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PRESIDENTIAL ADDRESS 1997: A NEW SPECIES OF *LITHOPHANE* (NOCTUIDAE), FROM THE MIDWESTERN UNITED STATES, DEDICATED TO THE PURPOSE OF THE LEPIDOPTERISTS' SOCIETY

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ABSTRACT. *Lithophane franclemonti*, new species, is described and illustrated from Killdeer Plains Wildlife Area, Wyandot County, Ohio. The new species is most similar to *L. innominata* (Smith) and *L. bethunei* (Grote & Robinson). The holotype and male and female genitalia are illustrated. The description is written in deference to the principle of collaboration between amateur and professional lepidopterists.

Additional key words: Ohio, Wisconsin, Illinois, Pennsylvania, Killdeer Plains Wildlife Area.

This presidential address coincides with the 50th anniversary of The Lepidopterists' Society. At this quintessential occasion, it seems appropriate to highlight the celebration, and thus I take the liberty of straying from the traditional erudite wisdom of former Presidents by dedicating this paper to the purpose of the Society, as eloquently penned by Cyril Franklin dos Passos (Kendall 1977), to wit:

"It shall be the purpose of the Society to promote internationally the science of lepidopterology in all its branches; to further the scientifically sound and progressive study of Lepidoptera; to publish periodicals and other publications on Lepidoptera; to facilitate the exchange of specimens and ideas by both the professional worker and the amateur in the field; to compile and distribute information to other organizations and individuals for purposes of education and conservation and appreciation of Lepidoptera; and to secure cooperation in all measures tending to that end."

The foresight and strength of this passage, now 50 years old, is supported by the success of the Society, and its impact on the thousands of professional and amateur enthusiasts who exemplify its meaning. This paper is written to honor all the Society's members. I speak for myself and many others when I express my heartfelt thanks for the support and invaluable assistance we have received from the people who comprise the Society. One source of encouragement, especially important to me, is expressed in the line: "to facilitate the exchange of ideas by both the

professional worker and the amateur." My activities as an amateur have been greatly enhanced by assistance from many professionals.

My research activities include documenting Lepidoptera in some of Ohio's finest natural areas (Rings et al. 1987, Rings & Metzler 1988, Metzler 1989, Metzler & Shuey 1989, Rings & Metzler 1989, Rings & Metzler 1990, Rings et al. 1991[92], Rings & Metzler 1992, Metzler & Zebold 1995), including Killdeer Plains Wildlife Area near Marion, Ohio. My field work is not restricted to summer months—unpredictable warm nights during the winter tend to induce long drives (Newman 1945) to sample "winter moths," including several species in the genus *Lithophane*. A new species of *Lithophane*, discovered on one of those outings, is described here, and its dedication is meant to honor all members adhering to the purpose of The Lepidopterists' Society.

MATERIALS AND METHODS

Specimens of the new *Lithophane* were collected in the evening crepuscular hours after attraction to baits consisting of homemade banana wine, black strap molasses, and brown sugar. Small sponges were soaked in the bait mixture and hung from tree branches or bushes. The illustrated genitalia were dissected in distilled water, stained with Safranin O in water, dehydrated in 98% isopropyl alcohol, cleared in xylene, and slide mounted in Canada balsam. To prepare the genitalia, I soaked abdomens of the moths in KOH (Clarke 1941, Hardwick 1950). I photographed the genitalia with the aid of a Leitz Aristophot photomacrographic apparatus using transmitted light. The photograph of the adult was illuminated with an Aristo DA-10 light box, background being an 18% gray card. The forewing lengths were estimated to the nearest mm, using a mm rule, and the measurements are from the base of the forewing to the tip of the apex. The colors are from Ridgway (1912) and Smithe (1974, 1975, 1981). Terminology for the morphology, elements of wing pattern, and genitalic structures follow Forbes (1954), Klots (1970), Hodges (1971), and Lafontaine (1987). The subfamily assignment follows Poole (1995) and Poole and Gentili (1996).

Lithophane franclemonti Metzler, new species

Diagnosis. *Lithophane franclemonti* is most similar to *L. bethunei* (Grote & Robinson 1868) and *L. innominata* (Smith 1893), and closely matches the generic characters provided by Franclemont and Forbes (1954). Compared to the other species, *L. franclemonti* looks yellow. It can be distinguished from *L. bethunei* by its color and larger size. The ground color of *L. bethunei* is pearl gray. The mean forewing length of *L. franclemonti* is 17.5 mm ($n = 18$) and *L. bethunei* is 15.9 mm ($n = 12$). The pale color of both forewings and hindwings, and the shape of the juxta, separate *L. franclemonti* and *L. innominata*. The forewing of *L. innominata* is more orange. The hindwing of *L. franclemonti* is a mixture of flesh and fuscous colored scales which makes the hindwing look pale and pinkish in comparison to the fuscous colored hindwings of *L. innominata*. The juxta of *L.*



FIG. 1. *Lithophane franclemonti* n. sp., holotype male. USA: OHIO, Wyandot County, Pitt Township, Killdeer Plains Wildlife Area, 40°42.5'N, 83°13.8'W, 27 March 1997, Eric H. Metzler.

franclemonti has two strongly delineated lateral ridges, the distal end of the juxta is spoon shaped and blunt. The juxta is narrow, without lateral ridges, and tapers to a point in *L. innominata*.

Description. *Adult male* (Fig. 1): *Head*: pale pinkish buff, tawny line across front between eyes, patch of tawny scales dorsad of clypeus on each side of head next to eyes, anterior lashes tawny, posterior lashes black; labial palpus concolorous; dorsal, distal, and ventral surfaces of second segment with some tawny- and black-tipped scales; antennae filiform, dorsal scaling concolorous with head, ventral surface naked; sensory setae on ventral surface of male antennae dense in comparison to that of female, setae no longer than width of flagellar segment. *Thorax*: concolorous with head, collar and tegulae partly outlined with black-tipped scales; ventral thorax with hair-like scales, mixed with tawny-tipped scales; legs concolorous with head, with scattered black-tipped scales; tibia lateral distal end with patch of black-tipped scales; tibial spurs encircled with black scales at middle, tip of each spur black; tarsus concolorous with head, basal dorsum of each tarsomere with patch of tawny-, fuscous-, and black-tipped scales. *Forewing*: length 16–18 mm, mean 17.5 ± 0.6 mm, $n = 18$; ground color pale pinkish buff, markings delineated with tawny-, fuscous-, and black-tipped scales; basal dash, obscure antemedial line, median shade, narrow filling of reniform, filling between median line and postmedial line, inner half of subterminal line, and terminal line defined by tawny-tipped scales; black-tipped scales at intersection of dentate antemedial and postmedial lines and veins, at basal, antemedial, and median lines at costa, and along veins in subterminal area; adterminal line, and costa near reniform with black-tipped scales; median shade between antemedial and postmedial lines, and subterminal inter-vein spaces below apex and above tornus filled with fuscous-tipped scales; orbicular obscure, outline of reniform defined by absence of tawny-tipped scales; underside pale horn color with tawny-tipped scales delineating some veins and terminal line; postmedial line obscure, pale pinkish buff. *Hindwing*: ground

