups, their characters, and remarks. Character states in **bold** are especially useful in delimiting that species group. Species synonymies follow Robbins (in press). The subspecies concept was not used in Robbins (in press), so we have designated geographically variable species as Synonyms and Subspecies.

STRYMON MELINUS GROUP. Characters: Male lacking a scent patch on the dorsal surface of the FW, no basal patch of white scales on the ventral surface of the HW (except *S. tyleri*), penis tip down-turned with a single slender cornutus, ductus bursae with simple sclerotized loop, ductus seminalis arises from the unsclerotized posterior end of the corpus bursae, female with 8th tergum unfurrowed and lacking imbedded vestigial spiracles. Remarks: Some members, such as *S. melinus*, *S. tyleri*, and *S. rufofusca*, can be exceedingly common where they occur.

1. *Strymon melinus* (Hübner, 1813)
   SYNONYMS AND SUBSPECIES: *Thecla hyperici* (Boisduval & Leconte, 1835), *Thecla humuli* (Harris, 1841), *Thecla pudica* (H. Edwards, 1877), *Strymon atrofasciata* McDunnough, 1921, *Strymon setonia* McDunnough, 1927, *Strymon meinersi* Gunder, 1927, *Thecla clarionensis* (Heid, 1933), *Strymon youngi* Field, 1936, *Strymon franki* Field, 1938, *Strymon caldasensis* Salazar, Vélez & K. Johnson, 1997
2. *Strymon avalona* (W.G. Wright, 1906)
3. *Strymon tyleri* (Dyar, 1913)
4. *Strymon sabinus* (C. Felder & R. Felder, 1865)
   SYNONYM: *Thecla promissa* (Möschler, 1883)
5. *Strymon rufofusca* (Hewitson, 1877)
   SYNONYMS AND SUBSPECIES: *Thecla (Uranotes) valentina* (Berg, 1896), *Thecla lucaris* (A.G. Weeks, 1901), *Thecla grisea* (Dufrane, 1939), *Thecla nigriplaga* (Dufrane, 1939), *Strymon guanensis* Le Crom & K. Johnson, 1997
6. *Strymon cyanofusca* K. Johnson, Eisele & MacPherson, 1990

STRYMON ALBATA GROUP. Characters: Male with a scent patch on the dorsal surface of the FW, no basal patch of white scales on the ventral surface of the HW (except *S. albata*), penis tip down-turned with a single slender cornutus, ductus bursae with simple sclerotized loop, ductus seminalis arises from the unsclerotized posterior end of the corpus bursae, female with 8th tergum unfurrowed and lacking imbedded vestigial spiracles. Remarks: The only consistent difference with the previous group is that the males have a scent patch.

7. *Strymon albata* (C. Felder & R. Felder, 1865)
   SYNONYM: *Thecla sedecia* (Hewitson, 1874)
8. *Strymon alea* (Godman & Salvin, 1887)
   SYNONYM: *Callicista laceyi* (Barnes & McDunnough, 1910)
9. *Strymon bebrycia* (Hewitson, 1868)
   SYNONYMS: *Thecla chonida* (Hewitson, 1874), *Strymon buchholzi* H.A. Freeman, 1950

STRYMON YOJOA GROUP. Characters: Male with a scent patch on the dorsal surface of the FW (except *S. ohausi*), no basal patch of white scales on the ventral surface of the HW (except *S. yojoa*), penis tip down-turned with a single slender cornutus that is barely sclerotized, **ductus bursae with a twist, but lacking a sclerotized loop,** ductus seminalis arises from the unsclerotized posterior end of the corpus bursae, female with 8th tergum unfurrowed and lacking imbedded vestigial spiracles. Remarks: Johnson et al. (1992) noted that *Thecla tegea* Hewitson does not belong to *Strymon*, but its male genitalia have anterior pointing teeth on the valvae, and its male and female genitalia are exceedingly similar to those of *S. yojoa*.

10. *Strymon yojoa* (Reakirt, 1867)
    SYNONYMS AND SUBSPECIES: *Thecla daraba* (Hewitson, 1867), *Thecla beroea* (Hewitson, 1868)
11. *Strymon tegaea* (Hewitson, 1868)
    SYNONYM: *Thecla seitzi* (Spitz, 1931)
12. *Strymon ohausi* (Spitz, 1933)

STRYMON MULUCHA GROUP. Characters: Male with a scent patch on the dorsal surface of the FW, with basal patch of white scales on the ventral surface of the HW, penis tip down-turned with a single slender cornutus, ductus bursae with simple sclerotized loop (except for some individuals of *S. cestri*), ductus seminalis arises from the unsclerotized posterior end of the corpus bursae, female with 8th tergum unfurrowed and lacking imbedded vestigial spiracles. Remarks: This species group is probably paraphyletic with respect to the previous group.

13. *Strymon mulucha* (Hewitson, 1867)
    SYNONYMS: *Tmolus invisus* (Butler & H. Druce, 1872), *Strymon necjebus* Le Crom & K. Johnson, 1997, *Strymon necjabus* Le Crom & K. Johnson (missp.), 1997, *Strymon novasignum* Austin & K. Johnson, 1997, *Strymon clavus* Austin & K. Johnson, 1997, *Strymon implexus* Austin & K. Johnson, 1997, *Strymon inmirum* Austin & K. Johnson, 1997, *Strymon incanus* Austin & K. Johnson, 1997
14. *Strymon cestri* (Reakirt, 1867)
    SYNONYMS AND SUBSPECIES: *Thecla cydia* (Hewitson, 1874), *Thecla crossoea* (Hewitson, 1874), *Strymon chamiensis* Salazar, Vélez & K.

Johnson, 1997, *Strymon germana* Austin & K. Johnson, 1997

15. *Strymon davara* (Hewitson, 1868)
    SYNONYMS: *Thecla joannisi* (Dufrane, 1939), *Thecla pallida* (Dufrane, 1939)
16. *Strymon crambusa* (Hewitson, 1874)
17. *Strymon astiocha* (Prittwitz, 1865)
    SYNONYMS: *Thecla faunalia* (Hewitson, 1868), *Thecla deborrei* (Capronnier, 1874), *Strymon halos* Austin & K. Johnson, 1997, *Strymon conspergus* Austin & K. Johnson, 1997

STRYMON MARTIALIS GROUP. Characters: Male with or without a scent patch on the dorsal surface of the FW, no basal patch of white scales on the ventral surface of the, penis tip down-turned **with a single "wide" cornutus,** ductus bursae with sclerotized loop complex, especially in *S. martalis* (Fig. 23), **ductus seminalis arises from the posterior end of the corpus bursae which is sclerotized dorsally,** female with 8th tergum unfurrowed and lacking imbedded vestigial spiracles. Remarks: A sister species relationship between the two included species is a new hypothesis, but one that appears to be reasonably strongly supported by the shape of the cornutus and by the sclerotized patch on the corpus bursae. This species group may be more closely related to the *S. melinus* species group than its position here indicates.

18. *Strymon martialis* (Herrich-Schäffer, 1865)
19. *Strymon christophei* (W.P. Comstock & Huntington, 1943)

STRYMON ISTAPA GROUP. Characters: Male with a scent patch on the dorsal surface of the FW (except for *S. oribata*), no basal patch of white scales on the ventral surface of the HW, penis tip down-turned with a single slender cornutus, ductus bursae with sclerotized loop simple except in *S. acis*, ductus seminalis arises either from the unsclerotized posterior end of the corpus bursae or from a point anterior of a sclerotized patch on the dorsal surface of the corpus bursae, **female with 8th tergum furrowed (except in *S. acis*) and with imbedded presumed vestigial spiracles.** Remarks: The inclusion of *S. bazochii* and *S. acis* in this group are new hypotheses. The latter species is included because it has imbedded presumed vestigial spiracles and basal spots on the ventral surface of the HW, which most of the species in this group share. Its inclusion is highly tentative because its female 8th abdominal tergum lacks furrows and the sclerotized loop of its ductus bursae is exceedingly complex, unlike any other *Strymon* species.

20. *Strymon istapa* (Reakirt, 1867)
    SYNONYMS AND SUBSPECIES: *Lycaena modesta* (Maynard, 1873), *Callicista ocellifera* (Grote, 1873), *Thecla cybira* (Hewitson, 1874), *Thecla arecibo* (W.P. Comstock & Huntington, 1943), *Thecla clarionica* (Vázquez, 1958), *Thecla socorroica* (Vázquez, 1958), *Strymon clenchi* Austin & J.F. Emmel, 1998
21. *Strymon bazochii* (Godart, 1824)
    SYNONYMS: *Hyreus thius* (Geyer, 1832), *Thecla agra* (Hewitson, 1868), *hecla infrequens* (A.G. Weeks, 1901), *Strymon gundlachianus* M. Bates, 1935, *Strymon diagonalis* Austin & K. Johnson, 1997
22. *Strymon acis* (Drury, 1773)
    SYNONYMS AND SUBSPECIES: *Papilio mars* (Fabricius, 1776), *Thecla gossei* (W.P. Comstock & Huntington, 1943), *Thecla bartrami* (W.P. Comstock & Huntington, 1943), *Thecla casasi* (W.P. Comstock & Huntington, 1943), *Thecla petioni* (W.P. Comstock & Huntington, 1943), *Strymon armouri* Clench, 1943, *Strymon leucosticha* Clench, 1992
23. *Strymon columella* (Fabricius, 1793)
    SYNONYMS: *Papilio dion* (Schaller, 1788), *Tmolus erytalus* (Butler, 1870), *Thecla antigua* (W.P. Comstock & Huntington, 1943)
24. *Strymon limenia* (Hewitson, 1868)
25. *Strymon toussainti* (W.P. Comstock & Huntington, 1943)
    SYNONYMS: *Strymon andrewi* K. Johnson & Matusik, 1988, *Strymon rhaptos* K. Johnson, Eisele & MacPherson, 1990, *Strymon amonensis* D.S. Smith, K. Johnson, J.Y. Miller & McKenzie, 1991
26. *Strymon bubastus* (Stoll, 1780)
    SYNONYMS AND SUBSPECIES: *Papilio minereus* (Fabricius, 1787), *Thecla salona* (Hewitson, 1868), *Thecla sapota* (Hewitson, 1877), *Thecla peruensis* (Dufrane, 1939), *Thecla ponce* (W.P. Comstock & Huntington, 1943), *Strymon vividus* Le Crom & K. Johnson, 1997
27. *Strymon eurytulus* (Hübner, 1819)
    SYNONYMS AND SUBSPECIES: *Thecla americensis* (Blanchard, 1852), *Thecla argona* (Hewitson, 1874), *Thecla rana* (Schaus, 1902, *Thecla tucumana* (H.H. Druce, 1907), *Thecla nigra* (Lathy, 1926), *Strymon peristictos* K. Johnson, Eisele & MacPherson, 1990, *Heoda nivea* (K. Johnson, L.D. Miller & Herrera, 1992)
28. *Strymon flavaria* (Ureta, 1956)
    SYNONYM: *Heoda erani* (Benyamini & K. Johnson, 1996)
29. *Strymon ollantaitamba* (K. Johnson, L.D. Miller & Herrera, 1992)

30. *Strymon colombiana* (K. Johnson, L.D. Miller & Herrera, 1992)
    SYNONYM: *Heoda lecromi* (K. Johnson & Lugo, 1997)
31. *Strymon bicolor* (Philippi, 1859)
    SYNONYMS AND SUBSPECIES: *Thecla quadrimaculata* (Hewitson, 1874), *Thecla heodes* (H. H. Druce, 1909), *Thecla leptocosma* (Hayward, 1949), *Thecla tricolor* (Ureta, 1949), *Heoda atacama* (K. Johnson & L.D. Miller, 1992), *Eiseliana probabila* (K. Johnson, L.D. Miller & Herrera, 1992), *Heoda suprema* (K. Johnson, L.D. Miller & Herrera, 1992), *Heoda shapiroi* (K. Johnson, L.D. Miller & Herrera, 1992)
32. *Strymon wagenknechti* (Ureta, 1947)
33. *Strymon oribata* (Weymer, 1890)
    SYNONYMS AND SUBSPECIES: *Thecla arenicola* (Jörgensen, 1934), *Thecla punona* (Clench, 1944), *Thecla rojasi* (Ureta, 1956), *Eiseliana koehleri* (Toledo, 1978), *Eiseliana patagoniensis* (K. Johnson, L.D. Miller & Herrera, 1992)

STRYMON SYLEA GROUP. Characters: Male with a scent patch on the dorsal surface of the FW, no basal markings on the ventral surface of the HW, penis tip up-turned with a single slender cornutus, ductus bursae straight without a loop or twist, ductus seminalis arises either from the unsclerotized posterior end of the corpus bursae, female with 8th tergum unfurrowed and lacking imbedded vestigial spiracles. Remarks: The upturned penis tip and straight ductus bursae, which is like most Eumaeini other than *Strymon*, suggest that the single species in this group may be sister to the remainder of the genus.

34. *Strymon sylea* (Hewitson, 1867)

STRYMON SERAPIO GROUP. Characters: Male with a scent patch on the dorsal surface of the FW, no basal patch of white scales on the ventral surface of the HW, penis tip down-turned **with paired cornuti,** ductus bursae with simple sclerotized loop, ductus seminalis arises from the unsclerotized posterior end of the corpus bursae, female with 8th tergum unfurrowed and lacking imbedded vestigial spiracles. Remarks: All larval foodplant records in this groups are Bromeliaceae, as noted.

35. *Strymon serapio* (Godman & Salvin, 1887)
    SYNONYMS AND SUBSPECIES: *Thecla lemnos* (H.H. Druce, 1890), *Thecla mesca* (Dyar, 1914), *Thecla inconspicua* (Lathy, 1930), *Strymon golbachi* K. Johnson, Eisele & MacPherson, 1990, *Strymon trunctogen* K. Johnson & Salazar, 1993, *Strymon altamiraensis* K. Johnson & Kroenlein, 1993, *Strymon henaoi* Salazar, Vélez & K. Johnson, 1997, *Strymon hurtadoi* K. Johnson, 1997, *Strymon rosari* Torres & K. Johnson, 1997, *Strymon originatus* K. Johnson, Hernández & Cock, 1997
36. *Strymon glorissima* K. Johnson & Salazar, 1993
    SYNONYM: *Strymon campbelli* K. Johnson & Salazar, 1993
37. *Strymon gabatha* (Hewitson, 1870)
    SYNONYMS: *Thecla balius* (Godman & Salvin, 1887), *Strymon alexandra* K. Johnson & Kroenlein, 1993, *Strymon alicia* Salazar, Vélez & K. Johnson, 1997
38. *Strymon monopeteinus* Schwartz & J.Y. Miller, 1985
39. *Strymon veterator* (H.H. Druce, 1907)
    SYNONYMS: *Strymon lorrainea* K. Johnson, Eisele & MacPherson, 1990, *Strymon coronos* K. Johnson, Eisele & MacPherson, 1990
40. *Strymon oreala* (Hewitson, 1868)
41. *Strymon dindus* (Fabricius, 1793)
42. *Strymon ochraceus* K. Johnson & Salazar, 1993
    SYNONYM: *Strymon baricharensis* Le Crom & K. Johnson, 1997
43. *Strymon lucena* (Hewitson, 1868)
    SYNONYMS: *Thecla cardus* (Hewitson, 1874), *Thecla canitus* (H.H. Druce, 1907), *Strymon specialus* K. Johnson, Eisele & MacPherson, 1997
44. *Strymon legota* (Hewitson, 1877)
45. *Strymon azuba* (Hewitson, 1874)
    SYNONYMS: *Strymon montevagus* K. Johnson, Eisele & MacPherson, 1990, *Strymon rojos* K. Johnson & Kroenlein, 1993
46. *Strymon eremica* (Hayward, 1949)
    SYNONYMS AND SUBSPECIES: *Strymon lariyojoa* K. Johnson, Eisele & MacPherson, 1990, *Strymon barbara* K. Johnson, Eisele & MacPherson, 1990, *Strymon nicolayi* K. Johnson, Eisele & MacPherson, 1990
47. *Strymon megarus* (Godart, 1824)
    SYNONYMS AND SUBSPECIES: *Tmolus basilides* (Geyer, 1837), *Thecla basalides* (W.F. Kirby, 1871) (missp.), *Thecla tigonia* (Schaus, 1902), *Strymon amphyporphyra* K. Johnson, Eisele & MacPherson, 1990, *Strymon rotundum* Austin & K. Johnson, 1997, *Strymon gallardi* Faynel & K. Johnson, 2000

STRYMON ZIBA GROUP. Characters: Male with a scent patch on the dorsal surface of the FW, no basal patch of white scales on the ventral surface of the HW, penis tip up-turned with two large unpaired cornuti, ductus bursae slightly twisted without a sclerotized loop, ductus seminalis arises from the sclerotized posterior end of the corpus bursae, female with 8th tergum unfurrowed and lacking imbedded vestigial spiracles. Remarks: The single included species is widespread and common. It is the only *Strymon* lacking the clear-cut anterior pointing teeth on the valvae.

48. *Strymon ziba* (Hewitson, 1868)
    SYNONYMS AND SUBSPECIES: *Thecla thulia* (Hewitson, 1868), *Thecla diaguita* (Hayward, 1949), *Strymon baptistorum* K. Johnson, Eisele & MacPherson, 1990, *Strymon dondiego* K. Johnson & Adams, 1997, *Strymon profusorubrus* Le Crom & K. Johnson, 1997, *Strymon lecromi* K. Johnson, 1997, *Strymon spinatus* Austin & K. Johnson, 1997, *Strymon latamaculus* Austin & K. Johnson, 1997, *Strymon pallidulus* Austin & K. Johnson, 1997, *Strymon tholus* Austin & K. Johnson, 1997

APPENDIX 2. Alphabetical list of specific names that were originally described in *Strymon* and that have been transferred to other genera (Bridges 1988). For those names that are junior synonyms, we note its senior synonym.

1. *Cyanophrys agricolor* (Butler & Druce, 1872)

2. *Satyrium aliparops* (Michener & dos Passos, 1942), a junior synonym of *Satyrium liparops* (Leconte)

3. *Satyrium borealis* (Lafontaine, 1969), a junior synonym of *Satyrium calanus* (Hübner)

4. *Satyrium caryaevorus* (McDunnough, 1942)

5. *Satyrium chlorophora* (Watson & Comstock, 1920), a junior synonym of *Satyrium saepium* (Boisduval)

6. *Lamprospilus coelicolor* (Butler & Druce, 1872)

7. *Satyrium coolinensis* (Watson & Comstock, 1920), a junior synonym of *Satyrium acadica* (Edwards)

8. *Satyrium desertorum* (Grinnell, 1917), a junior synonym of *Satyrium sylvinus* (Boisduval)

9. *Electrostrymon dowi* (Clench, 1941), a junior synonym of *Electrostrymon angelia* (Hewitson)

10. *Satyrium fletcheri* (Michener & dos Passos, 1942), a junior synonym of *Satyrium liparops* (Leconte)

11. *Satyrium godarti* (Field, 1938), a junior synonym of *Satyrium calanus* (Hübner)

12. *Calycopis gottschalki* (Clark & Clark, 1938), a junior synonym of *Calycopis cecrops* (Fabricius)

13. *Satyrium immaculosus* (Comstock, 1913), a junior synonym of *Satyrium titus* (Fabricius)

14. *Satyrium kingi* (Klots & Clench, 1952)

15. *Satyrium montanensis* (Watson & Comstock, 1920), a junior synonym of *Satyrium acadica* (Edwards)

16. *Satyrium muskoka* (Watson & Comstock, 1920), a junior synonym of *Satyrium acadica* (Edwards)

17. *Satyrium okanagana* (McDunnough, 1944), a junior synonym of *Satyrium saepium* (Boisduval)

18. *Cyanophrys pastor* (Butler & Druce, 1872), a junior synonym of *Cyanophrys longula* (Hewitson)

19. *Satyrium polingi* (Barnes & Benjamin, 1926)

20. *Satyrium provo* (Watson & Comstock, 1920), a junior synonym of *Satyrium saepium* (Boisduval)

21. *Satyrium swetti* (Watson & Comstock, 1920), a junior synonym of *Satyrium acadica* (Edwards)

22. *Satyrium violae* (Stallings & Turner, 1947), a junior synonym of *Satyrium favonius* (Smith)

23. *Satyrium watsoni* (Barnes & Benjamin, 1926), a junior synonym of *Satyrium titus* (Fabricius)

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LEPIDOPTERISTS' PERCEPTIONS OF A PROPOSED PERMITTING SYSTEM FOR BUTTERFLY COLLECTING ON PUBLIC LANDS

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ABSTRACT. There has been widespread and often rancorous discussion of the need for and desirability of regulation of insect collecting on public lands in the United States. In order to gauge the potential success and utility of a model "No-Fee Permitting System" (NFPS) for butterfly collecting, an anonymous survey was sent to all of the members of the Lepidopterists' Society in northern California, Oregon, and Washington in the spring of 1998. Over 52% of the surveys were returned. While many respondents feel they would use the system honestly, few of the respondents felt other lepidopterists would do so. Correlation analysis between the ranked questions using the Gamma statistic shows that those respondents who collect most often believe the NFPS would not be a useful tool for making management decisions. Likewise, the most frequent collectors are least likely to utilize the NFPS and have a tendency to believe the NFPS would worsen the relationship between collectors and government agencies. Respondents were invited to comment on the questions. The most widely discussed themes included: (1) 36% of the respondents felt the permit would be a nuisance and too difficult to fill out prior to the collection activity; (2) 27% felt the permit was a good idea and was worth trying; (3) 44% expressed a general mistrust of governmental regulation; and (4) 29% felt the permitting strategy is an improper conservation focus. The combination of the quantitative and qualitative responses demonstrates that the NFPS would not be used widely enough for it to be a worthwhile management tool. The relationship between collectors and federal agencies is laden with mutual mistrust, and the installation of a NFPS would only apparently amplify the tension between these two groups of people. We recommend that any future regulation be developed in an atmosphere of consultation and open communication.

Additional key words: conservation, land management, The Lepidopterists' Society, U.S. National Forests.

Garry Wills (1999) recently published A Necessary Evil: A History of American Distrust of Government, a book that shows that resistance to authority is truly "as American as apple pie." Such resistance is, moreover, closely tied to a characteristic animus against "cosmopolitanism" and "expertise" — a finding which should not surprise readers of Richard Hofstadter's classic Anti-Intellectualism in American Life (1963). These forces in the American polity have recently come into play in an unlikely arena — government regulation of butterfly collecting on federal lands.

The publication of Stainton's (1857) Manual of British Butterflies and Moths in the mid 19th century may mark the beginning of butterfly collection as a hobby popular with common people as well as the aristocracy. This manual was the first affordable, yet accurate guide to butterflies in Great Britain (Kirby 1903). By the late 1800's, butterfly collecting was common in the United States, and several popular manuals were in circulation (Edwards 1879, Maynard 1891, Scudder 1893, Holland 1898). The Lepidopterists' Society was founded in 1947. According to the 1996 Statement on Collecting Lepidoptera, the Society supports collection as "one of many legitimate activities enabling professional and avocational lepidopterists to further the scientifically sound and progressive study of Lepidoptera and education about Lepidoptera as well as encouraging interaction between professional and avocational lepidopterists" (Executive Committee of the Lepidopterists' Society 1996).

In 1965 Frederick H. Rindge, in his presidential address to the Twelfth Annual Meeting of the Pacific Slope Section of the Lepidopterists' Society, expressed the urgent need for butterfly collections as a tool for future conservation work (Rindge 1965). Today, most lepidopterists agree that loss and modification of habitat have caused reductions in butterfly diversity and abundance. Yet the role of butterfly collecting in this scenario is not well defined. Collecting may be viewed as either a source of distribution and abundance data critical for future work, or as a factor in the loss of diversity due to potential over-collection of sensitive species.

Recently butterfly collection has been a focus of controversy among lepidopterists, academics, federal and state agency employees, and conservationists. This controversy has received a fair amount of publicity in public media. In 1996 two articles describing federal prosecution of lepidopterists involved in illegal collection activities appeared in popular recreation magazines, Audubon (Williams 1996) and Outside (Alexander 1996). Among lepidopterists, the controversy boiled over in a heated exchange filling much of the April 1996 News of The Lepidopterists' Society, playfully nicknamed "The Collecting Issue." A variety of ideas and attitudes towards butterfly collecting were addressed. Most hailed the activity as an honorable pastime providing much-needed distributional data (Kral 1996, Sun 1996), while Jeffrey Glassberg (1996) highlighted the importance of "non-consumptive" butterfly enjoyment, such as photography and sight-identification.

The issue of butterfly collection is especially pertinent for federal land managers. For example, in southwestern Oregon — an area known for its high butterfly diversity — butterfly enthusiasts may conduct the majority of their activities on National Forest lands. Currently, the United States Forest Service does not require permits for the non-commercial collection of insects on such lands, but retains the right to regulate collecting administratively (Joslin 1998). On the Rogue River National Forest in Oregon two areas have been designated as "closed" to the collection of butterflies since 1990 [Title 36 Coded Federal Regulation 261.53(a)], including Dutchman's Peak and Observation Peak. This closure was based on anecdotal evidence of decline of the Small Apollo, *Parnassius phoebus sternitzkyi*. Forest Service biologists observed heavy collecting of *P. p. sternitzkyi* in previous years and had concerns about the extreme environmental conditions of the mountain peaks inhabited by the subspecies (B. Mumblo pers. com.).

There has been no study specifically addressing the effects of collection on population dynamics. In 1964 and 1965 heavy predation pressure was artificially applied to the Jasper Ridge Colony of *Euphydryas editha* without significant decreases in population sizes in 1965 and 1966 (Ehrlich et al. 1975). Yet, in this example of intended overcollection the authors concede that they were unable to remove more than 5 to 25% of the females from the population. Since the population structure and viability of each species is likely to vary, individual examples will not provide blanket answers for butterflies as a whole. Due to the lack of clear scientific guidance, conservationists and land managers alike usually have taken a conservative stance, thereby increasing the amount of regulation of butterfly collection. For example, the National Park Service has limited butterfly collection strictly to research purposes (Code of Federal Regulations, Title 36, Part 2, Section 2.5). Some lepidopterists shared with us their belief that information on species abundance and distribution within state and national parks has declined because amateur butterfly collectors can no longer monitor the changes in these parks. It is thus claimed on the one hand that over-regulation can stimulate the withdrawal of potential data sources, while under-regulation may allow the over-collection of sensitive butterfly species.

In the spring of 1998, on our own initiative but with the approval of biologists from the Rogue River National Forest, we attempted to design a permitting system that would be acceptable to lepidopterists and useful to forest managers. In an age when conservation is essential, it is crucial for managers to maintain the most up-to-date information on at least the most sensitive species within their domain. An effective permitting system for butterfly collection might assist in this daunting task by providing information on one particularly charismatic group of organisms. But what would such a system be like?

The development of this permitting system would itself be an experiment. Instead of creating it by fiat "from above," we approached this policy issue in a more inclusive manner. As described below, the proposed permitting system was "floated" with lepidopterists in the Pacific Northwest as a sort of trial balloon to determine its reception and potential utility.

MATERIALS AND METHODS

Creation of the permitting system. The "No-Fee Permitting System" (henceforth NFPS) was purposefully designed as a "user-friendly" means for butterfly collection within the bounds of forest service land. The procedure for using the NFPS was described in general terms in the belief that excess detail would merely distract from the aims of the system. It would work as follows: Upon arrival, a collector would voluntarily fill out a two-copy form detailing the date, location, the species desired and the quantity to be taken. One copy of the form would automatically serve as a free permit and would be retained by the collector. The second copy would be deposited in a drop box on-site, and provide the agency with information about which locations and species experience the most collection pressure.

Survey of the members of The Lepidopterists' Society. All of the members of The Lepidopterists' Society in northern California, Oregon, and Washington were surveyed. They were asked whether they would use the NFPS and their opinion of it as a management and conservation tool. Northern California was arbitrarily defined as any location north of Sacramento, California. All 86 members of the society in the defined region as of 1997 were mailed a packet containing a cover letter, survey, and a pre-addressed, stamped envelope in which to return their responses. The cover letter was designed to establish a disinterested position on the issue, detail the procedure for using the NFPS, and assure the respondent of anonymity (Appendix 1). The survey was made up of eight questions and the majority of the answers were rankings from one to five for particular, scaled responses (Appendix 2). The questionnaires were not coded in any way for individual tracking and were separated from their envelopes so that postmarks could not be used to identify respondents. A few respondents elected to in-

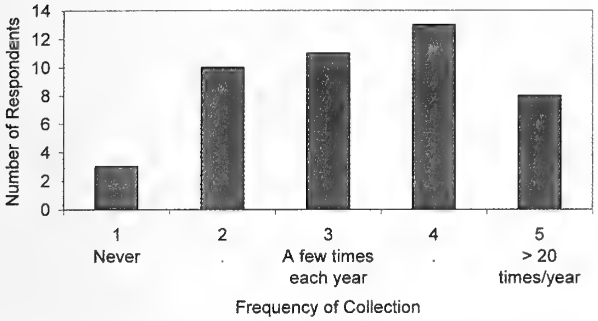

FIG. 1. Distribution of the survey responses to the first question, "How often do you collect butterflies?"

clude signed comments, sometimes quite lengthy, but none is identified in this paper.

Analysis of the survey response data. The responses to the quantitative rank questions were graphed in order to detect trends in the replies. Since the responses to the survey questions were ordered categories it was necessary to use nonparametric statistics for the correlation analysis. The Gamma Statistic (Siegel & Castellan 1988) was used to measure correlations between the responses of the different ranked questions. The Gamma statistic is most appropriate for calculating correlations with non-continuous data and, similarly to other correlation statistics, it produces results ranging from –1 to 1. A Gamma statistic close to 1 indicates a positive relationship between the responses of two different survey questions, while Gamma statistics approaching –1 indicate negative relationships between the responses.

All of the comments from the qualitative questions were compiled into individual documents and these responses were read and evaluated separately. The responses to each question were reviewed several times and "themes" that appeared in more than one answer were labeled and tallied. Once this exercise was completed it was evident that there was a significant amount of overlap in the responses to questions 4, 7, and 8. Thus, the responses to the three questions were combined for the most frequent themes and the total number of respondents expressing each particular theme was recorded. Each survey reply was given an identification number after being separated from its envelope to avoid double-counting sentiments expressed twice by the same respondent.

RESULTS

Quantitative survey questions. The responses to the survey were collected during the summer of 1998. Overall, 45 surveys were received, yielding a return rate of 52.3%. Responses to question 1 (Fig. 1), "How often do you collect butterflies?" demonstrate the presence of a wide variety of lepidopterists in our population, from those who collect quite frequently to others who do not collect at all. The second question, on the reasons for butterfly collection (Fig. 2), clearly points towards "personal collection" as the most widely cited rationale. "Museum collection," "enjoyment," and "research" all follow closely behind "personal collection" as reasons for butterfly collecting. Not a single respondent claimed to be collecting for "profit," and only a few respondents said they collect for "exchange" purposes.

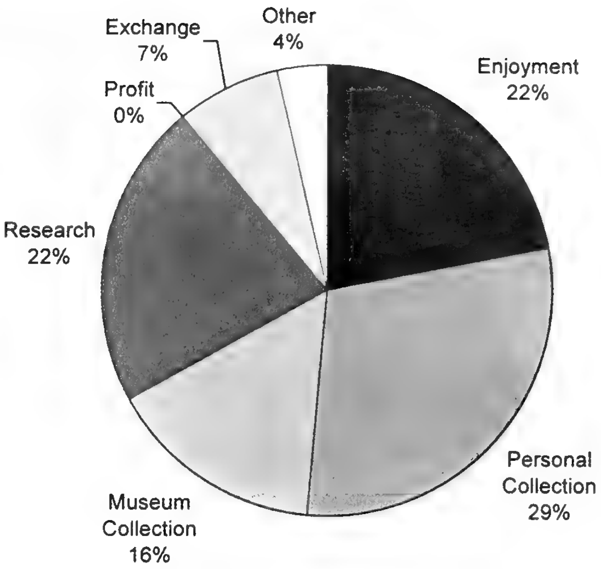

FIG. 2. The relative frequencies of the given responses to the second survey question, "Why do you collect butterflies?"

Question 3 asked respondents, "If you decided to collect butterflies and you went to a location that implemented a voluntary "No-Fee Permitting System" as described in the letter, (a) would you use it; (b) would you fill it out candidly and accurately; (c) do you think other collectors would use it; (d) do you think other collectors would fill it out candidly and accurately?" While many respondents claimed they would use the NFPS "every time" and would do so candidly and accurately "every time," they did not hold the same expectations of compliance for their fellow lepidopterists. The most popular response for questions 3A and 3B is 5, signifying "every time" (Fig. 3). Notably, this majority shifts to 3, signifying "sometimes," for questions 3C and 3D (Fig. 4): in other words, many respondents consider themselves better conservationists or more ethical than lepidopterists in general.

When asked in question 5, "Do you think the NFPS would be a useful tool for making management deci-

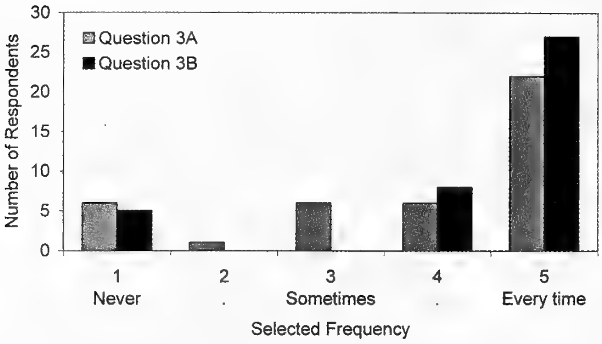

FIG. 3. Distribution of the survey responses to questions 3A and 3B. These questions asked, "If you decided to collect butterflies and you went to a facility or location that implemented a voluntary 'No-Fee Permitting System' as described in the letter, (3A) would you use it?" and (3B) "Would you fill it out CANDIDLY and ACCURATELY?"

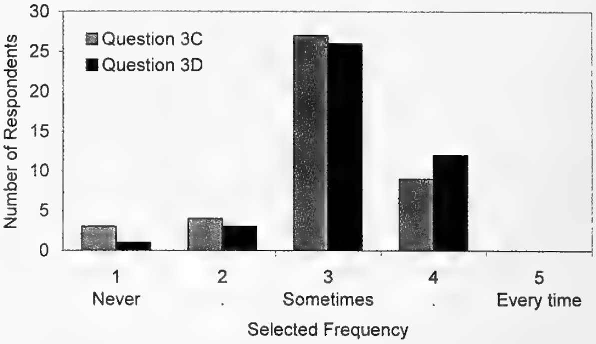

FIG. 4. Distribution of the survey responses to questions 3C and 3D. These questions asked, "If other butterfly collectors went to a facility or location that implemented a voluntary 'No-Fee Permitting System' as described in the letter, (3C) do you think they would use it?" and (3D) "Do you think they would fill it out CANDIDLY and ACCURATELY?"

sions about butterfly collecting?" the responses were extremely scattered. Almost an equal number of respondents circled "yes" as "no," and the majority of respondents answered "maybe." However, the responses to question 6 were more revealing. Over 20 respondents who answered the question, "How do you think the NFPS would affect relations between collectors and government agencies?" felt it would worsen the relationship (either a 4 or 5), while only ten respondents felt the NFPS would improve it (either a 1 or 2).

While the raw data are interesting to examine, the correlations between responses to particular questions reveal some of the most intriguing patterns in these data (Table 1). It is clear that the respondents who claim they would use the NFPS also express the likelihood of using it candidly and accurately ($p < 0.0001$). Likewise, those who felt other lepidopterists would use the NFPS also tended to think they would use it candidly and accurately ($p = 0.0005$). Since the responses to 3A and 3B are so tightly linked to each other, the additional correlations are only tested using comparisons with 3A with the understanding that a correlation with 3A indicates a similar level of correlation with 3B. This reasoning is also used for correlations with 3C and 3D.

Several interesting trends emerge from the correlation data. While not all of the trends produce results with statistical significance, the correlations mentioned here indicate potentially important relationships between survey responses. These trends include: (1) The respondents who collect butterflies the most frequently tend to be the ones who would not utilize the NFPS ($G = -0.35$, $p = 0.11$) and believe others would not use the permit either ($G = -0.26$, $p = 0.21$). (2) The respondents who collect butterflies the least are the ones who believe most strongly that the NFPS is a useful tool for making management decisions about butterfly collecting, while the most frequent collectors tend to hold the opposite opinion ($G = -0.46$, $p = 0.015$). (3) The respondents who claim to be the most likely to use the NFPS and believe others would do the same are also the ones who feel the NFPS may be a useful tool for making management decisions and could potentially improve the relations between butterfly collectors and government agencies (all correlations are significant at $p = 0.05$). (4) The collectors who collect with the highest frequency have a slight tendency to believe that the NFPS would worsen relations between butterfly collectors and government agencies ($G = 0.26$, $p = 0.18$).

Finally (5), there is a tight relationship between the respondents who feel the NFPS is a useful management tool and those who feel it will improve relations between the collectors and the agencies ($p = 0.0054$). This also indicates a tight relationship in the other direction; the respondents who feel the relationship will be worsened also feel the NFPS is not a useful management tool.

Qualitative survey questions. Besides the ranked survey responses, there were three questions that solicited comments from the respondents. Question 4 asked the respondent to "Explain your responses to question #3." Question 7 inquired, "What is your opinion of the NFPS?" Lastly, question 8 asked the respondent to write any additional comments they wanted to discuss regarding the NFPS. The writer was invited to attach additional sheets if necessary.

Since the qualitative questions were all fairly general in what they were asking, there was a great deal of overlap in the responses. Several themes continued to emerge in the written response data, therefore it is fitting to discuss the general trends detected in the re-

TABLE 1. Selected correlations between pairs of quantitative survey questions using the Gamma statistic (*G*), which ranges from –1.0 to 1.0. Highly significant correlations are emphasized with the following notations: °°° represents $p \le 0.001$; °° represents $p \le 0.01$; and ° represents $p \le 0.05$.

Pairs of questions tested for correlation		Gamma statistic (G)	p-value
3A: If you went to a location with the NFPS, would you use it? 1 = never, 5 = every time	3B: Would you fill it out candidly and accurately? 1 = never, 5 = every time	0.83	<0.0001 °°°
3C: Do you think other collectors would use the NFPS? 1 = never, 5 = every time	3D: Do you think other collectors would fill it out candidly and accurately? 1 = never, 5 = every time	0.85	0.0005 °°°
1: How often do you collect butterflies? 1 = never, 5 = >20 times/yr	3A: If you went to a location with the NFPS, would you use it? 1 = never, 5 = every time	–0.35	0.11
	3C: Do you think other collectors would use the NFPS? 1 = never, 5 = every time	–0.26	0.21
	5: Is the NFPS a useful tool for making management decisions about BC? 1 = No, 5 = Yes	–0.46	0.015 °
	6: How do you think the NFPS will affect relations between BC's and Govt. Agencies? 1 = Strongly Improve, 5 = Strongly Worsen	0.26	0.18
5: Is the NFPS a useful tool for making management decisions about BC? 1 = No, 5 = Yes	3A: If you went to a location with the NFPS, would you use it? 1 = never, 5 = every time	0.49	0.044 °
	3C: Do you think other collectors would use the NFPS? 1 = never, 5 = every time	0.56	0.027 °
	6: How do you think the NFPS will affect relations between BC's and Govt. Agencies? 1 = Strongly Improve, 5 = Strongly Worsen	–0.61	0.0054 °°
6: How do you think the NFPS will affect relations between BC's and Govt. Agencies? 1 = Strongly Improve, 5 = Strongly Worsen	3A: If you went to a location with the NFPS, would you use it? 1 = never, 5 = every time	–0.59	0.013 °
	3C: Do you think other collectors would use the NFPS? 1 = never, 5 = every time	–0.58	0.026 °

sponses to all three questions (4, 7, and 8) in order to consolidate the findings of the study.

Thirty-six percent of the respondents expressed the belief that the permit would be a nuisance and that it would be too difficult or impractical to fill out ahead of time. One respondent explains, "As you've described it, most collectors have to indicate what species and how many individuals they intend to take upon arrival . . . MOST collecting does not happen that way — it is rather a treasure hunt — you go out and see what you can find." Another says "quite often people go to a new area, especially on vacation, without prior knowledge of what can be found." Finally, another comment suggests a different approach to permits as a data source: "When I go to collect, the reason is never to pick up a certain number of a certain species, but rather to sample what is flying that day . . . the system you suggest is useless for me unless I get to fill out the species and count info after the fact — say at day end or even better later by mail."

Several replies included suggestions for alternate permit systems. Two respondents expressed their belief that the permit needs "teeth," in other words, some regulations specifically geared towards the enforcement of the system. Four respondents suggested that the permit have a third copy on which the actual species list can be recorded and submitted at a later time.

On the other hand, several respondents (27%) believed the permit was a good idea and it was worth trying to determine if lepidopterists would comply with the new system. One person felt the NFPS "might help gauge the pressure on a fragile population." Although 12 respondents included comments leaning in this direction, these responses tended to be brief and supportive, yet not as emphatic in tone as the negatives.

One of the most consistent trends in the qualitative data was a mistrust of government. Quotes from respondents include:

> "I am very nervous about the NFPS being put under the supervision of any state or federal agency," (underline original)

> "I will confess, my knee-jerk reaction anytime that it is suggested that government become more heavily involved in scientific endeavors, even if they be hobbyist endeavors such as collecting butterflies, that it is a bad idea."

> "I think the government screws up everything it touches."

> "Bad idea to involve 'the government' in any more of our lives than absolutely necessary."

These types of sentiments were recorded in 20 of the 45 returned surveys (44%).

Furthermore, many respondents (29%) felt that butterfly collecting is an ineffective conservation focus:

> "Collecting of several specimens of a population of insects in the vast majority of cases has absolutely no effect on the population whatsoever."

> "It is well known that the decline of species of any kind has been due to two principle (sic) causes — long term climate change and loss of habitat."

> "One issue is the immense hypocrisy perceived by lepidopterists when the USFS bans collecting… while permitting hunting, fishing, logging, bug zappers, and the spraying of vast acreages of forests with *Baccilus thuringiensis*, killing millions of leps."

There were several reasons advanced as to why lepidopterists would be unlikely to comply with this system. This opinion was expressed in 18/45 surveys (40%):

> "Some persons might feel guilty that they have overcollected and not report all of their catches."

> "Anyone pursuing larger numbers of specimens for whatever reason would be least likely to truthfully report their activities."

> "There are some people in it for money, these people seemingly have no thought about habitat, populations, future of a species or subspecies, just dollars."

Clearly, many lepidopterists feel that the collectors who take the highest numbers would be the least likely to use the NFPS, a trend that aligns with the correlation results from the quantitative data.

Several people worried that the data collected from the NFPS would not be of a high quality because so many different people with varying levels of skill in species identification would submit it. In addition, there seems to be a fear that agency personnel would interpret the data inappropriately. Concerns over data quality and interpretation were cited in six returned surveys (13%). Some of these respondents felt that a biologist working for the Forest Service may have little or no understanding of what factors have the most influence on butterfly populations. For instance, declines due to inclement weather may be wrongly associated with a modest level of collection, especially by agency personnel unfamiliar with insect (as opposed to tree or vertebrate) population dynamics.

Six respondents (13%) expressed the fear that the NFPS would not remain "No-Fee" after a few years. Three lepidopterists pointed out that they believe there are too few collectors to justify an effort. One respondent explained, "there are nowhere near as many collectors as the public is led to believe. In nearly 70 years of collecting, I rarely see another collector." Finally, six respondents (13%) expressed the belief that lepidopterists have an innate conservation ethic or highlighted the importance of butterfly collection for conservation purposes. They explain that amateur butterfly collectors are often the main group of lepidopterists that provide accurate distribution data for species occurrences on an annual basis. Further, many of the dot-distribution maps widely used in Oregon and Washington were based on specimens from private collections (Dornfeld 1980, Hinchcliff 1996). With only a few academic and professional research lepidopterists in the region, it is imperative to augment their data with the work of amateur collectors. Many point out that collectors out on exploratory jaunts are often the ones who discover new species and populations in an area. Regulation of this activity may have negative impacts on the willingness of these people to share their discoveries.

DISCUSSION

Analysis of the potential success and utility of the "No-Fee Permitting System." Based upon the responses to the first few questions on the survey, it is clear that this group of people was an appropriate population to be surveyed. Most of the 45 respondents collect several times per year with only three who claimed to never collect at all (Fig. 1). Collectors usually go out into the field with the intention of taking specimens, with the most widely cited rationale being "personal collection" (Fig. 2). While no one admitted to collecting for profit, 8/45 of the respondents (18%) collect with the intention of exchanging specimens. Collection for the purpose of "exchange" may imply the taking of more rarer or harder-to-catch species in order to increase their exchange value.

While approximately half of the respondents said they would utilize the NFPS every time they went to a participating location, an even greater proportion of respondents predicted a lower level of participation for other lepidopterists. Sixty percent of the respondents felt that other collectors would only use the NFPS "sometimes" at participating locations. Only 6/45 lepidopterists (13%) say they would "never" use the proposed system. Since some of these are the most frequent collectors, as indicated by the slight correlation between question 1 and question 3A (Table 1), this is a significantly negative response.

From the response data it is apparent that the reaction to the NFPS is not positive enough to justify initiating this sort of conservation strategy: it would, in fact, be counterproductive. Furthermore, from the comments and quantitative data it is apparent that the relationship between lepidopterists and government agencies is seriously in need of repair. While both groups would benefit from improved communication and cooperation, neither thoroughly understands the predicaments and concerns of the other. Yet, without cooperation, the future of butterfly conservation is needlessly compromised.

The approach of this survey was to involve the persons most affected by the model system in the decision-making process. We feel this is one of the first steps to improving the relationship between the two groups. It is critical that the U.S. Forest Service listen to the concerns of the respondents and make its policy decisions with these suggestions in mind: that is, only extremely compelling reasons would justify failing to heed the advice of the concerned public. In the *Parnassius phoebus sternitzkyi* case there are no such compelling reasons.

It is clear from the ranked data that the lepidopterists who collect most frequently have a tendency to be the ones who do not consider the NFPS to be a useful tool for making management decisions; they do not think it will improve the relations between collectors and government agencies, and they are the least likely to comply with the system (Table 1). When these results are combined with the comments regarding the success and utility of the NFPS, it becomes clear that the system will be ignored and disliked by many, perhaps most, frequent butterfly collectors. If implemented with only weak support from lepidopterists the NFPS would not only incite resentment, it would also be nearly useless as a source of reliable data, making it an essentially useless endeavor. In an era where the sentiment towards government agencies is laden with mistrust, agencies such as the US Forest Service should strive to open channels of communication, rather than close them by taking what would be perceived as arbitrary bureaucratic action.

Suggestions for policy improvement and future use. The NFPS was intended to improve the amount of data available to land managers. Even if the NFPS as we have described it would not be acceptable to the collecting public, perhaps it would be helpful for individual forests to set up voluntary data submission programs — carefully avoiding the word "permit" or other threatening buzzwords. Then lepidopterists might feel they are doing their part for conservation without the sense of unjustified regulation. This could be a primary step toward improving the relationship between collectors and government agencies. If legitimate, well-documented conservation concerns ultimately dictate some form of permitting system, it would be much more likely to succeed if lepidopterists understand its rationale and support its goals.

ACKNOWLEDGMENTS

This study would not have been possible without the survey respondents. Thank you for taking the time to think about our questions, write your comments, and mail the replies. Many people added creative ideas to this project. We would like to thank Rich Van Buskirk, Mikaela Huntzinger, Jim Fordyce, Nicole Jurjavcic, Tag Engstrom and Michelle Gadd for thinking about and discussing the NFPS. We also appreciate the contributions of two anonymous reviewers. Sy Schwartz facilitated an environmental policy seminar that helped to shape the direction of the data interpretation. Barbara Mumblo provided information on the recent history of butterfly collection closures on the Applegate Ranger District of the Rogue River National Forest. We gratefully acknowledge Joel E. Pagel, who coordinated the funding of this research through the Rogue River National Forest, Challenge Cost-Share Agreement.

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APPENDIX 1 – Letter to Lepidopterists.

Evolution and Ecology
University of California, Davis
Davis, CA 95616
email: kcmazzei@ucdavis.edu

June 17, 1998

Dear Member of The Lepidopterists' Society,

I am a graduate student at the University of California, Davis, and I am interested in the conservation biology of butterflies. Regulation of collecting has become a very controversial subject in part because of poor communication about the justification and goals of the regulation. As part of my Master's thesis research I would like to determine how a new butterfly collection monitoring program would be received by amateur, professional, and academic lepidopterists. Since the proposed system has not been used before, the results of the enclosed survey will be of key importance when determining whether such a program would be successful and worthwhile. Please read on!

As you may know, Apollo butterflies (genus *Parnassius*) are often under heavy collection pressure. Intense butterfly collecting in a particular region has been claimed to contribute to irreversible species decline. Both the collection and sale of Apollo butterfly species have been forbidden in Europe and similar protective actions could occur in the United States. Lepidopterists are commonly aware of "source" locations for particular species. The Siskiyou Mountains are the only habitat for a showy Apollo subspecies, *Parnassius phoebus sternitzkyi.* Most of its habitats are on public lands.

At this time there are no hard data on how much collecting of *Parnassius phoebus sternitzkyi* is occurring, or whether it is harming the populations. Because the subspecies has such a small geographic range and a low reproductive rate, it may be proposed for protection of some kind. Such proposals should not be made on pure instinct, however—protection might be urgently needed, but it also might be totally unnecessary!

One way to monitor the amount of collecting on public lands would be the installation of a "No-Fee Permitting System." It would work like this: (1) Upon arrival, a collector would voluntarily fill out a two-copy form detailing the date, location, the species desired and the quantity to be taken; (2) One copy of the form would automatically serve as a free permit. The second copy, which would be deposited in a drop box on-site, would provide the agency with information about which locations and species experience the most collection pressure.

Please take a few minutes and complete the enclosed survey regarding the "No-Fee Permitting System." This survey is being sent to Lepidopterists' Society members in Oregon, Washington, and Northern California. The completed survey should be returned in the stamped envelope provided. I would like to thank you for your honest participation in this important study. Let me assure you that there are no identifying marks on the survey and that all replies will be kept absolutely anonymous. The aggregate response may be published and/or provided to local, state, and federal agencies, and non-governmental conservation organizations. It may shape the future of *Parnassius phoebus sternitzkyi*—and of collecting on public lands. Thanks again!

Sincerely,
Kristine C. Mazzei

APPENDIX 2 – Survey on proposed "No-Fee Collection Permit System."

Return to (stamped envelope has been provided):
Kristine C. Mazzei
Evolution and Ecology
University of California, Davis
Davis, CA 95616
email: kcmazzei@ucdavis.edu

1998 Survey on Proposed "No-Fee Collection Permit System"

Please honestly respond to the following questions and feel free to explain any answers in the "ADDITIONAL COMMMENTS" section at the end of the survey. Thank you for your participation. Please omit any information that might identify you or your location.

(1) How often do you collect butterflies (circle the appropriate number)?

Never		**A few times each year**		**More than 20 times per year**
1	**2**	**3**	**4**	**5**

(2) If you answered between 2 and 5 on question #1, please circle all of the reasons why you collect butterflies:

Enjoyment **Personal Collection** **Museum Collection** **Research** **Profit**

Exchange **Other Reason:**

(3) If you decided to collect butterflies and you went to a facility or location that implemented a voluntary "No-Fee Permitting System" as described in the letter,

(A) would you use it?

Never		**Sometimes**		**Every Time**
1	**2**	**3**	**4**	**5**

(B) would you fill it out CANDIDLY and ACCURATELY?

Never		**Sometimes**		**Every Time**
1	**2**	**3**	**4**	**5**

(continued on back)

(C) Do you think other collectors would use it?

Never		**Sometimes**		**Every Time**
1	2	3	4	5

(D) Do you think other collectors would fill it out CANDIDLY and ACCURATELY?

Never		**Sometimes**		**Every Time**
1	2	3	4	5

(4) Explain your responses to Question #3:

(5) Do you think the "No-Fee Permitting System" would be a useful tool for making management decisions about butterfly collecting?

No		**Maybe**		**Yes**
1	2	3	4	5

(6) How do you think the "No-Fee Permitting System" would affect relations between collectors and government agencies?

Strongly Improve		**No Effect**		**Strongly Worsen**
1	2	3	4	5

(7) What is your opinion of the "No-Fee Permitting System?"

(8) ADDITIONAL COMMENTS (please write as much as you like, use additional sheets if necessary—but remember not to identify yourself).

Thank You!

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LIFE HISTORY AND LABORATORY HOST RANGE TESTS OF *PARAPOYNX SEMINEALIS* (WALKER) (CRAMBIDAE: NYMPHULINAE) IN FLORIDA, U.S.A.

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ABSTRACT. The native aquatic moth, *Parapoynx seminealis* (Walker), attacks big floating-heart, *Nymphoides aquatica* (S. G. Gmel.) Kuntze, in Florida. Eggs are laid on the lower surface of floating leaves. Neonates bore into the relatively thick leaf or drop off the leaf on a silken thread to feed on submersed leaves. Later instars build cases mostly by excising leaf pieces and attaching them to leaves. They feed from the case or out of the case on the margin of the leaf and on the upper surface. Cocoons are made in the cases. There were three, or possibly four, peak adult emergence periods in north-central Florida: June, August, mid-October, and possibly late March and April. Although the larvae are specialists on floating-hearts, they fed and developed for relatively long periods on some non-host species in laboratory host range tests. The two species most acceptable were *Egeria densa* Planchon and *Hydrilla verticillata* (L.fil.) Royle, both immigrant species in the non-related monocot family Hydrocharitaceae.

Additional key words: floating-heart, biocontrol, *Nymphoides, Hydrilla, Egeria.*

Aquatic moths in the genus *Parapoynx* (Crambidae: Nymphulinae) are of interest both to aquatic biologists and to researchers on the biological control of aquatic weeds. The caterpillars feed on aquatic macrophytes and cover themselves with cases, portable or stationary, which are made with the leaves of the host plant. They are the only aquatic caterpillars that have branched gills on all body segments except the prothorax (Habeck 1974). Six species are native to North America. All have been reported from Florida (Monroe 1972) although records for two species are suspect [*P. badiusalis* (Walker) and *P. curviferalis* (Walker)]. A seventh species, *P. diminutalis* Snellen, is an immigrant in Florida (Buckingham & Bennett 1996). No host plants have been recorded for *P. curviferalis*, but the other species, except the subject of this study, *P. seminealis* (Walker), have hosts in at least two genera and three have hosts in multiple families (Habeck 1974).

Parapoynx seminealis reportedly develops only on floating-heart, *Nymphoides,* and specifically on big floating-heart, *N. aquatica* (S. G. Gmel.) Kuntze (Menyanthaceae). A second native floating-heart, *N. cordata* (Ell.) Fern., occurs within the range of the moth. It has not been reported as a host, possibly because of lack of collecting or because often only the host genus is recorded. Herlong (1979) mentioned that a *P. seminealis* larva "on occasion was found on a nearby leaf of *Nymphaea odorata*" Aiton (Nymphaeaceae), but he did not indicate whether the larvae were actually feeding and developing.

Big floating-heart ranges from New Jersey to Florida and west to Texas (Godfrey & Wooten 1981). It has heart-shaped leaves, 5–15 cm long, that are green and smooth on the upper surface but purplish and rough or pitted on the lower surface due to an irregular layer of aerenchyma cells. The leaves are quite thick compared with leaves of most other native floating species. Mature leaves were at least 1.5–3.0 mm thick with about 50–66% of the thickness composed of spongy aerenchyma cells. Several leaf petioles arise from the tip of a stem near the surface of the water. The white flowers arise just below the petioles and often a cluster of short, stout, fleshy roots forms among or below the flower stalks (Godfrey & Wooten 1981). These roots are colloquially called "bananas" and are sold in the aquarium trade. "Bananas" excise and drop to the hydrosoil where they produce very thin submersed leaves and later new plants. Submersed leaves are also produced by rooted plants.

Several species of *Parapoynx* and other Nymphulinae have been of interest for the biological control of submersed aquatic weeds (Buckingham 1994), but none has been purposefully released in any country (Julien & Griffiths 1998). We became interested in *P. seminealis* while awaiting the results of foreign surveys for natural enemies of submersed weeds. We planned to conduct host range tests in quarantine with the potential control agents to determine their safety for release in the United States. Because of its reported host specificity, the native *P. seminealis* appeared to be an excellent test subject for developing techniques to rear and study aquatic caterpillars and for comparing the laboratory physiological host range with a known ecological (or realized) host range. We report below our studies on the life cycle and the host range of this interesting aquatic moth.

MATERIALS AND METHODS

Insects and plants. Insects and host plant material, big floating-heart, were collected by boat from Santa Fe Lake, Alachua County, Florida, near Melrose, one to three times a month from June 1980 to June 1981 except during December, February, April, and May. Damaged leaves were collected for observation and for recovery of immature stages. Undamaged leaves were collected for a food source. Anecdotal observations were made of leaf abundance and damage at the various sites.

Rearing. Undamaged leaves were held in outdoor pools or in a refrigerated temperature cabinet. Rearing was conducted in floating screen cages in the outdoor pools and in plastic pans in the laboratory (22–24°C). The large size of most floating leaves, 10–15 cm wide, precluded rearing in small cages. New leaves were added often because the leaves broke down, possibly because of disease or because they were excised from the roots. Efforts to transplant plants from the lake were not successful, although some new plants were grown from "bananas." New adults were collected from the cages, paired in the laboratory for mating, and then placed into new cages. Usually eggs or neonates were placed back into the cages after they were counted, but some were removed for studies. Initially, leaves were dipped in 0.01N potassium permanganate for 45 seconds to one minute to surface sterilize them and then were washed with water. However, even treated leaves continued to break down within a couple of days and this treatment was discontinued early in the study.

Life cycle studies. Insects were held for these studies (1) in the laboratory with natural lighting from a window and with fluorescent lighting during work hours (ca. 0700–1750 h), (2) in the quarantine laboratory with only fluorescent lighting during work hours, and (3) in a quarantine greenhouse with natural lighting supplemented with fluorescent lighting (16 h photophase). Laboratory temperatures usually ranged from 22–24°C and greenhouse temperatures from 26–32°C. Larval and pupal development was determined in a temperature cabinet at 27°C and 16 h photophase. Head capsules of living larvae were measured at 12× and of preserved larvae at 50× with an ocular micrometer in a dissecting microscope. All measurements are reported as mean ± standard error (number, range). Specimens have been deposited in the Florida State Collection of Arthropods (FSCA), Gainesville, Florida, and in the U.S. National Museum of Natural History (USNM), Washington, D.C.

No-choice host range tests. Test plants were field collected and were held in pools for a few days up to several weeks until used or in a refrigerated temperature cabinet for a few days. Tests were conducted in the laboratory at 22–24°C with eggs containing active larvae just prior to eclosion and with neonates. The cages for these tests were 30 ml plastic cups with their bottoms replaced by nylon organdy and capped with either organdy or plastic lids. The cups sat on coarse sand in a shallow pan filled partially with water aerated by an aquarium pump. The water was aerated because neonates had died within five days on floating-heart in a preliminary test with closed cups and no aeration. Pieces of test plants were cut to fit into the 30 ml cups, which were 30 mm wide at the bottom and 40 mm at the top and 45 mm deep. Stem tips or sections cut from broad leaves were used depending on the growth form of the plant. Each cup received one egg or neonate. There were two no-choice tests, each with six treatments (Table 1). Each test had two control treatments: one without plant material and one with floating-heart. The other treatments were common aquatic plant species. Both tests were initiated with 20 replicates in each treatment except the cage without plant material in test B, which had ten replicates. Replicate numbers (n) less than 20 in Table 1 are due to losses during handling. Test A was terminated when all larvae died. Test B was terminated at 22 days because floating-heart leaves were lacking. The cups were examined for larval survival every three to seven days in test A and four to seven days in test B. Plant material was changed as needed. Presence of feeding was recorded at each examination, but the amount was not estimated.

No-choice tests were also conducted with medium-sized larvae, 1 cm or greater in length, reared in the laboratory on floating-heart (test C – larval age was 63 days after oviposition, test D – larval age was 49 days after oviposition). Larvae were removed from their cases and placed individually on test plants in 177 ml Styrofoam drinking cups in the laboratory at 22–24°C. Plants were cut to fit into the cups. Pieces of elongate plants, ca. 9–18 cm long, and sections of large leaves, ca. 5–8 cm diameter, were used. Initially, there were eight replicates per treatment in test C and three replicates in test D, except in the treatment without plant material, which had five. One replicate in test C was lost in handling, and after six days *Vallisneria americana* Michaux (Hydrocharitaceae) was added to

TABLE 1. No-choice feeding tests with *Parapoynx seminealis* neonates.

			Longevity (days)				No. observations with damage[3] No. larvae[4]		
Plant species[1]	Plant family	Test symbol[2]	mean	SE	range	n	1	2–3	>4
Cage without plant material	——-	A	7.3	0.3	7–12	18			
Egeria densa Planchon	Hydrocharitaceae	A	61.2	9.9	7–89	15	4	3	10
Hydrilla verticillata (L. fil) Royle	Hydrocharitaceae	A	24.3	6.4	7–102	20	1	2	6
Nymphoides aquatica (J. G. Gmel.) Kuntze	Menyanthaceae	A	65.5	7.2	7–89	19	0	4	16
Sagittaria subulata (L.) Buch.	Alismataceae	A	8.2	0.5	7–12	17	3	0	0
Vallisneria americana Michaux.	Hydrocharitaceae	A	9.5	0.8	7–12	10	3	0	0
Cage without plant material	——-	B	6.8	0.2	5–7	10			
Limnobium spongia (Bosc.) Steud.	Hydrocharitaceae	B	14.4	1.0	5–22	20	11	4	0
Najas guadalupensis (Sprengel) Magnus	Najadaceae	B	11.9	1.0	5–22	19	13	2	0
Nuphar luteum (L.) Sibth. & Smith	Nymphaeaceae	B	10.4	0.7	5–18	19	2	1	0
Nymphoides aquatica	Menyanthaceae	B	19.7	1.2	5–22	17	2	4	12
Potamogeton illinoensis Morong	Potamogetonaceae	B	11.5	0.8	5–18	20	10	1	0

[1] *N. aquatica*, big floating-heart, is the field host plant.

[2] Cages were 30 ml plastic cups with organdy bottoms sitting in aerated water in the laboratory at 22–24°C. There were 20 larvae per treatment. Test A was conducted until larvae died. Test B was conducted for 22 days until the control plant, big floating-heart, was no longer available. Only three of 78 larvae were alive in test B at 22 days on test plants (*L. spongia* and *N. guadalupensis*) versus 12 of 20 on big floating-heart. Numbers (n) less than 20 are due to handling losses, except the "cage without plant material" treatment in test B, which was started with only 10 larvae.

[3] Cages were observed for feeding damage every three to seven days in test A, first observation at seven days, and four to seven days in test B, first observation at five days. Feeding was noted but not estimated. Plant material was changed as needed.

[4] Number of larvae (replicates) in the category: 1 – only one observation with damage, usually the first; 2-3–two or three observations with damage, >4 – greater than 4 observations with damage. When the total number of larvae is less than n, there were larvae that did not feed; when total numbers are greater than n, some larvae fed before they were killed or missed during handling.

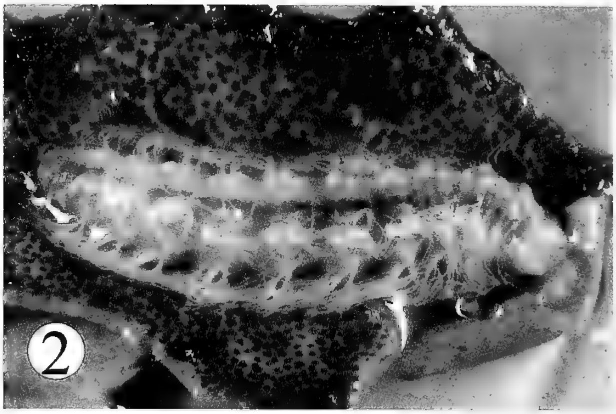
the five replicates of the treatment without plant material in test D. Frass pellets on the floor of the cup were counted as an indication of the amount of feeding. In test C, the cups were examined at eight days and at 15 days when the test was stopped. In test D, the cups were examined mostly daily from Monday to Friday until the larvae died. Survival and the number of frass pellets were recorded at each examination, the frass was removed, and plant material was changed as needed.

RESULTS

Phenology. Based on larval sizes and larval and pupal numbers, it appears that peak adult emergence occurred in June, early August, and mid–October. There were many large larvae at the end of March and some pupae, which suggests that there was probably also an emergence peak in April when we did not sample. Pupae might have been absent during winter since we found none in January, but we are unable to confirm that because we did not sample in February. Only two adults, one each in October and November, were observed in the field, but some were undoubtedly present most of the time based on our collections of other stages. Grass along the shore was swept with a net in October when pupae were common and the temperatures still warm, but without success. This suggests that adults rest away from the waterway during the day or move to emergent plants elsewhere in the waterway. However, we examined and collected emergent plants at times throughout the year for studies with other insect species, but we saw no adults.

Parapoynx seminealis eggs were found in August, October, and November 1980, and June 1981. All sizes of larvae were present from August 1980 to June 1981. Larvae were common at the beginning of the project in June and July 1980, but we did not record their sizes when we placed the unopened larval cases in the rearing cages. In late November there were small larvae among the "bananas" attached to the plants, and there were many small and large larvae among attached "bananas" in mid-January. There were also many at that time in cases on the leaves. "Bananas" that had fallen from the plants were common on the soil surface beneath plants in shallow water during a visit on 27 October 1999, but none were infested.

Plant damage. Larvae damaged the plants heavily throughout the year. Large sections were cut from the leaves by multiple larvae until there was often little remaining leaf material (Fig. 1 and Fig. 1 in Habeck 1974). Damaged leaves appeared to be more susceptible to pathogens especially *Pseudomonas marginalis* (Brown) Stevens pv *marginalis* (Brown) Stevens which caused the leaves to become mushy. Another patho-



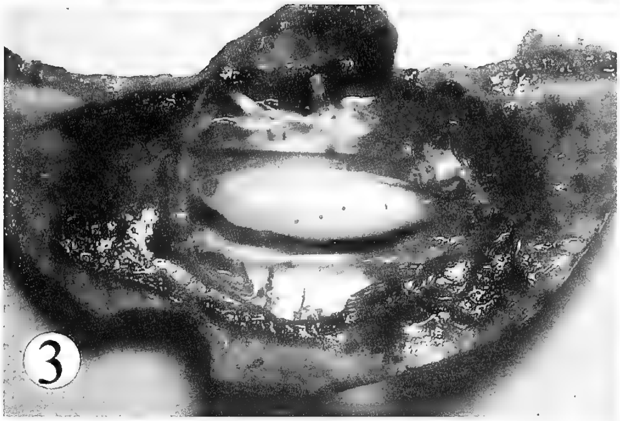


FIG. 1. *Parapoynx seminealis* feeding damage on floating leaves of big floating-heart, *Nymphoides aquatica*. Arrow points to larval case on lower left margin of the large leaf. FIG. 2. Mature larva of *P. seminealis*. FIG. 3. *P. seminealis* pupa, note shiny air layer in the cocoon silk around the middle of the pupa. FIG. 4. *P. seminealis* male.

gen, *Cercoseptoria nymphaeacea* (Cke. & Ell.) Deighton, was first recorded for Florida from our material. Damage from neonatal boring produced small holes in the leaves, which added to the leaf decline. We had five sites that varied greatly in available leaf material because of the damage from varying caterpillar populations.

Eggs. The newly deposited egg is a flattened, elliptical disc, length 0.90 ± 0.01 mm (17, 0.84–0.94), width 0.65 ± 0.01 mm (0.62–0.66). If the floating leaf was mature, each egg was deposited in a pit in the arenchyma layer on the lower surface that has been described as "dark-punctate or pitted" (Correll & Correll 1972). The margins of the eggs often overlapped on the raised margins of the pits. Younger leaves without a well-developed aerenchyma layer are smoother and the eggs did not overlap as much. The center of the fresh egg was pale yellow, but the margins were clear. The chorion appeared roughened with longitudinal ridges. The entire egg turned yellow as it aged, but the color disappeared as the visible embryo matured. The light brown head capsule and dark pronotal shield signaled the approaching eclosion. Eggs developed in six days at 27°C and in eight to ten days at about 24°C. The swollen egg was ovate when the embryo was developed, length 0.80 ± 0.01 mm (8, 0.76–0.81), diameter 0.55 ± 0.01 mm (0.52–0.58). Eggs were placed in loose rows, two to five eggs deep, along the leaf margin. The rows were 0.9 to 4.7 mm from the margin. The heads of most embryos were at the end of the egg closest to the leaf margin, but a few were oriented at the other end. Field egg masses were relatively small, 14.6 ± 2.6 eggs (15, 2–28).

Neonates. Upon eclosion, the neonate burrowed into the thick leaf or dropped from the leaf on a silken thread. The leaf entrance hole was often marked by light green frass. The first instar was distinguished by the lack of tracheal gills and by the dark brown pronotal shield and frontoclypeal triangle of the head capsule. Most of the head capsule was light brown like that of later instars. The larva tunneled either just beneath the lower epidermis or from there to the upper epidermis. Viewed from below, the tunnel beneath the lower epidermis appeared green from the frass;

viewed from above, the tunnel beneath the upper epidermis appeared as a dark blotch. However, if the leaf were held towards a light, the upper tunnel appeared transparent. The epidermis over the tunnel often broke down forming a hole in the leaf through which fungi invaded. Dark gut contents could be clearly seen in the whitish, almost transparent, neonate that was often visible in the tunnel. Younger floating leaves were sometimes too thin for a tunnel and the larva fed in a trench on the lower surface. It also fed on the petiole by scraping the surface or by boring into it. Submersed leaves are much thinner than floating leaves and the larva fed by scraping away all the material from the lower surface. This created windows in the leaf. Older first instars made small cases on the thin submersed leaves by bending the leaf margin inwards along a cut and fastening it to the leaf. Some fed on the "bananas" and on the flower buds, both of which are attached just below the floating leaves.

A larva dropping from a leaf through the water could be manipulated by intercepting the silken thread attached to the plant. The larva also attached a thread to the forceps whenever handled. If food were not available, larvae crawled actively around the container and even crawled out of 30 ml plastic cups into the air where they perished. When confined in capped 45 ml cups without water but with moist filter paper, they lived from 5.5 to 114.5 h (mean = 58.1 ± 7.0 h; median = 64.5 h; n = 29). In cups with dry filter paper all were dead at 2 h. Head capsules of living first instars were 0.34 mm wide and the larvae were 1.8–2.4 mm long. Development time was four to 12 days with most developing to second instars in five to eight days.

Older larvae. Second and later instars were distinguished readily from first instars by the presence of tracheal gills. They also were whitish and somewhat transparent with the gut easily seen. The head capsule was very light brown except the last instar's which was pale yellowish to whitish. Second instars fed in tunnels and externally on the lower surface and petiole, but they also began making small cases on the floating leaves and fed in channels on the upper surface of the floating leaves. As the larvae matured, the case-making habit intensified, but some larvae were also found feeding without cases. Cases were formed in several ways. A piece was cut from the edge of the leaf with the size weakly related to the size of the larva. This circular to semicircular piece was either attached to the upperside of the leaf by attaching the rough lower surface of the piece to the smooth upper surface of the leaf, or attached to the underside of the leaf by upper surface to lower, or lower to lower. Attachment to the upperside of the leaf was most common. Next most common was attachment to the underside by upper surface to lower surface. With both of these common orientations, the excised piece was camouflaged as part of the leaf.

To excise a piece, the larva started eating from the edge of the leaf and ate a cut inward, revolving its body around like the hand of a clock until reaching the margin again. The thickness of the leaf prevented the larva from merely cutting the leaf as reported for the *P. maculalis* (Clemens) case-making behavior on yellow waterlily, *Nuphar* (Welch 1916). The larva then held onto the excised piece with the hind legs and pulled itself onto the main leaf, dragging the piece behind it. The piece was then attached to the leaf with silk. The case was completed within an hour by medium to large larvae. Small larvae formed a silken gallery inside the case that pulled away from the leaf piece and remained around the larva on the main leaf when the case was pulled apart. Older larvae placed the silk in two parallel rows thus forming a tunnel with the two leaf pieces. When the case was pulled apart, the silk remained attached to both leaves leaving the larva naked. More silk was placed on the rough lower leaf surface than on the smooth upper leaf surface. Large larvae also webbed together the overlapping portions of two leaves to make a case without cutting pieces. When medium and large larvae made detached cases the two excised pieces were usually placed lower surface to lower surface. The case was thus green on both sides. The first pieces cut from leaf margins were roughly circular to semicircular, but as the leaves were cut up, the shape of the excised pieces became highly variable with multiple angles.

The size of the cases was also highly variable. Some examples of the sizes of excised pieces used in field collected cases of mid-instar larvae (10–15 mm long) were 10 × 10, 10 × 15, 10 × 20, 10 × 25, 15 × 25, 20 × 20, 25 × 35, 40 × 75 mm; and of large larvae (20–25 mm long) were 15 × 25, 20 × 25, 20 × 35, 20 × 40, 25 × 30, 30 × 30, 30 × 35, 30 × 40, 30 × 45 mm. All of these pieces were attached to floating leaves. Larvae in both attached and detached cases fed along the margins of the leaves and on the surfaces of the leaves near their cases. They also exited from their cases to feed naked on the leaf surface. Those on the upper surface ate down to the lower epidermis forming patches or channels and occasional holes. Larvae also fed somewhat on the inside of the cases. Feeding appeared to be mostly nocturnal, but larvae were observed during the day out feeding on the leaves, especially during the cooler period of autumn and winter. Most cases were attached along the leaf margin (Fig. 1) but many were away from the margin near the center of the upper surface. A thin layer of water from small holes in the leaf or from wash over the sides usually surrounded these cases. The larva often wiggled its body side to side which apparently moved water through the case as reported for *P. maculalis* (Welch & Sehon 1928). The gills of the mature larva are very long, white, and beautifully delicate (Fig. 2). Mueller and Dearing (1994) described similar case construction on *Nymphaea ampla* by *Parapoynx rugosalis* Möschler in Costa Rica.

A graph of measurements of the head capsules of 233 preserved larvae from both laboratory experiments and field collections did not have well defined separations between instars. It suggested that there might be as many as 10 or 11 instars in the field populations. These measurements and the presumed instars were 0.32–0.36 mm (n = 17) I°, 0.40–0.44 (n = 9) II°, 0.46–0.52 (n = 31) III°, 0.56–0.64 (n = 39) IV°, 0.66–0.74 (n = 32) V°, 0.76–0.90 (n = 30) VI°, 0.94–1.00 (n = 8) VII°, 1.04–1.22 (n = 30) VIII°, 1.28–1.40 (n = 14) IX°, 1.44–1.54 (n = 15) X°, 1.60–1.66 (n = 6) XI° (males?), 1.78–1.86 (n = 6) XI° (females?). Measurements of living larvae that were measured just before or after ecdysis confirmed the sizes of the first nine instars. However, the maximum head capsule size prior to pupation in the sample of live larvae was 1.40 mm. Possibly host plant quality was lower in the excised laboratory leaves and thus larvae pupated sooner that they did in the field. Most of the measurements above 1.40 mm in the preserved specimens were from larvae collected directly in the field. The approximate body lengths of larvae varied from 3.2 mm for II° to 24.2 mm for mature larvae.

The larval development period at 27°C was 41.1 ± 1.1 days (7, 36–44) and the development period from neonate to adult was 51.4 ± 1.4 days (5, 47–54).

Pupa. The mature larva formed a pupal chamber by tying the case together completely around the edges. A silken cocoon was formed in the case. The newly formed pupa (Fig. 3) moved actively when disturbed, but moved less as it matured. The central portion of the cocoon appeared silvery because of air trapped in the silk. Air was provided to the cocoon through small elliptical feeding spots in the surface of the leaf made before pupation. These spots, six to ten in a group, were near the center of the cocoon and the silk directly above them was the most silvery. The spots were 0.40–0.60 mm long and 0.30–0.40 mm wide. Some of the ridges on the lower aerenchyma surface of the attached excised piece also had similar feeding spots.

There was a distinct prepupal stage when the light yellow larva contracted into the three body regions with very obvious abdominal segments. The newly formed pupa was light yellow with three obvious orange spiracles on projections of the abdomen (2.0–2.5 mm long on segments A2–A4); as the pupa matured, the eyes darkened and the wing pads, legs, and antennae turned white before darkening. The afternoon of emergence, the pupa was brown with visible wing markings. The female pupa was distinguished by antennae that were obviously shorter than the wing pads and by the mesothoracic legs, which terminated just beyond the wing pads in the same body segment, A5. The male's antennae were as long or longer than the wing pads, and the mesothoracic legs ended in the anterior portion of segment A6. The abdomen of the new female pupa exceeded the hindlegs, but that of the new male was usually shorter than the hindlegs. Near emergence the male's abdomen lengthened and exceeded the hindlegs. The widest part of the body was between the spiracles of A3 and A4. The pupal size was: female, length = 12.2 ± 0.1 mm (9, 11.4–12.7), width = 3.3 ± 0 mm (3.2–3.5), width at spiracle = 3.8 ± 0.1 mm (3.5–4.2); male, length = 10.4 ± 0.1 mm (8, 10.0–11.0), width = 2.7 ± 0 mm (2.7–2.8), width at spiracle = 3.1 ± 0.1 mm (2.8–3.3). Pupal development time at 27°C was: female, 10.0 and 11.0 days (2): male, 10.0 ± 0.8 days (5, 7–11).

Adults. Forewings of the adults are sexually dimorphic. Females have more or less unicolorous reddish brown forewings compared with males that have grayish forewings with a white stripe parallel to the side and hind margins (Fig. 4). Both sexes have hindwings with two transverse black stripes on a white groundcolor and tan or orangish markings along the hind margin (for a detailed description see Monroe 1972). Adults emerged in outdoor cages all day although probably mostly at night because the largest numbers were present in early morning. Observed night emergence times were 2000 h, 2100 h, and 2100–2245 h for three females and 1800–2100 h for one male.

The newly emerged female calls the male by raising her abdomen above her resting wings and extending the tip. One mating was at 0200 h and lasted less than an hour. Colony females generally mated the next evening after they emerged. Females typically rested with their wings folded over their body. Males often rested with their wings extended so that the hind wings were visible, although they also rested with folded wings, especially after a disturbance. Adults were not strongly attracted to light in the laboratory. When they escaped, they flew erratically, landing on the walls rather than flying to the window or overhead light.

Oviposition was observed at 2000 h in an outdoor tank, and at 2100 h and later in laboratory cages. Fe-

TABLE 2. No-choice feeding tests with medium-sized larvae of *Parapoynx seminealis*.

Plant species[1]	Test symbol[2]	Longevity (days)				No. frass pellets/day[3]	
		Mean	SE	range	n	Mean	SE
Egeria densa	C	15.0	0	15.0	8	9.3	2.3
Hydrilla verticillata	C	15.0	0	15.0	7	5.0	0.5
Nymphaea odorata Aiton	C	15.0	0	15.0	8	8.0	1.7
Nymphoides aquatica	C	15.0	0	15.0	8	62.4	6.8
Potamogeton illinoensis	C	8.9	0.9	8–15	8	0.5	0.1
Cage without plant material	D	6.0	0	6.0	5	0.4	0.2
Egeria densa	D	51.3	29.6	6–107	3	12.2	3.5
Hydrilla verticillata	D	46.7	20.9	13–85	3	13.6	1.8
Limnobium spongia	D	18.7	4.7	14–28	3	10.7	3.8
Nymphaea odorata	D	26.7	8.1	12–40	3	14.7	2.0
Nymphoides aquatica	D	66.3	14.0	47–93	3	28.5	0.6
Sagittaria subulata	D	17.3	4.3	13–26	3	3.6	3.0
Vallisneria americana	D	23.7	2.3	19–26	3	13.6	1.4
Vallisneria americana	D	18.0	4.1	7–28	5	9.7	3.6

[1] *Nymphaea* is in the Nymphaeaceae, *N. aquatica* is the field host plant.

[2] Cages were 177 ml styrofoam cups with medium-sized larvae reared in the laboratory at 22–24°C on big floating-heart. Test C was terminated after 15 days; test D terminated when all larvae died.

[3] Individual frass pellets were counted and removed every one to three days. Plant material was changed as needed.

males sat at the edge of the leaf perpendicular to the margin with the fore and mid legs on the leaf and the abdomen curled under the leaf. They also sat halfway on the leaf parallel to the margin with the abdomen curved sideways under the leaf. Realized fecundity in the laboratory was 293.3 ± 25.5 eggs (17, 56–412). Thirteen of the females laid the largest number of eggs during their first night of oviposition, which was one to three nights after emergence, and eight of those laid the majority of their eggs during the first night after emergence. None oviposited during the night they emerged or after the fifth night. Longevity in the laboratory was 4.0 ± 0.4 days (16, 2–6) for females and 3.4 ± 0.4 days (14, 2–5) for males.

Host range tests. Some neonates fed briefly on each test plant species, but most feeding was before the first change of plant material (Table 1). Notable feeding and longevity was observed in test A on *Egeria densa* Planchon and *Hydrilla verticillata* (L. fil.) Royle, both in the family Hydrocharitaceae. Longevity and feeding were similar among the other test species in both tests. Larvae did not complete development in test A on floating-heart because of the lack of fresh plant material at the end of the field season. Although test B was terminated at 22 days because of lack of floating-heart, that had little impact on the longevity data for the test plants because only three of 78 test larvae were still alive at 22 days. It did, however, greatly reduce the longevity for floating-heart, which had 12 of 20 larvae still alive. Small differences in longevity among test plants might have been masked by the relatively long intervals of three to seven days between changes of plant material.

Medium-sized larvae that had developed on floating heart until tested survived longer than neonates and fed more on some of the same plant species (Table 2). Again, longevity on test plants was highest on *E. densa* and *H. verticillata* (test D), but feeding (as indicated by mean number of frass pellets per day) was similar on all test plants except on the little eaten *Potamogeton illinoensis* Morong (Potamogetonaceae) and *Sagittaria subulata* L. Buch (Alismataceae). In test C, most feeding on *N. odorata* was during the first eight days, 13.2 frass pellets per day, compared with 2.0 during the final seven days. It was vice versa in the other four species.

DISCUSSION

The life cycle of *P. seminealis* is quite similar to that reported for *P. maculalis* on *Nuphar* (Nymphaeaceae) (Welch 1916). One difference is that *P. maculalis* preferred to oviposit through oviposition holes of *Donacia* leafbeetles (Chrysomelidae) (Welch 1916), which were not present on big floating-heart.