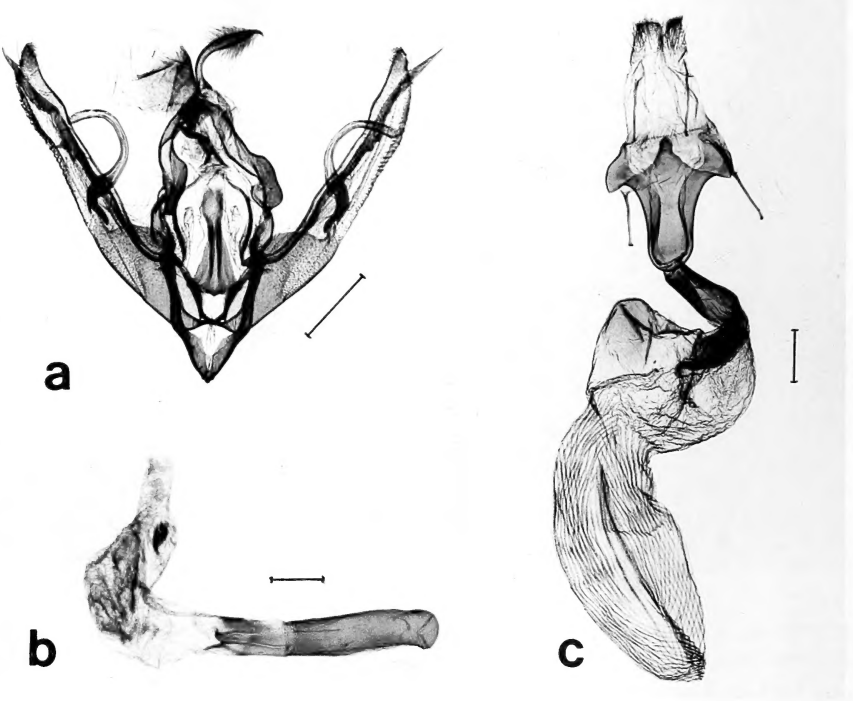


FIG. 2. Genitalia of *Lithophane franclemonti* n. sp. **a**, male genitalia (aedeagus removed) and **b**, aedeagus; slide EHM 218, paratype, USA: OHIO, Wyandot County, Pitt Township, Killdeer Plains Wildlife Area, 40°42.5'N, 83°13.8'W, 16 March 1995, Eric H. Metzler. **c**, female genitalia; slide EHM 219, paratype, USA: OHIO, Wyandot County, Pitt Township, Killdeer Plains Wildlife Area, 40°42.5'N, 83°13.8'W, 16 March 1995, Eric H. Metzler. Scale bars = 1 mm.

color flesh color, fuscous-tipped scales along veins and terminal line, paler fuscous-tipped scales in some spaces between veins; outer half of fringe contrastingly pale; underside as in forewing. *Abdomen*: first tergite closely scaled, buff; terga 2–8 heavily dusted with fuscous- and black-tipped scales; tufts absent; sterna dusted with tawny- and black-tipped scales. *Adult female*: similar to male. *Male genitalia* (Fig. 2): vinculum, tegumen, penicillus, uncus, and saccus as for genus; sacculus of valve broad with costal lobe, ventral margin between sacculus and terminal spine dentate, cucullus and corona reduced; digitus heavy, serrate at middle, extending from base of sacculus to a terminal spine; clasper sinuate; juxta elongate, broadest at the anterior end, gradually narrowing, posterior 1/3 spoon shaped, anterior 2/3 with strongly sclerotized parallel lateral ridges; aedeagus with broad terminal ventral tooth angled at tip; vesica with 90° angle to right, distal half lightly sclerotized, apical diverticulum with dense patch of cornuti. *Female genitalia* (Fig. 2): ovipositor lobes lightly sclerotized, anterior apophysis and posterior apophysis slender, sterigma elongate, broadly pointed ventrally; ductus bursae flattened, anterior ventral side heavily sclerotized, twisted 180° and bent 90° so that posterior sclerotized side is dorsal at junction with ostium bursae; corpus bursae broad and elongate, slightly narrowed at 2/3 length from anterior end, posterior end lightly sclerotized; 4 elongate signa, 2 lateral, 1 ventral, and 1 dorsal.

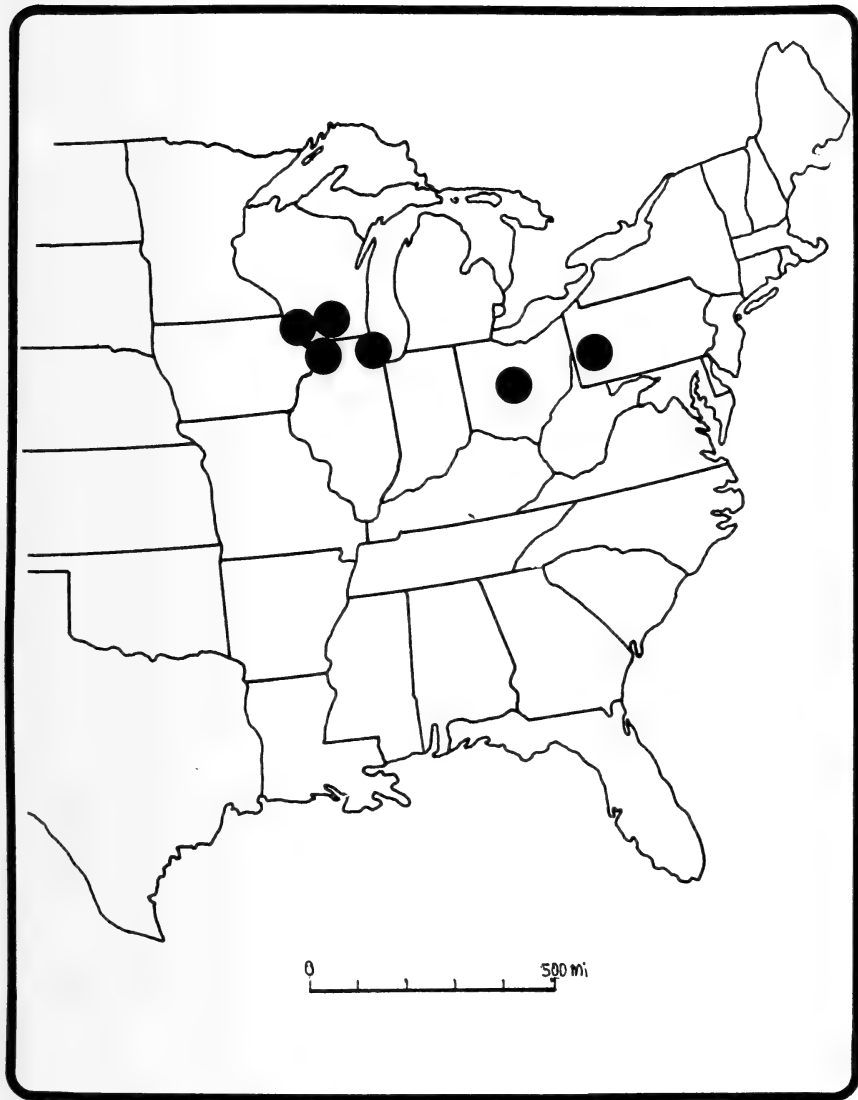


FIG. 3. Distribution of *Lithophane franclemonti* n. sp.

Types. *Holotype*: Male. USA: OHIO, Wyandot Co., Pitt Township, Killdeer Plains WLA, 40°42.5'N, 83°13.8'W, 27 March 1997, Eric H. Metzler, bait. *Paratypes*: 26 ♂ and 26 ♀ as follows. USA: Illinois: [Cook County] Evanston, 4/5/[18]97, ♀, coll. A. J. Snyder; [Jo Daviess County] Elizabeth, Sept. 12 1937, ♂, M.L. Bristol, Coll.; [Jo Daviess County] Apple River Canyon, Oct 5 1940, ♂, M.L. Bristol, Coll. Ohio: Wyandot County, Pitt Township, Killdeer Plains WLA, 40°42.5'N, 83°13.8'W, 16 March 1995, 2 ♂, 2 ♀, 27 March 1997, 7 ♂, 4 ♀, Eric H. Metzler. Pennsylvania: [Allegheny County] Pitts[burgh], Oct. 8 [19]04, 1

♂, Oct. 25 [19]04, ♀, [Beaver County] New Brighton, 10-10-[19]02, ♂, 10-3-[19]03 ♂, and IX-24-[19]05, ♀, H. D. Merrick. Wisconsin: Crawford County, T10N, R6W, Sec. 6, 6 May 1995, ♂, L. A. Ferge; [Dane Co.] Cross Plains, T8N, R7E, S33, 3/27/[19]97, 7 ♂, 13 ♀, 4/10/[19]96, ♀, T. Rocheleau coll.; Dane County, T7N, R7E, Sec. 16, 7 April 1981, ♀, 22 April 1979, ♂, ♀, 26 April 1978, ♂, and 5 May 1979, ♂, L. A. Ferge; Iowa County, T6N, R5E, Sec. 1, 22 March 1988, ♂, ♀, L. A. Ferge. The holotype male is in the United States National Museum of Natural History, Washington, D.C. Paratypes are deposited in the following collections: John G. Franclemont at Cornell University, Ithaca, New York; Field Museum of Natural History, Chicago, Illinois; Illinois Natural History Survey, Champaign, Illinois; Eric H. Metzler, Columbus, Ohio; The Ohio Lepidopterists, Ohio State University Museum of Biological Diversity, Columbus, Ohio; Thomas A. Rocheleau, Madison, Wisconsin; Leslie A. Ferge, Middleton, Wisconsin; Milwaukee Public Museum, Milwaukee, Wisconsin; Natural History Museum of Los Angeles County, Los Angeles, California; Michigan State University, East Lansing, Michigan; Ohio State University Museum of Biological Diversity, Columbus, Ohio; Canadian National Collection, Ottawa, Ontario; American Museum of Natural History, New York, New York; The Natural History Museum, London, England; Florida State Collection of Arthropods, Gainesville, Florida; and Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Biological Notes. *Lithophane franclemonti* has been recorded from western Pennsylvania (Allegheny and Beaver counties), central Ohio, northeastern Illinois, and southern Wisconsin (Fig. 3). The Ohio specimens were collected at the edge of, and in an old field adjacent to a second growth mixed mesophytic forest of oaks, hickories, wild black cherry, beech, various maples, and other hardwoods typical of central Ohio. The topography of Killdeer Plains Wildlife Area is flat. It is known for its remnant prairies and wetlands. However, I cannot link *L. franclemonti* to either of those habitats. Leslie Ferge describes the Wisconsin habitat as: "oak/hickory forest, the predominant habitat type of [his] three localities. However, the Crawford County specimen was collected on a dry hill prairie remnant surrounded by extensive forest." Thomas Rocheleau collected his Wisconsin specimens along a road at the top of a hill surrounded with mature (second growth) oak/hickory woods. Most of the specimens were collected at bait. The specimens collected in autumn are inseparable from specimens collected in spring. The immature stages are as yet unknown.

Etymology. As a young man, fully wet behind the ears, and bolstered by encouragement from my mentors at Michigan State University, I nervously called upon John G. Franclemont with a few boxes of Noctuidae and asked for his assistance. He immediately treated me as a colleague by demonstrating techniques, sharing knowledge and showing me the finest literature. The next several hours, and an invitation to go collecting, led to a friendship that has lasted many years. John Franclemont exemplifies what Alexander Barrett Klots later told me: "lepidopterists are the friendliest people in the world." In recognition of all the lepidopterists, who gladly give their time to help me and others more fully enjoy our common interest, I name this species after John Franclemont; *franclemonti* is the possessive genitive case. The genus *Lithophane* is one of his favorite groups of moths.

ACKNOWLEDGMENTS

Patricia A. Metzler, my wife and constant companion, faithfully carried collecting equipment, lent support, and provided excellent company while she contemplated the apparent pleasures of being married to a man who plays golf every weekend. John G. Franclemont provided me with abundant hours of learning and fellowship. Many other entomologists, several of whom are Franclemont's students, provided time, energy, knowledge, food, spirits, and patience while I attempted to absorb as much knowledge as possible. I cannot name them all for fear of omitting a few, yet it is clear to me that they epitomize the professional/amateur interaction extolled in the constitution of The Lepidopterists' Society. Dale Schweitzer and John Franclemont both inspected specimens of *L. franclemonti* and concur that it is a new species. For lending specimens I thank: Leslie A. Ferge; Kathleen R. Zeiders, Illinois Natural History Survey; Philip Parrillo, Field Museum of Natural History; Susan Borkin, Milwaukee Public Museum; John A. Rawlins, Carnegie Museum

of Natural History; Ronald W. Hodges, U.S. National Museum of Natural History; Mark F. O'Brien, University of Michigan; and Thomas A. Rocheleau. Charles V. Covell, Jr., J. Donald Lafontaine, Ron Leuschner, Mogens C. Nielsen, Eric L. Quinter, Roy W. Rings, and Sonja Teraguchi searched for specimens in collections under their care. This research was funded by the Ohio Division of Wildlife with funds donated to the Ohio Wildlife Diversity & Endangered Species Program, and a grant from the Partnerships for Wildlife Program, U. S. Fish & Wildlife Service, to the Wisconsin Department of Natural Resources. The project was administered by The Ohio Biological Survey. Brian J. Armitage, Steve Barry, Donna Daniel, Carolyn Caldwell, Douglas C. Ferguson, Richard A. Henderson, William Luckey, Steven Passoa, John A. Shuey, Charles A. Triplehorn, and John W. Wenzel provided professional courtesies. Michael G. Pogue, John W. Brown, M. Deane Bowers and Lawrence F. Gall made excellent suggestions that helped improve the manuscript.

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ECOLOGY, POPULATION BIOLOGY AND MORTALITY OF
EUPTOIETA HEGESIA CRAMER (NYMPHALIDAE)
ON JAMAICA

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ABSTRACT. We examine the ecology, population biology and potential sources of mortality of *Euptoieta hegesia*, a tropical lowland butterfly from Jamaica, using a combination of captive rearing, studies of natural populations, and experimental approaches. We provide detailed observations of the life cycle and methods for captive rearing of this species. We assess the relative performance of larvae on primary and secondary hostplants, distribution of larvae on the primary hostplant, hostplant population utilization, and the distribution of *E. hegesia* on the island. A mark-release-recapture study was conducted to estimate population parameters and we recorded sex, size, age (as estimated by wing wear), and wing damage sustained by the butterflies prior to their initial capture. We provide evidence that *Turnera ulmifolia* is the primary hostplant of *E. hegesia* on Jamaica and that butterfly population size is not limited by the availability of hostplants. These short-lived butterflies appear to be residents of discrete hostplant populations and experience high mortality levels. Females are damaged more frequently, show more total damage and more frequent symmetrical hindwing damage (attributable to ground-based predators) than do males. We compare the results of the population study with available studies of other tropical butterflies and suggest that lowland butterfly population structure and dynamics are significantly different from that of rainforest species.

Additional key words: tropical lowland habitats, *Turnera ulmifolia*, cyanogenesis, sexual dimorphism, predation.

Euptoieta hegesia Cramer (Nymphalidae) uses *Turnera ulmifolia* L. (Turneraceae) as its primary hostplant on the island of Jamaica in addition to several *Passiflora* spp. (Passifloraceae) to a lesser degree (see below). *Turnera ulmifolia* is known to exhibit extensive genetically-based variation for a putative defense trait, cyanogenesis (the ability of plants to liberate hydrogen cyanide upon damage to tissues), within and between populations on Jamaica (Schappert & Shore 1995) whereas the Jamaican species of *Passiflora* which have been investigated are uniformly cyanogenic (Spencer 1988, Schappert & Shore, unpubl. data). Our ongoing studies of the *T. ulmifolia*-*E. hegesia* hostplant-herbivore system are centered on this variation in the ability of the hostplant to liberate hydrogen cyanide and the interaction with *E. hegesia*. In the long term, we hope to investigate the strength of selection imposed by both organisms, one upon the other. For example, we are finding that the

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magnitude of cyanogenesis exhibited by the hostplant has little or no effect on the growth and development of *E. hegesia* larvae (Schappert & Shore, unpubl. data), suggesting that this species is capable of detoxifying and/or sequestering cyanogenic glycosides, perhaps for their own chemical defense.