This study has confirmed the limited observations on larval behavior and feeding reported by Forbes (1910), Habeck (1974), and Monroe (1972). Kimball (1965) reported adults collected throughout Florida in every month of the year, but not in north Florida during December and January, which agrees with our phenology data. This is the only species of *Parapoynx* recorded feeding on floating-hearts in North America, but a polyphagous relative, *Synclita obliteralis* (Walker) (Crambidae: Nymphulinae) has also been recorded from it (Habeck 1991). In Europe, the related floating-heart, *N. peltata* (Gmel.) O. Kuntze, is attacked by *Nymphula nymphaeata* L. (Crambidae: Nymphulinae) and possibly occasionally by *Cataclysta lemnata* (L.) (Crambidae: Nymphulinae) (Van Der Velde 1979). We were not surprised that the host feeding range in the laboratory was wider than that observed in the field, but we were surprised that the two plant species most heavily eaten were in the monocot family Hydrocharitaceae. Both species, *E. densa* and *H. verticillata*, are immigrants in North America and are thus new associations with *P. seminealis.* No host records were found for *P. seminealis* on the related North American genus *Elodea.* Interestingly, John and Nanjappa (1988) in India reported that *Parapoynx diminutalis* (Snellen), a native moth common on *H. verticillata,* fed upon and destroyed *Nymphoides cristata* (Roxb.) O. Kuntze. This moth, an immigrant in Florida, did not eat big floating-heart in our laboratory host range tests with it (Buckingham & Bennett 1989). The current study with *P. seminealis* demonstrates both the difficulty of accurately assessing in the laboratory the narrowness of the feeding host range of a biological control agent and the importance of good field host range data in the native range for interpreting laboratory data. We did not demonstrate that caterpillars could complete development on the test plants. However, if field data were lacking, the amounts of laboratory feeding we found might preclude use of even a truly specialized species like this as an introduced biological control agent.

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NYCTEOLA FRIGIDANA WALKER (NOCTUIDAE: SARROTHRIPINAE) REPORTED AT AN UNORTHODOX BAIT

Additional key words: Gadway Barrens, New York, *Salix bebbiana*, insect remains.

On 15 July 1998, while attempting to compare the efficacy of two different types of bait, I noted a commonplace occurrence. Yellow jackets (Hymenoptera: Vespidae; *Dolichovespula arenaria* (Fab.)) were feeding on the fresh spattered insect remains on the front of my vehicle. An hour later, at dusk, I hung out two 30–meter long strands of cotton clothesline rope that were soaked in different bait formulas: the more traditional beer/sugar/molasses bait (Holland 1903) was being compared to a simple bait of red wine saturated with sugar. I ran the trials through uniform jack pine/blueberry habitat on the Gadway Barrens, Clinton County, New York.

The vehicle I used for transportation was parked in a 10-meter gap between the bait trials. I would pass the front of the vehicle each time I traversed the two trials. No apparent differences in habitat existed in the immediate sample area.

Five *Nycteola frigidana* (Wlk.) were observed probing the fresh remains of insects spattered over the windshield and front of the vehicle over the course of the night. One *Caripeta piniata* (Pack.)(Geometridae) and one *Catocala gracilis* Edw. (Noctuidae) were also recorded probing the insect remains. The insect remains on the parts of the vehicle where the *N. frigidana* were observed feeding were determined to be mostly Diptera and definitely not that of Lepidoptera.

The two baited ropes produced many *Idia aemula* Hbn., *I. americalis* (Gn.), *I. lubricalis* (Gey.), *Catocala similis* Edw., *Apamea amputatrix* (Fitch), *A. lignicolora* (Gn.), *Phlogophora periculosa* Gn., *Apharetra dentata* (Grt.), *Pseudaletia unipuncta* (Haw.), *Leucania pseudargyria* Gn., *Agrotis ipsilon* (Hufn.), *Noctua pronuba* L., *Graphiphora auger* Fab. (all Noctuidae), and *Caripeta piniata* (Pack.)(Geometridae), but no *N. frigidana* or *Catocala gracilis*.

Nycteola frigidana comes poorly to both bait and light. I have taken only the occasional specimen at traditional bait on the Gadway Barrens. In June, *Nycteola* caterpillars can be found commonly on *Salix bebbiana* Sarg. (Salicaceae) at this site. Additional information on the range and systematics of *Nycteola* can be gleaned from several sources (Fletcher 1959, McDunnough 1943, Rindge 1961). It is apparent that alternative methods of sampling are possible for these difficult-to-attract moths.

As an aside, I detected no significant differences in numbers or composition of species at the two types of bait being tested.

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HEPIALUS CALIFORNICUS (HEPIALIDAE) OVIPOSITION PREFERENCE ON THE LUPINE *LUPINUS ARBOREUS*

Additional key words: dispersal, tanglefoot, aerially-dispersed eggs.

One of the consequences of complete metamorphosis in Lepidoptera is that larvae and adults experience very different environments and selective pressures. Adult Lepidoptera are far more mobile than larvae, allowing use of a larger portion of the habitat. Adults make important decisions regarding host plants and the location of oviposition sites on this larger scale, decisions that greatly affect larval survival (Setamou et al. 1999). While many Lepidoptera demonstrate specificity in host plant oviposition sites (e.g., Haribal & Renwick 1998), it is less clear whether Lepidoptera that aerially disperse their eggs are similarly selective. Falling into the latter category is the ghost moth *Hepialus californicus* (Lepidoptera: Hepialidae), a nocturnal moth native to the West Coast of the United States. Males of *H. californicus* perch on vegetation and release pheromones, forming leks at dusk and dawn to which females are attracted (Wagner 1985). Gravid females find a host plant for the larvae and release their eggs while hovering over the vegetation. Other species of Hepialidae, notably *Korscheltellus gracilis,* also exhibit similar 'hovering' oviposition behavior (Wagner et al. 1989, Wagner & Rosovsky 1991). The primary host plant for *H. californicus* at Bodega Bay is the bush lupine *Lupinus arboreus*, but larvae are polyphagous and have occasionally been found on *Eriophyllum staechadifolium*, *Helenium puberulum*, *Rumex* sp. and *Rubus* sp. (Wagner 1985).

Wagner (1985) suggested that females scatter their eggs over a wide range of potential host plants and surfaces, an assertion bolstered by a documented case of *H. californicus* ovipositing over asphalt. Widely-dispersed egg-laying by *H. californicus* at BML is questionable in light of: (1) the larval dependence on the bush lupine host plant for survival; and (2) the ability of Lepidoptera to detect the CO_2 signal of host plants (Stange 1997). Wagner (1985) and others (Strong et al. 1995, 1996) noted that *H. californicus* eggs are deposited into the detritus underneath lupine bushes, where the larvae hatch and have to find a lupine stem or root in which to burrow. Since the larvae are small (less than 2 mm at hatching) and extremely vulnerable, and the vast majority of *H. californicus* larvae at BML are found on bush lupines, being deposited closer to the lupine's stems and roots would seem to improve the chances of larval survival. In addition, larger lupine bushes have larger stems and roots, and *H. californicus* larvae are found on the largest stems and roots within a bush (pers. obs.). In this note I present data on non-random *H. californicus* oviposition within bush lupine, along with a technique for collecting aerially-dispersed eggs.

I tested the hypothesis that *H. californicus* oviposits non-randomly and has an increased frequency of oviposition near the center of lupine bushes. I collected *H. californicus* eggs at two sites at the Bodega Marine Reserve, Bodega Bay, California, USA. One was a large patch of lupine bushes east of the marine station (Upper Draw) and one was to the west of the marine station on the lee side of a hill (Mussel Point). At each site, I identified 14 lupine bushes for sampling (28 bushes total). I measured each bushes' length, width, and height in meters. Each bush had four 22.2 cm diameter white plastic plates, covered in "tanglefoot" sticky trap, placed at ground level beneath it. The four plates were allocated to 'interior' and 'perimeter' sites as shown in Fig. 1. Initially, I also placed traps one meter outside the bushes to check for outside-bush oviposition; however, after three trapping dates there had been no eggs laid on the outside-bush plates and I concentrated on within-bush sampling. There were a total of 56 traps/site × 2 sites, for a total of 112 traps. The traps were placed under bushes before sunset (between 1730 and 1900 h, depending on date) and collected in the morning starting at 0645 h. I examined each trap for ghost moth eggs, which were removed after being counted. The numbers of eggs on the two 'perimeter' plates were added to get each bush's perimeter number of eggs, and two 'interior' plates were added to get the interior number of eggs. I sampled during the mating and oviposition period of *H. californicus* over six dates, from late March through early May, 2000.

Over six sampling dates I recovered 187 eggs: 125 eggs in interior traps and 62 in perimeter traps. This difference between the two areas was significant (chi-square: df = 1, $p < 0.001$). This trend was significant across both sites (Fig. 2) and was supported by an analysis of how many traps at each location caught eggs. Of the 23 (out of 28) traps that caught eggs, 13 had interior > perimeter eggs, 7 had perimeter > interior eggs, and 3 had equal numbers – a significant difference (chi-square: df = 2, $p < 0.01$). In comparison, an analysis of bush height, volume (length × width × height), or 'ground coverage' (length × width) on the total number of *H. californicus* eggs laid found no significant correlation (height: df = 1, 26, F = 2.19, $p < 0.15$; volume: df = 1, 26, F = 2.57, $p < 0.12$; ground coverage: df = 1, 26, F = 2.59, $p < 0.12$).

Despite variation in the numbers of eggs oviposited between sites and bushes, I did note a preference by *H. californicus* for oviposition in the center of lupine

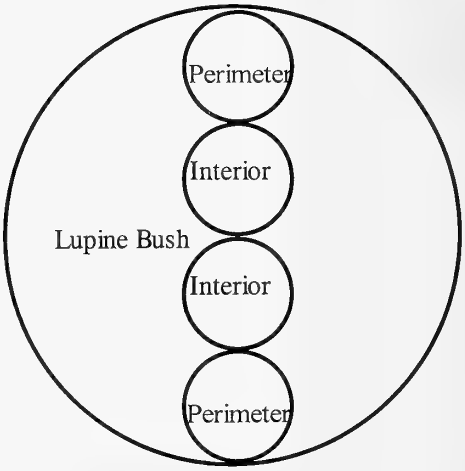

FIG. 1. Trap placement in lupine bushes. The two perimeter and interior traps are added together for the number of perimeter and interior eggs collected per date, respectively.

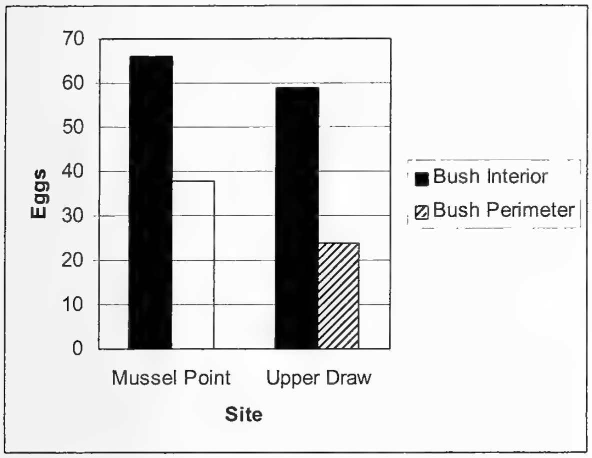

FIG. 2. Total eggs caught per site vs. placement. At both sites, more eggs were caught in interior versus perimeter traps.

bushes. This conclusion is supported by comparisons of both the total numbers of eggs laid as well as the number of bushes with more eggs in the interior than on the perimeter. This preference is reasonable given the additional risk incurred by *H. californicus* larvae that have to travel extensively through a predator-filled zone like the detritus (D. Strong pers. com.). Females capable of detecting the thickest part of a lupine bush and releasing their eggs closer to it would thus increase larval survival.

The above logic might also be applied to oviposition that depends on the size of the lupine bushes; however, there was no evidence of any correlation between oviposition and several indices of bush size. It may be that intraspecific competition for lupine stems and roots is so low due to larval mortality that bushes have approximately the same chance of supporting larvae; however, this is impossible to evaluate without quantifying larval mortality in the detritus. Wagner (1985) suggested that female moths may preferentially oviposit on the lee- versus wind-ward side of bushes, something that may be especially important given BML's strong coastal winds. This hypothesis, however, was not tested in the current study.

The sampling technique used here makes it possible to quantify the amount of 'egg rain' that lupine bushes experience due to *H. californicus*, an important factor in establishing a life-cycle model of *H. californicus* for addressing larger ecological issues. Some of the questions that could be answered by this technique in conjunction with additional experiments include: do different sites have different numbers of eggs, or at different times? Does the location of leks influence where females oviposit? What is the survival rate of eggs deposited close to roots versus at the perimeters of bushes? All of these questions could be answered with further applications of this technique, providing a better sense of the ecological and population dynamics of *Hepialus californicus*.

I would like to thank Rick Karban, Don Strong, Lynne Adler and the Bodega Marine Lab support staff. This project was supported by in-class funds from the UC-Davis Population Biology and Entomology departments.

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STATUS OF *PIERIS VIRGINIENSIS* (PIERIDAE) IN NEW YORK STATE

Additional key words: conservation, Brassicaceae.

Since the introduction of the cabbage butterfly, *Pieris rapae* (L.) (Pieridae), into Quebec around 1860 (Scudder 1889), many changes in the distributions and abundances of members of the genus *Pieris* have been observed in northeastern North America. *Pieris rapae* has spread through most of the continent, while *P. oleracea* Harris and *P. virginiensis* Edwards disappeared from many localities. Competition from *P. rapae* was thought to be the cause for the decline of the native species (Scudder 1889, Forbes 1926), but *P. rapae* does not frequent forested habitats and the two native species prefer to remain beaneath the forest canopy (Klots 1935, Chew 1981). The likely cause of the decline of the native species was the reduction of forest habitat (Klots 1935, Chew 1981, Cappuccino & Kareiva 1985), possibly exacerbated by the introduction of non-native Brassicaceae which are lethal to larvae (Bowden 1971, Chew 1978) but to ovipositing females are not distinguished from the natural hosts (Chew 1980).

I attempted to clarify the current distribution of *P. virginiensis* in New York State to assess the need for attention by the conservation community. The present distribution and abundance of *P. virginiensis* in New York State is poorly understood, partly due to the long-standing synonymy with *P. oleracea* which is sympatric with *P. virginiensis* in New York State (e.g., Hovanitz 1963, dos Passos 1965, 1966). Historic reports without specimens for verification are not reliable. However, the loss of well-known *P. virginiensis* colonies and a paucity of modern reports are seen as symptoms of a general decline within New York State (Forbes 1926, Shapiro 1974). Similar concerns in Ontario proved unwarranted after previously unknown populations were located in the 1980s (Layberry et al. 1998).

I searched the literature for historic (before 1974) and recent (1974–1999) reports of *P. virginiensis* within New York State. The dividing point between "historic" and "recent" was based on reports that Shapiro (1974) would have been aware of. In addition to the literature, the collections at the New York State Museum and Cornell University were examined, the New York Natural Heritage Program database was consulted, and localities with appropriate habitat were visited during the flight periods in 1998–1999.

Pieris virginiensis is broadly distributed in New York (Fig. 1), having been documented from 28 counties. Recent accounts were found from 12 counties and historic accounts were found from 22 counties. During field surveys I encountered the species at 12 localities within 7 counties. Five recent localities were documented in the News of the Lepidopterists' Society Season Summary (1974, 1977, 1987, 1997). Two recent reports were found in the New York Natural Heritage Program database. Sixteen counties have reports dating only from before 1974, while six have strictly recent accounts. Only two localities have reports dating from both time periods.

Localities in which I searched forested habitat for populations included areas in the vicinity of historic records and areas near localities where I found extant populations. Regions from which historic documentation of the species exists but where I did not locate extant populations were the southern Catskill Mts. in Sullivan and Ulster Counties, and the area around Trenton Falls in both Oneida and Herkimer Counties. Extensive deciduous forest remains in these areas, but most of the potential habitat is inaccessible. I did not search in the eastern portions of the Catskill Mountains or the western counties.

The narrow overlap of historic and recent accounts of *P. virginiensis* within New York State suggests that the information available is insufficient to elucidate changes in distribution. Newly discovered localities on the Tug Hill Plateau and central and western counties do not necessarily represent newly colonized habitat. The presence of *P. virginiensis* in southern Ontario and one historic specimen from Potsdam (St. Lawrence County, New York) (Shapiro 1974) suggest the species has gone unnoticed in the Tug Hill region

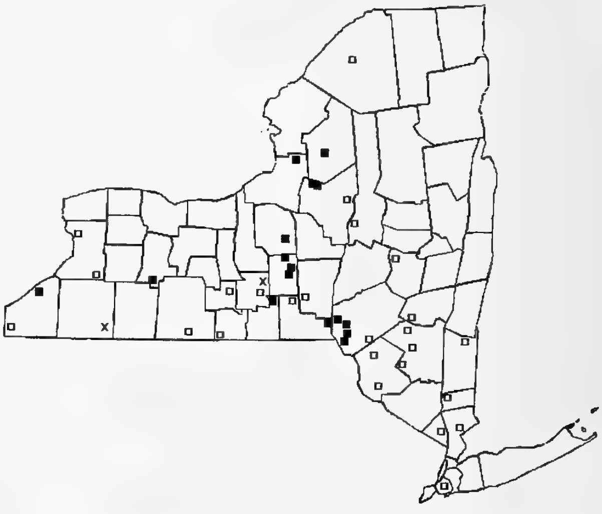

FIG. 1. Map of New York State showing old (before 1974) and recent (1974–1999) collection localities for *Pieris virginiensis* (open square, old; solid square, recent; **x**, both time periods).

until my explicit attempts to locate it there. The possibility also exists that historic records of *P. oleracea* included individuals of *P. virginiensis*, although all specimens I have seen were correctly identified.

Populations in western counties may also have long escaped notice. *Pieris virginiensis* was last reported from the Buffalo metropolitan area in 1873 (Forbes 1926), but has recently been found in adjacent Chautauqua County (Season Summary 1987). Reports from the vicinity of Olean in Cattaraugus County spans both time periods considered here (Shapiro 1974, Season Summary 1993) but could have included an extirpation followed by recolonization, as was documented in McLean Bog (R. Dirig, Season Summary 1974).

The possibility also exists that *P. virginiensis* populations have shifted hosts and are moving into areas previously unoccupied. Courant et al. (1994) and Porter (1994) discussed the strong selective pressures associated with the use of non-native Brassicaceae by native pierines. Porter (1994) presented three possible outcomes for a population encountering the spread of non-native Brassicaceae, including the initial decline of the native *Pieris* population as the lethal effects of the new host remove individuals feeding on the lethal host, followed by an increase due to two potential responses. Selection would favor females that recognize the lethal host and refuse to oviposit, or selection would favor larvae capable of utilizing the new host. The third outcome would be loss of populations as the non-native, lethal host expands its range and dominance across the landscape. The host association of populations at most of the localities in which I found *P. virginiensis* could not be ascertained. All sites where large colonies were found were associated with native *Dentaria*. The relationship between *P. virginiensis* and the native and non-native Brassicaceae continues to be a question requiring research. The populations in and around Tompkins and Cortland Counties, which include the recolonized McLean Bog, may offer an arena for such observation.

The loss of forest continues to be the greatest threat to the viability of *P. virginiensis* populations. Historic extirpations typically have been noted in areas of urban expansion. Colonies are occasionally found in woodlands within suburban areas. These habitats are more suitable to *P. rapae*, but the responses of native *Pieris* species to habitat conversion are not understood.

Although *P. virginiensis* is likely less common than in the past (Cappuccino & Kareiva 1985), it remains in many forested areas throughout New York State. However, no conclusion regarding its long-term viability can be made until additional information on the population dynamics within a series of localities in New York State is gathered. The number of unknown populations I found during only a few days within two flight seasons indicates that additional surveys will find this species more widespread than is made apparent by the distribution map included here (Fig. 1), particularly in the Catskill Mountains and the vicinity of Allegany State Park. Additional survey efforts should also be given to localities with historic documentation but lack recent specimens.

I would like to thank James Liebherr for permitting access to the collection at Cornell University, Tim McCabe for supplying label data from specimens in the New York State Museum, Kathy Schneider for supplying copies of reports in the New York Natural Heritage Program database, and F. Chew and A. Porter for their reviews of this manuscript. Vouchers taken during field studies were deposited in the collection of the New York State Museum in Albany.

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FLYING JEWELS—BUTTERFLY IMAGES, by Yasutaka Murata & Daisaburo Okumoto. 2001. Publisher: Shueisha Inc, 5-14, Sarugaku-cho, 1-chome, Chiyoda-ku, Tokyo, 101-8050 Price: 4,410 Japanese yen [written in Japanese] ISBN4-08-532058-0.

This slim book is a collection of 76 butterfly portraits photographed in natural habitats. The photographic localities range from Japan, China, Indonesia, Europe, North America, Mexico, Central and South America. Each photograph is accompanied by minimal text describing the location and behavior of the butterflies, and occasionally, the impression of the authors. I confess that, given the number of pretty picture books in the world dedicated to butterflies, I did not anticipate being taken by Flying Jewels—Butterfly Images. However, it became clear that this book includes images that are truly unique, beautiful and show a patient understanding of both photography and subject.

In particular I was impressed by those images taken with a 15 mm lens. These not only provide an astonishing butterfly's view of the world, but considering the balance of light, the user hostility of a 15 mm lens, and the color balance that is involved in film photography, these images are mini-miracles. How does *Morpho amathonte*, *Teinopalpus aureus* or *Papilio glaucus* see the world when flying along a forest edge? What does the world look like to puddling males of *Agehana maraho* or *Trogonoptera trojana*? What view of the world does *Lycaena phaleas* have when feeding on a sunflower, or *Polygonia c-aureum* when feeding on a persimmon fruit that still hangs from the tree? Thanks to the images in this book, we have come much closer to knowing the answers.

Following these extraordinary images there is a section (in Japanese) stressing the worldwide need for conservation to preserve butterflies in particular, and natural habitats in general. The final text encompasses brief technical descriptions of where each photo was taken and what equipment was employed. Although Flying Jewels – Butterfly Images is decidedly not a scholarly work, the images in this book form a connection between the reader and the projected sense of wonder of the photographer for the subject. And that is natural, reflective art.

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SESIIDAE—CLEARWING MOTHS. HANDBOOK OF PALAEARCTIC MACROLEPIDOPTERA. VOLUME 1. Karel Špatenka, Oleg Gorbunov, Zdeněk Laštůvka, Ivo Toševski, and Yutaka Arita, 1999. Watercolor illustrations by Bohumil Starý, Ruth Holzinger, and František Gregor. Genitalic illustrations by Oleg Gorbunov and Ivo Toševski. Clas M. Naumann, Managing Editor. Published by Gem Publishing Company, Brightwood, Brightwell cum Sotwell, Wallingford, Oxfordshire, UK OX10 0QD. ISBN 0-906802-08-3. xv + 569 pp., 487 color illustrations, 504 male and female genitalic illustrations, and 309 distribution maps; all reproduced by off-set printing. Hardbound with color jacket. Price £120, $170.00 (US). Shipping, £5, $7.12 (US) for first copy, £3, $4.30 (US) for additional copies; overseas shipping, £10 for first copy, £5 for additional copies. Subscriptions to The Gem Publishing Company are accepted by check or banker's draft in sterling or US dollars. Payment may also be made directly into Giro Account No. 467-6912.

In 1991, an editorial board for The Handbook of Palaearctic Macrolepidoptera (HPM) was formed. As stated in Volume 1, HPM "is not meant to cover the entire field of the butterflies and the larger moths," but to "provide a basis for the treatment of those groups where critical, reliable and experienced taxonomists are available and willing to devote themselves to preparing modern revisions to their special groups." Moreover, "HPM will not compete with Microlepidoptera Palaearctica." Given the above, and the fact that the placement of Sesiidae within the Microlepidoptera is unlikely to be challenged, it is difficult for this reviewer to ascertain how the editorial board of HPM has determined taxonomic coverage of its publications. Clearly, there appears to be a taxonomic inconsistency between what is being advertized (by HPM) and what is being published. That said, I think that volume 1 on Sesiidae is one of the more comprehensive and superbly illustrated works published on any lepidopteran taxon.

This book is divided logically into several parts in the following order: introduction; check-list of Palaearctic Sesiidae; known host-plants; keys to the subfamilies, tribes, and genera; a taxonomic treatment, including Insertae sedis; bibliography; color and black-and-white illustrations of the imagos; and indices to insect names and technical terms, and plant names.

The introduction contains several concise, well written parts that include an historical review, diagnostic characters of the family, morphology, biology, natural history, mimicry and behavior, distribution, economic importance, collecting, and rearing. Although a phylogenetic classification of the tribes within Sesiidae is presented (Fig. 10a), no summary of supportive characters is provided.

The check-list of Palaearctic Sesiidae appears complete with all species arranged to reflect some degree of relatedness. The authors have provided all synonymies. In addition, a list of host-plants is arranged alphabetically by the species-group names. All moth species are arranged, as within the check-list, within their respective taxonomic categories, with all authors and dates given. In addition, all associated host-plants are provided with their respective family names in an easily readable table.

Keys to the subfamilies, tribes, and genera emphasize features of the antennae, wing venation and degree of wing transparency, legs, and male and female genitalia. The couplets are dichotomous, easy to read, and emphasize features that are relatively easy to diagnose. The keys to the species are a pleasure to read because they emphasize body maculation. However, in a group such as the Sesiidae, the authors recommend, especially when trying to identify a "rubbed" specimen, that the genitalia be used to confirm the identity.

The taxonomic treatment for all species included provides the bulk of the text. It is divided into several sections that include a complete synonymy, diagnosis, variation, including sexual dimorphism, male and female genitalia, bionomics, habitat, and distribution maps. Because the male and female genitalia of the type-species of *Zhuosesia* Yang, 1977 could not be examined, its subfamilial and generic placement could not be made; and consequently it is placed Insertae sedis.

Although this volume has several coauthors, its descriptions are surprisingly uniform. However, there are some general inconsistencies to be noted. First, relative lengths given for the apophyses posteriores and antrum in females, are too general. Terms like "comparatively long" or "quite short" are not informative. On occasion, lengths relative to some other structure are given, e.g., "the antrum is twice the length of the eighth segment." It may have been better to use these ratios or some other ratio throughout the text more consistently. In addition, the position of the ductus seminalis in the female is inconsistently illustrated (either present or absent), and its position relative to the ostium bursae and the inception of the corpus bursae would have been valuable to include in the description of the female genitalia. Other inconsistencies include the description of the "thorns" on the distal part of the aedeagus in the male and the "bifid" nature of the coecum penis of the aedeagus in the male; are probably due to reduction of the original illustration and the orientation of the specimen when it was illustrated.

Several errors of omission or interpretation were noted during a detailed review of the species descriptions of Tinthiini and Sesiini. For example, in *Tinthia tineiformis* (p. 38) the corpus bursae is described as having "a small rounded signum in upper part," while the associated text Fig. 276 lacks a signum. The uncus in males of *Tinthia myrmosaeformis* and *T. hoplisiformis* are described as being "hooked and bifurcate," but these features are not illustrated in text Figs. 13 and 15, respectively. The text includes a description of the female genitalia of *Tinthia mianjangalica* (p. 42), but the text figure is omitted. The description of *Paradoxecia gravis* (p. 50) indicates that the corpus bursae "has a sclerotized field," yet it appears only partially illustrated. Moreover, the corpus bursae appears to have a long crescent-shaped signum, which is not mentioned in the description. Descriptions of the female genitalia for *Sesia repanda* and *S. przewalskii* erroneously indicate that the antrum is V-shaped. In these cases, it is the anterior margin of the ostium that is V-shaped.

An extensive bibliography contains 830 references, including the most important references dealing with the Palaearctic Sesiidae. However, many faunistic, biological, and other references were prudently excluded from an already useful bibliographic listing.

There are 489 beautifully reproduced color illustrations of the imagos with several accompanied by illustrations of the head and its appendages and/or other diagnostic body features. The original illustrations were rendered in water color. The reproductions are 2× original size. Some of the illustrations of species that have heads and other body appendages illustrated separately could have been made larger as their small size restricts the reader from seeing diagnostic color patterns.

Genitalic features represented by 276 male illustrations and 228 female illustrations were rendered in black ink. One male illustration (text fig. 5) and 1 female illustration (text fig. 7) are accurately labeled to offer the user a clear understanding of the terms given in the descriptive text. Five male illustrations and 3 female illustrations appear to be added to accommodate 8 species that were discovered after the position of the bulk of the illustrations of the book plates were already "fixed." Although, the addition of a section to accommodate these additional species appears awkward, it does not detract from the work, but adds to its completeness. Easy-to-read distribution maps for all 309 species are provided.

Two indices are provided, one for insect names and technical terms and one listing the species of host-plants included. I found it very convenient that for each moth species listed in the index that the primary locator pages are in bold, the page the species is found in the species key is indicated, and pages for all plates and text figures are given. Additionally, a square symbol precedes the page number on which each distribution map for a given species is found. In the host-plant index, I found it very useful to have the family name provided for each species of plant listed.

In conclusion, I find this volume a very useful contribution to the taxonomic understanding of Palaearctic Sesiidae and of Lepidopterology in general. If a phylogenetic classification had been included with a presentation and discussion of supportive characters, the volume would have been a standard for future works edited by any organization. The taxonomic completeness and depth, along with the fine color and black-and-white line illustrations greatly overshadow the few errors and inconsistencies found in the text.

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MARIPOSAS ARGENTINAS: GUÍA PRÁCTICA E ILUSTRADA PARA LA IDENTIFICACIÓN DE LAS PRINCIPALES MARIPOSAS DIURNAS Y NOCTURNAS DE LA PROVINCIA DE BUENOS AIRES, by Andrés E. Varga. 2000. Published by the author. 148 pp. Paper. ISBN: 987-43-1671-3. Approximately US $60. Price available from the author: museo@mariposasdelmundo.com; fax (54) (11) 4664-2108; mail address Calle Italia 650, San Miguel 1663, Pcia. Buenos Aires, Republica Argentina. (In Spanish.)

What do you know about the Southern Cone—the south-temperate zone comprising Chile, Argentina and Uruguay? (It is cone-shaped; look at a map.) You probably have some notions of tango and gauchos and military dictatorships, but did you know that the region embraces some of the greatest natural beauty on the planet, an incredible array of biomes, and a unique flora and fauna? Long better-known to Europeans, the Southern Cone only recently has begun to attract significant eco-tourism from the USA.

What do you know about the butterflies there? For most people, Lepidopterists or not, South America equals big, shimmering blue Morphos and gaudy swallowtails. But things change beyond the Tropic of Capricorn, and for most of us the Southern Cone is terra incognita. The biggest problem has been the lack of a field guide or faunistic treatment for any of the countries. Here is a paradox. All three countries have strong entomological traditions going back to the middle of the nineteenth century, with indigenous journals and abundant Lepidopterological literature—but until very recently, nothing one can actually use afield. There are taxonomic catalogues of all three faunas. They are antiquated, not very accessible, and typically not illustrated. Uruguay has the least interesting fauna. The country is small, nearly flat, and mostly agriculturalized. Virtually everything found there occurs in Argentina too.

The first breakthroughs to a popular field guide occurred in Chile. Butterfly studies in Chile were dominated for half a century by two arch-rivals, the academic José ("Pepe") Herrera G. and the accomplished amateur Luis E. ("Lucho") Peña G. Peña was better-known outside Chile: he sold specimens of the Chilean entomofauna worldwide and collaborated in the filming of nature documentaries for the BBC and others. He prepared a small pocket guide to Chilean butterflies that was distributed as a subscription premium by a newspaper in the 1970s. This was later expanded into a real book, Las Mariposas de Chile (with coauthor Alfredo J. Ugarte P.), appearing in 1997 (Editorial Universitaria, Santiago) after Peña's death. Even as this work was in preparation, many new species of lycaenids were being discovered by the Israeli Dubi Benyamini and others, and described by Kurt Johnson, Zsolt Balint, and Benyamini. These were worked into the manuscript. Thus we have an up-to-date and effectively complete reference work available for Chile.

The Argentine situation is much more daunting. The Argentine fauna is perhaps an order of magnitude richer. Unlike Chile, Argentina extends into the humid lowland tropics. Elements of the enormous fauna centered on Amazonia extend through the Argentine northeast and as far south as the subtropical forests of Tucumán. Argentina is a land of great physiographic, climatic and ecological complexity. The lowland tropical fauna articulates with the tropical Andean and altiplano fauna in the dissected yungas of Salta and Jujuy. In places one can drive from rain forest (selva) through Andean-alpine habitats to mesquite and columnar cactus desert in four hours. To the south lie zones of subtropical thorn scrub (espinal), creosote-bush desert (monte), subhumid to subarid bunchgrass prairie (pampa), cool Patagonian desert-steppe (including southern juniper woodland) and the cool to cold montane forests of the Patagonian Andes and southwestern Tierra del Fuego. What a country! Unlike Chilean Patagonia, Argentine Patagonia is relatively dry and sunny, fostering a rich butterfly fauna. And recent studies have revealed tremendous evolutionary dynamism there and along the steppe-forest ecotone, a veritable "ferment of variability." How to deal with such a fauna?

In 1973 Kenneth Hayward, an Englishman long resident in Argentina, published a taxonomic catalogue of the butterflies and skippers of the entire country. It contained hardly any biology, had no range maps or plates, and was rife with errors, but it has had to serve as the foundation of modern Argentine butterfly studies. Hayward was also responsible for an extraordinary four-volume work on Argentine butterflies, in oversize format with magnificent lithographic plates in the style of Edwards and Scudder. Published between 1948 and 1967 under the pompous series title "Genera et Species Animalium Argentinorum," this rare and ponderous work was intended to initiate a complete zoological inventory of the country. It represents the acme of Peronist pretension; indeed, Juan Domingo Perón himself patronized the initial volumes. This work does contain some biology, but it is hardly useful as a field guide, nor is it widely or readily accessible even within the country.

Andrés Eugenio Varga has undertaken to change the situation for the better. Argentina is an entrepreneurial country, and in the Buenos Aires suburb of San Miguel, about 30 km from the city center, Varga has opened a Museum of Butterflies of the World displaying some 70,000 mounted specimens in uniquely-constructed concave display cases (intended for ease in viewing) under filtered light. There is a biology lab, a rearing facility and a library. The museum—first of its kind in the Southern Cone—is open to guided tours only Monday through Friday, and on a drop-in basis to the general public on Saturdays. It has a support group, the Friends of the Museum, and has initiated its own journal. Meanwhile, Varga has published the first in a projected series of four volumes intended to cover the butterfly fauna of the entire country. Unsurprisingly, it focuses on the Province of Buenos Aires. Volumes 2 through 4 will cover (in order) "Mesopotamia" (the humid tropical northeast), the pampa and cuyo (the desert-Andean contact zone centered on Mendoza), and Patagonia and Tierra del Fuego. He's made a good, if not perfect, start.

Mariposas Argentinas is lavishly produced, in 20 × 28 cm format, with color illustrations on nearly every page. The color reproduction is remarkably true—even capturing the elusive near-UV purple sheen on the upper surfaces of *Colias lesbia* (p. 27). There is an introductory essay by Varga emphasizing global change and the biodiversity crisis. This is followed by six pages of basic butterfly biology and anatomy and a résumé of basic taxonomy (the Linnean hierarchy, binomial nomenclature and the Code—cladistics is not mentioned). The main part of the book—the species accounts, about which more anon—occupies pp. 17–94. This is followed by a very detailed 20-page section on collecting and preserving butterflies. Some may find this material retrograde in emphasis, or at least inconsistent with the author's conservationist rhetoric. There is a 2-page overview of the Museum and its projects, a 4-page glossary (84 terms), a 7-page bibliography (118 items), and 2 pages of maps. The bibliography contains both Argentine and foreign references. Of the former group three were new to me, and one of those—in an obscure agricultural extension venue—is not in Lamas, Robbins and Field's Annotated Bibliography of the Neotropical Butterflies and Skippers (Scientific Publishers, Gainesville, Florida, 1995) although it dates from 1968. Varga has published most of the material other than species accounts previously as freestanding articles in Argentine magazines.

The species accounts cover 171 butterflies and skippers, most of which are illustrated. Many show sexual and seasonal dimorphism, and both dorsal and ventral surfaces. The nature of the variation is usually explicit in the captions; an exception is the pierid *Tatochila vanvolxemii* (p. 25), which has seasonal forms analogous to our *Pieris napi*, but they are not identified as such. In addition to the butterflies, a selection of large and showy moths is presented. The Black Witch represents the Noctuidae. There are 14 saturniids, 13 sphingids, and miscellaneous arctiids, pericopids, lasiocampids, ctenuchids, etc.—all common and familiar. There are also several pages of photos of representative (again, showy) larvae.

The text accompanying these photos is somewhat disappointing. Frequently it consists merely of a verbal description of what is evident in the photo. (Since the pictures are natural size, this is hardly necessary.) There is little biology, and some of what is given is suspect. This is especially true of host plant records, which are given without attribution and (as Varga told me) sometimes straight out of Hayward. Opening randomly to page 72, I immediately saw the familiar fiery Skipper, *Hylephila phyleus*, which is as much a lawn and garden "weed" in Buenos Aires as in Los Angeles or Houston. In B.A. it routinely breeds on (surprise!) Bermuda Grass, *Cynodon dactylon* ("Pasto Bermuda," "Gramilla Blanca," "Pato de Perdiz") and other lawn grasses and on *Paspalum* ("Pasto Miel," "Gramilla

Dulce") and other weedy species. Varga says: "The caterpillars eat grasses, including Sugarcane, Achiras, etc." "Achira" is the Spanish name for *Canna*, which is not a grass but is a skipper host. I do not know if either Sugarcane or *Canna* really is a host of *H. phyleus*, but they are certainly not the most important ones. On the same page is the Argentine Least Skipper, *Ancyloxypha nitidula*. No host is specified. In my experience this species is often intimately associated with the grass *Leersia hexandra*; at any rate, it should be easy to find out what it eats. One hopes later editions and volumes will rely more on information from life and less on antique and questionable published sources.

The taxonomy appears up-to-date and was vetted by Profs. Carlos Mielke and André Victor Lucci Freitas of Brazil and a local Argentine specialist, Joaquin Carreras.

There are too many typographical errors. Many of the bibliographic citations are incomplete.

Factual errors are rare, but there is one important bit of confusion that appears on p. 17. Under *Euryades corethrus* (Papilionidae) we read: "They are characterized by two mighty extremities (harpagones) in the posterior part of the abdomen, which the females possess in order to hold on during copulation and prevent new fertilizations." This refers, of course, to the sphragis—a "chastity belt" secreted by the male during copulation, not an integral part of the female. The sphragis of *Euryades* is indeed "mighty." It is also flamboyant, bilobed, and—when fresh—bright green (!). What are "harpagones?" In the glossary this Spanish term is given as a synonym of harpes, which are correctly defined as "periphallic moveable processes . . . which usually function in subjugating the female during copulation." The lobes of the sphragis no tienen nada que ver con harpagones.

This book is a vast improvement over what was available before. It is not cheap. Books have always been expensive in the Southern Cone, despite the fact that Buenos Aires shares with Mexico City the traditional intellectual leadership of Latin America. Mariposas Argentinas, the set, will however be indispensable to any serious student of the butterflies of the region: the later volumes all the more so. The fauna of the Province of Buenos Aires is probably the least interesting of the lot, but it has its biogeographical charms. It is mostly derived from the lowland Neotropics. A number of such taxa enter the Province only in the riverine and swamp forests of the Tigre Delta; from the capital south the Neotropical element is very dilute. Endemic austral-Patagonian elements enter in the grasslands. The admixture is well illustrated by the Satyridae. Two radiations are represented. The euptychiines are lowland-Neotropical. The pronophilines have radiated twice in South America, with one large radiation in the tropical Andes (often associated with bamboos) and the other in the temperate grasslands, extending into alpine steppe and grassland. It is the latter group that reaches its northern limit in the littoral in the Province of Buenos Aires. One species, *Etcheverrius* (=*Cosmosatyrus*) *chilensis*, extends from there to far-southern Patagonia, and also occurs widely in Chile. Except for some of the skippers, the Buenos Aires fauna is fairly well-known. The same cannot be said for the fauna of any other region. Varga's emphasis on collecting is justified in places where one can still collect three new species in one day (as I once did in Patagonia). He asks on p. 6: "How can we claim to conserve that which we still don't know?" A good question, and this book may stimulate others to get out and learn the Argentine fauna while it is still in place. Otherwise, he says, we will all too soon "lament, as we remember this beautiful world that we had but couldn't take care of."