As is the case for many tropical insects, few data are available on the natural history of *E. hegesia*. In this paper, therefore, we present the results of the first comprehensive study of the ecology and life history of this species. These data provide necessary background information as a prelude to more detailed investigations of chemical mediation of the interaction between the hostplant and this butterfly. Specifically, our objectives are to: (1) provide detailed observations of the life cycle of *E. hegesia* using captive-reared individuals, providing methods for captive rearing; (2) compare the lifespan and size of individuals in captivity and the field; (3) examine the age-structure, size and sex ratio of populations in nature; (4) examine the distribution of larvae on hostplants; (5) compare relative survival and performance of larvae on commonly used hostplants; (6) assess the degree of butterfly movement between hostplant populations; and (7) provide information on the level and kinds of mortality sources experienced by adult butterflies.

MATERIALS AND METHODS

Study organisms. There are two extant species in the genus *Euptoieta*. *Euptoieta hegesia* Cramer is limited in its distribution to Mexico and Central America south to Colombia in South America and to the islands of the Caribbean (Brown & Heineman 1972, DeVries 1987, Smith et al. 1994). *Euptoieta claudia* Cramer has a similar but broader distribution that extends both further north and south of the range of *E. hegesia*. There is some debate as to whether additional taxa, including *E. hortensia* Blanchard (Brown & Heineman 1972, A. Shapiro, pers. comm.), and *E. bogotana* Staudinger (DeVries 1987; possibly a high Andean race of *E. claudia*, K. Brown Jr., pers. comm.), warrant recognition as distinct species. *Euptoieta* is generally placed in the subfamily Argynninae, allied with both the North American and Old World argynnines and the Neotropical Heliconiinae (Dos Passos & Grey 1945, Clark 1947, Ehrlich 1958). Scott (1985) suggested that *Euptoieta* shares many ancestral traits with these two lineages, noting that the wing venation of *Euptoieta* is almost identical to that of *Agraulis vanillae* L., a heliconiid with a number of primitive characteristics. This classification is supported by more recent analyses (Ackery 1988, Harvey 1991, Martin & Pashley 1992). Recent molecular work by Weller et al. (1996) and A. Brower (pers. comm.) suggests that the Argynninae, Heliconiinae and Acraeinae form a monophyletic clade.

Turnera ulmifolia is the primary larval hostplant of *E. hegesia* on Jamaica (see below, Brown & Heineman 1972). *Euptoieta hegesia* is also known to use other *Turnera* species and varieties including *T. scabra* Mills. in the Dominican Republic (JSS, pers. obs.), *T. ulmifolia* (probably *T. subulata* Smith) in Brazil (K. Brown Jr., pers. comm.) and Colombia (Hallman 1979) as well as cyanogenic *Passiflora* species, particularly *P. suberosa* L. and *P. foetida* L. on Jamaica (T. Turner, pers. comm., PJS, pers. obs.) and *P. foetida* in Costa Rica (Smiley 1983). *Euptoieta claudia* is also found on Jamaica (but is confined to a region of the Blue Mountains above 1220 m) where it feeds on *Viola patrinii* DC., an acyanogenic plant (PJS, pers. obs. and unpubl. data, T. Turner, pers. comm., Smith et al. 1994).

While no detailed work exists on the life history and ecology of *E. hegesia*, most of the available information is attributable to the work of Tom Turner (*in* Brown & Heineman 1972, Smith et al. 1994). Turner indicates that eggs are laid on the upper or terminal leaves of hostplants in the wild, that the egg stage lasts five days, that larvae develop over 9–12 days and that pupae develop over eight days. These data yield a published egg to adult (i.e., generation) time of 22–25 days. Larvae are brick red with black spines until their third instar when the ground colour deepens to maroon and a silver/white dorsal line edged with black and two similar lateral lines appear—suggesting that larvae are aposematically colored. Pupae vary from tan to black (pers. obs.) with silver and gold markings. Adults are “medium-size orange-tawny butterflies” (Brown & Heineman 1972:210) with extensive black markings on the upperside (similar to *A. vanillae* but lacking the elongated forewings) and with the undersides mottled brown and purple. Published, mostly anecdotal, accounts of various aspects of the anatomy, life cycle and hostplant use of *E. hegesia*, with particular reference to Jamaica, include Swainson (1901), Longstaff (1908), Kaye (1926), Brown and Heineman (1972) and Smith et al. (1994). Further accounts are found in Scudder (1889), D’Almeida (1923), Ross (1964) and DeVries (1987).

Turnera ulmifolia L. is a weedy shrub common to roadsides and coastal scrub habitats throughout the Neotropics (Barrett 1978, Barrett & Shore 1987). It is a perennial that produces many ephemeral (<1 day) flowers and is known to show a wide range of morphological and reproductive variation on Jamaica (duQuesnay 1971, Barrett & Shore 1987). Plant populations are generally discrete, often small and widely separated, with potentially little gene flow among populations (Barrett 1978, Belaoussoff & Shore 1995). Shore and Obrist (1992) documented extensive variation for cyanogenesis across a number of species, taxonomic varieties and populations of *Turnera*. There is a wide range of cyanogenesis in *T. ulmifolia* from Jamaica (Schappert & Shore 1995). The presence of cyanogenic glycosides with a cyclopentenoid structure, in addition to morphological, embryological, and DNA sequence data, ally the Turneraceae with the Passifloraceae and other members of the order Violales (Vijayaraghavan & Kaur 1966, Cronquist 1981, Spencer et al. 1985, Spencer 1988, Chase & Swenson 1995). Interestingly, the patterns of host use by related species of butterflies led Ehrlich and Raven (1964:594–595) to “confidently predict” that the biochemical basis for the association of these plant families would eventually be found.

Rearing in captivity. To investigate the life cycle and conduct laboratory experiments, larvae were reared on potted plants of *T. ulmifolia* on which eggs had been laid. When larvae began wandering in later instars, or if individual rearing was needed, they were transferred to rearing cups. Rearing cups consisted of 260 ml disposable plastic cups with an inner circle, approximately 42 mm in diameter, cut out of the transparent lid. A 30 ml cup with a small hole punched in its lid was filled with water, capped, a small shoot of hostplant inserted and was placed in the bottom of the larger cup. A 100 mm × 100 mm square of bridal veiling was sandwiched between the cup and the transparent lid to prevent larvae from escaping, and allow sufficient air movement to prevent the build-up of fungus. The netting also provided a preferred pupation site for this species. Single larvae kept in cups generally needed cleaning and replenishing of the hostplant every 2–5 days. Groups of similar sized larvae were reared on potted plants in large (10–12 L) plastic pails with veil tops secured by an elastic. All rearing was conducted in the glasshouse at York University in Toronto, Ontario, Canada under natural summer photoperiod conditions.