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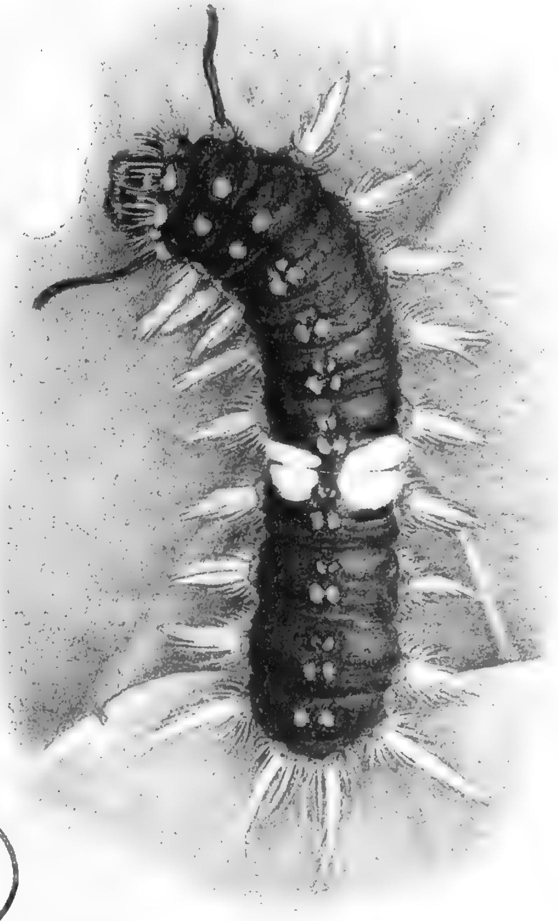

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REVIEW OF *REBINEA* RAZOWSKI AND *ELIACHNA* RAZOWSKI (TORTRICIDAE: EULIINI)—SISTER GROUPS ENDEMIC TO CHILE AND ARGENTINA

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ABSTRACT. *Rebinea* Razowski and *Eliachna* Razowski, two formerly monotypic genera known only from males, are redescribed based on large series of specimens (n = 320) including both sexes. As presently defined, *Rebinea* is monotypic, with a single variable species, *R. erebina* (Butler, 1883), and its synonym, *Arotrophora balsamodes* Meyrick, 1931. It is possible that two (or more) species are concealed within the variation, but we were unable to separate them using traditional morphological characters. *Eliachna* is represented by three species: *E. chileana* Razowski, 1999, ***E. digitana* Brown and McPherson, new species,** and ***E. hemicordata* Brown and McPherson, new species.** Both genera are restricted to south-central Chile and southwestern Argentina, ranging from coastal lowlands (5 m) to middle elevations (1200–1700 m) at the southern end of the Andes. A phylogenetic analysis of the four species (plus two out-group species) provides support for the sister relationship of *Rebinea* and *Eliachna* based on the following synapomorphies: (1) elongate labial palpi (length 3–4 times horizontal diameter of the compound eye); (2) a pair of stout, digitate, submedial processes on the dorsum of the transtilla; (3) a deep, rounded excavation near the mid-venter of the valva; and (4) a pair of semicircular, lateral flanges from the posterior edge of the sterigma.

Additional key words: new species, genitalia, phylogenetics, leafrollers.

The tortricid fauna of Chile and Andean Argentina is distinct from that of the remainder of South America, comprised primarily of endemic, or nearly endemic genera (e.g., *Accuminulia* Brown, *Acmanthina* Brown, *Argentulia* Brown, *Chapoania* Razowski, *Chileulia* Powell, *Eliachna* Razowski, *Haemateulia* Razowski, *Nesochoris* Clarke, *Proeulia* Clarke, *Rebinea* Razowski, *Recintonia* Razowski, *Varifula* Razowski). Although the contributions of Razowski (1995, 1999) and Brown (1998, 2000a, b) have added substantially to our knowledge of Euliini of this region, phylogenetic relationships among genera of the tribe are unresolved and many species remain undescribed. Prior to this study, *Rebinea* and *Eliachna* were considered monotypic, known only from a handful of males. The discovery of additional specimens of the two genera, including both sexes, reveals a close phylogenetic relationship between them and the presence of two new species. The purposes of this paper are to redescribe *Rebinea* and *Eliachna* based on new information, describe two new species of *Eliachna*, provide data on the geographic distribution of the included species, and examine the phylogenetic relationship between the two genera.

MATERIALS AND METHODS

We examined 320 pinned adults of *Rebinea* and *Eliachna* deposited in the following institutions: American Museum of Natural History, New York, New York, U.S.A. (AMNH); The Natural History Museum, London, England (BMNH); Mississippi Entomological Museum, Mississippi State, Mississippi, U.S.A. (MEM); Essig Museum of Entomology, University of California, Berkeley, California, U.S.A. (UCB); National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (USNM); and Zoological Museum, Copenhagen, Denmark (ZMC). Specimens were sorted by forewing pattern, geographic location, and sex. The resulting groups then were examined for differences in male and female genitalia, which have been shown to provide the most reliable morphological features for distinguishing among related species of Tortricidae. Preparation of genitalia slides followed the methodology summarized in Brown and Powell (1991). Because of the phenotypic similarity of, and variation within the treated species, we examined the genitalia of all male specimens. For undissected specimens, we used a fine camel-hair brush to remove scales from the external margin of one valva, which provided enough detail to convincingly assign all males to a species-level taxon. Specimens were examined using a Wild M3Z dissecting microscope; slide mounted genitalia were studied using the dissecting microscope and a Zeiss compound microscope. Illustrations of genitalia were drawn with the aid of a Ken-A-Vision microprojector (model X1000-1). Unless indicated otherwise, genitalia illustrations are of a single preparation. Text descriptions of all characters are composite, based on all available specimens. Measurements of forewing and labial palpi were made with an ocular micrometer mounted in a Wild M3Z dissecting microscope under low power (×10–16). Forewing length was measured in a straight line from the base to the apex of the wing, including the fringe. Forewing width was measured at the widest place perpendicular to the length measurement. Where available, a minimum of 15 individuals of each sex were measured. Colors follow Ridgway (1912); terminology for wing venation and genitalia structures follows Horak (1984). Abbreviations and symbols are as follows: DC = discal cell; ca. = circa (approximately); n = number of individuals examined; $\bar{x}$ = mean; N, E, S, W = compass points.

Polymorphism or moderate variation in phenotype is uncommon to rare in most Euliini. However, many euliine species in Chile and Argentina (e.g., *Chileulia*, *Proeulia*, *Haemateulia*), including the two genera treated here, are variable in forewing pattern and maculation. Consequently, examination of the genitalia is the only reliable method for accurately identifying species. Comparison with the illustrations provided is highly recommended. For males, the profile of a single valva is adequate; females must be dissected.

SYSTEMATICS

Rebinea Razowski, 1986

Rebinea Razowski, 1986:22; Powell et al., 1995:145; Razowski, 1999:84.

Type species. *Sericoris erebina* Butler, 1883:72, by original designation.

Diagnosis. Adults of *Rebinea* are superficially and morphologically most similar to those of *Eliachna* among described Euliini genera. The two share a similar forewing shape, size, and pattern; extremely elongate labial palpi (3–4 times horizontal diameter of the compound eye); a pair of stout, digitate, submedial processes from the dorsum of the transtilla; a deep, rounded excavation near the mid-venter of the valva; and a pair of semicircular, lateral flanges at the posterior edge of the sterigma. Superficially, males of many *Rebinea* can be distinguished from *Eliachna* by their slightly longer forewings and paler ground color. Genitalia characters that distinguish *Rebinea* from *Eliachna* include its broad, straight aedeagus, with a single, large, compound conutus; the absence of an elongate, free process at the distal end of the sacculus; and an extremely short, broad ductus bursae.

Redescription. Head: Antennal cilia approximately 1.5 times width of flagellomere in male; cilia short, unmodified in female. Labial palpus porrect, 3–4 times horizontal diameter of eye in both sexes (i.e., without dimorphism). Vertex with overhanging tuft of scales. Proboscis present, presumably functional. Ocellus moderately large. Chaetosema present. Thorax: Smooth scaled. Male without foreleg hairpencil. Forewing (Figs. 5, 9): Length 2.3–2.6 times width; length of DC ca. 0.6 times forewing length; width of DC ca. 0.2 times DC length; CuA_2 originates 0.6–0.7 along DC length; all veins separate beyond DC; chorda and M-stem absent; CuP weak, present only at margin. No upraised scale tufts; male without costal fold. Hindwing: Sc + R and Rs closely approximate at base; Rs and M_1 stalked; M_3 and CuA_1 connate or short-stalked; CuP present; M-stem absent; tuft of hairlike scales at base of 1A + 2A in both sexes. Abdomen: Smooth scaled; dorsal pits absent; no modified corethrogyne scaling in female. Male genitalia (Fig. 10): Uncus short, moderately stout, curved, strongly sclerotized; socius moderately short, hairy, drooping, slightly expanded distally; gnathos arms slender, with a delicate terminal plate; transtilla a transverse band with a pair of stout, digitate, submedial processes on dorsum, sometimes with tips slightly expanded; valva broad at base, with deep, rounded excavation near mid-venter; sacculus restricted to basal portion of valva, strongly sclerotized, ending in short, dorsal-projecting hook; pulvinus absent; vinculum well developed, strongly sclerotized; juxta large, stout arrowhead-shaped. Aedeagus large, straight, with a single large, compound, capitate cornutus, consisting of several fused filaments; vesica finely spiculate. Female genitalia (Fig. 14): Apophyses anteriores and posteriores moderate in length, slender. Sterigma relatively broad, with narrow, shallowly U-shaped, sclerotized band and a pair of semicircular lateral flanges from posterior edge. Ductus bursae extremely short, broad, with a short membranous region immediately anterad of antrum; a frail, obovate, accessory bursa from a moderately long ductus originating from dorsum of corpus bursae in posterior one-third; corpus bursae moderately large, ovoid, with dense spiculae and a large, irregularly rounded, sclerotized plate, usually along lateral wall.

Distribution and biology. *Rebinea* is known from Chile and Argentina between about 30° and 45°S latitude, ranging from the coastal lowlands (50 m) to the middle elevations (1400 m) of the southern Andes (Fig. 1). Collecting localities seem to have little in common in terms of habitat type, ranging from

Nothofagus forest (e.g., Alto Tregualemu) to xeric areas dominated by succulents and leguminous trees (e.g., Nague, Los Vilos) (see Davis 1986 for descriptions of the habitat at many of the collecting localities listed below). Adults have been captured primarily in October (n = 16), November (n = 118), and December (n = 95), with a few specimens recorded from January through March. The early stages are unknown.

Remarks. Razowski (1986) included two species in *Rebinea*: *R. erebina* (Butler) and *R. balsamodes* (Meyrick). Powell et al. (1995) synonymized the two without explanation. Although the types of the two nominal taxa are fairly distinct in forewing size and facies, they have extremely similar genitalia. The abundance of material now available from Chile and Argentina suggests that the two probably represent forms of an extremely variable species. Alternatively, there may be more than one species concealed within this variation (see discussion below).

Rebinea erebina (Butler, 1883)

(Figs. 1, 5, 9, 10, 14)

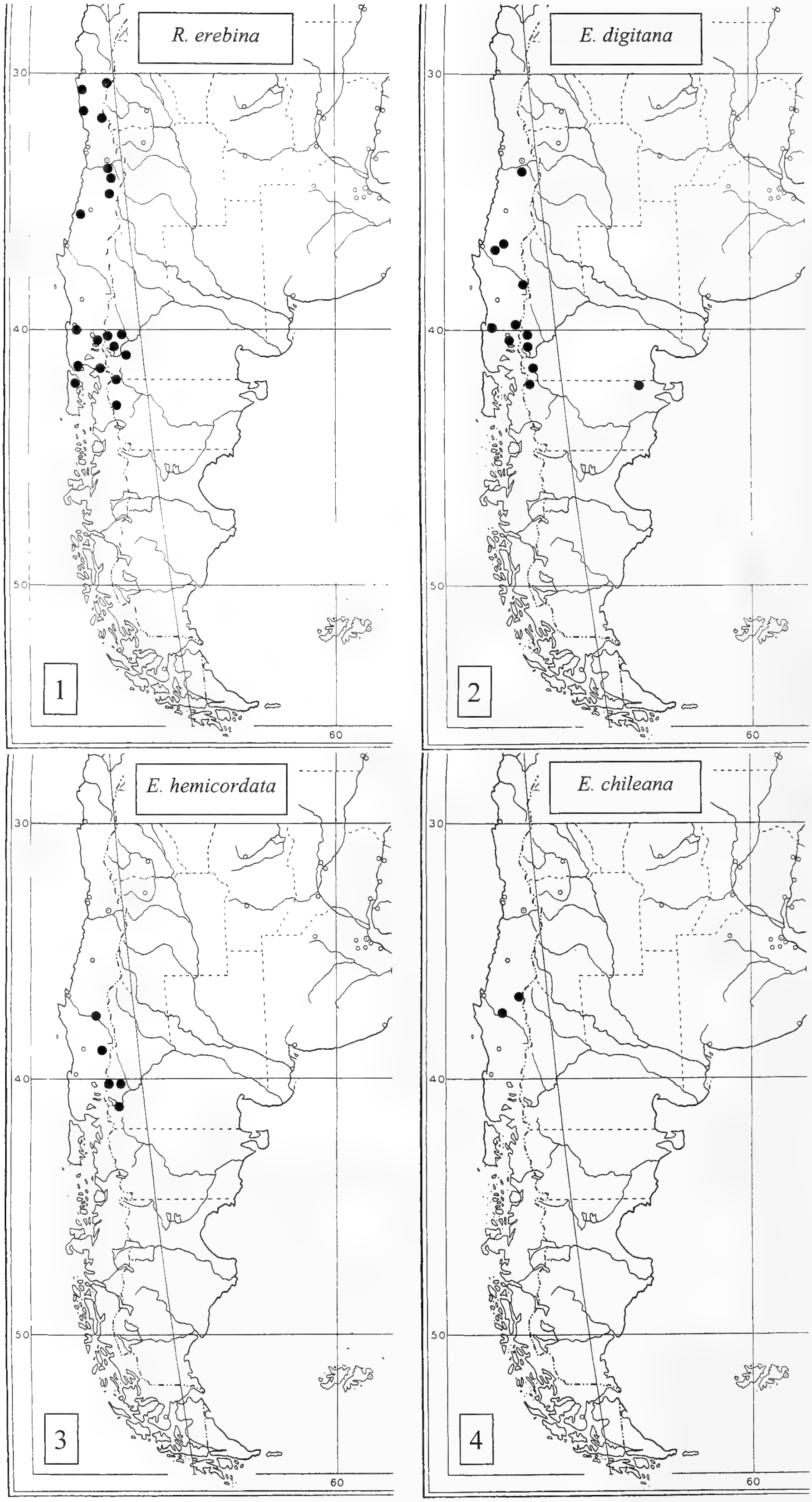
Sericoris erebina Butler, 1883:72.
Arotrophora balsamodes Meyrick, 1931:381; Clarke, 1963:8 [illustration of adult and male genitalia].
Rebinea balsamodes: Razowski, 1986:22.
Rebinea erebina: Razowski, 1986:22 [illustration of male genitalia]; Powell et al., 1995:145; Razowski, 1999:84.

Diagnosis. *Rebinea erebina* resembles *Eliachna* species in general facies; most individuals (especially females) cannot be separated by forewing length and pattern. The male genitalia of *R. erebina* can be distinguished easily from those of *Eliachna* by its broad, straight aedeagus with a large compound cornutus, and the absence of the elongate, free process of the sacculus. In addition, the overall shape of the valva is distinct, with a short hooklike process at the terminal end of the sacculus; the latter likely represents an autapomorphy for *Rebinea*. The female genitalia of *R. erebina* are similar to those of *Proeulia*, *Argentulia*, and other related Chilean-Argentinean genera, with an extremely broad ductus bursa and an irregularly sclerotized, highly spiculate corpus bursa.

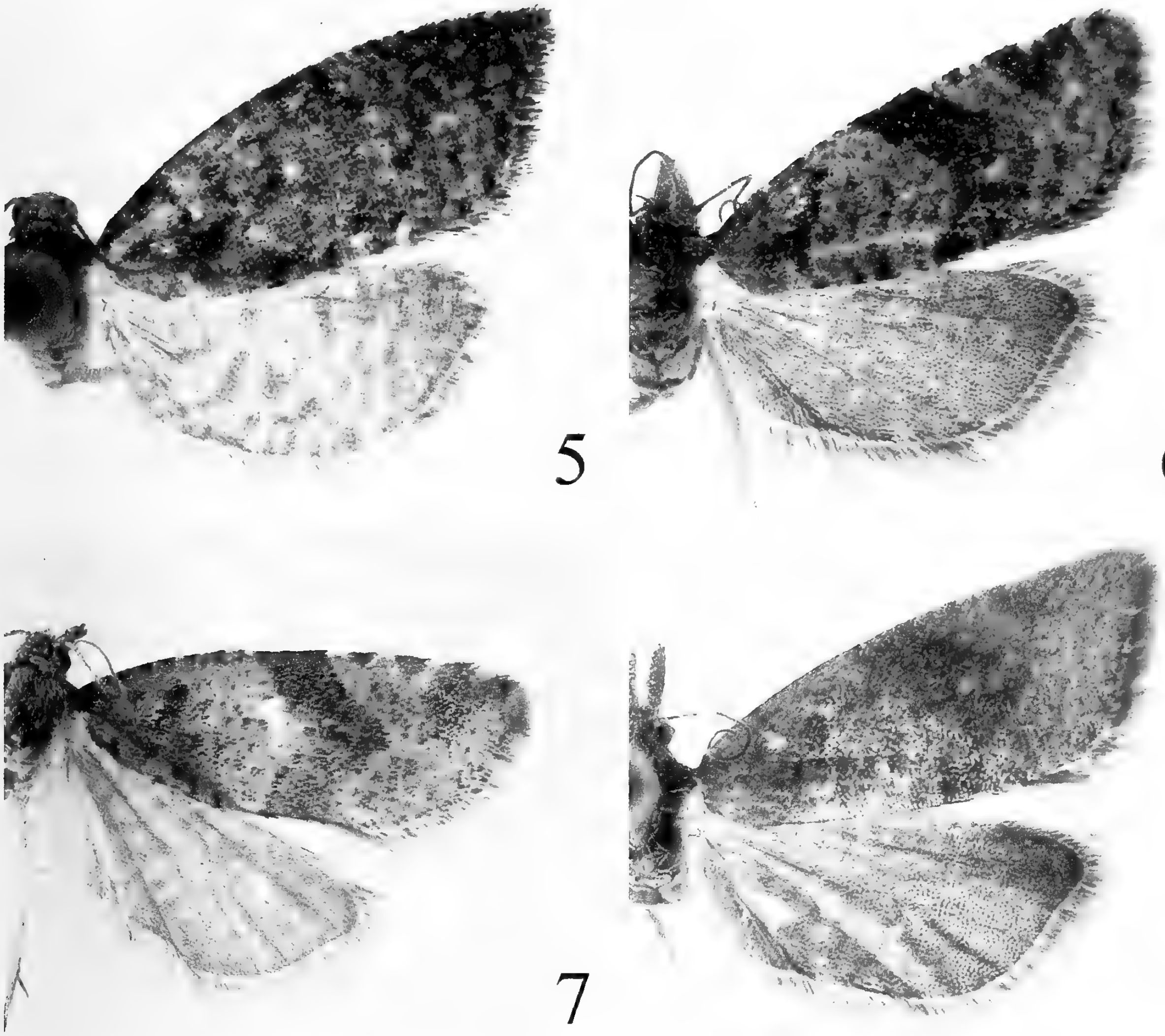
Redescription. Male. Head: Lower frons pale tan to cream; upper frons gray brown. Labial palpus light brown. Thorax: Mostly brown. Forewing (Fig. 5): Length 6.6–8.8 mm ($\bar{x}$ = 7.9 mm; n = 25); ground color pale gray to burnt umber, with small, scattered, indistinct patches of orange-brown, orange-red, and cream scales; frequently with faint, parallel bands in distal one-third of wing represented by series of slightly disjunct, darker scales; often with a variably developed, diagonal fascia of darker brown from near mid-costa to dorsum, angled outward near middle of wing. Hindwing: White to pale brown, usually with brownish-gray mottling. Abdomen: Pale yellow brown to dark brown. Genitalia (Fig. 10): As described for genus (drawn from USNM slide 90383; 15 preparations examined). Female. Head, thorax, and abdomen: Essentially as described for male. Forewing: Length 6.2–8.2 mm ($\bar{x}$ = 7.4; n = 15); ground color burnt umber to cinnamon, with indistinct patches of orange-brown, orange-red, and cream scales; a variably defined, red-brown fascia from near mid-costa to dorsum, angled outward near middle of wing. Genitalia (Fig. 14): As described for genus (drawn from USNM slide 81239; 10 preparations examined).

Types. Holotype ♂ (*erebina*), Chile, [Mountains of the hacienda of Cauquenes, Butler 1883] (BMNH). Lectotype (new designation) ♂ (*balsamodes*), Argentina, Territory Río Negro, Lake Gutierrez, 3–14.XI.1926 (F. & M. Edwards, BMNH).

Material examined. ARGENTINA: Chubut Province: El Bolsón, Lago Puelo, 220 m, 2 ♂, 17.XI.1978, 1 ♂, 2 ♀, 21.XI.1978 (Mision Cientifica Danesa, ZMC), 1 ♀, 22.X.81, 3 ♀, 23.X.1981 (Nielsen & Karsholt, ZMC); Esquel, Lago Menéndez, El Sagrario Puerto, 600 m, 1 ♂, 1 ♀, 2–4.I.1982 (Nielsen & Karsholt, ZMC). Neuquén Province: Lago Lacar, Pucará, 750 m, 4 ♀, 10.XI.1978, 2 ♂, 2 ♀, 25.XI.1978, 5 ♂, 2 ♀, 1.XII.1978, 3 ♂, 7 ♀, 2.XII.1978, 5 ♂, 3 ♀, 3.XII.1978 (Mision Cientifica Danesa, ZMC); Lago Lacar, Pucará, 600 m, 21 ♂, 3 ♀, 28–29.XI.1981, 1 ♂, 1 ♀, 26–27.XII.1981 (Nielsen & Karsholt, ZMC); Lago Lacar, 5 km E Hua-Hum, 640 m, 2 ♂, 3 ♀, 6.XI.1981, 2 ♂, 1 ♀, 25.XI.1981, 1 ♀, 26–27.XII.1981 (Nielsen & Karsholt, ZMC); San Martín de los Andes, 640 m, 1 ♂, 14.X.1981, 1 ♂, 1 ♀, 17–31.X.1981, 4 ♂, 16.X.1981, 3 ♂, 2.XI.1981, 1 ♀, 5–6.XI.1981, 3 ♂, 6 ♀, 7–15.XI.1981, 1 ♀, 26.XI.1981 (Nielsen & Karsholt, ZMC); San Martín de los Andes, Cerro Chapelco, 1400–1600 m, 2 ♂, 2–19.XII.1981 (Nielsen & Karsholt, ZMC). Río Negro Province: San Carlos de Bariloche, Colonia Suiza, 810 m, 1 ♀, 6.XI.1978, 1 ♂, 15.XI.1978, 3 ♀, 28.XI.1978, 3 ♂, 29.XI.1978, 1 ♀, 4.XII.1978, 1 ♀, 5.XII.1978, 3 ♀, 11.XII.1978, 1 ♂, 12.XII.1978, 1 ♂, 15.XII.1978, 1 ♀, 9.I.1979 (Mision Cientifica Danesa, ZMC); San Carlos de Bariloche, Colonia Suiza, 800 m, 1 ♂, 26.X.1981, 1 ♂, 31.X.1981, 1 ♂, 11.XI.1981, 2 ♂, 1 ♀, 12–20.XI.1981, 4 ♂, 21–22.XI.1981, 1 ♀, 23.XI.1981, 1 ♂, 24.XI.1981, 1 ♂, 2 ♀, 29–30.XI.1981, 2 ♂, 3 ♀, 3.XII.1981, 2 ♂, 1 ♀, 5–6.XII.1981, 1 ♂, 7.XII.1981, 1 ♂, 8.XII.1981, 1 ♀, 22.XII.1981, 1 ♀, 5–7.I.1982 (Nielsen & Karsholt, ZMC); San Carlos de Bariloche, Camino de Tronador, 2 ♀, 29.XI.1978 (Mision Cientifica Danesa, ZMC); Lago Nahuel Huapi, Puerto Blest, 770 m, 1 ♂, 27.XI.1978, 1 ♀, 18.XII.1978, 1 ♂, 30.XII.1978 (Mision Cientifica Danesa, ZMC), 1 ♂, 3.XII.1981 (Nielsen & Karsholt, ZMC). CHILE: Aconcagua Province: Los Andes, Curimon, 700 m, 1 ♂, 28.III.1979 (Mision Cientifica Danesa, ZMC). Chiloé Province: Puntra, ca. 30 air km S Ancud, 50 m, 1 ♂, 1 ♀, 21–22.XII.1981 (D. Davis, USNM). Coquimbo Province: Fray Jorge National Park, ca. 70 km W Ovalle, 4 ♂, 2 ♀, 6–9.XI.1981 (D. & M. Davis, USNM); Nague, 11 km N Los Vilos, 1 ♂, 4–5.XI.1981 (D. & M. Davis, USNM); Coquimbo, 1 ♀, 1.VII–19.X.1883, "Walker" (BMNH). Llanquihue Province: Casa Pangue, 1 ♀ (paralectotype of *balsamodes*), 4–10.XII.1926 (F. & M. Edwards, USNM); Peulla, 1 ♀ (paralectotype of *balsamodes*), 12–13.XII.1926 (F. & M. Edwards, BMNH). Maule Province: Paso Garcia, ca. 23 km NW Cauquenes, 300 m, 1 ♀, 29–30.XI.1981 (D. R. Davis, USNM); Río Teno, ca. 40 km E Curico, 800 m, 1 ♂, 1 ♀, 25–27.XI.1981 (D. R. Davis, USNM). Ñuble Province: Alto Tregualemu, ca. 20 km SE Chovellen, 500 m, 5 ♀, 1–3.XII.1981 (D. R. Davis, USNM). Osorno Province: P. N. Puyehue, Ag. Calientes to 3 km W, 600 m, 2 ♂, 12–20.XII.1981 (D. R. Davis, USNM); Parque Nacional Puyehue, Aguas Calientes, 450 m, 6 ♂, 1 ♀, 12.XI.1981, 1 ♂, 2 ♀, 13.XI.1981, 6 ♂, 5 ♀, 10.XII.1981, 4 ♂, 1 ♀, 11.XII.1981, 1 ♂, 6 ♀, 12.XII.1981, 2 ♀, 13.XII.1981 (Nielsen & Karsholt, ZMC); Parque Nacional Puyehue, Anticura, 350 m, 2 ♂, 2 ♀, 17.XI.1981, 2 ♂, 2 ♀,



FIGS. 1–4. Geographic distribution of *Rebinea* and *Eliachna*. **1,** *R. erebina;* **2,** *E. digitana,* new species; **3,** *E. hemicordata,* new species; **4,** *E. chileana.*



FIGS. 5–8. Adults of *Rebinea* and *Eliachna*. **5,** *R. erebina;* **6,** *E. chileana;* **7,** *E. hemicordata*, new species; **8,** *E. digitana*, new species.

18.XI.1981, 2 ♀, 19.XI.1981, 1 ♀, 15.XII.1981, 3 ♀, 17.XII.1981, 1 ♀, 18.XII.1981 (Nielsen & Karsholt, ZMC). Santiago Province: Los Maitenes, Colorado River, 33°22′S, 70°17′W, 1200–1400 m, 2 ♂, 16.X.1954 (L. Peña, USNM); Pilay, Río Pueco, ca. 45 km S Santiago, 800 m, 1 ♂, 23–24.XI.1981 (D. R. Davis, USNM). Valdivia Province: 20 km S Valdivia, Rincon de la Piedra, 180 m, 2 ♀, 14.XI.1981, 1 ♂, 3 ♀, 15.XI.1981 (Nielsen & Karsholt, ZMC). Valparaiso Province: Valparaiso, 1 ♂, 30.IX– 8.X.1883, "Walker 3074" (BMNH). Unknown Province: Central Austral, 2 ♂, I–III.1898 (V. Izquerdo, USNM).

Discussion. *Rebinea erebina* is either a single, highly variable species or two (or more) extremely similar species that cannot be separated reliably using traditional morphological characters. At one extreme are specimens with a large forewing length (7.3–8.8 mm), a pale (gray to beige) forewing ground color, a poorly defined forewing pattern, and a pale hindwing, usually mottled with gray brown (similar to the type of *erebina*). Although a majority of the specimens of this phenotype are males, a few females approach this general aspect. At the other extreme are specimens with a shorter forewing length (6.6–7.7 mm), a darker (red brown to brown) forewing ground color, and a more uniformly dark hindwing (similar to the type of *balsamodes*). Although this phenotype is typical of females, some males approach this aspect (see Clarke 1963). Male genitalia are only slightly variable among all the specimens examined (n > 100), and the variation is concordant with neither differences in facies, forewing length, nor geographic distribution. In some male specimens, the distal end of the venter of the valva is somewhat pointed and slightly reflexed, while in others it is somewhat rounded. The width of the paired processes from the transtilla is somewhat variable, as is the development of the hooklike process at the distal end of the sacculus. Apparent variation in the latter feature, however, is likely an artifact of slide mounting of genitalia.

Remarks. In his description of *Arotrophora balsamodes*, Meyrick (1931) indicated that he had six examples from "Argentina, Territory Rio Negro, Lake Gutierrez, November; S. Chile, Llanquihue Province, Casa Pangue and Peulla, December." Three of these specimens are in the BMNH, one of which is a female of *Eliachna;* one specimen is in USNM. Clarke (1963) identified the male from Argentina as "type" without formally designating it as the lectotype. Because the type series consists of more than one species, we formally designate a lectotype, and we select the specimen labeled as such in the BMNH and identified as such by Clarke (1963). This designation is necessary to establish the concept of the species and promote nomenclatural stability.

Eliachna Razowski, 1999

Eliachna Razowski 1999:87.

Type species. *Eliachna chileana* Razowski 1999:87, by monotypy.

Diagnosis. *Eliachna* is most similar to *Rebinea* in forewing length, shape, pattern, and venation (see diagnosis of *Rebinea* above for details), and most specimens are difficult to distinguished superficially from *Rebinea*. Genitalic differences between the two genera are conspicuous and are detailed above under *Rebinea*.

Redescription. Head: Antennal cilia approximately 1.5 times width of flagellomere in male; cilia short, unmodified in female. Labial palpus elongate, porrect, length 3–4 times horizontal diameter of compound eye, slightly longer in female. Vertex with overhanging tuft of scales. Proboscis present, presumably functional. Ocellus moderately large. Chaetosema present. Thorax: Smooth scaled. Legs unmodified, male without foreleg hairpencil. Forewing (Figs. 6–8): Length ca. 2.4 times width; length of DC ca. 0.6 times forewing length; width of DC ca. 0.2 times DC length; CuA2 originates 0.6–0.7 along DC length; all veins separate beyond DC; chorda and M-stem absent; CuP weak, present only at margin. No upraised scale tufts; male without costal fold. Hindwing: Sc + R and Rs closely approximate at base; Rs and M_1 stalked ca. one-third distance from DC to margin; M_3 and CuA_1 connate or short-stalked; CuP present; M-stem absent; tuft of hairlike scales at base of 1A + 2A in both sexes. Abdomen: Dorsal pits absent; no modified corethrogyne scaling in females. Male genitalia (Figs. 11–13): Uncus slender, short, simple, strongly sclerotized; socius moderately short, broad, hairy, slightly expanded distally; gnathos with slender lateral arms connected to terminal plate by membrane. Transtilla a simple band, highly sclerotized laterally, weaker medially, with a pair of submedial, digitate processes, slightly rounded apically. Valva broad basally, with variable excavation near mid-venter; sacculus well defined, with free, elongate-digitate terminal process of variable shape and length; pulvinus absent; juxta strongly sclerotized, stout arrowhead-shaped. Aedeagus somewhat elongate, variably curved near middle, usually with distal spine projecting dorsoposteriorly; vesica with or without minute spinules and/or small patch of tiny cornuti. Female genitalia (Figs. 15–16): Papillae anales somewhat slipper-shaped. Apophyses anteriores and posteriores slender, nearly equal in length. Sterigma usually crescent-shaped, with a pair of rounded, sclerotized lateral flanges at posterior edge. Ductus bursae moderately short; corpus bursae ovoid, with dense spicules, at least in posterior one-half.

Distribution and biology. *Eliachna* apparently is confined to south-central Chile and adjacent Argentina, ranging from coastal lowlands (5 m) to montane areas (1700 m). Adults have been collected from October to April. Nothing is known of the early stages.

***Eliachna digitana* Brown & McPherson, new species**

(Figs. 2, 8, 11, 15)

Diagnosis. Superficially, *E. digitana* is difficult to distinguish from other species in the genus; the forewing length is usually a little shorter and the ground color slightly more orange brown rather than gray brown. The male genitalia can be distinguished easily from its congeners by the subrectangular distal portion of the valva; the short, straight, digitate process at the termination of the sacculus; and the weakly curved aedeagus. Female genitalia, likewise, are easily distinguished; the lateral pouches of the sterigma and the sclerotized, knoblike diverticula of the ductus bursae are unique to this species.

Description. Male. Head: Labial palpus dark brown. Forewing (Fig. 8): Length 5.9–7.0 mm ($\bar{x} = 6.5$; n = 15); ground color and maculation somewhat variable; ground color usually gold gray to red brown, with faint, dark brown reticulations, infrequently with ill-defined, darker area in basal one-third; a variably developed median fascia from costa to dorsal margin, brown to red brown, angled outward near middle of forewing; apex frequently with darker patch. Hindwing: Brownish gray, infrequently with faint mottling. Abdomen: Gold brown to dark brown. Genitalia: As in Fig. 11 (drawn from USNM slide 90484; 7 preparations examined). Uncus, socius, gnathos, and transtilla as described for the genus. Valva long, subrectangular, only slightly narrowed near middle and slightly broadened distally; sacculus broad basally, with a free, mostly straight, digitate process distally. Juxta as described for the genus. Aedeagus weakly undulate; spine at termination of coecum strongly sclerotized, slightly disjunct from coecum; vesica densely punctate, especially in distal three-fourths; a row of minute cornuti near the base. Female. Essentially as described for male. Forewing length 6.5–7.6 mm ($\bar{x} = 6.9$; n = 15). Genitalia: As in Fig. 15 (drawn from USNM slide 81228; 6 preparations examined). Sterigma subrectangular, with a pair of shallow lateral pouches at anterior edge. Ductus bursae short, with a short, stout, knoblike, sclerotized diverticula dorsally; corpus bursae oblong, uniformly covered with fine spinules.

Type. Holotype ♂, Chile, Ñuble Province, 17.5 km S Curanipe, near coastal stream, 50 m, 25.I.1979 (D. & M. Davis & B. Akerbergs, USNM).

Paratypes. ARGENTINA: Chubut Province: El Bolsón, Lago Puelo, 220 m, 1 ♂, 18.XI.1978 (Mision Científica Danesa, ZMC), 1 ♀, 13.X.1981 (Nielsen & Karsholt, ZMC); Esquel, 550 m, 1 ♂, 1.I.1982 (Nielsen & Karsholt, ZMC); Sierra Colorada, 800 m, 1 ♂, 29.I.1983

(M. & P. Gentili, USNM). Neuquén Province: San Martín de los Andes, 640 m, 1 ♀, 13.X.1981, 1 ♂, 7–15.XI.1981 (Nielsen & Karsholt, ZMC); Lago Lucar, Pacará, 650 m, 1 ♂, 10.XI.1978 (Mision Científica Danesa, ZMC), 1 ♂, 26–27.XII.1981 (Nielsen & Karsholt, ZMC). Río Negro Province: Lago Gutierrez, 1 ♀ (paralectotype of *balsmodes*), 3–14.XI.1926 (F. & M. Edwards, BMNH); San Carlos de Bariloche, Colonia Suiza, 810 m, 1 ♂, 2.XII.1981, 1 ♀, 20.XII.1981, 1 ♂, 23.XII.1981, 1 ♂, 5–7.I.1982 (Nielsen & Karsholt, ZMC), 1 ♀, 9.XI.1978, 1 ♂, 19.XI.1978, 1 ♂, 29.XI.1978, 1 ♀, 9.XII.1978, 1 ♀, 12.XII.1978, 1 ♀, 9.I.1979, 1 ♀, 10.I.1979, 1 ♀, 11.I.1979 (Mision Científica Danesa, ZMC). CHILE: Cautin Province: Fundo Neltume, 2 km N Villarrica, 200 m, 1 ♂, 1 ♀, 27.II.1979 (D. & M. Davis & B. Akerbergs, USNM); Fundo el Coigue, 27 km NE Villarrica, 500 m, 2 ♂, 28.II– 3.III.1979 (D. & M. Davis & B. Akerbergs, USNM). Malleco Province: Rio Manzanares, 5 ♀, 19.X.1979 (Flint & Barria, USNM). Ñuble Province: Forel Carrizalillo, 250 m, 1 ♀, 30.I–5.II.1981 (L. E. Peña, USNM); Alto Tregualemu, 500 m, 1 ♀, 27–28.I.1981 (L. E. Peña, USNM); Alto Tregualemu, ca. 20 km SE Chovellen, 500 m, 2 ♂, 26–27.I.1979 (D. &. M. Davis & B. Akerbergs, UCB), 4 ♀, 1–3.XII.1981 (D. Davis, USNM); 17.5 km S Curanipe, near coastal stream, 50 m, 3 ♂, 2 ♀, 25.I.1979 (D. & M. Davis & B. Akerbergs, USNM); Pierdra de la Iglesia, 8 km N Cobquecura, 5 m, 4 ♀, 25.I.1979 (D. & M. Davis & B. Akerbergs, USNM), 1 ♂, 4 ♀, 24.I.1979 (D. & M. Davis & B. Akerbergs, USNM); Cachapoal, Cajon de Lisboa, Alhue, 800 m, 1 ♂, 19–21.XII.1987 (L. E. Peña, USNM). Llanquihué Province: Llanquihué, Petrohue, 1 ♂, 8.III.959, 1 ♂, 12.III.959 (J. F. G. Clarke, USNM). Osorno Province: Parque Nacional Puheyue, Anticura, 250 m, 1 ♂, 17.XII.1981 (Nielsen & Karsholt, ZMC). Santiago Province: Rinconada Maipú, 450 m, 35°31′S, 70°47′W, 1 ♂, 14.IV.1966 (W. Hichins & M. E. Irwin, UCB); Pilay, Río Peuco, ca. 45 km S Santiago, 800 m, 1 ♂, 23–24.XI.1981 (D. Davis, USNM). Valdivia Province: Valdivia, 1 ♀, 7.III.1960 (E. Krahmer, ZMC); 20 km S Valdivia, Rincón de Piedra, 180 m, 1 ♂, 24.XI.1981 (Nielsen & Karsholt, ZMC).

Distribution and biology. *Eliachna digitana* occurs from Santiago Province, Chile, to Chubut Province, Argentina (Fig. 2), ranging from coastal *Nothofagus* forests (5 m) to arid uplands (1300 m) dominated by Fabaceae and Lauraceae. Capture records are from October (n = 3), November (n = 5), December (n = 11), January (n = 20), February (n = 4), March (n = 3), and April (n = 1). Nothing is known of the early stages.

Etymology. The species name refers to the digitate process that comprises the distal portion of the sacculus.

Remarks. N. Obraztsov probably was the first to recognize this species as distinct and undescribed; he labeled the specimen from Llanquihué, Peulla (USNM) with a manuscript name.

Eliachna hemicordata Brown & McPherson, new species

(Figs. 7, 13)

Diagnosis. *Eliachna hemicordata* has a slighter greater forewing length and a paler ground color than other species in the genus. Males can be distinguished from other *Eliachna* by the somewhat cordate distal portion of the valva; the elongate, curved, digitate, free process of the sacculus is similar to that of *E. chileana*. The female is unknown.

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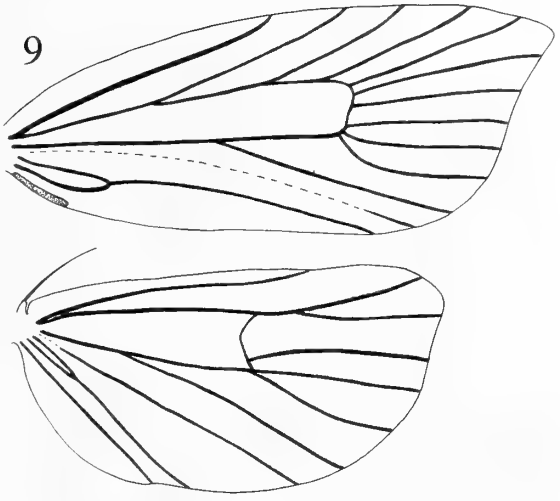

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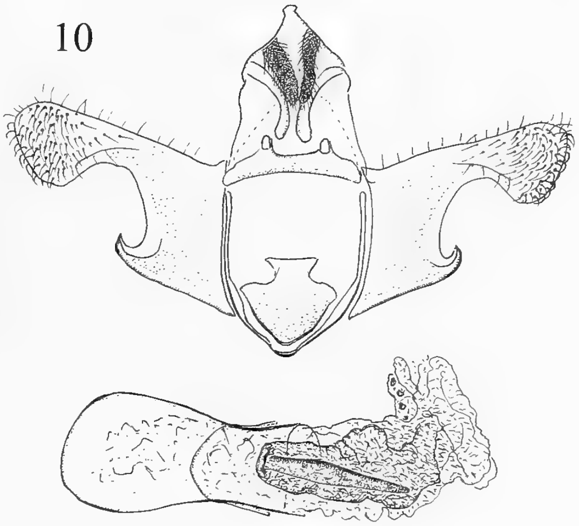
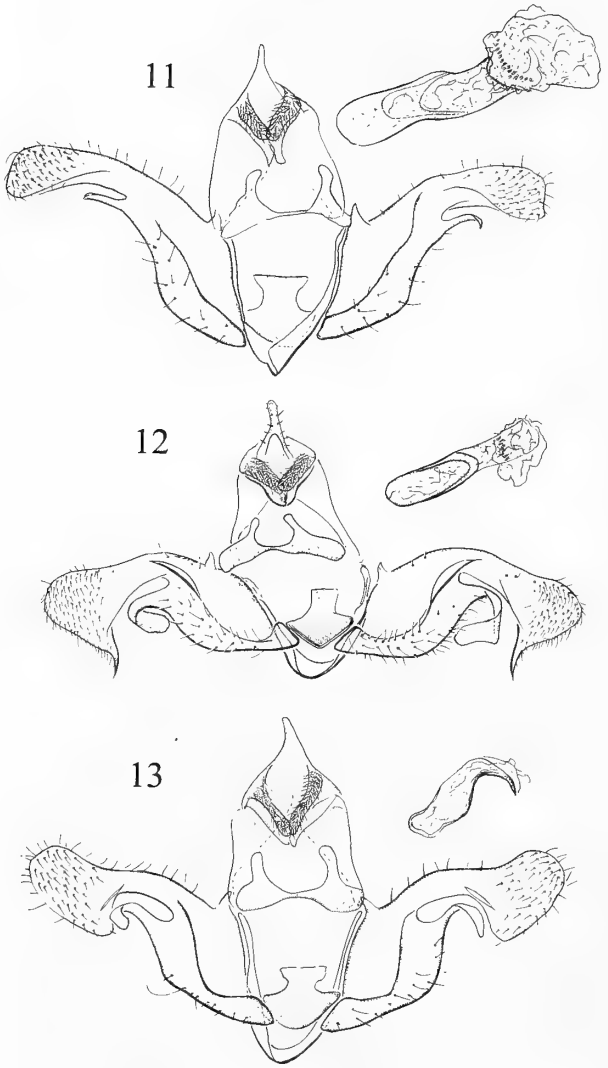


FIGS. 9–10. *Rebinea erebina*. **9,** Wing venation; **10,** Male genitalia, aedeagus removed, valvae spread.

Description: Male. Head: Labial palpus dark brown. Thorax: Brown to dark brown. Forewing (Fig. 7): Length 7.8–8.0 mm ($\bar{x}$ = 7.9; n = 5); ground color pale orange cream, with tiny black specks throughout; moderately broad median fascia, extending from costa ca. 0.6–0.7 from base to apex, to dorsum ca. 0.7–0.8 from base to tornus, angled outward near middle of forewing Hindwing: Pale gray brown with variably developed darker mottling. Abdomen: Gold brown to dark brown. Genitalia: As in Fig. 13 (drawn from USNM slide 81222; 7 preparations examined). Uncus, socius, gnathos, transtilla as described for genus. Valva long, distal portion ovoid, with short hooklike process from venter of apex; sacculus with elongate, slightly flattened, weakly curved free process. Juxta as described for genus. Aedeagus curved dorsad just beyond coecum, with dorsoposteriorly projecting spine at distal end; vesica without spicules. Female. Unknown.

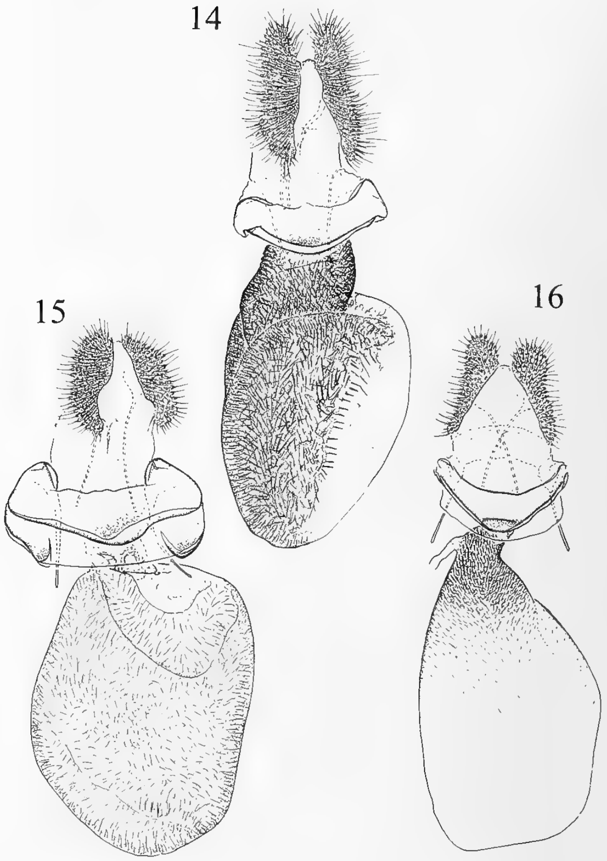


FIGS. 11–13. Male genitalia of *Eliachna*, aedeagus removed, valvae spread. **11,** *E. digitana*, new species; **12,** *E. chileana*, new species; **13,** *E. hemicordata*.

Type. Holotype ♂, Argentina, Nuequén, Chapelco Lenga, 1700 m, 24.I.1984 (M. & P. Gentili, USNM).

Paratypes. ARGENTINA: Neuquén Province: Chapelco Techos, 1400 m, 1 ♂, 21.I.1982 (M. & P. Gentili, USNM); Lago Lacar, Trompul, 1200 m, 1 ♂, 6.I.1983 (M. & P. Gentili, USNM); San Martín de los Andes, Tr. Kura, 1000 m, 1 ♂, 29.XII.1985 (M. & P. Gentili, USNM). Río Negro Province: Lago Nahuel Huapi, Puerto Blest, 1 ♂, 23.XII. 1978 (Mision Científica Danesa, ZMC). CHILE: Bío-Bío Province: Lago El Barco, Guallali, Sta. Barbara, 1200 m, 1 ♂, 25–28.II.1981 (L. E. Peña, USNM). Cautin Province: [Parque Nacional] Conguillio, 1200 m, 1 ♂, 4–8.II.1988 (L. E. Peña, USNM). Unknown Province: V. Villarica, 16 km S Pucon, 1 ♂, 20.XII.1982 (R. Brown, MEM).

Distribution and biology. *Eliachna hemicordata* is known from Neuquén and Río Negro provinces, Argentina, and Bío-Bío and Cautin provinces, Chile, between 1000 and 1400 m (Fig. 3). Capture records are from January (n = 3), February (n = 2), and December (n = 3). Nothing is known of the early stages.



FIGS. 14–16. Female genitalia of *Rebinea* and *Eliachna*. **14,** *Rebinea erebina*; **15,** *E. digitana*, new species; **16,** *E. chileana*.

Etymology. The species name refers to the half-hearted shape of the distal portion of the valva.

Eliachna chileana Razowski, 1999
(Figs. 6, 12, 16)

Eliachna chileana Razowski, 1999:88 [male genitalia illustrated].

Diagnosis. The male genitalia of *E. chileana* can be distinguished from those of other species in the genus by the greatly expanded distal portion of the valva, terminating in an attenuate, pointed tip. The female genitalia can be distinguish by the simple U-shaped sterigma.

Redescription. Male. Head: Labial palpus light brown. Thorax: Mostly brown. Forewing (Fig. 6): Length 7.1–7.8 mm ($\bar{x}$ = 7.5 mm; n = 4); ground color dull silvery gray, faintly overscaled with red orange and copper orange; basal one-fourth usually with patch of slightly darker scales; variably defined, red-brown median fascia from near mid-costa to dorsum, angled outward near middle of forewing; terminal area with irregular patches of black and orange-red scales, decreasing toward apex. Hindwing: Pale olive brown, with faint brown-

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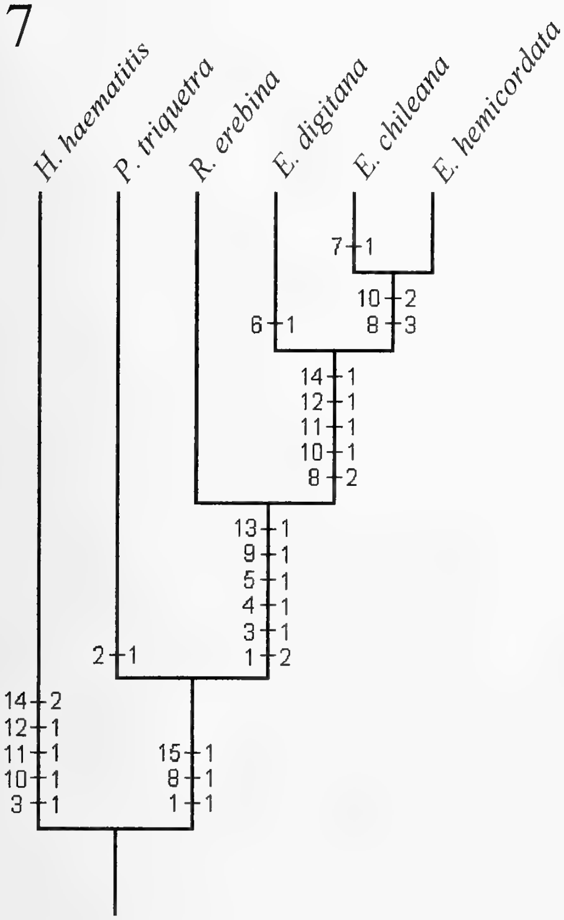

FIG. 17. Hypothesis of phylogenetic relationship among the taxa. Numbers on the left refer to characters (1–15); numbers on the right refer to character states (see Table 1).

ish-gray reticulations. Abdomen: Pale yellow brown to dark brown. Genitalia: As in Fig. 12 (drawn from USNM slide 81223; 5 preparations examined). Uncus, socius, and gnathos as described for genus. Valva broad basally, narrowed at middle, greatly expanded distally, with elongate, curved, beaklike process directed ventrally; sacculus with elongate, free, slightly flattened, curved, digitate process. Juxta as described for genus. Aedeagus strongly curved near middle; vesica with several minute spines and a few short, capitate cornuti. Female. Essentially as described for male. Forewing: Length 6.7–7.0 mm (x̄ = 6.9; n = 4). Genitalia: As in Fig. 16 (drawn from USNM slides 90493 and 90177; 5 preparations examined). Sterigma weakly U-shaped, uniform in thickness. Ductus bursae moderately short, with large ductus seminalis originating dorsally about midway between ostium and corpus bursae. Corpus bursae as described for the genus.

Type. Holotype ♂, Chile, Ñuble Province, Las Trancas, Shangri-la, Chillan area, SE Recinto, 1500 m, 15.XII.1983 (L. Peña, AMNH).

Additional specimens examined. CHILE: Malleco Province: nr. Los Gringos Camp, Nahuelbuta Nat. Park, 1300 m, 3 ♂, 2 ♀, 6–11.I.1982 (D. R. Davis, USNM). Ñuble Province: Shangri-la, SW side Volcan Chillan, 1600 m, 1 ♂, 19–21.I.1979 (D. &. M. Davis & B. Akerbergs, USNM); Las Trancas, 21 km E Recinto, near high waterfall, 1300 m, 1 ♂, 3 ♀, 17.I.1979 (D. &. M. Davis & B. Akerbergs, USNM).

Distribution and biology. *Eliachna chileana* is known only from Malleco and Ñuble provinces (Fig. 4). With all captures between 1300–1600 m, this species appears to be restricted to higher elevations than its congeners. Capture records are from December (n = 1) and January (n = 10). Nothing is known of the early stages.

EXPLANATION OF CHARACTERS AND PHYLOGENETIC ANALYSIS

A phylogenetic analysis was performed on the four species that comprise *Rebinea* and *Eliachna,* plus two out-group species, *Proeulia triquetra* Obraztsov and *Haemateulia haematitis* (Meyrick). The use of *Proeulia* and *Haemateulia* as out-groups is somewhat arbitrary because sister group relationships within this clade of Euliini previously have not been demonstrated. However, the two genera share a variety of features with *Rebinea* and *Eliachna* (e.g., forewing pattern, polymorphism, broad, short valvae, etc.), and all appear to belong to a complex of endemic Chilean-Argentinean genera that is taxonomically isolated from other Euliini present in South America. The primary purposes of the analysis were to confirm the sister relationship of *Rebinea* and *Eliachna*, and ensure that the two in-group genera are monophyletic with respect to each other. The analysis was based on 15 morphological characters (11 binary and 4 multistate), including two of the head, one of the thorax, nine of the male genitalia, and three of the female genitalia. Character state polarity was determined through the out-group method and using Horak's (1984) assessment of characters of Tortricinae. The character state data were subjected to parsimony analysis using the "mhennig*" command of Hennig86 (Lipscomb 1994). Characters used in the analysis are listed and discussed briefly below; the character matrix is present in Table 1.

1. Labial palpi: (0) upturned, ca. 1.5–2.0 as long as horizontal diameter of the compound eye; (1) somewhat porrect, ca. 2.0–3.0 as long as horizontal diameter of the compound eye; (2) porrect, 3–4 times the horizontal diameter of the compound eye. While elongate labial palpi occur in several groups scattered throughout Euliini (e.g., *Proeulia*, *Seticosta* Razowski, *Anopinella* Powell, etc.), none of these taxa have palpi as long as those of *Rebinea* and *Eliachna*.

2. Male antennal cilia: (0) conspicuous, elongate, ca. 1.0–1.5 times the width of the flagellomere; (1) inconspicuous, extremely short, ca. 0.5 times the width of the flagellomere. The value of this character is diminished somewhat by its variability in the out-group taxa (e.g., length of male antennal cilia varies among species of *Proeulia*).

TABLE 1. Character matrix ("?" = missing data).

haematitis	00100	00001	11020
triquetra	11000	00100	00001
erebina	20111	00110	00101
digitana	20111	10211	11111
chileana	20111	01312	11111
hemicordata	20111	00312	11???

3. Male foreleg hairpencil: (0) present; (1) absent. The presence of a male foreleg hairpencil is assumed to represent the plesiomorphic condition in Euliini (Brown 1990). However, because the structure is evolutionarily labile, there is no evidence that its shared absence is truly a synapomorphy for the taxa that lack it.

4. Transtilla: (0) a simple bridge; (1) with a pair of stout, digitate, submedial processes on dorsum. Although digitate structures are present on the dorsum of the transtilla of *Inape* Razowski and *Ortognathosia* Razowski (see Razowski 1988 for illustrations), few other features of the male or female genitalia of the latter two genera indicate a close relationship with *Rebinea* and *Eliachna*. Hence it is suspected that the structures represent convergent development in *Inape*, *Ortognathosia*, and *Rebinea* + *Eliachna*.

5. Valva: (0) venter uniform; (1) venter with a deeply excavated portion near middle resulting in a broad basal portion, a narrow "neck" near the middle, and an expanded distal portion. The distinctive shape of the valva is apparently unique to *Rebinea* and *Eliachna*, and is reminiscent of the valva of some Eucosmiini (Olethreutinae).

6. Valva: (0) distal one-third somewhat club-shaped; (1) distal portion narrowed, somewhat elongate-rectangular. The latter character state is considered an autapomorphy for *E. digitana*.

7. Valva: (0) distal one-third somewhat club-shaped; (1) distal portion greatly expanded into an elongate, curved, beaklike process directed ventrally. The latter character state is considered an autapomorphy for *E. chileana*.

8. Sacculus: (0) weak, lacking free terminal process; (1) well-defined, with short, free, distal termination; (2) well-defined, with slender, digitate process; (3) well-defined, with long, slightly flattened, curved process. A sacculus lacking a free terminal process, such as that in the genitalia of *Haemateulia*, is considered the plesiomorphic condition. A well-defined sacculus with a short, free, distal termination, such as that in the genitalia of *Proeulia*, is considered derived; and the development of the free tip into an elongate, digitate process is considered a synapomorphy for *Eliachna*. Its further development into an extremely long, slightly flattened, curved process is considered a synapomorphy for *E. chileana* and *E. hemicordata*.

9. Juxta: (0) shield-shaped, unmodifed; (1) stout arrowhead-shaped. The presence of a stout, arrowhead-shaped juxta is not particularly compelling as a synapomorphy for *Eliachna* and *Rebinea* because other genera of Chilean-Argentinean Euliini may possess a similarly shaped juxta. The structure frequently is not included in illustrations of male genitalia or is distorted by slide mounting.

10. Aedeagus: (0) broad, straight, relatively large; (1) slightly more slender, weakly curved; (2) conspicuously more slender, strongly curved. A broad, straight, relatively large aedeagus, characteristic of *Proeulia* and *Rebinea*, is considered the plesiomorphic condition. A slightly more slender, weakly curved aedeagus is considered the first step in a transformation series leading to a conspicuously more slender, strongly curved aedeagus.

11. Aedeagus: (0) without external projections; (1) with a small dorsoposteriorly projecting spine from near junction of the coecum and the phallobase. The latter character state appears to represent a synapomorphy for *Eliachna*.

12. Vesica: (0) with one or few large capitate cornuti; (1) with numerous tiny non-capitate cornuti. The presence of one or few large cornuti, assumed to represent the plesiomorphic condition, is typical of *Proeulia*; the vesica of *Rebinea*, likewise, has a single, large, compound cornutus.

13. Sterigma: (0) unmodified; (1) with a pair of semicircular sclertotized flanges located at the posterior edge. The latter character state appears to represent a synapomorphy for *Rebinea* and *Eliachna*.

14. Ductus bursae: (0) extremely broad, nearly as broad as the corpus bursae; (1) slightly more narrow, weakly differentiated from corpus bursae; (2) relatively narrow, clearly differentiated from corpus bursae. In *Proeulia*, *Argentulia*, and related Chilean-Argentinean genera, the ductus bursae is extremely broad. This condition, considered the plesiomorphic state, also is present in *Rebinea*. The slightly more narrow ductus bursae of *Eliachna* is considered a synapomorphy for this genus, and the relatively well defined ductus bursae of *Haemateulia* is considered the most advanced state. Because this character varies throughout Euliini (sometimes even within a single genus), it is a less compelling indicator of relationship.

15. Corpus bursae: (0) finely punctate; (1) densely spiculate. A densely spiculate corpus bursae is shared by *Proeulia*, *Rebinea*, *Eliachna*, *Argentulia*, and additional related Chilean-Argentinean genera. The finely punctate corpus bursa of *Haemateulia*, similar to most

Euliini, is considered the plesiomorphic state for this character.

The parsimony analysis of the 15 characters described above resulted in one most parsimonious tree with a length of 24, a consistency index of 0.83, and a retention index of 0.69. The consistency and retention indices are biased by the fact that the data set includes characters that are non-informative in a phylogenetic context (i.e., autapomorphies and characters consistent within the in-group). The cladogram (Fig. 17) shows strong support for the monophyly of *Rebinea* + *Eliachna* on the basis of the following characters: labial palpi extremely elongate and porrect (character state 1.2); male foreleg hairpencil absent (character state 3.1); transtilla with a pair of stout, digitate, submedial processes on the dorsum (character state 4.1); venter of valva with a deeply excavated mesal portion (character state 5.1); juxta stout and arrowhead-shaped (character state 9.1); and sterigma with a pair of semicircular slertotized flanges located at the posterior edge (character state 13.1). The most convincing of these are characters 1, 4, 5, and 13.

The monophyly of *Eliachna* is supported by the presence of a digitate process at the termination of the sacculus (character state 8.2); a slender, weakly curved aedeagus (character state 10.1); a dorsoposteriorly projecting distal spine from near the junction of the coecum and the phallobase (character state 11.1); numerous tiny cornuti in the vesica of the aedeagus (character state 12.1); and a slightly more narrow ductus bursae (character state 13.1). The most convincing of these are characters 8, 11, and 12.

While the sister relationship of *Eliachna* and *Rebinea* is well supported in the context of the genera used in this analysis, their relationship to other euliine genera endemic to Chile and Argentina remains unknown. Fortunately, the unique leafroller fauna of this region is receiving greater attention from systematists and pest managers worldwide, as many of the native species have broadened their host ranges to include economically important crops (Brown 2000b). An anticipated increase in specimens and host information will undoubtedly shed additional light on phylogenetic relationships among these genera.

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THE LIFE HISTORY OF *DASYPYGA ALTERNOSQUAMELLA* RAGONOT (PYRALIDAE) FEEDING ON THE SOUTHWESTERN DWARF MISTLETOE (*ARCEUTHOBIUM VAGINATUM*) IN COLORADO

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ABSTRACT. The immature stages, feeding and oviposition behaviors, patterns of larval abundance, and associated arthropod fauna of *Dasypyga alternosquamella* Ragonot (Pyralidae) on *Arceuthobium vaginatum* susp. *cryptopodum* (Hawks.), the Southwestern dwarf mistletoe, are described and illustrated. The study was conducted at the Manitou Experimental Forest, U.S.D.A. Rocky Mountain Research Station, Woodland Park, Colorado, where the Southwestern dwarf mistletoe parasitizes *Pinus ponderosa* (Laws.) *scopulorum*.

Additional key words: biological control, herbivory, Phycitinae, *Promylea lunigerella*, Blue Hairstreak.

Dwarf mistletoes have significant economic and ecological impacts on coniferous species throughout the West and have been called "the single most destructive pathogen of commercially valuable coniferous timber trees in several regions of Mexico, western Canada, western United States, and parts of Asia" (Hawksworth & Wiens 1996). Past work has catalogued the lepidopteran and other arthropod fauna associated with dwarf mistletoes (Stevens & Hawksworth 1970), but there is little or no natural- or life-history information is available for many of these species. *Dasypyga alternosquamella* Ragonot (Pyralidae, Phycitinae), a common herbivore of dwarf mistletoes can have significant effects on dwarf mistletoe standing biomass (e.g., Reich 1992), and could be an important agent of biological control for this important conifer parasite.

Dasypyga alternosquamella feed on multiple species of dwarf mistletoes (*Arceuthobium* spp. [Viscaceae]) throughout western North America (Heinrich 1920). This species was described by Ragonot (1887) from specimens collected in California. A description of larva and pupa were first given by Heinrich in 1920, and relevant information was again summarized by Heinrich in 1956. This is the first published work to provide basic natural- and life-history information on this species. In this paper I describe the immature stages of *D. alternosquamella*, larval feeding and oviposition behaviors, and a brief account of other dwarf mistletoe-associated arthropods at a field site on the eastern slope of the Colorado Rockies.

MATERIALS AND METHODS

This work was conducted at the Manitou Experimental Forest, an administrative unit of the U.S. Department of Agriculture Forest Service Rocky Mountain Experiment Station located in Woodland Park, Colorado. The field portion of the work was in a stand of pure 50 to 60 year old ponderosa pines (*Pinus ponderosa* var. *scopulorum* Laws.) growing at an elevation of 2414 m (39°06′40″N, 105°06″50′W). These trees are heavily parasitized by Southwestern dwarf mistletoe (*A. vaginatum* subsp. *cryptopodum* Hawks.).

All dwarf mistletoes (*Arceuthobium* spp.) are leafless, have highly reduced flowers, and are dioecious. Plants of *A. v. cryptopodum* (Fig. 1) reach a maximum height of approximately 20 cm and a single plant consists of multiple shoots emerging directly from the bark of host pine trunks and branches. Individual shoots range from 2–5 mm in diameter. Coloration is uniform within plants, but highly variable among plants including yellows, pale greens, and browns, often with reddish tints.

Southwestern Dwarf Mistletoe plants were collected from the field between 30 June and 1 August 1999 in individual plastic bags and brought into the lab on eight separate occasions. Individual plants ranged from 3 to 10 cm in height and in most cases only one or two plants were taken from any single host-pine. Both eggs and early instar larva were isolated from these plants using a dissecting microscope, as well as other arthropods associated with dwarf mistletoe.

Because dwarf mistletoes are not free-living and only grow on conifers, *D. alternosquamella* were not reared on living host plants, but instead they were

FIG. 1. The Southwestern dwarf mistletoe parasitizing ponderosa pine. Scale bar 10 cm.

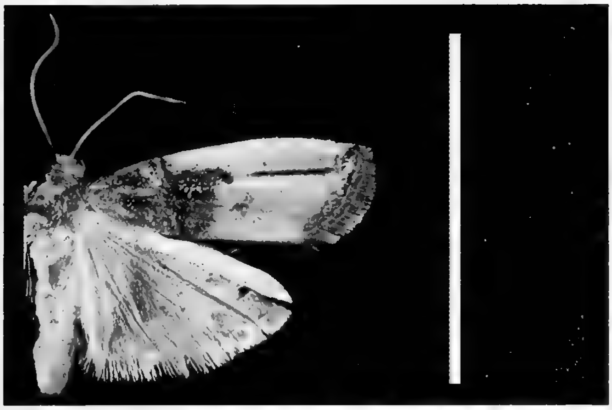

FIG. 2. *Dasypyga alternosquamella* adult. Scale bar 1 cm.

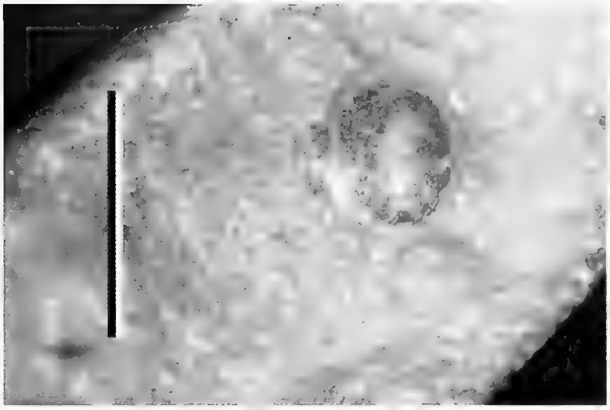

FIG. 3. *Dasypyga alternosquamella* egg on Southwestern dwarf mistletoe. Scale bar 1 mm.

reared individually in clear plastic petri dishes lined with filter paper in a laboratory facility. The larvae were fed small (2–5 cm) shoots of dwarf mistletoe collected from the same general location as the larvae themselves, and they were replenished with fresh plant material approximately every third day. The filter paper linings of each petri dish were wetted on a daily basis. The lab building was neither heated nor cooled, and petri dishes were stored in the open near a window where they received indirect but not direct sunlight. Although every precaution was taken to maintain a "natural" rearing environment within the laboratory facility the quality of harvested food plants, as well as other environmental variables, likely differ to some extent from that of a living plant.

Larval head capsule widths and resting body lengths were measured using a stereomicroscope with an ocular micrometer. Head capsule widths were taken daily while resting body lengths were taken only at the time of molting. Five larvae were reared from eggs through pupation, three larvae were collected at second instar and reared through pupation, and one additional larva was collected at the third instar and reared through pupation. All pupae were measured and weighed approximately two months after pupation. Voucher specimens of adults reared for this work are housed at the University of Colorado Museum in Boulder, Colorado.

To determine egg hatch-time 25 field-collected eggs were reared at least through first instar. To document pupation behavior several late-instar larvae were reared on dwarf mistletoe plants still attached to clipped pine branches in a terrarium with several centimeters of soil and needles in the bottom. The pine branch, dwarf mistletoe, and soil were subsequently searched for pupae. Larval feeding behaviors both in the laboratory and in the field were recorded.

RESULTS

Oviposition. Eggs and first instar larvae appeared in the field beginning 30 June 1999 and the last eggs were found on 3 August 1999. As the egg stage lasts approximately seven days (see below), adult emergence likely began sometime in the middle of June. In two years of fieldwork at this site, I have seen an adult (Fig. 2) only once in the field during the day and have not observed oviposition and other adult behaviors. These behaviors may be occurring nocturnally. Eggs were laid singly, although the frequent presence of multiple larvae of different instars on a single plant suggests that ovipositing females may not make any effort to avoid plants on which previous oviposition has occurred.

Eggs. Eggs are circular, approximately 0.5 mm in diameter, and slightly domed in shape (Fig. 3). They are light red in color with slight white mottling, especially along the margins, and adhere tightly to the surface of the dwarf mistletoe shoots, thus becoming readily visible in the field. Eggs were never found on the pine foliage or branches. The dates of oviposition of the 25 eggs collected from the field are not known, but all hatched within eight days. Specifically, one hatched eight days after collection, six hatched seven days after collection, and the other 18 hatched in less than seven days, suggesting a maximum egg stage of seven to eight days. Without knowing the actual dates of egg laying minimum egg stage duration can not be estimated.

Larvae. *Dasypyga alternosquamella* has six instars. Heinrich (1920) provides a formal description and illustration of larval characters. The size (head capsule width and larval length) and instar duration of each stage are shown in Table 1. The average duration from egg hatch to pupation was 47 days (N = 7, SE = 0.76) over which time larvae grew from a mean length of 1.19 mm (N = 5, SE = 0.048) at hatching to 16.56 mm (N = 9, SE = 1.034) at pupation (Table 1).

First instar larvae feed on the plant surfaces including terminal shoots and flowers, presumably because they are unable to penetrate the harder exterior surface of the dwarf mistletoe shoots. Later instars (Fig. 4) frequently mine shoots, often entering the shoot at the base and moving distally. Large aggregations of frass can accumulate at the

TABLE 1. Mean values for head capsule width, pre- and post-molt body lengths of resting larvae, and instar duration for *Dasypyga alternosquamella*. Sample sizes (N) given in column two, standard errors (SE) follow each measurement. Post-molt body length for instar one is size at time of hatching.

Instar	N	x̄ head capsule width mm (SE)	x̄ post-molt body length mm (SE)	x̄ pre-molt body length mm (SE)	x̄ instar duration days (SE)
1	5	0.15 (0.005)	1.19 (0.048)	1.61 (0.093)	7.33 (0.558)
2	8	0.20 (0.004)	1.62 (0.093)	2.30 (0.088)	6.5 (0.563)
3	9	0.29 (0.010)	2.31 (0.088)	3.25 (0.124)	6.38 (0.263)
4	9	0.43 (0.012)	3.26 (0.124)	5.36 (0.288)	6.33 (0.471)
5	9	0.64 (0.011)	5.37 (0.288)	8.25 (0.310)	7.11 (0.351)
6	9	0.96 (0.111)	8.26 (0.310)	16.56 (1.034)	14.78 (0.760)

entry holes to the shoots, and is not typically found within shoots. Because *D. alternosquamella* begins feeding at shoot bases, even small amounts of feeding result in the death of the entire shoot.

Whether or not the larvae move among separate dwarf mistletoe plants is unclear. However, when disturbed, larvae of all instars will either drop from the plant on a line of silk or depart and travel across pine branches. There are typically many dwarf mistletoe plants on a single tree at this study site, making larval movement among plants feasible in at least some instances. Frequently a larva which has dropped will then ascend the same line of silk to return to its original location.

Heinrich (1920:84) notes that "the color of the individual larvae varies in harmony with the color of the individual batches of mistletoe on which they feed." The coloration of larvae is variable, and generally this range of variation is similar to some host plant colors, but no close association between larval color and host plant color was observed. Furthermore, larval coloration did not change as a function of color of the dwarf mistletoe plants on which they were fed in the laboratory.

Pupae. *Dasypyga alternosquamella* has a single generation per year and over-winter as pupae. Sixth instar larvae drop to the ground and in the litter and soil they construct a small chamber of frass, soil and silk where they pupate. This chamber is approximately 10 mm in length and 4 mm in width and just encloses the pupae with little excess room. Pupae (Fig. 5) average 9.1 mm in length (N = 8, SE = 0.34) and 2.8 mm in width (N = 8, SE = 0.11). Two months after pupation average pupal weight was 35.4 mg (N = 7, SE = 1.94).

Larval abundance. During the course of this study 284 larvae were collected on 112 plants for an overall average of 2.5 larvae per plant. Most of these larvae were used in an unrelated field experiment. Larval abundance was quite variable in both space and time. For instance, on 12 July only five of the 10 *A. vaginatum* (collected from approximately as many host pines) had larvae, and the mean was 0.5 larvae per plant. On 3 August all of 16 *A. vaginatum* (collected from approximately as many host pines) had larvae, and larval abundance ranges from 1 to 10 per plant with a mean of 3.25 per plant. On this same date (3 August), an additional 146 larvae were collected from 18 dwarf mistletoe plants all growing on a single tree for a mean of 8.0 larvae per plant. In general, larval abundance appeared to increase over the course of the summer, peaking in mid-August, but larvae were still common into the middle of September.

Associated fauna. In addition to *D. alternosquamella*, at least three other species of lepidopteran herbivores were also found feeding on *A. vaginatum*. The most abundant of these three, *Promylea lunigerella glendella* Dyar (Pyralidae, Phycitinae), was only slightly less abundant than *D. alternosquamella*. These two phycitines can be distinguished by the fact that the head capsule widths of sixth instar *P. l. glendella* is a mean of 0.75 mm (N = 6, SE = 0.0097; Mooney in prep.), approximately 20% smaller than the mean of 0.96 mm (N = 9, SE = 0.111) for *D. alternosquamella*. Although Heinrich (1920) describes and

FIG. 4. Sixth instar *D. alternosquamella* and Southwestern dwarf mistletoe. Scale bar 2 cm.

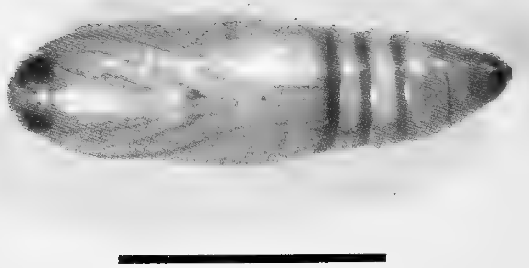

FIG. 5. Pupae of *D. alternosquamella*. Scale bar 5 mm.

illustrates larval *D. alternosquamella*, the only description of *P. l. glendella* is that of the adult (Dyar 1906, Heinrich 1956). Far less common, but also feeding on *A. vaginatum* was *Callophorys* (*Mitoura*) *spinetorum* Hewitson (Lycaenidae), the Blue Hairstreak. On three occasions cryptically colored geometrid larvae were also found feeding on the dwarf mistletoe. Most attempts at rearing *C. spinetorum* (nine of 10) and all attempts at rearing the geometrids were unsuccessfully due to parasitoids. In addition to lepidopterans, *Neoborella tumida* (Hemiptera: Miridae) and unidentified mites (Acari) were common and, especially the latter, present on most plants. The relatively high abundance of both *N. tumida* and the mites, along with the fact that no predation events were observed, suggests they are herbivores.

DISCUSSION

The feeding behavior of *D. alternosquamella* is consistent with the general patterns previously described for related taxa: Almost all pyralids are concealed feeders, and the Phycitinae in particular are known to feed within host plants (Neunzig 1987). What may be somewhat unique is that *D. alternosquamella* apparently changes feeding modes during their development; they are terminal shoot feeders early in their ontogony and later progress to mining modes. Because dwarf mistletoes are leafless, it is the shoots that are mined, and this feeding might more properly be compared to stem boring.

This mining has significant consequences for dwarf mistletoes. *Dasypyga alternosquamella* can be abundant, and because it feeds on shoots even low levels of herbivory results in death of all plant tissue distal to the site of herbivory. Other, unrelated work has documented the nearly complete destruction of all dwarf mistletoe shoots by *D. alternosquamella* in a several-hectare area of heavily parasitized ponderosa pines near Boulder, Colorado during the summer of 1998 (unpubl. data). At the Boulder site, *D. alternosquamella* was the only abundant herbivore. At the Manitou Experimental Forest the lepidopteran assemblages appeared to be more diverse; *P. l. glendella* was nearly equal in abundance to *D. alternosquamella*. The nature and consequences of interactions between *D. alternosquamella* and other dwarf mistletoe associated fauna are unknown, but diversity between sites can vary.

ACKNOWLEDGMENTS

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RECOGNITION OF WESTERN POPULATIONS OF *SPEYERIA IDALIA* (NYMPHALIDAE) AS A NEW SUBSPECIES

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ABSTRACT. Western populations of *Speyeria idalia* are described as separate subspecies, ***S. idalia occidentalis*, new subspecies.** Eastern and western populations can be diagnosed morphologically by differences in the size of spots on the underside of the hindwings. Furthermore, mitochondrially encoded cytochrome oxidase I and II genes reveal five synapomorphies for an extant eastern population in Pennsylvania, indicating a unique genetic diversity possessed by this population. Recognition of subspecies status for the eastern population may lead to a petition for an emergency listing under the Endangered Species Act of 1973.

Additional key words: Mitochondrial DNA, morphology, conservation, taxonomy.

Taxonomy within the genus *Speyeria* Scudder has long been a troublesome issue among lepidopterists (dos Passos & Grey 1945, 1947, Moeck 1957, Arnold 1983). No consensus has been reached on the number of species within the genus and relationships among subspecies are even less well resolved (Howe 1975, Arnold 1983, Hammond 1985, Scott 1986). Confusion among taxa stems from numerous examples of polymorphism, sexual dimorphism, convergence and clines (Hovanitz 1941, 1943, Moeck 1957, Rindge 1987, Grey 1989, Hammond 1991). Most of the variation within the genus is found among western North American species and subspecies, whereas eastern taxa are perceived as relatively well resolved. However, because previous research has been focused on the problematic western species, intraspecific variation in the eastern fauna may have been overlooked.

Speyeria idalia (Drury) is an example of an eastern species that has not been an issue of contention (Moeck 1957, Hovanitz 1963). Because *S. idalia* is so easily identified among *Speyeria* species, intraspecific variation may not have been thoroughly examined. The original range of *S. idalia* extended from the plains of North Dakota and Colorado, east to Virginia and Maine (Howe 1975, Scott 1986). However, within the last century, populations of *S. idalia* have been extirpated over most of the species' range due to habitat destruction (Hammond & McCorkle 1984, Hammond 1995, Swengel 1997). Only two populations are known to exist east of Illinois, one in Pennsylvania and the other in Virginia. Hence, if differences do exist between eastern (=Pennsylvania and Virginia) and western (=all other) populations, taxonomic status could have important implications for the conservation of the remaining eastern populations. The purpose of this research is to examine mitochondrial DNA (mtDNA) and morphological variation among populations of *S. idalia* to determine if: (1) significant intraspecific variation exists, (2) there is a pattern to the variation, and (3) any patterns of variation are worthy of taxonomic recognition.

MATERIALS AND METHODS

Morphological variation was examined via measurements of the size of white spots on the underside of the hindwings. All measurements were taken from museum specimens at the American Museum of Natural History (New York, NY). Sample sizes and collecting localities are provided in Table 1. No specimens from counties adjacent to the extant Pennsylvania population could be found in the American Museum collections; therefore, analyses of eastern populations used specimens from extinct populations from nearby counties in Pennsylvania, New York, and New Jersey to represent morphological variation of the extant Pennsylvania population (Table 1). Traits selected for analyses (Table 2, Fig. 1) were those determined by a pilot study to be most variable and therefore most likely to provide information on patterns of intraspecific variation. Maximum diameter of each spot was measured using a hand held digital micrometer. To account for allometric relationships all measures were transformed using the equation $X' = \log(X/Y)$, where Y = size measure. The size measure used was the length of the second cubital vein. An alternative measure for size, wingspan, was not incorporated because not all specimens had both wings and because some specimens had wings folded for display. A regression of second cubital vein length on wingspan was significant ($r^2 = 0.62$, $p < 0.001$), suggesting that second cubital length is a valid size measure. Analysis of morphological data included both a MANOVA, incorporating all 11 traits as a group, and univariate F-tests, to examine variation at each trait independently. Both analyses tested the effects of region (eastern vs. western; Table 1) and sex on patterns of variation. All analyses were completed using Systat v. 5.0.

Mitochondrial DNA analysis used samples collected from extant populations found across the range of the species. Sample sizes and locales are provided in Table 3. Collection of tissue from those populations of special

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TABLE 1. Sample sizes and collection locales for morphological measurements from museum specimens.

State	County	Male	Female
Eastern populations			
Pennsylvania	Montgomery	2	1
	Alleghany	6	3
	Butler	11	3
New York	Renssalaer	2	0
	Albany	1	5
	Columbia	1	0
	Westchester	12	6
	New York	6	5
	Unknown	2	6
New Jersey	Passiac	4	3
	Essex	9	3
	Morrris	14	6
	Hunterdon	2	1
	Unknown	3	3
Total eastern		75	45
Western populations			
Nebraska	Pawnee	2	0
	Otoe	5	0
	Lancaster	14	1
	Douglas	3	3
	Stanton	2	0
	Dixon	4	3
	Cedar	0	3
	Knox	1	1
	Keyapaha	4	0
	Cherry	5	0
	Douglas	2	2
	Johnson	3	0
	Riley	2	0
Iowa	Dickinson	3	1
	Plynouth	3	0
	St. Clair	2	4
	Franklin	8	6
	Polk	5	0
	Guthrie	6	0
	Pocahantas	3	0
Illinois	Cook	21	5
	Mercer	3	3
	Iroquois	7	0
Total western		108	32

TABLE 2. Traits selected for analysis and the corresponding abbreviations used in Figs. 1–3. Cell names follow Scott (1986) (Figure 53, p. 146).

Trait	Abbreviation
Basal-most spot in cell 1A + 2A	1A2A
Basal spot in cell CuA2	CUA2-A
Median spot in cell CuA2	CUA2-B
Basal-most spot in cell CuA1	CUA1
Basal-most spot in cell M3	M3
Basal-most spot in cell M2	M2
Basal-most spot in cell M1	M1
Basal-most spot in cell Rs	RS
Basal-most spot in cell Sc + R1	SCR1-A
2nd most basal spot in cell Sc + R1	SCR1-B
Basal-most spot in the hindwing cell	HCELL

conservation concern (Pennsylvania, Illinois, Iowa, and Wisconsin) consisted of the removal of the anterior leg on the right side so that specimens could be released alive. Anecdotal observations of seven captive females suggested no decrease in survivorship or oviposition ability following leg removal. These results indicate that this method may be useful for future genetic studies in other insect species of conservation concern, although more thorough, species specific, studies should be conducted. DNA extractions were carried out by digesting homogenized tissue at 65°C for 3–12 hours in: 10 mM Tris-HCl, 10 mM EDTA, 50 mM NaCl, 2% SDS, 20 µl dithiothreitol, and 0.4 mg Proteinase K. Nucleic acids were extracted with an equal volume of phenol, the aqueous phase was transferred to a new microcentrifuge tube and the organic extraction repeated with 24:1 chloroform:isoamyl alcohol. Total nucleic acids were precipitated with the addition of 1/10 volume 3 M sodium acetate and 3 volumes of cold 95% ethanol. Nucleic acids were resuspended in 50–100 µl of sterile water.

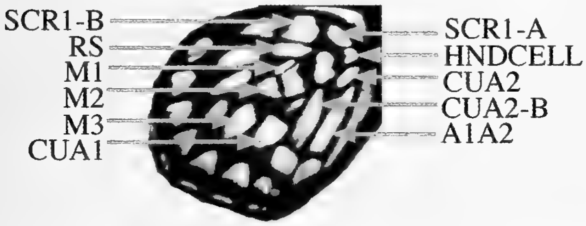

FIG. 1. Arrows indicate underside hindwing spots measured for morphological analysis. Trait abbreviations correspond with Table 1.