This method of individual rearing provides a good balance between space requirements, labour intensiveness and the maintenance of reasonably sanitary conditions because cups can be contained in plant trays to allow easy movement and to allow visual checks for food and cleanliness in a timely manner. Cleaning and re-feeding were quickly accomplished by removing the larvae and old inner cup, wiping, inserting a new inner cup with fresh foodplant, and reintroducing the larvae. The pupae were easily removed from the bridal veiling with their silk pads intact. The pads were sandwiched between two pieces of marking tape and hung on the side walls of rearing cages with wire paper clips. Adults were housed in cages and mating and oviposition occur even in very small cages (30 cm × 30 cm × 30 cm). However, we commonly used 64 cm × 71 cm × 85 cm high wooden frame cages with wire screen floors and covered in bridal veiling for the maintenance and breeding of adults. Sex ratio in the cages can be maintained by monitoring the sex of pu-

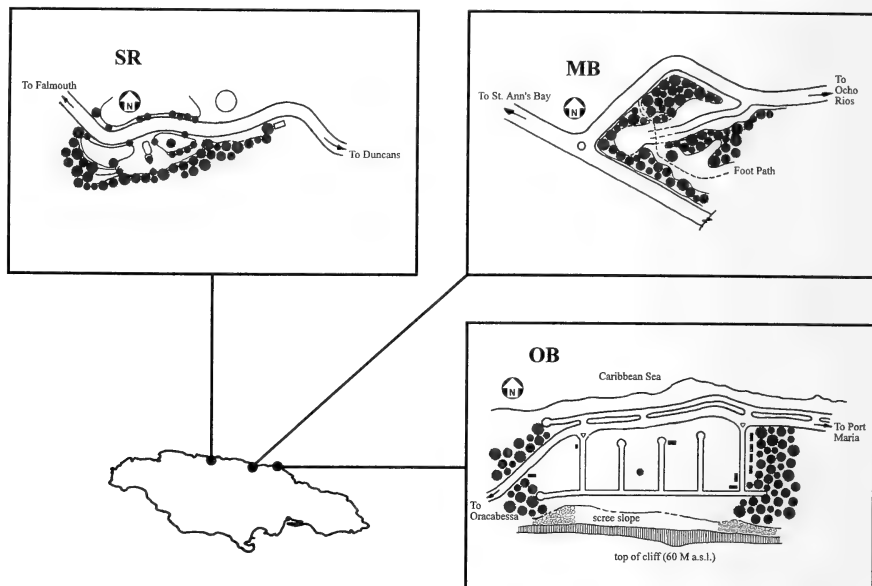


FIG. 1. Location and site plans for three *T. ulmifolia*/*E. hegesia* populations studied in Jamaica. Not to scale.

pae (determined by pupal mass—females are significantly larger than males, see below and Table 1). Mating of females as they eclose is common.

Adults were fed daily with a honey water/salts/amino acid supplement (Lederhouse et al. 1990) placed in *T. ulmifolia* flowers on oviposition plants and in individual flowers inverted on the top of the cage. In addition, *Lantana* spp. (Verbenaceae), *Pentas* sp. (Rubiaceae) and *Ageratum* sp. (Compositae) are provided as nectar sources in the cages. Some individual butterflies (e.g., ovipositing females) were fed manually by uncoiling their proboscis into nectar supplement contained in *T. ulmifolia* flowers on the cage bottom. Recently we have begun using a long-lived artificial nectar, modified from Lederhouse et al. (1990) and O. R. Taylor (pers. comm., for captive rearing of Monarchs), presented to butterflies in shallow cups clipped to the corner posts of the cages approx. 20 cm from the top of the cage. The nectar is resistant to fermentation and can be left for up to three weeks with daily additions of distilled water to offset evaporation. It has proven to be very attractive to the butterflies and has greatly reduced manual feeding requirements of females. Our recipe for artificial nectar is as follows: to 1 L of distilled water, add 150 g high-grade natural honey (or sugar); 4 g ascorbic acid (vitamin C); 2 g 2,4-hexanedienoic acid (sorbic acid); 2 g p-hydroxybenzoic acid methyl ester (methylparaben or Tegosept®); 5 g bovine casein, acid hydrolysate; 7.2 g Potassium chloride (KCl); 0.24 g Calcium chloride (CaCl₂); and 0.10 g Sodium chloride (NaCl).

Performance of larvae on hostplants. We conducted experiments to assess the performance of larvae on the three most commonly used Jamaican hostplants: *T. ulmifolia*, *P. foetida* and *P. suberosa*. A sample of fresh-hatched larvae (total 72) was selected from four *T. ulmifolia* oviposition plants that had each been available to at least five ovipositing females (reared on *T. ulmifolia*) in each of four cages for four hours. The larvae, therefore, were even-aged and likely represented the progeny of at least 20 matings. The larvae were reared in groups of 12 in six rearing buckets containing abundant, mature, flowering hostplants: two with potted plants of *P. foetida*, two with *P. suberosa* and two with *T. ulmifolia*. The presence/absence of larvae was monitored every 2–3 days. We

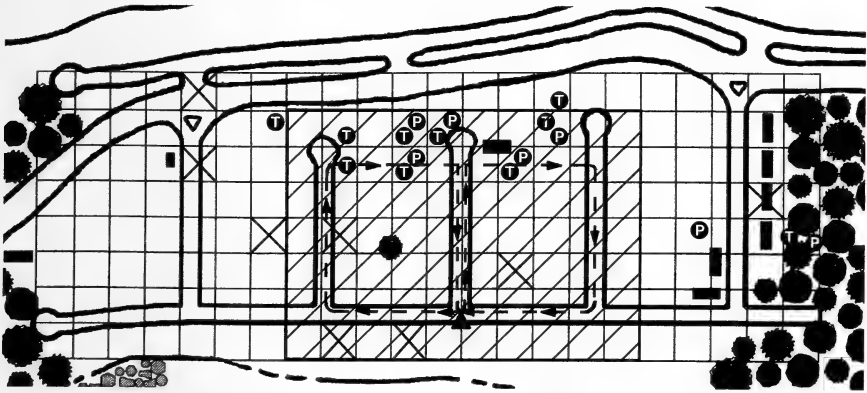


FIG. 2. Site plan of OB showing location and approximate effective area of the *E. hegesia* population studied (crosshatched), the length and direction of the survey transect used in the MRR study (dotted line), and the location of the hostplants found and quadrats surveyed during the hostplant survey. T = *T. ulmifolia*, P = *Passiflora* spp., X through quadrat denotes a surveyed quadrat where no hostplants were found. Each quadrat is 30.5 m square.

recorded the date of pupation and the mass of the pupa the following day. The entire experiment was replicated in the subsequent generation, again with larvae from eggs laid by *T. ulmifolia*-reared adults.

Study sites and distribution of *E. hegesia* on Jamaica. A survey of numbers of potential hostplants was conducted at one large (OB, near Oracabessa, St. Mary, >20 ha) and two small (MB, near Mammee Bay, St. Ann, & SR, near Duncans, Trelawny, <2 ha each) *T. ulmifolia* populations on the north coast of Jamaica in June to August of 1991 (Fig. 1). A survey was conducted at OB in August by mapping and dividing the site into 176 contiguous 30.5 × 30.5 m quadrats (Fig. 2), counting all plants of *T. ulmifolia* encountered, and recording the presence/absence of *Passiflora* species in 20 randomly selected quadrats. A complete count of all of the available hostplants was made at the two small populations (MB & SR) in late-June and again in August. On the final visits to each site, the numbers and distributions of eggs and larvae found on *T. ulmifolia* were recorded (an exhaustive search was carried out at MB and SR and a random sample of 100 plants was examined at OB and at another large site 1 km east of OB). The distributions of eggs and larvae on plants was also recorded at MB and SR in June and December of 1992 and at an inland site, EW (near Ewarton, St. Catherine), in June 1991 and June 1992.

To determine the distribution of *E. hegesia* on the island of Jamaica, the presence of larvae and adults was recorded at more than forty *T. ulmifolia* populations from around the island that were systematically surveyed in June of 1990 and June to August of 1991. Additional data on presence of larvae in a number of plant populations were recorded in January of 1989 by JSS, and for adults and larvae in June and December of 1992 and June and December of 1995 by PJS.