Mitochondrial DNA sequences were generated by direct sequencing of PCR products from partial cytochrome oxidase I and II genes (COI and II). Primers used for PCR amplification were: C1-J-2183 (alias Jerry) 5′-CAACATTTATTTTGATTTTTTGG-3′ (Simon et al. 1994) and TK-N-3772 5′-GACCATTACTTGCTTTCAGTCATCT-3′ (listed as TK-N-3782 in Sperling & Hickey 1995). PCR reactions were carried out using: 60 ng genomic DNA, 20 mM Tris-HCl, 50 mM KCl, 3 µM MgCl$_2$, 0.25 mM of each dNTP, 2 µM each primer, 1 Unit Taq DNA polymerase, and water to a final volume of 20 µl. Each PCR reaction was then subjected to 30 cycles of amplification at the following conditions: 94°C for 30 seconds, 45°C for 30 seconds, 72°C for 1 minute. PCR reactions were purified using Qiagen (Valencia, CA) PCR purification columns, following manufacturers recommendations.

Sequencing reactions used two internal primers, sequencing in opposite directions, with 30 base pairs of overlap. Sequencing primers were: TL2-N-3014 (alias PAT) 5′-TCCAATGCACTAATCTGCCATATTA-3′ (Simon et al. 1994), modified to 5′-TCCATTACATATAATCAGCCATATTA-3′ and C1-J-2983 (alias LANAE)

FIG. 2. Comparison of similarly-sized males (upper) and females (lower) from western (left) and eastern (right) populations. Western specimens were from Nebraska and eastern specimens from New York.

5′-TACCTCCTGCTGAACATTCT-3′. Sequencing reactions were carried out using the Perkin Elmer (Foster City, CA) Big Dye cycle sequencing kit, following manufacturer recommendations. Sequences were visualized on an ABI 377 automated sequencer at the University of Illinois Biotechnology Sequencing Center. All sequences were edited using EditView V1.0.1 and aligned using Sequencher V3.0.

Phylogenetic hypotheses were constructed using PAUP* V4.0b3 (Swofford 1998) via maximum parsimony analysis with a heuristic search and tree bisection and reconnection (TBR) branch swapping. Sequences generated from *Speyeria cybele* (Fabricius) and *S. nokomis* (Edwards) were used as outgroups to root the tree. Phylogenetic reconstructions were without weighting schemes because all substitutions but one within *S. idalia* were transitions. Statistical support for nodes was estimated using 100 bootstrap replicates.

RESULTS

Morphological analyses revealed that all traits examined were significantly different between eastern and western populations in both the multivariate test (Wilks' lambda = 0.381, F = 36.006, df = 11, 244, $p < 0.001$) and all univariate F-tests ($p < 0.001$ for all traits). As an example, Fig. 2 shows a male and female from an eastern population next to a similarly-sized male and female from a western population. Only one of the traits, the basal-most spot in the third median cell, was significantly different between the sexes (Univariate F = 7.523, df = 1, 254, p = 0.007); however, the multivariate results suggest that as a group, the traits did not differ between the sexes (Wilks' lambda = 0.946, F = 1.254, df = 11, 214, p = 0.252). Figure 3 graphically represents the differences in the trait means between eastern and western populations for the non-transformed data.

Results of mtDNA sequence analysis revealed 30 variable sites, 18 of which were parsimony-informative (Genbank accession number AF295040). Within the COI gene there were 11 parsimony-informative sites: three first-position and one second-position nonsynonymous substitutions and seven third-position synonymous substitutions. Within the COII gene there were seven parsimony-informative sites, all third-position synonymous substitutions. Maximum parsimony analysis resulted in five most-parsimonious trees of 126 steps. All individuals in the Pennsylvania population shared the same unique haplotype, which has five synapomorphies (Fig. 4). All other populations sampled revealed a total of 22 unique haplotypes with no apparent geographic associations among them, with the possible exception of some Wisconsin haplotypes (Fig. 4). Also, 45 out of 84 individuals sampled from the 17 western populations shared the same haplotype (haplotype 1, Fig. 4), suggesting little genetic structuring among those populations.

Speyeria idalia idalia (Drury [1773])

See dos Passos and Grey (1945, 1947) for a description and type specimens of *S. i. idalia*. Diagnostic characters that separate subspecies are provided below.

***Speyeria idalia occidentalis* Williams, new subspecies**

Diagnostic characters. *Speyeria idalia occidentalis* can usually be diagnosed by eye because the hindwing spots are usually much larger than in *S. i. idalia*. The basal-most diffuse white spot (not included as a trait used in this study) in the second cubital cell (Figs. 1, 2) is often entirely absent in *S. i. idalia* but usually present in *S i. occidentalis*. While all of the ventral hindwing spots included in this study are significantly larger in *S. i. occidentalis*, the most pronounced differences are in cells A1A2, M1 and RS (Figs. 3, 4). In *S. i. occidentalis* the spot in A1A2 is usually greater than 10 mm, whereas *S. i. idalia* it is usually less than 8 mm (these numbers are general rules of thumb for quick reference and therefore do not incorporate size or sex differences). For M1, *S. i. occidentalis* is usu-

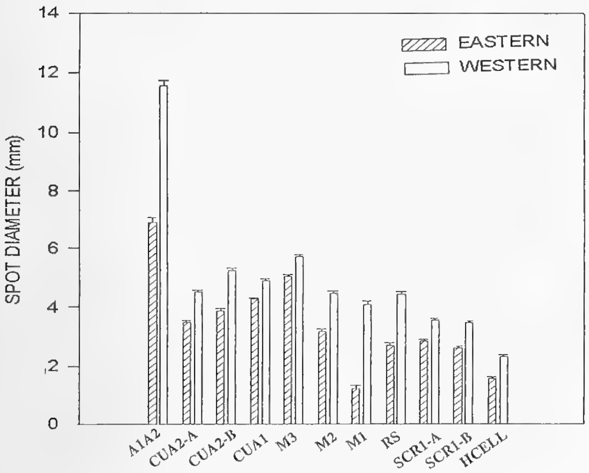

FIG. 3. Means and standard errors of underside hindwing cell spots for raw data. Trait abbreviations correspond with Table 1 and Fig. 1.

ally >3 mm, whereas *S. i. idalia* is usually <3 mm. For RS, *S. i. occidentalis* is usually >4 mm, whereas *S. i. idalia* is usually <4 mm.

Description. Male wingspan 63–92 mm (N = 108). Dorsal surface of forewing with orange background coloration and the usual *Speyeria* pattern of black spots and bars. Black outer marginal border with a row of white spots. Hindwing is orange with hints of blue-black basally and entirely with blue-black background color from the submedian to outer margin. A postmedian row of orange or fulvous spots, a submarginal row of white spots and an outer marginal row of white spots. Ventrally, forewing lighter orange background with submarginal and outer margin rows of white spots. Also, varying numbers of diffuse apical and subapical white spots. Hindwing is unique to *Speyeria idalia*. Background is entirely yellow to black with white spots, either single or multiple, in every cell. Female wingspan 71–110 mm (N = 33). Dorsal surface, forewing with larger marginal black border than in males and a marginal row of white spots. Black apical and subapical background color with white spots. Hindwing as in male except with a post median row of white spots, rather than orange. Ventrally, same as the male except for a deeper fulvous background coloration in the forewing, more black background coloration apically and in the margin.

Types. HOLOTYPE: (male), 1 mile S.E. of Crete, IL, 7 July 1965 (R.R. Irwin). ALLOTYPE: (female), same location data as holotype, 23 August 1965 (R.R. Irwin). PARATYPES: Two males, one female, all with same collection and data as holotype. Deposition of specimens: All specimens at the Illinois Natural History Survey collections.

DISCUSSION

Morphological data suggest that eastern and western populations were distinct entities; in that specimens from eastern populations had spots on the underside of the hindwing that were significantly smaller. The genetic basis for these morphological traits has not been determined, so the potential exists for differences between eastern and western populations to be correlated with as of yet undetermined environmental variables, rather than indicative of a unique evolutionary history. However, mtDNA sequence analysis suggests that the Pennsylvania population is a distinct evolutionary lineage that can be diagnosed with 5 synapomorphies, which are unique and fixed in the population. Hence, mtDNA support, in part, differentiation of the eastern populations. Based on these data I recommend that the eastern (=Pennsylvania) and western (=all other) populations be recognized as separate subspecies, and the morphological characters be used as a means for external diagnosis of each subspecies. Fortunately, the subspecies of *S. idalia* named here can be identified on the basis of easily quantified measures (spot size), which make diagnosis relatively straightforward when compared with other *Speyeria* species, in which subspecies are typically differentiated by slight differences in basal

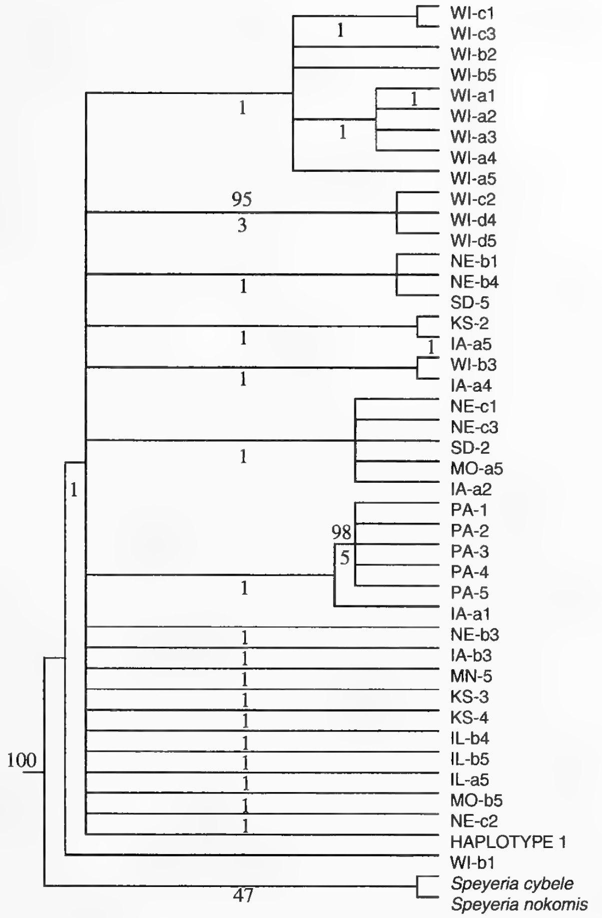

FIG. 4. Strict consensus of the five most-parsimonious trees resulting from maximum parsimony analysis of mitochondrial DNA sequence data from cytochrome oxidase I and II genes (126 steps, consistency index = 0.96). Bootstrap values >60 are shown above branches and the number of synapomorphies for each clade are shown below branches. Forty-five specimens that shared a single haplotype were collapsed together into "haplotype 1" to conserve space. Sample labels correspond with collection locations in Table 3 and numbers in parentheses indicate which of the five individuals per sample correspond to a given haplotype.

TABLE 3. Sample sizes and collection locales for mitochondrial DNA tissue collection.

State	County	Sample Size
Pennsylvania	Lebanon	30
Nebraska – a	Keyapaha	5
Nebraska – b	Greeley	5
Nebraska – c	Kearney	5
Kansas	Riley	5
Iowa – a	Muscatine	5
Iowa – b	Plymouth	5
Illinois – a	Ogle	5
Illinois – b	Mason	5
Illinois – c	Cass	4
Wisconsin – a	Crawford	5
Wisconsin – b	Iowa	5
Wisconsin – c	Dane	5
Wisconsin – d	Portage	5
Missouri – a	St. Clair	5
Missouri – b	Vernon	5
Minnesota	Lincoln	5
South Dakota	Hughes	5
Total sample size		114

coloration of the hindwing discal area (Howe 1975, Scott 1986). Figure 3 can be used as a guide to distinguish among *S. idalia* subspecies. For example, the maximum diameter of the A1A2 cell spot used in this study (Fig. 1) is less than 8 mm in *S. i. idalia* but greater than 10 mm in *S. i. occidentalis* (Fig. 3).

If the relationship between mtDNA, morphology and longitude were to be generalized, then the Virginia population would be recognized as the same subspecies as the Pennsylvania population. However, the formal status of the Virginia population will remain undetermined until data from this population can be included in the analyses. Assuming that the neotype designation for *S. idalia* (New York, NY) of dos Passos and Grey (1945) applies to the eastern populations in general, the name for the Pennsylvania subspecies becomes *Speyeria idalia idalia*. Western populations therefore fall under the subspecies name *Speyeria idalia occidentalis*, new subspecies.

An initial examination of the male genitalia from five eastern and 25 western specimens did not result in any distinguishable differences (unpubl. data). However, other anecdotal evidence of differentiation does exist. Previous descriptions of habitat use note that eastern populations are typically found in xeric habitats whereas western populations are found in mesic habitats (Scudder 1889, Opler & Krizek 1984). Also, Barton (1996) notes that *Viola saggitatta* is the preferred host plant for the Pennsylvania population, whereas other studies focusing on western populations have noted *V. pedatifida* and *V. pedata* as preferred host plants (Swengel 1997, Kelly & Debinski 1998).

Subspecies status for the eastern population has important conservation implications. The Pennsylvania population is found on a military installation where current land use practices threaten to destroy the remaining *S. i. idalia* habitat (Barton 1996). Because this population resides on federally owned land, formal protection can only be afforded under federal legislation, i.e., the Endangered Species Act of 1973 (ESA). Therefore, the designation of *S. i. idalia* may result in a petition for an emergency listing under the ESA.

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POPULATION STUDIES OF *AERIA OLENA* AND *TITHOREA HARMONIA* (NYMPHALIDAE, ITHOMIINAE) IN SOUTHEASTERN BRAZIL

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ABSTRACT. Populations of *Aeria olena* and *Tithorea harmonia pseudethra* (Lepidoptera: Nymphalidae: Ithomiinae) showed large variations in abundance along the year in four sites, with peaks at the end of the wet season. The sex ratio of captures in *A. olena* was male biased. In *A. olena*, males showed longer residence times than females. Both species differ from other members of the Ithomiinae community in the region by feeding on Apocynaceae vines as larvae, not congregating in "ithomiine pockets" and having low population numbers in the dry season.

Additional key words: mark-recapture, Ithomiinae pockets.

The Ithomiinae (Nymphalidae) are an exclusively Neotropical butterfly group (Fox 1967, Brown & Freitas 1994) except possibly for the Australian genus *Tellervo* Kirby (Ackery & Vane-Wright 1984). The subfamily is distributed from Mexico to Argentina and is largely restricted to moist forest habitats from sea level up to 3000 m (Fox 1967, DeVries 1987).

Ithomiinae populations are considered difficult to study due to low adult recapture rates, even in dense pockets (Gilbert 1993). Thus there are few published population studies in this subfamily (Drummond 1976, Haber 1978, Young & Moffett 1979, Vasconcellos-Neto 1980, 1991, Trigo 1988, Freitas 1993, 1996, Pinto & Motta 1997). Knowledge of population parameters is important to the understanding of this family and of the whole butterfly community (DeVries 1994, Freitas 1996).

The genera *Tithorea* Doubleday (two species) and *Aeria* Hübner (three species) both belong to basal branches of the Ithomiinae (Brown & Freitas 1994), with aposematic "danaoid" larvae feeding on Apocynaceae (such as *Prestonia acutifolia* (Benth.) K. Schum. and *P. coalita* (Vell.) Woodson) and bearing fleshy tubercles (Brown 1987, Brown & Freitas 1994, Trigo et al. 1996). In Southeastern Brazil, both species are most common in semi-deciduous forests of the interior, being scarce in the humid forests of the Atlantic mountain slopes and coastal plain.

This paper describes the population parameters of three populations of *Aeria olena olena* Weymer and one of *Tithorea harmonia pseudethra* Butler in semideciduous forest fragments in SE Brazil, comparing them with other populations of Ithomiinae in Brazil.

STUDY SITES AND METHODS

The present study combines four data sets collected by different researchers from 1974 to 1998 in four different sites in São Paulo state, southeastern Brazil. Although the basic method to study all the populations was mark-recapture (see Freitas 1993, 1996), there were some differences among data sets, requiring that methods and results be presented separately. The regional climate in the four sites is markedly seasonal, with a warm wet season from September to April and a cold dry season from May to August.

The most recent study area was in the Santa Genebra Forest Reserve (SG, 22°49′S, 47°07′W), a 250 ha forest fragment in Campinas. The study area is covered by semideciduous forest, with annual rainfall near 1400 mm and an average annual temperature of 20.6°C (Morellato & Leitão-Filho 1995). A large part of the forest is old secondary growth, with a predominance of forest edge plants and lianas.

In this area, a mark-recapture census of *A. olena* extended from January 1997 to June 1998 (AVLF and FV), along an interior trail 1100 m long, with 103 field days of about four hours each at intervals of 2 to 15

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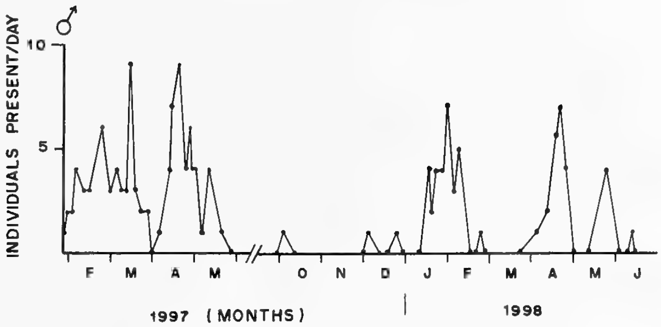

FIG. 1. Number of male *A. olena* present per day (NIPD) from January 1997 to June 1998 in Santa Genebra.

days. Butterflies were captured with an insect net, individually numbered on the underside of both forewings with a felt-tipped pen, and released. Wing wear, forewing length, point of capture, sex and food sources were recorded (as in Freitas 1993, 1996). The age of individual butterflies was estimated based on wing wear, initially using the six categories described by Ehrlich and co-workers (Ehrlich & Davidson 1960, Brussard & Ehrlich 1970, Ehrlich & Gilbert 1973). These six categories were later regrouped into three: fresh, intermediate and old as in Freitas (1993, 1996). Age structure was calculated as the daily proportion of each category, and grouped into monthly means.

The other three populations were studied by JV and KSB from August 1974 to December 1976 (Sumaré, SP), and by JRT from December 1983 to August 1985 (Campinas—Costa e Silva and Moji-Guaçu, SP), with the same methods for capturing, marking and gathering data (Vasconcellos-Neto 1980, Trigo 1988).

The Horto Florestal de Sumaré (HS, 22°50′S, 47°16′W; Brown & Vasconcellos-Neto 1976), where the population of *A. olena* was censused weekly, had a climate similar to that of Campinas. The population of *A. olena* censused in the "Mata de Costa e Silva" of the Fazenda Santa Elisa, Instituto Agronômico de Campinas (CS, 22°51′S, 47°06′W), occupied a 12-ha fragment of semideciduous forest, with the same climate as Santa Genebra. Most of the area is covered with secondary forest, with a predominance of forest edge plants and lianas. Marking was done along four trails (total of 1000 m), during two consecutive days each month.

A population of *Tithorea harmonia pseudethra* was censused from September 1984 to August 1985 in the "Mata da Pedra" of the Estação Experimental Mogi-Guaçu (Fazenda Campininha) (MP, 22°17′S, 47°12′W), a 30 ha area covered by riparian forest within "Cerrado" vegetation along the Moji-Guaçú river near Martinho Prado. The annual rainfall is about 1500 mm, and the average annual temperature is 21°C. In this area, a mark-recapture census was conducted on a 900 m long trail, for two consecutive days each month. Because the sex ratio was close to 1:1 in this population (see results), the sexes were lumped in some analyses.

The Santa Genebra mark-recapture data were analyzed by the Jolly-Seber method (Southwood 1971) for estimating population parameters. Only males were analyzed because of the low number of females. Daily results were presented as "number of individuals captured per day" (NICD), and "number of individuals present per day" (NIPD), as in Ramos and Freitas (1999). In estimating the NIPD, recaptured individuals were considered to have been present in the population on all previous days since the day of first capture (that is, they were "marked animals at risk").

RESULTS

Population biology of *Aeria olena*. In SG, adults of *A. olena* were captured on 51 of the 103 study days. Males were present on 47 days and females on 23 days. In total, 110 males and 28 females were marked. The NICD (for 51 days with captures) varied from zero to 9 in males (mean = 2.71, SD = 1.99); and from zero to 4 in females (mean = 0.67, SD = 0.93) (Fig. 1). Based on the NIPD, males were most abundant during the end of the wet season (February to May), diminishing in June, and virtually absent along the trail from July to January (Fig. 1). Jolly-Seber analysis for males gave estimated population numbers for only 12 days, varying from one to 19 individuals, with a maximum possible of 80 individuals.

In the HF, 217 males and 145 females were marked on 67 days during the three years of study (Table 1). Males were present on 63 days and females on 54 days. The NICD (for 67 days) varied from zero to 14 in males (mean = 4.82, SD = 3.99) and from zero to 11 in females (mean = 2.85, SD = 2.65). Based on the

TABLE 1. Sex ratio of marked individuals of *Aeria olena* in the three study sites in São Paulo state; rec (%) = percentage of recaptures. An asterisk indicates a male biased sex ratio (chi-square test [X^2], $p < 0.05$).

Study site and dates	Males	Females	Sex ratio	X^2	rec (%)	
					m	f
Sumaré 1974	28	18	1.5:1	2.2	7.0	11.0
Sumaré 1975	131	91	1.4:1	7.2*	27.4	25.9
Sumaré 1976	58	36	1.6:1	5.1*	14.0	17.0
Sumaré (three years)	217	145	1.5:1	14.3*	21.2	22.1
Costa e Silva 1983-84	182	116	1.6:1	14.6*	9.8	12.9
Costa e Silva 1985	180	85	2.1:1	34.1*	14.4	4.7
Costa e Silva (three years)	362	201	1.8:1	46.0*	12.2	9.4
Santa Genebra 1997–1998	110	28	3.9:1	48.7*	20.0	14.3

NIPD, both males and females were rare or absent throughout the early wet season (October to February) and most abundant at the end of the wet season (March to May) (Fig. 2).

In CS, 362 males and 201 females were captured. In 36 days of study, males were seen on 35 days and females on 33 days. The NICD (in 36 days) varied from zero to 29 in males (mean = 11.2, SD = 8.36) and from zero to 17 in females (mean = 6.25, SD = 5.04). The results of the censuses showed that the population increased in numbers from February to June, decreasing after July and maintaining low numbers from September to January (Fig. 3). In both 1984 and 1985, peak number of individuals were reached from April to June (Fig. 3).

In SG and CS, the maximum number of recaptures was two for both males and females; in HS, males were recaptured from one to three times, and females from one to four times. In the three populations, single recaptures were more than 68% of all recaptures.

Sex ratio. The sex ratio of individuals captured and marked was male biased in all sites (Figs. 4–6, Table 1). In SG, the sex ratio was male biased in all months (Fig. 4), and males were always more than 60% of the total. The recapture rate of males (20.0%) was higher than of females (14.3%), but due to the low number of recaptures of females (n = 4) no statistical comparison could be made.

In HS, the sex ratio was also male biased in all months (Fig. 5), and males were always more than

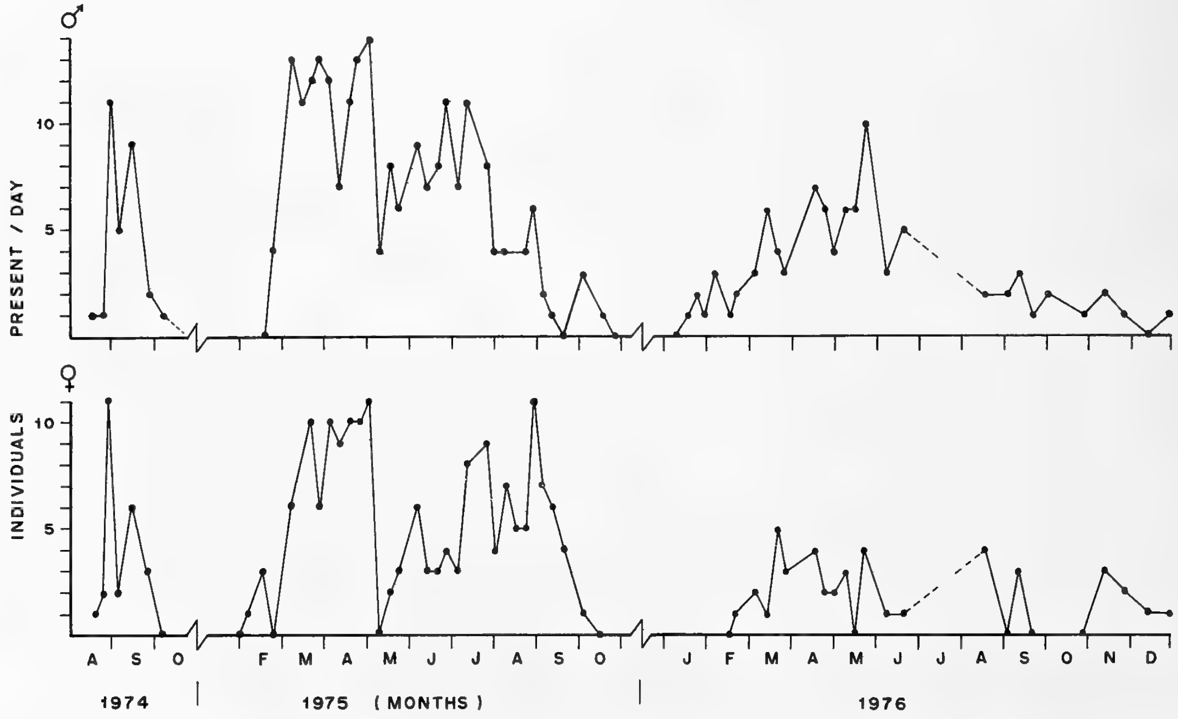

FIG. 2. Number of male and female *A. olena* present per day (NIPD) from August 1974 to December 1976 in the Horto Florestal de Sumaré.

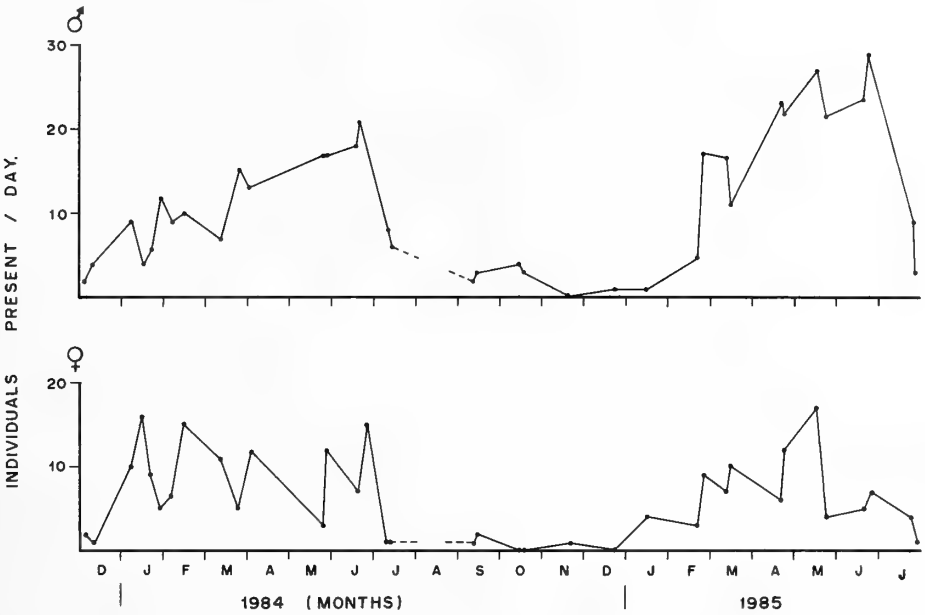

FIG. 3. Number of male and female *A. olena* present per day (NIPD) from December 1983 to July 1985 in Costa e Silva.

60% of the total. The recapture rate of males was higher than that of females in one of the three years (Table 1).

In CS, the sex ratio was male biased from May to July in 1984 and from April to June in 1985 (Fig. 6), and the recapture rate of males was higher in one of the three years (Table 1).

In laboratory rearing, the sex ratio was also male biased, with 29 males and 12 females obtained from larvae from CS ($X^2 = 7.05$, df = 1, $p < 0.01$).

Age structure. Age structure was not stable in the three sites; in general, "fresh" individuals were most common from February to May, replaced by intermediate ones in the dry season.

In SG in 1997, "fresh" individuals were common from February to May, and "old" individuals became more common after April; this pattern was not observed in 1998 (Fig. 7).

In HS (Fig. 8), the variation in age structure was similar in 1975 and 1976, with "fresh" individuals increasing from February to March, decreasing after this to be replaced by the "intermediate" ones in the dry season.

In CS in 1984 (Fig. 9), the age structure was stable in most of the months, with a small decrease of "fresh" and increase of "old" individuals in the dry season months; this pattern was not observed in 1985, when the "fresh" individuals increased in proportion after February, reaching a maximum in July.

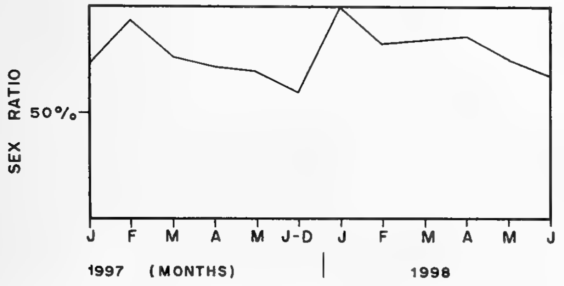

FIG. 4. Sex ratio in *A. olena* in Santa Genebra from January 1997 to June 1998, as percent of males in each day's captures.

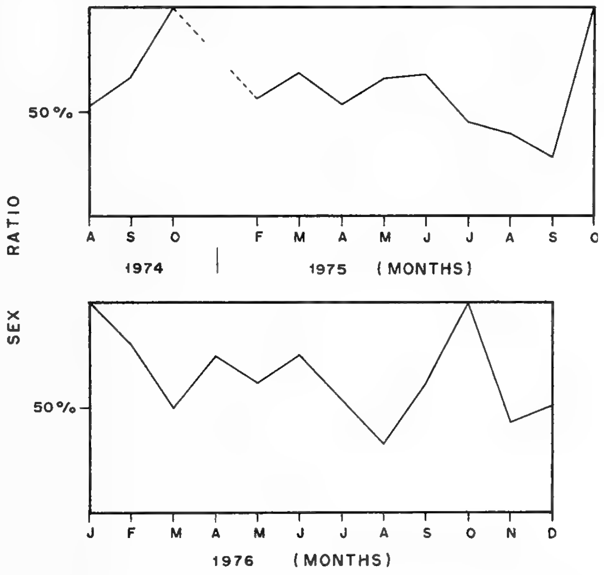

FIG. 5. Sex ratio in *A. olena* in the Horto Florestal de Sumaré from August 1974 to December 1976, as percent of males in each day's captures.

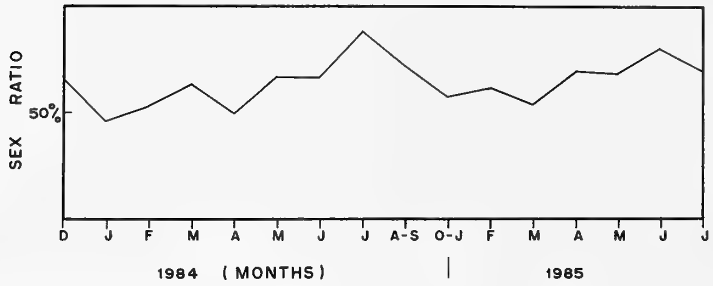

FIG. 6. Sex ratio in *A. olena* in Costa e Silva from December 1983 to July 1985, as percent of males in each day's captures.

Residence time. In SG, females had a residence time (mean = 9.5 days, SD = 4.04, n = 4) almost equal to that of males (mean = 9.14 days, SD = 5.34, n = 22); the significance could not be calculated due to low numbers of females. Estimated residence time for males ("life expectancy" of Cook et al. 1967) was 6.8 days. The maximum individual permanence (survival) was at least 24 days for a male and 13 days for a female.

In HS, females had a residence time (mean = 23.2 days, SD = 14.38, n = 32) statistically the same as that of males (mean = 20.7 days, SD = 19.24, n = 46) (t = 0.615, df = 76, p = 0.54). The maximum individual permanence was at least 120 days for a male and 56 days for a female.

In CS the residence time for males (mean = 6.79 days, SD = 7.36, n = 44) was considered equal to that for the females (mean = 11.1 days, SD = 10.38, n = 19) (t = 1.898, df = 62, p = 0.06). The maximum individual permanence was at least 24 days for a male and 27 days for a female.

Vagility. In SG, most males were recaptured away from the point of first capture (59.1%), with the maximum distance recorded being 800 m (male number 6, seven days after first capture), but in general ranging from 50 to 250 m (mean = 84.1 m, SD = 172.78, n = 22). All females recaptured were at the same place as the first capture.

In CS, 54% of the individuals were recaptured away from the point of first capture; the average distance traveled by an individual *A. olena* was 107.4 m (SD = 82.69, n = 34), with the maximum distance recorded being 300 m (for three males and one female).

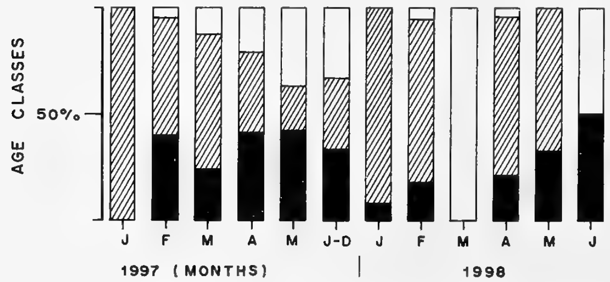

FIG. 7. Age structure of *A. olena* males (black = fresh individuals, hatched = intermediate, white = worn individuals) from January 1997 to June 1998 in Santa Genebra.

In HS numerous recaptures showed individuals moving 100–400 m in a single day.

Population biology of *Tithorea harmonia pseudethra*. The number of individuals was highest from March to May 1984, and decreased after June 1985 (Fig. 10). The sex ratio was statistically equal to 1:1 in all months except August 1985 (Fig. 11). The sex ratio in the laboratory was also 1:1, with 10 males and 9 females obtained from larvae from this region (X^2 = 0.05, df = 1, p > 0.2). The proportion of recaptures of males (3.9%) was almost equal to that for females (3.6%). Except for September 1984, the age structure (with both sexes lumped) was stable, with "fresh" and "intermediate" individuals equivalent in proportions and more abundant than the "old" individuals (Fig. 12). The maximum residence time was 34 days, recorded for three males. The average distance traveled by an individual *T. harmonia pseudethra* was 83 m (SD = 58, n = 6).

DISCUSSION

The general pattern observed in the three populations of *A. olena* indicates that population numbers decrease in the dry season, the same time that all other Ithomiinae reach maximum numbers in Ithomiinae "pockets" (Brown & Benson 1974, Brown & Vasconcellos-Neto 1976, Vasconcellos-Neto 1980, 1991, AVLF unpubl. data). This discrepancy may be related to the low availability of the leaves of the larval host plant *Prestonia coalita* (Trigo 1988) during the dry season. The low numbers continue until the next wet season, when populations start to increase and reach maximum size at the end of the wet season, possibly due to high recruitment of new individuals during the periods of maximum availability of new and mature leaves. In *Heliconius* butterflies, periods of dry climate were also observed to cause a decrease in popu-

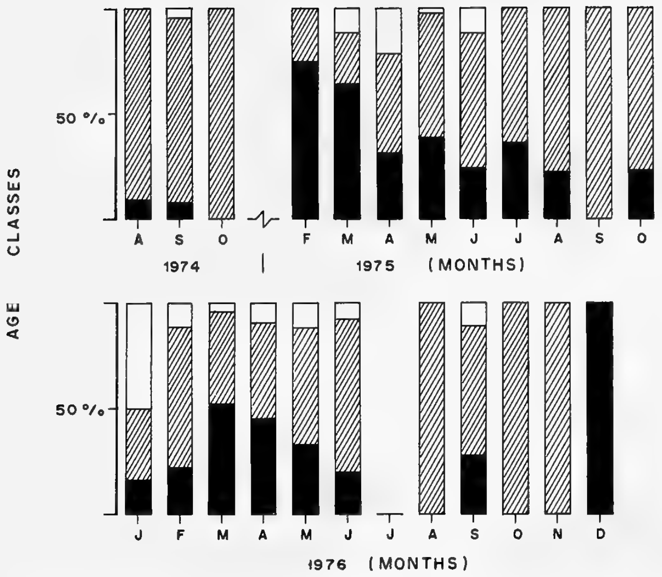

FIG. 8. Age structure of *A. olena* males (black = fresh individuals, hatched = intermediate, white = worn individuals) from August 1974 to December 1976 in the Horto Florestal de Sumaré.

lation numbers (Benson 1978, Ramos & Freitas 1999), probably as a result of low availability of meristems of Passifloraceae, eaten by the larvae of most species in this genus.

Some population parameters of *A. olena* are similar and others dissimilar to those observed in other Ithomiinae species. The male biased sex ratio in the field, low recapture rates of adults and a moderate adult survival rate are often observed in Ithomiinae (Brown & Benson 1974, Drummond 1976, Haber 1978, Young & Moffett 1979, Vasconcellos-Neto 1980, Trigo 1988, Freitas 1993, 1996, Pinto & Motta 1997), and considered as typical for species of this subfamily (even if more studies are needed to confirm these tendencies). The absence of adults in Ithomiinae pockets and low numbers in the dry season are clearly distinct from patterns recorded in other species of Ithomiinae.

The results indicate that *A. olena* occurs in areas where other Ithomiinae species are scarce or appear mostly as individuals moving between humid areas. Males are often found visiting flowers that have PAs (pyrrolizidine alkaloids) at the end of the wet season, showing a marked sex-bias for these sources (Trigo et al. 1996). Early observations suggested that *A. olena* usually flew outside the perimeters of the Ithomiinae pockets, being more tolerant of dry areas of the forests even during the early dry season, when the remaining species concentrate in the wettest spots. However, in the very strong dry season of 1997, even *A. olena* became scarce along the main trail of SG, probably as a result of both decrease in recruitment and migration away from the bright, hot trail.

The population structure of *T. harmonia pseudethra* appears to follow the same tendencies as that of *A. olena*, including the fluctuation in numbers throughout the year, the low recapture rates, and a moderate

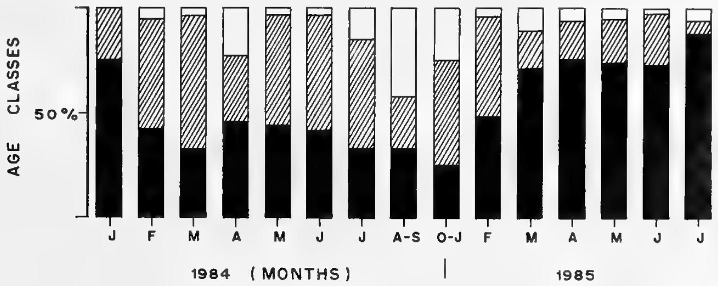

FIG. 9. Age structure of *A. olena* males (black = fresh individuals, hatched = intermediate, white = worn individuals) from January 1984 to July 1985 in Costa e Silva.

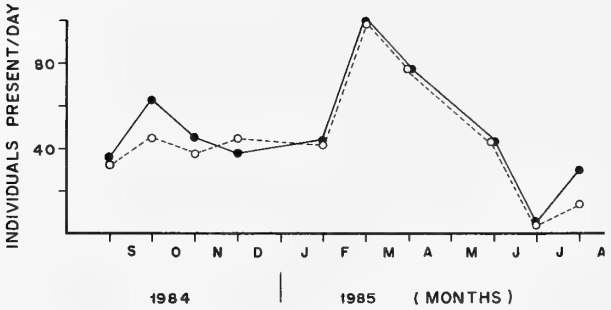

FIG. 10. Number of *T. harmonia pseudethra* individuals present per day (NIPD), males (solid line), females (hatched line), from August 1994 to August 1985 in the Mata da Pedra.

adult rate of survival. However, the sex ratio was equal in most months, differing from the pattern observed in most other Ithomiinae (Freitas, 1993, 1996). As in *A. olena*, the fluctuations appear to be related to seasonal changes in climate, with a marked decrease after the beginning of the dry season. Again, the effects of climate on the availability of fresh leaves and seedlings of their larval host plant *Prestonia acutifolia* during the dry season could be the main factor in the population decrease in the dry months (Trigo 1988). Adults of *T. harmonia pseudethra* do not occur frequently in Ithomiinae pockets, and are more common in forests near rivers. Both sexes were little attracted to PA sources, but frequently visited flowers without PAs (Brown 1985, 1987, Trigo et al. 1996).

Tithorea harmonia pseudethra and *A. olena* belong to the most basal branches of the Ithomiinae (Brown & Freitas 1994 and unpubl. data), with larvae feeding on Apocynaceae vines and immatures probably sequestering PAs (Brown 1985, 1987, Brown & Freitas 1994, Trigo et al. 1996). They also represent unique syndromes in behavior and population variation (not concentrating in Ithomiinae pockets, low numbers during the dry season). This suggests that population studies of other Ithomiinae genera are needed for a better understanding of the evolutionary biology of this butterfly subfamily.

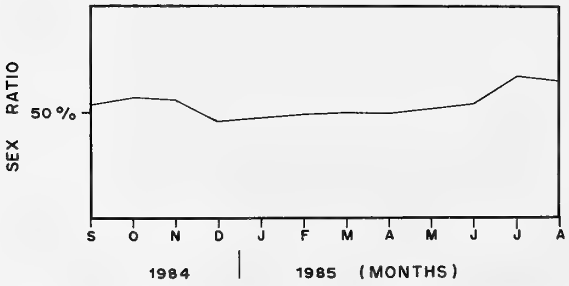

FIG. 11. Sex ratio in *T. harmonia pseudethra* in the Mata da Pedra from September 1984 to August 1985, as percent of males in each day's captures.

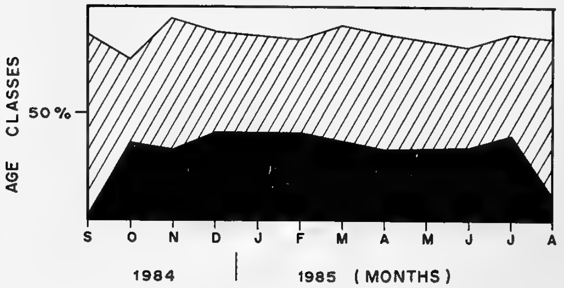

FIG. 12. Age structure of *T. harmonia pseudethra* males (black = fresh individuals, hatched = intermediate, white = worn individuals) from September 1984 to August 1985 in the Mata da Pedra.

ACKNOWLEDGMENTS

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A NEW SPECIES OF *EUPHYES* SCUDDER FROM WESTERN MEXICO (HESPERIIDAE: HESPERIINAE)

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ABSTRACT. A new species of *Euphyes* Scudder 1872 is described from seven males and four females from the western Mexican states of Oaxaca, Guerrero, Michoacán and Nayarit. It has been found in tropical deciduous forest and thorn forest from 100–680 m elevation.

RESUMEN. Se describe una especie nueva de *Euphyes* Scudder 1872 a partir de siete machos y cuatro hembras provenientes de los estados occidentales Mexicanos de Oaxaca, Guerrero, Michoacán y Nayarit. Se encuentra esta especie en bosque tropical subperennifolia y caducifolia, entre 100–680 msnm.

Additional key words: biogeography, butterflies, skippers, systematics, taxonomy.

The Mexican fauna of skipper butterflies (Hesperiidae) is slowly becoming better known. Fieldwork by John Kemner in Mexico between 1988 and 1995 clearly demonstrated what potential remains for the study of the Hesperiidae in that country. During those years in the field, Kemner collected specimens of over 15 species of skippers that proved to be new to science, almost entirely in Oaxaca. Four of these species have been named to honor Kemner and his persistent collecting efforts (see Freeman 1990; Steinhauser 1991, 1996; Burns 1992). The new species of *Euphyes* Scudder 1872 described below is yet another example of a new species taken by Kemner in Oaxaca, and has since been found to occur as far north in western Mexico as Nayarit.

While the fauna of Papilionoidea in the Sierra de Juarez, Oaxaca and Sierra de Atoyac, Guerrero is now surprisingly well known (see Luis et al. 1991 and Vargas et al. 1991), the Hesperiidae were not included in those studies. Recent studies in Jalisco and Colima states have included the Hesperiidae (see Vargas et al. 1996 and Warren et al. 1998). The first known collected specimen of this new *Euphyes* species was collected by Armando Luis Martínez (Museo de Zoología [MZFC], Universidad Nacional Autonóma de México, Mexico City) in Guerrero in 1985, but was not discovered among papered material at the MZFC by ADW until 1997. Hugh Avery Freeman (Garland, Texas) was the first to recognize this *Euphyes* species as being undescribed, based on two males collected by John Kemner in Oaxaca in 1989. Freeman subsequently forwarded specimens to SRS for eventual description. It has subsequently been taken in the Balsas depression in Michoacán on several occasions (at two localities) by Lamberto González Cota and Maximo Martínez (Uruapan, Michoacán), and recently as far north as southern Nayarit. All localities where this new species has been found are composed of seasonally dry tropical deciduous forest, or thorn forest at Rancho Nuevo, Michoacán. Additionally, permanent small streams or rivers flow through these habitats (except perhaps at Candelaria, with which we are not familiar).

Euphyes canda Steinhauser & A. Warren, new species

Description. Male: Forewing length by width varies from 19.5 × 9.5 mm (holotype) to 17.5 × 9 mm (in two paratypes), averaging 18.43 × 9.29 mm (N = 7). Dorsal surface (Fig. 1): Forewing silky brown with sparse ochreous scales on basal third of Cu2–1A and basal fifth of Cu1–Cu2, proximad of stigma. Faint indications of a discal band of paler spots from M2–M3 to Cu1–Cu2. Narrow tripartite black stigma (Fig. 5) rather prominent and offset slightly at Cu2; the upper section (Cu1–Cu2) distally bordered by an area of upturned scales forming a vague dull gray patch about twice the width of the stigma. Fringes concolorous at apex, becoming slightly paler and grayish at tornus. Hindwing same brown as forewing, unmarked, rather evenly covered with long brown hair-like scales. Fringes slightly paler and grayish. Ventral surface (Fig. 2): Forewing rufous brown, darker in discal cell and basad of poorly defined pale discal band which extends from M2–M3 to 2A, becoming much wider in Cu2–2A but not reaching termen. Pale discal band faintly continued forward at right angle into M1–M2, R5–M1, R4–R5. Fringes concolorous, becoming slightly paler at tornus. Hindwing same rufous brown color as forewing: poorly defined narrow, curved, discal band of pale spots from Rs to 1A; ground color slightly paler distad of discal band, somewhat grayish in 1A–2A and anal cell. Fringe concolorous, becoming paler at tornus. Head brown with admixed whitish scales around eyes and base of antennae, white beneath eyes. Palpi flattened, third segment short, stout, barely protruding above hairs of second; brown above, heavily scaled with white beneath. Antennae about half length of costa, nearly reaching end of Sc; shaft brown above, checkered brown and white beneath.

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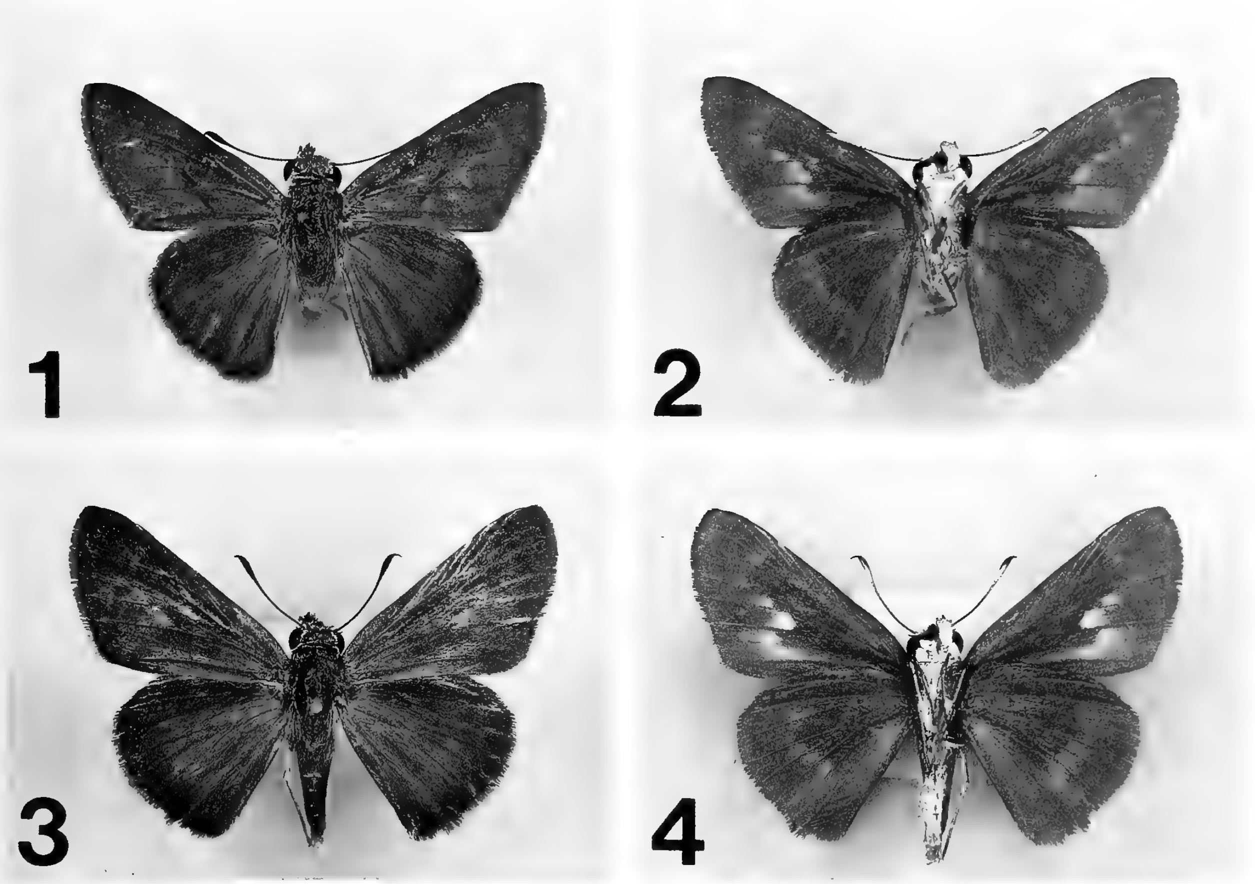

FIGS. 1–4. Adults of *Euphyes canda*, new species. **1** (dorsal), **2** (ventral), holotype ♂ from MEXICO: Oaxaca: 2 miles north of Candelaria, 1800 ft., 29 Oct 1989, John Kemner. **3** (dorsal), **4** (ventral), paratype ♀ from MEXICO: Guerrero: Mpio. Atoyac: Río Santiago, 680 m, 5 May 1985, Armando Luis-M.

Club stout, dark brown above, checkered brown and white beneath, about one-third of shaft length; apiculus reddish brown, about 1.5 times club width, nudum varies from 7/8 (holotype and three paratypes) to 8/9 (one paratype), averaging 15.6 segments; N = 8. Thorax and abdomen brown above, whitish beneath; legs brown, overscaled white or buff on one side; mid-tibiae with single pair of spurs, hind-tibiae with two pairs, the upper pair shorter. Genitalia (Fig. 6) of general *Euphyes* form (see Shuey 1993). Uncus shallowly bifurcate (Fig. 6D); at distal end, the dorsal half of each arm projects laterally beyond ventral half, the ventral edge of this projection appears as a short dark line (or small lateral posterior suture) in lateral view (Fig. 6A). Gnathos deeply bifurcate, protrudes caudad slightly beyond uncus, distally pointed in ventral view (Fig. 6E). Valvae symmetrical (Fig. 6C); harpe produced dorsad as broad rounded process; sacculus not produced dorsad (Fig. 6B). Saccus moderately long, slender. Penis long; vesica opening dorsad; vesica with eight small, separated, sclerotized teeth as cornuti (Figs. 6F–G). Juxta prominent and well sclerotized (Fig. 6F–H). **Female:** Forewing length by width varies from 19.5 × 10.5 mm to 21 × 11 mm, averaging 20.25 × 10.63 (N = 4). Dorsal (Fig. 3) and ventral surfaces (Fig. 4) as male, but with more rounded wings and lacking stigma. Antennal nudum varies from 7/8 (3 paratypes) to 7/9 (one paratype), averaging 15.25 (N = 4). Genitalia (Fig. 7A–B): Corpus bursae rather elongate, non-erect, rounded at distal end, and constricted at junction with ductus. Ductus bursae elongate, straight, well sclerotized dorsally (and ventrally caudad of the ductus seminalis); of a fairly uniform width the entire length but slightly restricted at caudal end. Ductus bursae without lateral projections or any indication of posterior bending. Lamella antevaginalis sclerotized, poorly developed, bending anteriorly to cover part of ductus. Lamella postvaginalis well sclerotized, forming a V-shaped structure typical for *Euphyes* (see Shuey 1993 for illustrations of other female *Euphyes* genitalia). Papillae annales fairly short, more or less flattened posteriorly (Fig. 7A).

Types. Holotype ♂ (Figs. 1–2): MEXICO: OAXACA: 2 miles north of Candelaria, 1800 ft. elev.; 29 October 1989, leg John Kemner, bearing the following labels: hand printed white label, MEX:

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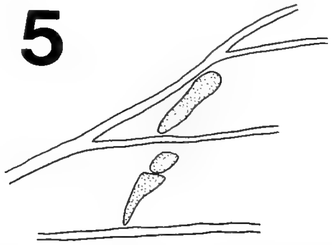

FIG. 5. Forewing stigma (dorsal view) and associated wing veins of holotype ♂ of *Euphyes canda*, new species. Data as in Figs. 1–2.

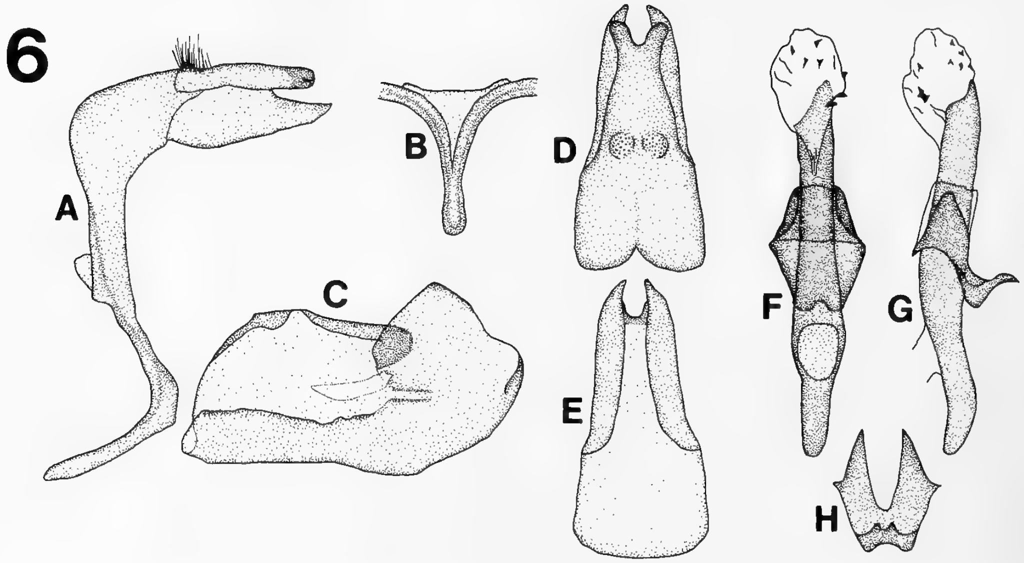

FIG. 6. Male genitalia of holotype of *Euphyes canda*, new species (data as in Figs. 1–2), genitalia vial SRS-3798. **A,** Uncus, gnathos, tegumen, and saccus in ventral view. **B,** Saccus in ventral view. **C,** Right valve, medial view of inner surface. **D,** Uncus, tegumen and gnathos in dorsal view; **E,** same, in ventral view. **F,** Penis, juxta and everted vesica with cornutus, dorsal view; **G,** same, in left lateral view. **H,** Juxta in ventral view.

Oaxaca - 2 mi. N. Candelaria—29 Oct. 1989 John Kemner—El. 1800′; hand printed red label, Holotype—*Euphyes canda* ♂ - S. R. Steinhauser & A. D. Warren; printed and hand printed white label, Allyn Museum Acc. 1990–12; printed and hand printed white label, Allyn Museum Photo No. 930818A,20. Paratypes N = 10 (6 ♂, 4 ♀): same data as holotype (1 ♂); GUERRERO: Mpio. Atoyac: Río Santiago, 680 m, 5 May 1985, Armando Luis-M. (1 ♀, Figs. 3–4); MICHOACAN: Mpio. Arteaga: Rancho Nuevo, ± 600 m, 2 Mar 1997 Lamberto González-Cota [LGC] (1 ♂); same locality and collector, 8 Mar 1997 (1♂); same locality and collector, 10 Nov 1996 (1 ♀); Mpio. Arteaga: El Higueral, 650 m, 28 Jun 1996, LGC (1 ♂, 1 ♀); same locality and collector, 25 May 1997 (1 ♂); same locality and collector, 5 Sept 1996 (1 ♀); NAYARIT: Mpio. San Blas: Mecatan, Ojo de Agua, 100 m, 22 Jun 2000, Tom W. Ortenburger (1 ♂). The holotype and one ♀ paratype are deposited in the Allyn Museum of Entomology; two ♂ and two ♀ paratypes will be deposited in the MZFC (Mexico City); one ♂ in the collection of LGC (Uruapan, Michoacán); and the remainder, temporarily, in the collection of ADW.

Etymology. The name *canda* is a meaningless combination of letters suggested by the type locality, Candelaria.

Diagnosis and discussion. *Euphyes canda* might be confused with several of the dark species of *Arotis* Mabille, 1904, from which it can be distinguished by its more elongate forewing, form of stigma, its longer and more slender penis, and by the "lateral posterior suture" on the uncus. These last three characters were used by Shuey (1987, 1993) to distinguish *Arotis* from *Euphyes*. The *Euphyes* species superficially closest to *E. canda* are *E. leptosema* (Mabille), *E. peneia* (Godman), *E. fumata* Mielke, *E. eberti* Mielke and *E. ampa* Evans. *Euphyes canda* differs superficially from *E. leptosema* in having fainter and less extensive ventral wing markings; from *E. peneia* in being more rufous than ochreous ventrally; from *E. fumata* and *E. eberti* in having a tripartite stigma (rather than bipartite) and being larger (forewing length of *E. fumata* and *E. eberti* is 15–16.5 mm); and from *E. ampa*, by being larger (*E. ampa* forewing length of 17 mm) and by lacking a large double, pale yellowish spot in Cu2–1A of the ventral forewing.

Genitalically, the terminal configuration of the penis of *E. canda* differs from *E. leptosema*, *E. peneia*, *E. fumata* and *E. eberti* in lacking spines. Its overall valva shape is similar to *E. subferruginea* (Hayward) and *E. eberti* but with a simple sacculus instead of the greatly produced and dentate sacculus of *E. eberti* (found also in *E. ampa*). There are other genital differences, but these should suffice to distinguish *E. canda* from others.

We have placed *canda* in the genus *Euphyes* rather than *Arotis*, primarily because of its long slender penis, pointed tips of the gnathos, and its uncus prongs with a small lateral posterior suture, noted as a probable synapomorphy for *Euphyes* by Shuey (1993). At first glance, *E. canda* does not appear to fit well into any of the species groups proposed by Mielke (1972:182–183) and Shuey (1993:271–272). It has the cornutus form similar to the *dion* (W. H. Edwards) and *subferruginea* groups, but not the tawny wing pattern of the former, and has a stigma unlike the latter. The stigma of *E. canda* is similar to that of *E. peneia* and *E. leptosema*, but the valvae are very different, quite elongate in the latter two, shorter and broad in *E. canda*. A future phylogenetic revision of the genus, through direct examination of all taxa and elaboration of Shuey's (1993)

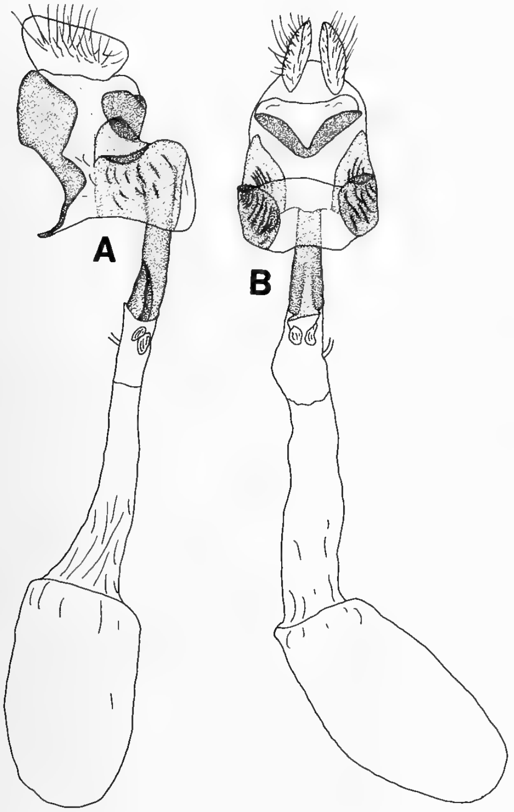

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FIG. 7. Female genitalia of *Euphyes canda*, new species, from MEXICO: Michoacán: Mpio. Arteaga: El Higueral, 650m, 28 Jun 1996, Lamberto González-C. ADW genitalia vial # 98-69. **A,** Papillae anales, lamella, ductus bursae (showing end of ductus seminalis), and corpus bursae in left lateral view; **B,** same in ventral view.

data matrix, would hopefully clarify *E. canda's* position, as well as the species-group relationships in the genus.

ACKNOWLEDGMENTS

We are grateful to our good friend Avery Freeman for supplying the holotype and one male paratype of this skipper (both taken by Kemner in Oaxaca) and for correcting the earlier determination by SRS of these specimens as *Euphyes peneia*. Thanks to Lamberto González Cota and Maximo "Chimo" Martínez for collecting specimens of *E. canda* and for Lamberto's hospitality to ADW in August, 1997, when skipper material containing *E. canda* specimens was examined. Thanks to Armando Luis Martínez, America Castaneda Sortibran and Esperanza Sortibran Davila (Mexico, City) for hospitality on numerous occasions when *E. canda* material was found among Michoacán material housed at the MZFC. Thanks to Jorge Llorente Bousquets, Armando Luis Martínez, and Isabel Vargas Fernandez (MZFC) for coordinating research efforts and permits with ADW. Thanks to Boris C. Kondratieff (Colorado State University, Fort Collins) for use of his camera lucida to prepare some illustrations used herein and to Thomas W. Ortenburger (Wheat Ridge, Colorado) for logistical support. Thanks also to George Austin, Deane Bowers, Andy Brower, John Burns, and Ray Stanford for comments on our manuscript. Support to ADW was provided, in part, by the CONABIO grant DGAPA IN-211397 to the MZFC and by the Ferguson Endowment for Systematic Entomology at Oregon State University.

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MONARCH BUTTERFLY (*DANAUS PLEXIPPUS* L., NYMPHALIDAE) FALL MIGRATION: FLIGHT BEHAVIOR AND DIRECTION IN RELATION TO CELESTIAL AND PHYSIOGRAPHIC CUES

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ABSTRACT. To learn more about the specific routes that monarch butterflies take from their breeding grounds in the northern United States and Canada to overwintering areas in the Transvolcanic Belt of central Mexico, and to investigate the guidance mechanism by which they locate these small overwintering sites, vanishing azimuths were taken during different times of day and at different locations in Texas and Mexico. Monarchs were shown to employ either a time compensating sun/sky compass or to follow other non-solar cues over open terrain. Upon reaching the Sierra Madre Oriental of eastern Mexico, monarchs change their course and follow these ranges. The implications of this course change for orientation and the use of the Sierra Madre Oriental as a focusing mechanism to insure that the maximum numbers of butterflies reach the Mexican overwintering sites are discussed.

Additional key words: orientation, Sierra Madre Oriental, Texas, Mexico.

Among invertebrates, the monarch butterfly, *Danaus plexippus* L. is the best known and most extensive migrant (Baker 1980). Long term mark and recapture records carried out by Urquhart have disclosed the extent and the general direction of the migration (Urquhart 1960, 1965, 1966). The final destination of the eastern population of monarchs was learned in 1974 (Urquhart 1976). Unlike most migrants, whose movements are into broad habitats favorable for winter foraging, monarchs fly to specific sites of very limited extent in Mexico's Transvolcanic Belt, where they aggregate by the tens of millions (Calvert & Brower 1986). The fidelity of monarchs to these circumscribed sites that are a few hectares or less in extent taxes the imagination and must require precise navigational skills.

Several studies have addressed navigational aspects of the monarch migration. Monarchs intentionally displaced longitudinally from their fall range and released did not compensate for the displacement (Urquhart 1965) as do species that home (Baker 1978). Studying monarch migrants in cages under various conditions of visibility and lighting, Kanz (1977) found orientation to the sun, but little evidence of compensation for time of day. On the basis of these findings, he hypothesized that, if the butterflies flew towards the sun between 1000 h and 1400 h, they would eventually end up at their overwintering destination. In contrast to Kanz's findings, Schmidt-Koenig (1985), recording flight vanishing azimuths of migrating monarchs in the eastern United States, found them to be highly directional and little affected by overcast conditions. He concluded that they use a magnetoclinic system for orientation similar to that used by birds (Kiepenheuer 1984). More recent studies revealed that monarchs use a sun/sky compass that is best discerned by body orientation, not direction of travel (Perez et al. 1997), and that the solar agent by which they orient is likely plane polarized light (Hyatt 1993).

Due to the physiographic constraints to migration afforded by the Gulf of Mexico and the Rocky Mountain and their extension into Mexico, the Sierra Madre Oriental, the monarchs' flight path at the latitude of the southern tip of Texas is approximately 8% of the width it was when they started from their breeding grounds in the north. This flight-path compression results in enormous numbers of monarchs traveling through the mountainous areas in the Mexican states of Coahuila and Nuevo Leon and further south. Almost everyone who lives in this flyway is aware of the migratory phenomenon. Many can give the exact date(s) when they pass through, when, as one campesino put it, "the sky was pure butterfly". Further south, closer to the overwintering grounds in Michoacan and the state of Mexico, the Mazahua Indians have a special word in their language for "the butterfly that passes in October and November" (Muro 1975). In spite of the high profile of the monarch migration, little is known about the breadth and duration of the migration or the orientation mechanisms of the butterflies. Here I report observations of behavior and flight azimuths of migrating and non-migrating monarchs and document for the first time a change in course that occurs during the migration to the Mexican overwintering sites.

Materials and Methods

To establish flight directions of migrating monarchs, vanishing azimuths were taken with a Suunto sighting compass in the plains of Texas, and in the mountains (Sierra Madre Oriental) of Mexico during the falls of 1977 and 1978. To avoid parallax problems, only butterflies that flew directly over head were sighted. For comparison, vanishing azimuths of non-migrating individuals were taken in fields near Amherst, Massachusetts during the summer of 1978. Vanishing azimuths

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taken during the summer months are referred to as summer monarchs; those taken during the fall are referred to as fall monarchs.

The large numbers of migrants in the Mexican Sierra Madre Oriental presented a problem. Sometimes hundreds, even thousands passed by each minute, all going in the same direction. Taking individual azimuths did not convey the magnitude of the phenomenon. In instances where many hundreds were passing by, all in the same direction, the count was stopped at 100. The total number counted in migration in the Sierra Madre Oriental using this limit was 3099. However, for statistical computations, each observation, no matter how many individuals were flying in the same direction, was treated as one observation. This number is reported in the tables. Also noted were the location and time of the day and, when appropriate, the sun's azimuth, the wind direction and magnitude, and the facing direction or heading of monarchs being blown by the wind. The facing direction is the direction towards which the body of the butterfly is oriented, as opposed to the direction it is traveling. Wind speeds were estimated by the author in mph and converted to kmph. When available, smoke, flags, or other blowing objects were used to improve the accuracy of the estimation.

Orthodromic (great circle) directions were computed using a program derived by Paul Donn. The sun's azimuths were computed for various latitudes and longitudes using a Hewlett-Packard # Nav-07A program. Loxodromic (map) directions and mountain range azimuths were obtained from Instituto Nacional de Estadistica Geografia e Informatica topographic maps Ciudad de Mexico and Monterrey, 1:1,000,000 scale (Anon. 1982, 1984). Orthodromic directions from the approximate center of the cluster of open plains observations at Austin, Texas (97.7°W, 30.3°N) to the western boundary of the overwintering zone (100.8°W, 19.7°N) were computed using the Donn program. Loxodromic directions were measured from the map. These directions were obtained for the cluster of mountain observations from Avila y Urbina, Tamaulipas (99.6°W, 23.7°N), the approximate geographic center of the mountain group, to the eastern boundary of the overwintering zone (99.9°W, 19.1°N).

All mean flight azimuths were corrected for magnetic declination and averaged vectorially. A circular statistics program (Watson's U^2 test) was applied to distinguish differences between the mountain and open plain distributions. Standard statistical tests, such as Student's *t* and Fisher PLSD, were used to compare deviations from expected directions. Mean angles derived vectorially differed from arithmetic means by only 1.7° and 3.7° for butterflies flying over open plains and in mountains, respectively. These differences are small enough so that the arithmetic means and standard deviations are very close approximations of mean angles and angular deviations. Therefore standard, non-circular statistical comparisons may be applied (Batschelet 1972). Vanishing azimuths and the associated circular statistics were computed using a circular graphics program Vector Rose 3.0 written by P. Zippi (1997).

For comparison, the loxodromic (map) azimuths are also given. They are more familiar and easier to understand that orthodromic (great circle) azimuths. I do not wish to imply that monarchs use to orient map azimuths that are the result of projections of spherical surfaces onto flat ones.

RESULTS

Observations of summer versus fall behavior. Monarchs observed during mid-summer were occupied mainly with feeding and oviposition. Occasionally courtship investigations and chases also occurred. Flight normally was confined to the first 3 m above the ground except during courtship chases, where the pair might fly up to 15 m before descending. In their search for nectar, mid-summer monarchs cruised over or among prospective plants in ziz-zag or circular paths. Flight in any one direction was short, usually less than 2 m, and flight direction was random (Fig. 2). The mean flight azimuth for 101 mid-summer monarchs was not significantly different from zero (Rayleigh test, $z = 0.87$, $p > 0.4$; Batschelet 1972).

In contrast, fall monarchs flying over the plains of Texas and in the Sierra Madre Oriental exhibited highly directional flight (Figs. 3 and 4). Mean flight azimuths computed for these two groups were 239.0° and 174.6° for open plain and mountainous terrain, respectively (Rayleigh test, Batschelet 1972; $z = 40.4$, $p < 0.001$ for open plains; $z = 158.2$, $p < 0.001$ for mountainous terrain).

Migratory flight behavior. Fall monarchs also differed from summer monarchs in their use of rising air currents to avoid powered flight. During the fall, the arrival and departure of migrating monarchs generally is associated with the arrival of cold air masses (see also Gibo 1987). Monarchs often ride the rising layers of warm air preceding these fronts and also take advantage of northerly winds that may blow for days in association with such fronts. On calm days or when winds were favorable, e.g., from a northerly direction, migrants were found flying at elevations from one me-

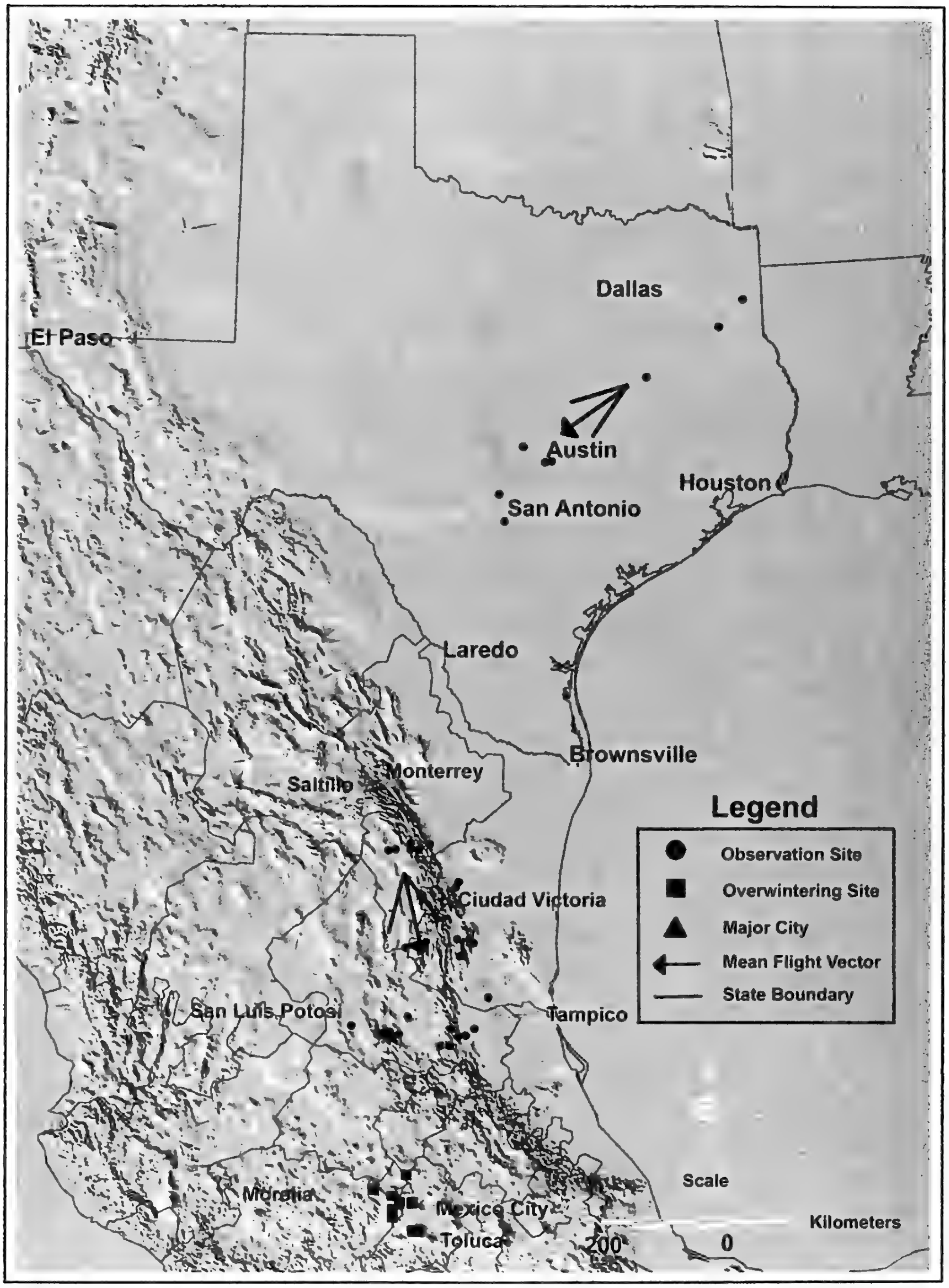

FIG. 1. Average flight vectors and confidence intervals for open plains and mountainous terrain in Texas and Mexico respectively. Without a course correction, monarchs flying over open plains would fly too far west to attain the overwintering sites. Monarchs flying in the mountains would miss all but the easternmost sites.

ter to the limits of binocular vision (ca. 300 m). When opposed by southerly winds, they could be found in riparian areas sheltered from the wind in loose gregarious roosts.

Convection thermaling was common. When winds were calm or blowing from the north, monarchs rose on thermals, and then glided. During the course of the glide they lost altitude. At some point they ceased gliding, and began again to circle in thermals to gain altitude. Often monarchs were seen in thermals with hawks and vultures. In mountainous area, monarchs often used orographic lift, riding on winds pushed up by the mountain ranges. The greatest concentrations of low flying migrants were nearly always encountered

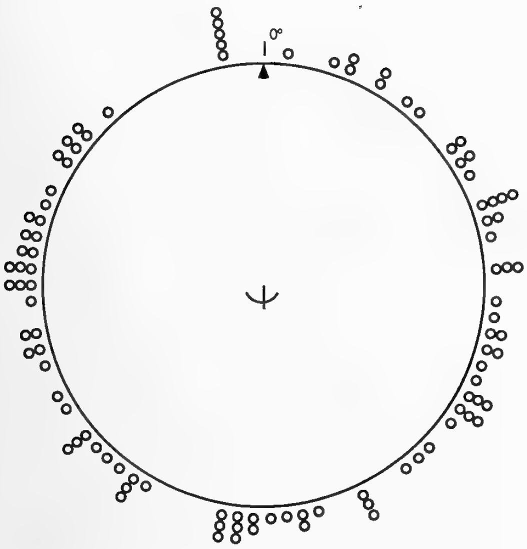

FIG. 2. Flight azimuths of monarchs during mid-summer near Amherst, MA, indicate no directional tendency. (mean vector = 180.3°; angular deviation = 124.9°; n = 101; r = 0.09; p = ns).

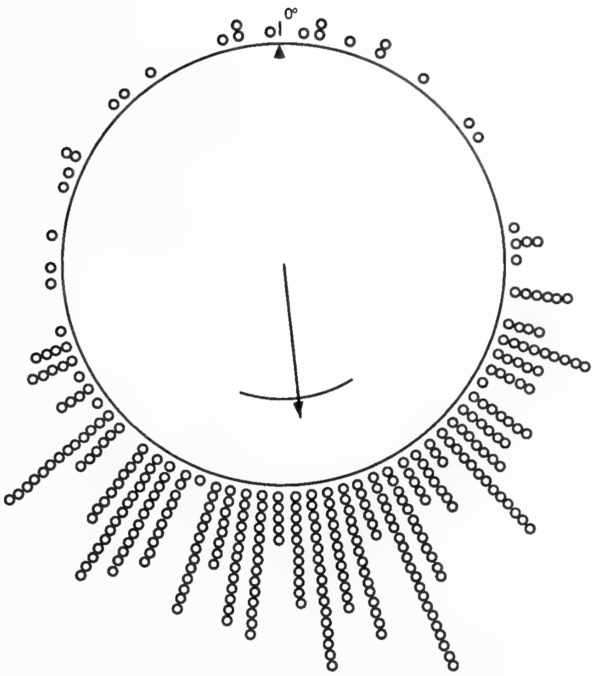

FIG. 4. Flight azimuths of fall monarchs in mountainous areas of Mexico showing that flight is highly directional, but now towards the SSE (mean vector = 174.6°; angular deviation=49.4°; n = 333; r = 0.84; p < 0.001).

on the east face of ranges of the Sierra Madre Oriental riding prevailing easterly winds (Mosiño-Aleman 1974).

Monarchs adapt to changing wind speeds and high velocity winds, but did not always appear to be in full control. A group of ca. 40 monarchs flying between 30 and 40 m altitude in nearly calm air, immediately dropped vertically to 1–3 m when headwinds suddenly increased (see also Gibo & Pallett 1979). Monarchs appear to have difficulty flying in high velocity winds. On one occasion near Monterrey, Mexico, a large concentration of migrants (>500 passing through a plane perpendicular to their flight path per minute) was found flying in the lee of a ridge, the windward face of which was receiving winds in excess of 30 kmph. On another occasion near Brownsville. Texas, monarchs were seen tumbling in the air apparently out of control in high velocity north winds gusting to 50 kmph.

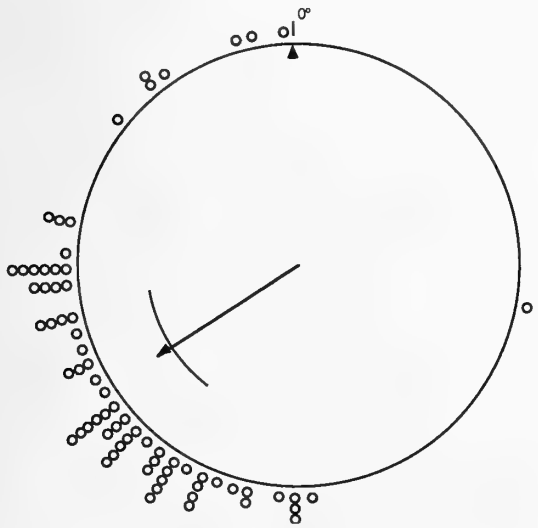

FIG. 3. Flight azimuths of fall monarchs in the plains of Texas showing that flight is highly directional towards the SSW (mean vector = 239.0°; angular deviation = 42.5°; n = 70; r = 0.76; p < 0.001).

Migration over open plains. Over open plains, in Texas, the mean of 70 vanishing azimuths was 239.0° (vector length = 0.76; Fig. 1, Table 1). Surprisingly, the 99% confidence interval of 15° included neither the orthodromic nor the loxodromic direction to the western edge of the Mexican overwintering zone located 1300 km SSW ca. 30 km west of Cd. Hidalgo in the state of Michoacan. If monarchs flying over open terrain continued on this course, they would fly too far to the west and miss the entire distribution of known overwintering sites.

Migration within the mountains. Within the Sierra Madre Oriental, the mean vanishing azimuth for 333 sightings shifted significantly eastward from 239.0° to 174.6° (99% confidence interval = 9°; vector length = 0.69). The 99% confidence interval barely includes the orthrodromic direction to the eastern boundary of the overwintering area (Table 1). Thus butterflies flying over open terrain fly in a direction that will take them too far to the west to strike any part

TABLE 1. Comparison of mean flight azimuths with directions to the overwintering areas for various locations in the United States and Mexico.

Migratory status/ location	N	Mean flight azimuth	99% conf. interval	Orthro-dromic	Loxo-dromic	Vector length	Prob.[1]
Non-migratory/Amherst, MA	101	209.3°	—	—	—	0.09	>0.4
Migratory/Open plains,Texas	70	239.0°	224–254°	195.4°[2]	195.5°[2]	0.76	<0.001
Migratory/Sierra Madre, Mexico [4]	333	174.6°	166–176°	182.9°[3]	184°[3]	0.69	<0.001
Migratory/Eastern US [4]	477	220.0°	216–224°	223°	228°	0.88	<0.001

[1] Rayleigh test for uniformity from Batschelet 1972. If $p > 0.05$, the distribution of observations is random.

[2] From Austin, TX (97.7°W, 30.3°N) to the western extreme overwintering site at Mil Cumbres (19.7°N, 100.8°W).

[3] From the approximate center of mountain observations at Avila y Urbina (99.6°W, 23.7°N) to the the eastern extreme overwintering site at Palomas (99.9°W, 19.1°N).

[4] Data from Schmidt-Koenig 1979.

of the overwintering zone, while those flying in the Sierra Madre Oriental will fly too far to the east to strike all but its eastern-most fringe. The distribution of azimuths observed in the mountains differed significantly from the distribution over open terrain (Watson's U^2 test: $U^2 = 2.10$, n = 333, m = 82, $p < 0.001$).