Butterfly population and damage surveys. We conducted a mark-release-recapture (MRR) study of *E. hegesia*, using Bailey's Triple Catch design (Bailey 1952), in the large (OB) and both small (MB & SR) *T. ulmifolia* populations in June of 1991, with continued study in the large population through July and August of 1991 (see Fig. 1 for site maps). A transect slightly more than 1 km in length through representative habitat (6.5 ha, approx. 35% of the habitat) was followed at OB (Fig. 2). At MB, a relatively flat and wind-protected glade surrounded by trees, we traversed the length of the access road plus the foot path. At the SR site, we wandered haphazardly throughout the uneven terrain in the

area. The OB site, described as "raised coral beach" by Asprey and Loveless (1958), is bounded by the sea to the north and a cliff-face to the south with secondary forest bounding the east and west. A large plant population located 1 km east of OB and separated from the MRR site by second growth forest was monitored in August for butterflies marked at the OB site, to assess interpopulation movement over relatively short distances.

On the first three visits to each site (and each month at OB) all captures were carefully marked on the underside of the left hindwing using an indelible fine point marker to show the mark day and a unique individual number. A different marker color was used for each of the three mark occasions. For each initial capture we recorded sex, size (maximum length of forewing), a qualitative estimate of age (wear, as loss of scales, in 5 classes: very fresh, fresh, medium, worn, very worn), and wing damage recorded for each wing (left, right, fore, or hind), damage location (tip, outer margin, trailing edge), type (tear, notch, frayed), and whether damage was symmetrical (i.e., mirror image) or asymmetrical between adjacent wing pairs. As many butterflies as could be captured at each site were carefully netted. Capture effort was standardized by time: short visits of 1 h sufficed at MB & SR while 3.5–4 h were required to traverse the transect on each occasion at OB. Captures commenced at 0830 h at OB and SR and at 1300 h at MB. All marking, age estimation and categorization of damage was done by PJS.

Marking visits to the sites were spaced 2–3 days apart to minimize the effects of handling on butterflies and to ensure that marked butterflies mixed with the unmarked population (Morton 1982, Gall 1985, Mallet et al. 1987, Orive & Baughman 1989). Subsequent visits, 3–7 days apart, were made to obtain data on the lifespan of adult butterflies. Mark visits in 1991 were conducted on 7, 9, and 11 June at OB and MB and 8, 10 and 12 June at SR. A total of six visits was made to each site over 16 days. At OB, mark visits only were made on 6, 8 and 10 July while mark visits in August were conducted on 4, 7, 10 and 13 August with one subsequent visit on 21 August. A fourth mark occasion was necessary in August due to the interruption of the first visit by inclement weather. There were 29 days between the onset of marking in June and July and between July and August at OB, roughly corresponding to the generation time in captivity (see below). On subsequent visits, only the number of unmarked butterflies and the identity and number of recaptures was recorded. Change in condition and new damage sustained by previously undamaged butterflies was recorded for a subsample of individual recaptures ($n = 26$) made at OB in June.

The frequency and type of wing damage sustained by *E. hegesia* during this population study was compared to a previous collection of a series of 30 specimens and a subsequent collection of a series of 25 specimens, taken from the OB site in June of 1990 and June of 1995, respectively. At the latter time we also collected a short series of 12 specimens each of 2 species which co-occur at the OB site—the close relative *Agraulis vanillae* L. (Heliconiinae) and more distantly related *Anartia jatrophae* Möschler (Nymphalinae)—to assess whether *E. hegesia* is unusual in the frequency of wing damage. A series of 25 specimens of the sister taxon, *E. claudia*, taken below Cinchona Gardens in the Blue Mountains (approx. 1300 m) in August 1991 was also examined for frequency and type of damage. All of these species are of similar size and are remarkably alike in their adult behaviour.

Data analysis. Population and lifespan (i.e., residence time) estimates including estimates for subsets of the data by sex, as well as tests of MRR assumptions, including equal catchability, and absence of marking and handling effects, were calculated using the PC program CAPTABLE (Arndt & Arnold 1994). Since *a priori* evidence was not available, and because one of our objectives was to assess interpopulation movements, population estimates were calculated for both open and closed population models to avoid potential bias due to application of the incorrect model (open model: Bailey's Triple Catch, Bailey 1952—a special case of the Fisher-Ford model, Gall 1985; closed model: Lincoln-Peterson, Begon 1979). Lifespan estimates were calculated using Scott's Method I, based on Jolly-Seber population estimates, which provides a single minimum daily survival rate for the duration of each study at each site and month (Scott 1973).

Total damage scores were assigned by summing the presence of damage for each wing (minimum score = 0, maximum = 4). For subjects with damage, total symmetry was calculated similarly (minimum score = 0, maximum = 2). Statistical analyses including t-tests and analyses of variance (ANOVA) were conducted using SAS (1988) unless otherwise in-

licated. Homogeneity of variance assumptions were tested; where the assumptions failed, t-tests were performed using Satterthwaite's approximation (SAS 1988). Tests of independence and correlation analyses were conducted using Minitab (1994) Release 10. Where comparisons involved the ranked age data, Mann-Whitney or Kruskal-Wallis tests were used, and we used Spearman's rank correlation (r_s) to examine the relationship between age and size. Distributions of eggs and larvae on plants were tested against Poisson and negative binomial distributions following Ludwig and Reynolds (1988).

RESULTS

Life history of *E. hegesia* in captivity. Our laboratory rearing methods proved to be quite successful, as numerous butterfly progeny could be raised fairly readily. The major limiting factor in rearing is the number of host plants that can be grown to feed the larvae. Typical results of lab rearing, from June of 1990, are as follows: a total of 212 *E. hegesia* larvae and pupae, in varying numbers, were collected from 10 sites in Jamaica and brought back to our glasshouse facilities in Toronto; approximately 75% of the sample pupated and eclosed normally yielding 156 adults; in the first lab-reared generation we obtained 4189 eggs from 21 crosses (approximately 200 eggs/mating) yielding a total of approximately 3800 larvae. Captive populations are easily maintained.

It is intriguing to note that in the years 1990 through 1992 we collected and reared 136 wild-collected eggs and 973 wild larvae of all stages, with a number of pupations having occurred in the field prior to our return, and have never found a parasitoid. Larvae that died and eggs or pupae that failed to eclose were monitored for up to two weeks without encountering parasitoids. None of the more than 1375 eggs, larvae and pupae that we have collected in the wild over a six year period has yielded a parasitoid.

In captivity, the life history of *E. hegesia* encompasses approximately five days in the egg stage (mean \pm SD: 4.97 ± 0.38 days, $n = 907$ eggs), with the larvae progressing through five instars in 12–15 days (13.8 ± 1.5 days, $n = 112$), and the pupal period lasting 8–9 days (8.5 ± 0.8 days, $n = 112$). Eggs are laid singly, predominately on the underside of terminal leaves on *T. ulmifolia* (but not exclusively so), and average 0.183 ± 0.013 mg each ($n = 43$ groups containing a total of 3311 eggs). Full sib progeny show a 1:1 sex ratio with peak male eclosion occurring approximately two days before females and the number of days from egg hatch to eclosion being one day longer, on average, for females (Table 1). Female butterflies are immediately receptive to mating upon eclosion—time from eclosion to mating is significantly shorter for females (Table 1), however, oviposition has not been recorded on the day of eclosion. Overall, *E. hegesia* has a 28–30 day egg-to-egg cycle in captivity and may prove to be a useful species for genetic studies as a result of its short generation time and high fecundity.

TABLE 1. Sexually dimorphic characters in captive-reared and wild *E. hegesia* from Jamaica. A Kruskal-Wallis test was used for Field age class and the statistic shown is a chi-square approximation; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Character	Males			Females			t
	N	mean	(SD)	N	mean	(SD)	
Lab							
adult size (mass at eclosion, mg)	190	111.1	(38.9)	220	145.5	(49.1)	7.78 ***
mass at pupation (mg)	56	260.0	(26.0)	39	311.1	(27.2)	9.18 ***
total development time (days)	56	26.9	(1.4)	39	27.6	(1.2)	2.43 *
larval development time (days)	56	13.5	(1.4)	39	14.2	(1.3)	2.47 *
pupation period (days)	56	8.5	(0.5)	39	8.4	(0.6)	0.48
eclosion to mating time (days)	24	1.7	(1.5)	22	0.8	(1.0)	2.37 *
adult lifespan (days)	123	6.8	(4.0)	103	6.5	(3.2)	0.75
Field							
adult size (wing length, mm)	267	27.2	(1.2)	208	29.4	(1.5)	17.45 ***
age class (wing wear class)	272	2.50	(1.16)	211	2.52	(1.15)	0.09
total damage	272	0.54	(.92)	210	0.78	(1.04)	2.59 *
damage frequency	272	0.34	(.47)	210	0.46	(.50)	2.75 **
age at subsequent damage (days)	5	5.8	(1.6)	8	3.5	(.3)	3.00 *
total symmetrical damage	272	0.06	(.25)	210	0.12	(.34)	2.16 *
symmetrical damage frequency	91	0.17	(.37)	96	0.25	(.44)	1.43

TABLE 2. Survivorship and relative performance of captive-reared *E. hegesia* on the three most commonly used hostplants on Jamaica. Means with the same letter are not significantly different at $p < 0.05$, SNK test following one-way ANOVA.

Hostplant	Generation	N	Survival to			Mean mass (SE) at pupation (g)	Mean time (SE) to pupation
			3rd instar	pupation	eclosion		
<i>T. ulmifolia</i>	1	24	100	100	—	0.253 (0.009) ^a	11.8 (0.21) ^a
<i>P. suberosa</i>		24	96	42	—	0.281 (0.013) ^{ab}	16.3 (0.34) ^b
<i>P. foetida</i>		24	58	46	—	0.336 (0.016) ^b	15.0 (0.54) ^b
<i>T. ulmifolia</i>	2	24	100	100	75	0.264 (0.010) ^a	13.4 (0.25) ^a
<i>P. suberosa</i>		24	100	92	67	0.291 (0.008) ^{ab}	18.0 (0.50) ^b
<i>P. foetida</i>		24	83	79	54	0.306 (0.010) ^b	15.5 (0.34) ^c

There is considerable dimorphism between the sexes. Females are significantly larger than males both in nature (wing length; Table 1) and in captivity (fresh adult mass and pupal mass; Table 1). Size dimorphism may be related to the increased time required for larval development in females—females take significantly longer to develop from date of oviposition through to eclosure (total development time; Table 1), largely as a result of increased larval development time since pupation periods do not differ between the sexes (Table 1). Captive females lay an average of 27 eggs per day (27 ± 11.2 , $n = 14$ females over 4 consecutive days) and lifespan in captivity does not differ between sexes (Table 1).

Performance of larvae on hostplants. There is some ambiguity in the literature about whether *T. ulmifolia* or a species of *Passiflora* is the primary hostplant of *E. hegesia*. Turner has commented that “the larva takes the longer time to mature when fed on *Turnera*” (Brown & Heineman 1972:210). To address this issue we conducted experiments to assess the performance of larvae on the three most commonly used Jamaican hostplants: *T. ulmifolia*, *P. foetida* and *P. suberosa*. Larvae reared on *T. ulmifolia* had the highest survivorship and a significantly faster development time but had the lowest pupation mass (Table 2). Larvae had lower survivorship on both species of *Passiflora*. Larvae reared on *P. foetida* had an intermediate development time and highest pupation mass whereas those reared on *P. suberosa* had the longest development time and median pupation mass. Two consecutive generations exhibited identical patterns (Table 2). Interestingly, mortality of larvae on *P. foetida* was in early instars, possibly due to the extensive glandular trichomes of this species, whereas mortality of larvae on *P. suberosa* occurred in later instars. All larvae reared on *T. ulmifolia* survived to pupation. Eclosion success in the second generation was lowest for *P. foetida* and highest for *T. ulmifolia*. These data suggest that overall host plant suitability for Jamaican *E. hegesia* is *T. ulmifolia* > *P. suberosa* > *P. foetida*.

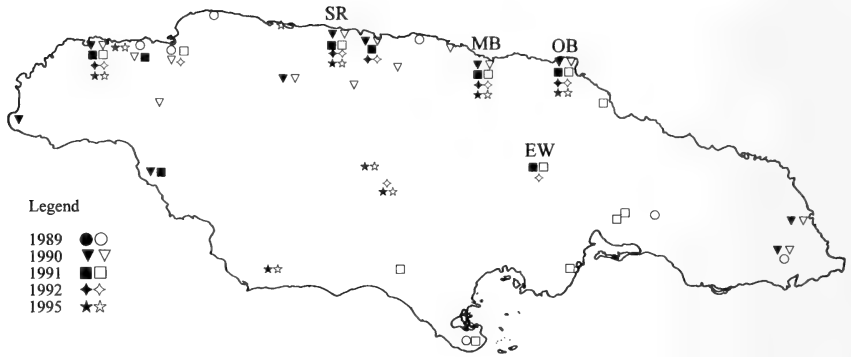


FIG. 3. Distribution of *E. hegesia* larvae and adults encountered on Jamaica from 1989 through 1995. Open symbols denote larvae, closed symbols adults. Study sites mentioned in the text are denoted by two-letter codes.

Distribution of *E. hegesia* on Jamaica. Larvae and adults of *E. hegesia* have been found at many *T. ulmifolia* populations; however, their abundances vary greatly. Our findings suggest that *E. hegesia* is more common in the largely acyanogenic hostplant populations on the north coast at least during the summer months (see Fig. 3, and Schappert & Shore 1995). Observations from the winter of 1989, 1992 and 1995 indicated the presence of larvae at highly cyanogenic southern populations more commonly than do all of our summer records.

Hostplant population size and distribution of larvae on hosts. The hostplant survey at OB (Fig. 2) yielded 311 *T. ulmifolia* plants in 11 (55%) of the 20 quadrats. Multiplying the 176 total quadrats by the mean number of *T. ulmifolia* in the surveyed quadrats (15.6, range: 0–82) yields an estimate of more than 2700 plants at this site. Four species of *Passiflora* were found in 7 quadrats (35%) but the percentage of quadrats occupied by the species varied (*P. suberosa*, 25%; *P. perfoliata* L., 20%; *P. rubra* L., 15%; *P. foetida*, 10%). *Turnera ulmifolia* and *Passiflora* spp. were commonly found in the same quadrat (Fig. 2). Repeated surveys of all available *T. ulmifolia* hostplants during 1991 and 1992 at the two small study sites revealed that the MB site fluctuated between 14 and 30 plants while SR varied from 18 to 47 plants. We did not find any species of *Passiflora* at either site.

The results of surveys for numbers of eggs and larvae on plants at the three main study sites (OB, MB & SR), the site immediately east of OB and a fifth site near Ewarton in the center of the island, conducted in 1991 and 1992, are presented in Table 3. The distribution of larvae on plants is non-random (8 of 11 larval distributions are significantly different from Poisson) and clumped (9 of 11 are not significantly different from negative binomial). A count of larvae on one of two large *P. foetida*

TABLE 3. Distribution of larvae of *E. hegesia* on *T. ulmifolia* and chi-square goodness of fit tests against random (Poisson) and clumped (negative binomial) distributions in five *T. ulmifolia* populations on Jamaica. 1992a = early June, 1992b = late June, 1992W = Dec. Asterisks indicate significant departure from listed distribution at $p < 0.05$.