Diel flight periods. Most overnight monarch roosts broke up within 15 minutes after the rays of the morning sun struck them. Unless the sun's radiation was blocked by topography or vegetation, this occurred between 0745 and 0830 h (CST). At roost breakup, initially most butterflies flew at least a short distance towards the sun before alighting to bask or beginning to ride morning thermals upwards. Occasionally morning thermaling commenced as early as 0715 h. Migratory flight usually ceased from mid- to late afternoon when monarchs descended to take nectar, to form nighttime roosts, or both. But directional flight was observed as late as 1745–1800 h. After 1800 h, most monarchs were either searching for or forming roosts. Rarely, a monarch was seen in directional flight until nearly dark (ca. 1900 h in central Mexico at latitude 24°N). Monarchs flew at the same azimuth during all times of the day over open plains (Table 2; ANOVA F = 0.96, n = 70, $p < 0.39$). In mountainous terrain, they flew at the same azimuth until 1400 h and slightly more westerly after 1400 h (F = 8.51, n = 333, p = 0.0002).

Comparison of mean flight azimuths to the sun's azimuth and to the direction of the mountain ranges. Azimuths of monarchs flying over open terrain and in the mountains both differed significantly from the sun's azimuth (ANOVA, F = 8.4, n = 57 $p < 0.0007$ and F = 38.6, n = 313, $p < 0.0001$ respectively; Table 1). To test Kanz's hypothesis that monarchs fly towards the sun between 1000 and 1400 h, deviations of monarch flight azimuths from the sun's azimuth were calculated for 3 diel time periods: <1000 h, between 1000 and 1400 h, and >1400 h. The flight azimuth of most groups remained significantly different from the sun's azimuth (Table 2). As would be expected, the open terrain group flew closest to the sun after 1400 h, and the mountain group flew in the direction of the sun between 1000 and 1400 h.

The direction of individual ranges composing the Sierra Madre Oriental often deviated from the general axis of the ranges (163°) as measured from the two Instituto Nacional de Estadistica Geografia e Informatica topographic maps that covered the region. In general, the northern ranges run more easterly than the southern ones. Monarchs flying in the intermontane valleys of the Sierra Madre Oriental flew an average of 11.6° to the west of the general direction of the ranges as indicated on the map (Table 1).

TABLE 2. Flight azimuths and deviations from potential cues for various time periods.

	Location							
	Open terrain				Mountains			
Time period	N	Mean azimuth	Dev.[2] sun	Prob.[3]	N	Mean azimuth	Dev.[2] sun	Prob.[3]
<1000 h	2	247.5 a[1]	–147.5	—	42	161.7[a]	–53.8	0.0001
1000–1400 h	9	221.7 a	–68.1	0.01	117	167.6[a]	+3.2	NS
>1400 h	59	243 4 a	–22.1	0.001	174	189.6[b]	+34.0	0.0001

[1] Different letters in columns indicate that the means differ significantly among times at 0.05 (Fisher PLSD test).

[2] Deviation from the sun. A negative deviation means that the butterfly is flying to the west of the sun or the axis of the Sierra Madre Oriental.

[3] Probability (Students *t*-test) that the butterfly azimuths are different from the sun's azimuth. In the first case (<1000 h over open plains) there were insufficient data to make a statistical determination.

DISCUSSION

Without physiographic markers such as mountains or shore lines, monarch butterflies in Texas and Mexico maintained a strongly directed course to the SSW (Table 1). Monarchs migrating in the eastern United States followed a similar course (Schmidt-Koenig 1979), although my measurements in Texas indicated that group flew slightly more westerly than the eastern group (Table 1). By the time the migrants reach south-central Texas, both the loxodromic and orthdromic directions to the overwintering areas are directly south. Yet, over open plains the monarchs continue to fly SSW which, if continued, would take them far to the west of the overwintering zone. When they reach the ranges of the Sierra Madre Oriental, they change their course to the SSE. If they continued in this direction, they would pass to the east of the major overwintering area centered around Angangueo, Michoacan (19.6°N; 100.3°W).

Assuming that monarchs cannot home, and correct the consequences of a miss, migrants flying in from the north must strike the Transvolcanic Belt somewhere within a 1.1° (115 km; 99.9°W–101.0°W) corridor to find the overwintering sites. The dimension and extent of this narrow corridor is based on the locations of the known overwintering sites (Urquhart 1976, Calvert & Brower 1986) and on extensive searching for additional sites by the Mexican Forestry Department (J. de la Maza, pers. com.) and others (de la Maza & Calvert I992). Small aggregations were located as far west as the states of Jalisco and Colima and as far south as the Sierra de Juarez in eastern Oaxaca, but none of these compared in size to the major overwintering colonies located from the west face of the Nevado de Toluca, state of Mexico (99.9°W) to Mil Cumbres, state of Michoacan (101.0°W).

Monarch migrants' failure to follow orthodromic or loxodromic directions to the overwintering area suggests a complex guidance senario. In the absence of physiographic cues, they must use a genetically programmed sun/sky, magnetic, or other based guidance system that takes them to the SSW. A course correction is necessary to avoid missing the overwintering sites by flying too far to the west. The ranges of the Sierra Madre Oriental apparently provide cues for this course correction. The monarchs follow these ranges to the SSE. But this correction is too great and, if continued, would take them too far east. Either another course correction to the SSW takes place in the relatively rangeless plains and mountains of the states of Hidalgo, Queretaro and southern San Luis Potosí, or perhaps the constant pressure of prevailing easterly winds (Mosiño-Aleman 1974) eventually displaces them the proper distance to reach their objective.

The Sierra Madre Oriental and Rocky Mountains may also be a focusing mechanism. Monarchs traveling across the continental United States from breeding areas scattered across the mid-west and eastern seaboard would be expected to proceed along a broad front. Reports to the National Monarch Watch (unpubl. archived reports to Dplex-L@raven.cc.ukans.edu) indicate that they migrate through a wide area of the mid-western states. Some years even western Kansas and New Mexico are traversed. Traveling SSW along such broad fronts, they would strike the Rocky Mountains and Sierra Madre Oriental at many places in Texas, northeastern Mexico, and possibly as far north as New Mexico or Colorado. Once encountered, turning to follow these ranges would insure that they eventually joined with other migrants proceeding in the same direction. This focusing mechanism could result in monarchs that were born a thousand miles apart traveling within the same intermontane valley in the Sierra Madre Oriental.

Yet another advantage may be afforded migrant monarchs once they enter the intermontane valleys and ridges of the Sierra Madre Oriental. By following mountain crests, they enter into extensive areas of rising air currents (orographic lift) caused when prevailing easterly winds (Mosiño-Aleman 1974) are pushed up by the mountain ranges. By soaring on the windward slopes of these intermontane valleys, monarchs may be able to travel long distances with little powered flight and thereby conserve energy.

Gibo and Pallett (1979) estimated that if soaring requires only a basal level of metabolism, a butterfly with an initial supply of 140 mg of fat could soar as long as 44 days without replenishment. Thermaling and gliding may be especially important during the segment of the migratory pathway between central Texas and the Sierra Madre Oriental. Nectar resources in the desert and chaparral regions of north-central Mexico and southwestern Texas are sporadic, and their abundance depends upon unpredictable rainfall. Preliminary evidence indicates that monarchs lose approximately 12 mg or about 2% of their wet weight in crossing this ca. 300 km area (Calvert unpubl.).

Riding rising currents generated by mountain ridges may be even more important for migrant lipid conservation further south within the Sierra Madre Oriental where a pronounced rain shadow is evident. The driest area through which monarchs migrated by the thousands was Tula in the Chihuahuan Desert region of the state of Tamaulipas. Many monarchs that cross the first major range through the Novilla Canyon near Ciudad

Victoria must traverse a ca. 200-km dry desert region from Jaumave to Ciudad del Maize where more mesic conditions are found.

Although there are some unexplained small variations in flight direction during the three diel periods (Table 2), clearly monarchs do not fly towards the sun as proposed by Kanz (1977), nor is their flight restricted to mid-day between 1000 and 1400 h. Directed migratory flight was observed before 0800 h and after 1800 h. Flying towards the sun would not be sufficient to get them from breeding to overwintering grounds since such flight would, over the course of a day, take them due south. This would be inappropriate for longitudes east of 99°W longitude where much of the breeding area is located.

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GENERAL NOTES

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NEWLY DISCOVERED POPULATIONS AND FOOD PLANTS EXTEND THE RANGE OF THE ENDANGERED QUINO CHECKERSPOT BUTTERFLY, *EUPHYDRYAS EDITHA QUINO* (NYMPHALIDAE) IN SOUTHERN CALIFORNIA

Additional key words: *Plantago*, *Castilleja*, *Antirrhinum*, *Cordylanthus*, Scrophulariaceae, Orobanchaceae, Veronicaceae.

The federally endangered quino checkerspot (*Euphydryas editha quino* (Behr) is restricted to the coastal slope of southwestern California. When the quino checkerspot was petitioned for listing in 1988, it was already believed extinct. However, several populations were detected in the early 1990's in southwestern Riverside County (Oak Mountain, Murrieta Hot Springs, and Temecula) and north-central San Diego County (Oak Grove). Furthermore, a year before the species was listed as endangered on January 16, 1997 (Rogers 1997), several quino checkerspots were observed on the western slopes of Otay Mountain in southwestern San Diego County. Since then, additional quino checkerspot populations have been found in southeastern (Jacumba) and south central (west Tecate Peak) San Diego County (Mattoni et al. 1997).

All of the known historical records of the quino checkerspot (i.e., captures and observations) were used to infer the elevational range and habitat associations (e.g., Mattoni et al. 1997). The historical records placed the quino checkerspot from the coast to a few high-elevation sites, including Black Star Canyon (625 m) in Orange County, Gavilan Hills (660 m) and Sage (765 m) in Riverside County, and San Miguel Mountain (660 m), western Mount Palomar (940 m), Jacumba Peak (1050 m), and Tecate Peak (1200 m) in San Diego County. These higher-elevation observations (>1000 m) were of hilltopping males on the highest peaks in the area. The food plants and butterflies were largely believed to occur well below 1000 m in the surrounding valleys. Also it was assumed that the quino checkerspot was restricted to open clay flats in the following habitats: native grasslands, coastal sage scrub, scattered juniper woodland, and chaparral.

Intensive and extensive quino checkerspot surveys (>1300 man hours) were conducted during the 1998 spring flight season to document presence/absence, relative abundance, and distribution of the butterfly in Orange, Riverside, Los Angeles, and San Diego Counties. Because most of the known records of the species were below 1000 m, with higher-elevation records representing hilltopping males, surveys were concentrated below this elevation. A number of new sites for the species were documented, but all within its recognized elevational (100–1000 m) range (GFP & EWH pers. obs., McMillan pers. com.). Many of the occupied sites support the larval host plant *Plantago erecta* Morris (Veronicaceae), and a suspected alternate host plant, *Castilleja exserta* (A. A. Heller) Chuang & Heckard (Orobanchaceae) (see Olmstead et al. 2001 for new plant families). Similar to *E. e. editha* (Boisduval) (formerly *E. e. bayensis*), we believed these two plants and other Veronicaceae and Orobanchaceae might be important for population survival of the quino checkerspot (Singer 1971, 1972).

East of Aguanga, the elevations of the valleys rapidly climb above 1000 m. For this reason, the area had not been surveyed during much of the quino checkerspot flight season. However, *Castilleja exserta* was observed in early May 1998 growing abundantly throughout an area east of Aguanga and south of Anza, well above 1000 m (M. Shaughnessy pers.). One of us (GFP) surveyed the area on 20 May 1998, to determine the suitability of habitat and the likelihood of quino occupancy. During the survey, two male quino were collected, one south of Anza near 1200 m and the other east of Iron Springs Mountain at approximately 1500 m elevation (Fig. 1). Both specimens have been placed as vouchers in the Entomology Research Museum at the University of California, Riverside, CA. These checkerspots were a significant eastward range and elevational extension for the species; even the valleys in this area were largely above 1200 m elevation. Other new populations, including additional sites in the Anza area, have extended the range of quino checkerspot populations (Fig. 1).

The habitat for both the south of Anza and Iron Springs Mountains sites were largely red shank (*Adenostoma sparsifolium* Torr., Rosaceae) chaparral, with other scattered chaparral bushes such as oaks (*Quercus* sp., Fagaceae), mountain mahogany (*Cercocarpus betuloides* Nutt. ex T. & G., Rosaceae), and buckthorns (*Ceanothus* sp., Rhamnaceae). Interestingly, no *Plantago* species was observed within several hundred m of either of these sites. Instead *Antirrhinum coulterianum* Benth. in DC. (Veronicaceae) was found common at the south of Anza site, and *Collinsia concolor* Greene (Veronicaceae) and

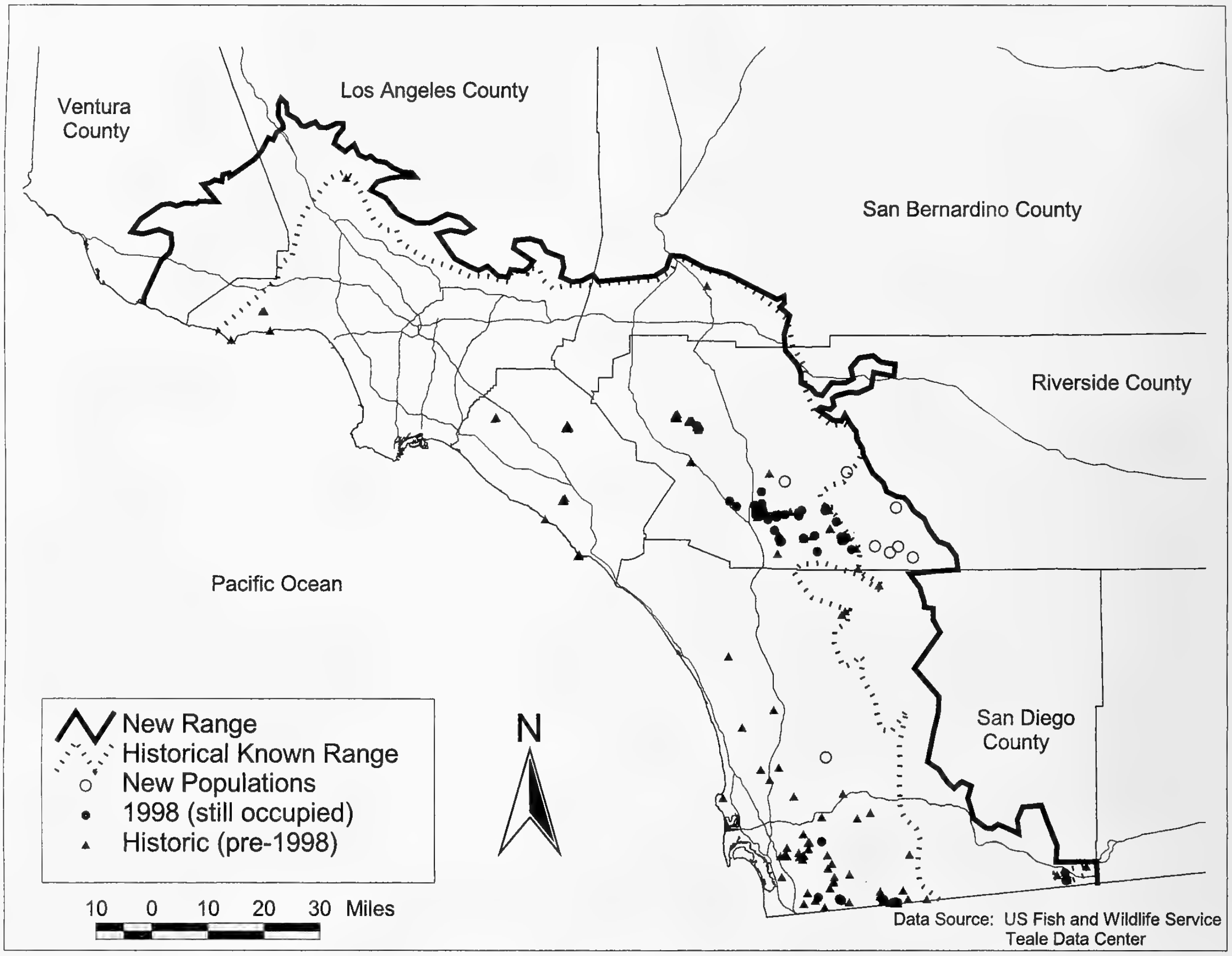

FIG. 1. New populations and inferred range of the quino checkerspot butterfly (*Euphydryas editha quino*) in southern California. The range extension was extrapolated from the higher elevation sites found near Anza, California.

Castilleja exserta were detected at the Iron Springs Mountain site. These three plants support larval development of the quino checkerspot to the adult in the laboratory (GFP unpubl. data). Furthermore, *Collinsia* spp. and *Castilleja* spp. are larval food plants for other *Euphydryas editha* subspecies (Singer 1971, 1972, 1982, White 1974, Garth & Tilden 1986).

Additional quino checkerspot adults and larval clusters were observed at and between the south of Anza and east of Iron Springs Mountain sites during the springs of 2000 and 2001. A single interconnecting silken shelter with 40 to as many as a couple of hundred first and/or second instar larvae was used to identify a single larval cluster. Between 11 April and 9 May, 2000, 39 males and five females were observed and between 3 and 18 May, 2000, 54 prediapause larval clusters were found on *Plantago patagonica* Greene (Veronicaceae) (GFP pers. obs.). From 24 April to 16 May, 2001, an additional 40 males and six females were observed, while between 9 and 28 May, 2001, 134 larval clusters were observed on *Antirrhinum coulterianum* and none on *Plantago patagonica*, even though thousands of *Plantago* were searched (GFP pers. obs.).

We believe these new populations are not a new *Euphydryas editha* subspecies. They are similar in color pattern and size to other quino checkerspot populations. Although prediapause larvae from this new population fed on a new food plant *Antirrhinum coulterianum* in 2001 (which suggested a new *Euphydryas editha* subspecies), in 2000 they fed on *Plantago patagonica*, the same genus as the major quino checkerspot food plant. Other quino checkerspot populations were observed to use even more divergent food plants. For instance larval clusters were found on the western and northern slopes of Tecate Peak of southern San Diego County on *Cordy-*

lanthus rigidus (Benth.) Jeps. (Orobanchaceae) (also a new food plant for the species) and *Plantago erecta* during the springs of 1999 and 2001 (GFP pers. obs.). Recent molecular studies suggest these food plants (*Cordylanthus* and *Plantago*) are more distantly related (separate families) than are *Antirrhinum* and *Plantago* (same family) (Olmstead et al. 2001). The food plant therefore may not be the most important character used to distinguish *Euphydryas editha* subspecies.

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PRECEDENCE OF *CATOCALA LOUISEAE* BAUER, 1965 AS A NOMEN PROTECTUM OVER *CATOCALA PROTONYMPHA* BOISDUVAL, 1840 (NOCTUIDAE)

ABSTRACT. The name *Catocala protonympha* Boisduval has heretofore been considered a junior synonym of the Palearctic species *Catocala fulminea* Scopoli. Examination of Bosiduval's type and relevant literature demonstrates that *Catocala protonympha* is in fact a disused senior synonym of the Nearctic species *Catocala louiseae* Bauer. Article 23.9.2 of the Code is invoked to give precedence to the established name *Catocala louiseae,* and maintain nomenclatural stability in the genus.

Additional key words: taxonomy, synonymy, types, Boisduval, Guenée, Staudinger, Culot.

In 1840, J. A. Boisduval described a new species of *Catocala* Schrank (1802) as *Catocala protonympha*, as follows: "Species distinctissima antennis crassioribus dentatis; statura *Callinympha*; alae posticae fere ut apud jam dictam; anticae cinereo-fuscae fasciis vix angulosis" [A species very distinct, by thick dentate antennae; size of *callinympha*; hindwings about the same as with those I have already described; forewings ash grey-brown with bands slightly angled]. The type locality was listed as "P." [=Paris, France].

Guenée (1852:103) figured *protonympha* on his Plate 15, Fig. 2, comparing it to *Catocala paranympha* L., which is a synonym of the widespread Palearctic species *Catocala fulminea* (Scopoli 1763), and stated "Environs de Paris, en aout. Coll. Bdv. Un ♂" [vicinity of Paris, in August. Collection of Boisduval. One male]. Guenée's original illustration of *Catocala protonympha* is reproduced here in Fig. 1c. Guenée also remarked on the apparent extraordinary rarity of *protonympha*: "C'est jusqu'ici, une des plus grandes raretes. Pourtant, M. Begrand m'a affirme avoir vu, sur un mur, au bois de Boulogne, une certaine quantite de petites *Catocala* jaunes qui ne pouvaient appartenir qu'a cette espece, la *paranympha*, avec laquelle la confusion est impossible" [Up to now, it is one of the great rarities. However, Mr. Begrand is positive about having seen a certain number of small yellow *Catocala* on a wall in the Boulogne woods, they necessarily belonged to the species *paranympha* with which no confusion is possible].

Subsequently, *Catocala protonympha* was listed with questionable provenience by Berce (1870:242): "est regardée comme douteuse par beaucoup de lépi-

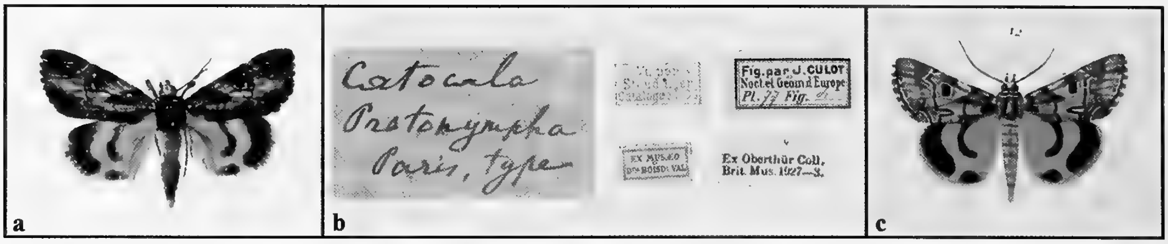

FIG. 1. *Catocala protonympha* Boisduval 1840. **a,** male type in the Natural History Museum (London), approx. 3/4 size. **b,** specimen labels on the type. **c,** painting of the type by Guenée (1852).

doptéristes" [is seen as doubtful by many lepidopterists], and the possibility of a hybrid or misattributed specimen was raised by Staudinger and Wocke (1871:138): "uno ♂ condita; an Eutychea al. posterioribus Hymenaeae adulterata? an sp. exotica?" [one male preserved; is it *eutychea* or otherwise from descendants of a cross with *hymenaea*?; or an exotic species?]. Despite the fact that Guenée's illustration of *protonympha* does not resemble *Catocala fulminea* in either size or pattern, Staudinger and Rebel (1901:249) later placed *protonympha* as a dwarfed aberration of *fulminea*, believing then that Guenée's illustration was wanting: "t. 15, f. 2 [fig. non quadrat bene]; (sec. specim. typ. Stgr. ab. nana esse videtur)" [the figure does not agree well; according to the type specimen of Staudinger from which it seems to be dwarf]. Both Spuler (1908) and Hampson (1913) also treated *protonympha* as an aberration of *fulminea*, and in the Seitz (1913:319) volume on Palearctic noctuids, Warren treated *protonympha* as a form of *fulminea*. The Seitz figure of *protonympha* is nearly identical to the Seitz figure of *fulminea* (both appear on Plate 57 row D), the former differing from the latter only nominally in having the hindwing ground color lighter and the hindwing medial band somewhat reduced.

Culot (1913:201–203, Plate 77, Fig. 4) refigured Boisduval's type of *protonympha*, and correctly pointed out that the type did not at all resemble the Seitz figures of *protonympha* or *fulminea*. Although Culot clearly felt *protonympha* and *fulminea* were different, and that some sort of error might be involved, he left the taxonomic position of *protonympha* unchanged, as he was unable to resolve fully the puzzle that Boisduval's specimen presented:

> "Quant a la soi-distant forme *protonympha* Bdv., elle parait etre fort peu connue des entomologistes et ne correspond en aucune facon a l'exemplaire reproduit soue ce nom sur la Planche 57, ligne D, de l'ouvrage de Seitz. Pour ma part, je trouve la *protonympha* Bdv. si differente de *fulminea* qu'il me parait temeraire de la rattacher specifiquement a cette derniere. Grace a la si large obligeance de mon ami M. Charles Oberthur, j'ai le plaisir de figurer ici le type *protonympha* de Boisduval. . . . En resume, je vois dans la *protonympha* Bdv. une espece tres particuliere, don't on ne connait que le seul exemplaire ♂ figure ici et qui fut capture aux environs de Paris. C'est un cas evidemment fort rare en entomologie, mais a moins qu'il ne s'agisse d'une erreur don't j'ignorerais la source, je ne puis trouber aucune autre solution." [As for the so-called form *protonympha* Bdv., it seems to be mostly unknown to entomologists and in no way corresponds to the example presented under this name in Plate 57, line D of Seitz' work. As far as I am concerned, I consider *protonympha* Bdv. to be so different from *fulminea* that it seems farfetched to relate it specifically to that species. Thanks to the kindness of my friend Charles Oberthur, I have the pleasure to illustrate here the type of *protonympha* by Boisduval. . . . In short, I see in *protonympha* Bdv. a very particular species of which only one male specimen, illustrated here, is known and that was captured around Paris. It is naturally a case seldom seen in entomology, but I cannot think of any other solution except for a mistake that I cannot explain].

Despite Culot's misgivings, in later systematic works the name *protonympha* has also been listed as a synonym of *fulminea* (e.g., Lhomme 1923–1935, Poole 1989, Hacker 1990), or has been omitted from the synonymy of *fulminea*, even in works covering France or nearby areas (e.g., Bergmann 1954, Forster & Wolfhart 1971, Leraut 1980). The most recent use of the name *protonympha* as a valid species name appears to be by Staudinger and Wocke (1871).

In 1965, Bauer described *Catocala louiseae* as a new Nearctic species from Florida. This local and generally uncommon *Catocala* occurs primarily in the southeastern United States, from North Carolina to Florida and westward along the Gulf Coast to Texas. The name *louiseae* has been used exclusively for this species, having appeared in catalogues treating Nearctic (Hodges 1983) and Holarctic Noctuidae (Poole 1989), a book devoted to *Catocala* (Sargent 1976), a moth field guide (Covell 1984), the experimental zoological literature (Gall 1991), regional surveys and compilations (Cromartie & Schweitzer 1997), and in numerous shorter reports on *Catocala* distributions and life histories in the News of the Lepidopterists' Society and the Southern Lepidopterists' News (e.g., Baggett 1994, Neal 1999).

We recently located Boisduval's type specimen of *Catocala protonympha* at the Natural History Museum, London in one of the "miscellaneous" type drawers. The male type (Fig. 1a) bears the following labels (Fig. 1b): "Catocala/protonympha/Paris, type"; "Vu par/Staudinger/Catalogue 1900"; "Fig. par J. CULOT/Noct et Geom d'Europe/Pl. 77 Fig. 4"; "EX MUSAEO/BOISDUVAL"; "Ex Oberthur Coll./Brit. Mus. 1927–3." The type is in fact a specimen in good condition of *Catocala louiseae*, and not an aberrant dwarfed specimen of *Catocala fulminea*.

Because the name *protonympha* actually refers to a local and generally uncommon Nearctic *Catocala* species, this explains prior lepidopterists' difficulties in placing *protonympha* as a Palearctic taxon, and the absence of any Palearctic specimens other than Boisduval's type. The type locality of Paris, France for *protonympha* is undoubtedly erroneous, and likely the result of a labeling error or other misattribution. Boisduval's type could even be one of John Abbot's 18th or early 19th century Lepidoptera specimens from Georgia, as *Catocala louiseae* inhabits the counties in Georgia where Abbot worked, and Abbot did depict *louiseae* in one of his unpublished watercolors in the Oemler compilation at the Houghton Library at Harvard University (the Francillon compilation of Abbot's unpublished watercolors at the Natural History Museum, London does not contain a painting of *louiseae*). Note that even though Guenée's illustration of *protonympha* is stylized, it matches the type well, and is nevertheless recognizable as *louiseae*. Staudinger and Rebel's (1901) mischaracterization of Guenée's illustration seems all the more peculiar in light of the data label that indicates Staudinger examined Boisduval's specimen, and especially since Staudinger and Wocke (1871) initially felt that *protonympha* might not be a Palearctic species.

Thus, the name *protonympha* Boisduval (1840) has been mistakenly tabulated throughout the 20th century in the Palearctic *Catocala* literature as a junior subjective synonym of *fulminea* Scopoli (1763). The name *protonympha* has never appeared in the Nearctic *Catocala* literature, and reintroducing the name *protonympha* for *louiseae* Bauer (1965) would upset established nomenclatural usage. Since the provisions of both Articles 23.9.1.1 and 23.9.1.2 of the Code appear to be met, the name *Catocala louiseae* Bauer (1965) is hereby given precedence per Article 23.9.2 as a ***nomen protectum*** over its disused senior subjective synonym *Catocala protonympha* Boisduval (1840), which becomes a ***nomen oblitum.***

We thank Martin Honey for his hospitality at the Natural History Museum (London), and for providing access to specimen material there. Julie Harvey, Michael Pogue and John Rawlins chased down several literature leads. Louis Hanfield assisted with the French translations, and Stephanie Spaulding, Leo Hickey and Victor Bers with the Latin. Don Lafontaine offered helpful comments on the manuscript.

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THE GUIDE TO BUTTERFLIES OF OREGON AND WASHINGTON, by William Neill, photography by Doug Hepburn and William Neill. Published by Westcliffe Publishers, Inc., Englewood, Colorado, 2001. 160 pp., 155 color photographs. ISBN 1-56579-392-7. Price $17.95.

Perhaps the most astonishing part of the book is hidden away in a place most would not read—on the back of the title page! Here we find a disclaimer that, perhaps in my naivety, I could never have imagined in a book on butterflies. The last sentence is worth quoting—"The author and publisher disclaim any liability for injury or other damage caused by backcountry traveling or performing any other activity described in this book." As I gaze to the right at the facing full page photograph in living color of a copulating pair of *Glaucopsyche lygdamus*, I must wonder, in my gutter of a mind, if this disclaimer also applies to illustrated activities.

This said, *The Guide to Butterflies of Oregon and Washington* is small and not all encompassing, but a preview of some butterflies of the northwestern United States aimed at the interested novice. The first one-third of the book consists of introductory chapters, is followed by 100 single page (except two pages for *Danaus plexippus*) accounts of species, and ends with a few pages of supplementary information (butterfly gardens, collections, and rearing), a glossary, a short bibliography, and an index.

The introductory sections are rather superficial and could have been improved with a little further research. A few errors leapt into view such as wing fringes being hairs, although these are nothing more than scales at the edges of wings. I am still trying to envisage a butterfly bending "its knees." We are told on p. 15 that "the animal kingdom is dominated by two principal groups: vertebrates and arthropods." True for arthropods, but there are certainly more species of mollusks, and undoubtedly more nematodes than vertebrates. The lock and key genital fit is advocated for "many" species. It seems to me that Shapiro and Porter (1989) and Porter and Shapiro (1990) more or less laid this concept to rest for butterflies. Additionally, the wings are said to "act as heat collectors." This is partially true. They do absorb radiation, but apparently only their bases act in transferring a significant portion of this to the body (Wasserthral 1975, Kammer & Bracchi 1973) and the wings of some pierids actually reflect heat energy to the body (Kingsolver 1985).

The accounts deal with over one-half of the species occurring in the two state region, and are divided into fifteen groups that are largely taxonomic at the family or subfamily level, although these divisions are not formally noted. Nomenclature is largely conservative. Each account includes a brief description, often a sentence on major variation in the region, distribution, habitat, some hostplants, the author's anecdotes, and photographs of the adult and occasionally early stages (usually larvae). The ventral surface of the wings is called the underside, but the dorsal surface is annoyingly called the "top." What ever happened to upperside? The myth that the spread of *Pieris rapae* was perhaps detrimental to "related indigenous species," especially *P. napi* is perpetuated. Decline of these species was much more likely due to habitat alteration (Chew 1981, Shuey *et al.* 1987). No mention is made that *Limenitis archippus* may be unpalatable in some areas (Ritland 1991). One of the characters given for distinguishing *Vanessa annabella* from *V. cardui* is blue-centered macules on the dorsal hindwing. Many *V. cardui* also have these, as is shown by the photographed individual on the previous page. Neill says that the forewings and hindwings of *Epargyreus clarus* are held at different planes. They are not. This is a characteristic of hesperiine skippers as shown a few pages later in the photograph of *Hesperia juba*. *Epargyreus clarus* usually perches with both sets of wings closed dorsally (e.g., Scudder 1889).

Larval hostplants off some interesting fodder: *Colias philodice* feeding on "clover and legumes," *Plebejus idas* on "lupine and legumes," and *Plebejus shasta* on "astragalus, legumes." Last time I looked, clover, lupine, and astragalus were all legumes. A similar *faux pas* was noted for *Euchloe ausonides*—"mustard family and rock cress." Currant is probably not an important hostplant of *Polygonia faunus* (Scott 1986); birch or willow may have been better choices here.

Various books (e.g., Scott 1986) would have us believe that *Habrodais grunus* may not feed as an adult on flowers. The text on this hairstreak tells us that "they use chinquipin flowers as a source of food" and lo and behold, the photograph shows an adult apparently feeding on the flowers of this oak. This is an interesting contribution.

The more than 150 photographs are largely excellent and taken in the field with natural light, a result I find very pleasing. A few include habitats and early stages. Some butterflies are out of focus, including *Papilio eurymedon* (p. 19), *Incisalia polios* (p. 92), and *Vanessa atalanta* (p. 134). The first is surprising since a much better photograph of this species appears on p. 50. One wonders why some of the images are used more than once. All six on the cover are repeated within (that of *Papilio multicaudatus*, twice). Four additional photographs are used twice in the book. Either there were no others available to use as fillers or I have nothing better to do than to look for repeats.

A few comments are needed concerning the glossary. The abdomen includes the several posterior segments; the author surely meant the posterior region of the body rather than posterior segment. This also applies to the thorax. The anal angle, apex, and costal margin occur on both wings. It is interesting to learn that a subspecies is "the subset of a population within a species that has its own distinctive features and is usually reproductively isolated." Reproductively isolated from what?

The book serves its intended audience and the photographs will allow identification of most species. The price is a bit steep and those who have more than a passing interest would want to spend a few more dollars for something like Opler's (1999) western field guide. As I reread this critique, I wonder if maybe I am getting old, picky, and cranky. Maybe. But then again, maybe not. Neill considered a coupled pair as in a predicament. This still sounds like a pretty good predicament to me. Do I need a disclaimer? If so, I take no responsibility.

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THE SESIIDAE OF EUROPE. 2001. Zdeněk Laštůvka & Aleš Laštůvka. Apollo Books. Stenstrup, Denmark. 245 pp., 9 colour plates. 17 cm by 24 cm. ISBN: 87-88757-52-8. Retail cost DKK 370,00 (approximately USD 45.00). Hard cover.

Sesiid moths, bee and wasp mimics, are popular amongst lepidopterists and lay persons alike. Often not seen, these creatures quickly catch the imagination and attention of many people. Lepidopterists, intrigued by the mimicry, anonymity, and diversity of so many species, wonder why they don't see more of the moths. Others, when presented with the true identity of these wasps as harmless moths, are awestruck, often responding with "You've got to be kidding!" For many years in the USA, only Beutenmuller's tome extra ordinaire (Beutenmuller, William, 1901, Monograph of the Sesiidae of America North of Mexico, Memoirs American Museum of Natural History, 1(5):215–352) with one plate reproduced in Holland's *Moth Book* (Holland, William Jacob, 1903, Doubleday, Page and Company, New York, 479 pp., 48 color plates) was available as the sole source of information. In Europe, as in the Western Hemisphere, the popularity of sesiids did not subside, and two recent books help fill the desire for knowledge. In 1999 Gem Publishing Company delivered a striking volume on Sesiidae (Spatenka, Karel et al. 1999. Handbook of Palaearctic Macrolepidoptera Volume 1 Sesiidae - Clearwing Moths, Gem Publishing Company, Wallingford, England, 569 pages, 57 color plates). Apollo Books now brings us The Sesiidae of Europe, and a fine book it is.

A quick examination of the book reveals a polished colorful hard binding that is Smythe sewn. A Smythe sewn book has threads through the folds of the paper on the inside margin. A Smythe sewn book lies flat when open, and individual pages never fall out. I urge all publishers and authors to take note of the superior quality of Smythe sewn books. The insides are clean, and clearly written with a comfortable typeface and large font. The color illustrations are very sharp. The lighting is so even the specimens appear at first to be paintings, but the pins belie the fact that they are real, nearly perfect specimens. The 1.8× natural size of the specimens allows inspection of all details even on small species. The consistently and artistically drawn interpretations of the genitalia are well done, although I prefer techniques of drawing that show exactly what the genitalia look like. The range maps are easy to use, but the heavily drawn political boundaries compete for attention with the black shading delineating species' distributions. The production of the book is consistently very high quality.

After reading it in detail I consider the book both an identification manual, and revision of European Sesiidae. Since it proposes many taxonomic changes at the species and subspecies level (summarized in the abstract) it is required for European lepidopterists, and the one synonym: *Synansphecia* Capuse, 1973 = *Pyropteron* Newman, 1832 will be of interest to students of Sesiidae everywhere. Other reviewers, more familiar with European fauna, are likely to comment on the correctness of the taxonomy and nomenclature. Most revisionary works contain more details, with specific citations, than are included in the section of Phylogeny and Classification. The authors should have explained why they chose the classification used in this book. A systematic list highlighting taxonomic revisions is followed by comprehensive keys; a key to subfamilies, tribes, and genera, followed by keys to the genera.

I like keys that are clearly dichotomous and well written because such keys can be used to show the characters the authors use to differentiate between species. In this book, some couplets are excellent; "Antenna without terminal scale pencil (text figure 1a)" versus "Antenna with terminal scale pencil (text figure 1b)." The previous couplet is truly dichotomous and illustrated, whereas the following couplet should be more clearly written, and since it includes no illustrations, interpretation is left to the reader. "Abdominal rings on segments 2, 4, 6, or additional rings only indicated" versus "Abdominal rings or margins also on other segments." I don't have any European species to test the keys presented in this book.

The book presents several other sections as well. A nicely illustrated section on the morphology is brief with some details, such as the coupling of the wings, unillustrated. A one page summary of the biology of Sesiidae is followed by an excellent list of larval hosts. The last few pages include an easy to use distributional check-list and an excellent bibliography.

The identification part of the book illustrates the great similarity between species. The assertion by the authors on page 8 "In a few isolated cases, even the combination of external and genitalic characters may not lead to a satisfactory result, . . ." is an understatement when compared to the illustrations of male and female genitalia along with wings for the genus *Chamaesphecia*. My head began to hurt when I considered the similarities as I examined several pages illustrating just a few species. It is clear that without complete facts, including larval host data and other bionomic information, differentiating some of the species of Sesiidae will be nearly impossible.

The meat of the book lies in the species accounts, the color illustrations, and the genitalia drawings. There are about two species accounts per page, and each includes the name of the insect, the author and year of description, reference to color illustration, and taxonomic information. For each species and synonym, the original description is referenced. The full literature citation for the original description should have been included. The type locality is specified, location of the type material, when known, is given, followed by notes about lectotypes and other taxonomic designations.

Each species account is divided into four sections; Diagnosis, Genitalia, Biology and Habitat, and Distribution. A fifth section, Remarks, is sometimes present. The detailed Diagnosis does not often tell how to distinguish one species from another. It is awkward that the reader will be required to reconcile distinguishing characters presented in the keys with the written descriptions in the Diagnosis. The section on Genitalia provides reference to the drawings, and in the case of *Chamaesphecia*, several entries simply refer the reader to another, nearly identical, species. This is a tough genus. The entries for Biology and Habitat, when known, are detailed and well referenced. The Distribution section is a verbal description of the maps.

I want to know more about Sesiidae. The two paragraphs about collecting and rearing are too brief and lack detailed information. The Introduction quickly mentions the increased knowledge of Sesiidae through the use of synthetic sex pheromones, yet this single phrase is the only place sex pheromones are discussed. The almost casual mention of other workers' knowledge without literature citations could be frustrating to a newcomer to the study of Sesiidae. The references to this as the second edition without clearly identifying the first edition will lead bibliographers 100 years from now, without additional knowledge, to search in vain for the first edition.

As I recommend this book to lepidopterists, especially those interested in Sesiidae, I suggest that readers of English in the Western Hemisphere not be put off by the odd hyphenation, including splitting the word "here" with two letters on each side of the hyphen. I am willing to credit these slips to the software or typesetters rather than think the translation so bad as to question the credibility of the text. This is a good book.

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ERRATA

INFLUENCE OF MOSQUITO CONTROL CHEMICALS ON BUTTERFLIES (NYMPHALIDAE, LYCAENIDAE, HESPERIIDAE) OF THE LOWER FLORIDA KEYS

In the above paper by Mark H. Salvato (Journal of the Lepidopterists' Society 55(1):8–14), there were seven typographical errrors:

pg. 10: *Proteus urbanus* (L.) should read *Urbanus proteus* (L.), *P. urbanus* should read *U. proteus*, *Pygrus oileus*(L.) should read *Pyrgus oileus* (L.).

pg. 11: *Pygrus oileus*(L.) should read *Pyrgus oileus* (L.).

pg. 13, Table 4: *Proteus urbanus* should read *Urbanus proteus*, *Pygrus oileus* should read *Pyrgus oileus*.

pg. 14: *Proteus urbanus* should read *Urbanus proteus*.

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