Site	Year	Tot. no. plants	Tot. no. larvae	Number of plants with 0, 1, 2, ... larvae										Mean (SD) larvae per plant	Poisson χ^2 (df)	NegBinom χ^2 (df)			
				0	1	2	3	4	5	6	7	8	9				>9		
EW	1991	51	25	39	7	2	1	1	1	0	0	0	1	0	0	0	0.49 (1.24)	6.5 (1)*	0.2 (1)
	1992	38	50	21	7	2	3	2	0	1	1	1	1	0	1	0	1.32 (2.17)	20.9 (2)*	0.9 (1)
MB	1991	20	16	14	2	1	2	0	0	0	1	0	0	0	0	0	0.80 (1.58)	6.6 (1)*	0.6 (1)
	1992a	14	13	9	3	0	0	0	2	0	0	0	0	0	0	0	0.93 (1.77)	3.6 (1)	1.4 (1)
	1992b	16	22	11	3	0	0	0	0	1	0	0	0	0	1	0	1.38 (3.44)	16.2 (1)*	2.0 (1)
	1992W	30	21	18	6	3	3	0	0	0	0	0	0	0	0	0	0.70 (1.02)	2.9 (1)	0.4 (1)
OBW	1991	100	121	82	4	4	1	1	2	2	0	0	0	0	0	4	1.19 (4.79)	134.8 (2)*	1.0 (1)
OBE	1991	100	68	78	1	10	7	2	0	0	0	0	0	0	2	0	0.68 (1.59)	66.8 (2)*	15.4 (1)*
SR	1991	18	39	7	5	1	1	0	2	0	1	0	0	1	0	0	2.17 (3.22)	8.0 (1)*	1.4 (1)
	1992	47	69	25	9	2	4	0	1	4	1	1	0	0	0	0	1.47 (2.25)	30.2 (2)*	1.8 (1)
	1992W	24	54	11	0	3	4	0	4	0	0	0	0	2	0	0	2.25 (2.59)	2.8 (1)	5.7 (1)*

TABLE 4. Species and flower color of nectar sources used by *E. hegesia* on Jamaica.

Taxon	Flower color
Acanthaceae	
<i>Blechnum pyramidatum</i> (Lam.) Urb.	lilac/blue
Asclepiadaceae	
<i>Asclepias curassavica</i> L.	red/orange
Boraginaceae	
<i>Heliotropium indicum</i> L.	white
Compositae	
<i>Ageratum houstonianum</i> Mill.	blue
<i>Bidens pilosa</i> L.	white/yellow
<i>Bidens reptans</i> (L.) G. Don	yellow
<i>Borrchia arborescens</i> (L.) DC.	yellow
<i>Eupatorium odoratum</i> L.	pink/blue
<i>Spilanthes urens</i> Jacq.	white
<i>Wedelia trilobata</i> (L.) Hitchc.	yellow
Rubiaceae	
<i>Borreria laevis</i> (Lam.) Griseb.	white/pink
Sterculiaceae	
<i>Melochia tomentosa</i> L.	white/pink
Turneraceae	
<i>Turnera ulmifolia</i> L.	yellow
Verbenaceae	
<i>Lantana camera</i> L.	yellow/orange
<i>Stachytarpheta jamaicensis</i> (L.) Vahl	blue

plants at OB yielded four *E. hegesia* and eight *A. vanillae* larvae. Larvae were not seen on a number of other *P. suberosa* and *P. foetida* that were surveyed; however, *E. hegesia* females have been observed to oviposit on all of the species of *Passiflora* found at the OB site. The vast majority of the ovipositions we observed occurred on *T. ulmifolia*.

Butterfly behavior and population structure. Our observations of adult *E. hegesia* revealed very fast, straight-line flights from shortly after dawn until about 8 am. At about this time flight behavior changes remarkably and becomes characterized by relatively slow, wandering flights within 30–45 cm of the ground. Butterflies stop frequently to rest or to nectar at many low herbs and shrubs, which are also commonly used by other butterflies. The flowering species visited span several plant families that exhibit a wide range of flower color and morphology (Table 4). Flowers of *T. ulmifolia*, used by a variety of other nectaring butterflies, were not commonly used by *E. hegesia*. Resting behavior also changes during the day from open-wing “basking” early in the day to folded-wing stances later in the day. Males appear to spend more time in flight, presumably patrolling in search of mates, and they inter-

TABLE 5. Common butterfly species found in typical *T. ulmifolia*/*E. hegesia* habitat on Jamaica.

Papilionidae
<i>Battus polydamas</i> Rothschild & Jordan
<i>Papilio andraemon</i> Hübner
Pieridae
<i>Ascia monuste</i> Godart
<i>Eurema lisa</i> (Ménétriés)
Lycaenidae
<i>Strymon acis</i> (Comstock & Huntington)
<i>Hemiargus hanno</i> (Fabricius)
Nymphalidae
<i>Anartia jatrophae</i> Möschler
<i>Junonia evarete</i> Felder & Felder
<i>Danaus gilippus</i> (H. W. Bates)
<i>Phyciodes frisia</i> Poey
<i>Mestra dorcas</i> Fabricius
<i>Agraulis vanillae</i> L.
Hesperiidae
<i>Urbanus proteus</i> (L.)
<i>Polygonus leo</i> Evans
<i>Pyrgus oileus</i> (L.)

act frequently with other males, females and a variety of other butterfly species, most notably the similarly sized and coloured *Agraulis vanillae*. Other butterfly species common in the habitats in which *E. hegesia* and *T. ulmifolia* are found are listed in Table 5.

We netted a total of 730 individuals with 483 (66%) being marked during the first three visits to each of the three sites over the length of the study. Most of the captures (622) and 427 of the marked individuals (68%) were from the large hostplant population (OB). No marked butterflies were recaptured at the site 1 km east of OB. The proportion of marked butterflies recaptured on subsequent visits was generally high (range 10–23%, up to 11 days after the initial visit) and the maximum length of time elapsed between marking and last recapture for any particular individual (i.e., the minimum age of those individuals) was 14 days. Population size estimates, whether from closed (Lincoln-Peterson) or open (Bailey's Triple Catch) population models, were very similar. Table 6 provides estimates of the total population sizes derived using the two methods as well as separate estimates of the numbers of males and females at MB and for the months of June and August at OB. Observed sex ratios, daily survival rates, expected residence times (i.e., estimated lifespan), and maximum observed lifespans are also presented in Table 6.

Tests of the assumptions made in MRR studies—including lack of marking effects, equal catchability of sexes, independence of recapture

TABLE 6. Population size estimates (second visit), observed sex ratio, survival rates and expected lifespan (residency) and maximum observed lifespan of *E. hegesta* at three sites on Jamaica. BTC = Bailey's Triple Catch, L-P = Lincoln-Peterson, Expected lifespan calculated using Scott's Method I (Scott 1973).

Site	Month	Captures included	Estimation Method				Observed sex ratio (% males)	BTC survival \bar{s} (SE)	Expected lifespan (residence time)	Maximum observed lifespan
			BTC	L-P	N	(SE)				
OB	June	all	233	(75)	282	(82)	0.81	(0.21)	5.6	14
		males	131	(57)	176	(72)	0.73	(0.26)	7.2	14
	July August	females	78	(36)	88	(40)	0.86	(0.32)	2.4	9
		all	474	(346)	247	(101)	0.17		2.1	5
		all	540	(596)	517	(164)	0.78	(0.71)	3.9	12
		males	343		315	(157)	0.56	(0.77)	5.8	12
females	121	(183)	178	(80)	0.76	(1.10)	10.6	7		
MB	June	all	22.5	(11.7)	24.3	(9.2)	1.29	(0.45)	8.5	12
		males	14.5	(7.6)	15.0	(6.2)	1.24	(0.29)	7.1	12
	females	12.0	(13.4)	7.0	(9.3)	0.81		11.7	12	
SR	June	all	12.5		25.7	(12.8)	0.46		3.6	9

from previous capture, and assumptions of constant survival or residency (Begon 1979, Tabashnik 1980, Gall 1985, Arndt & Arnold 1994)—revealed that there was no increase in mortality due to marking and no dependence of the probability of recapture based on previous capture (all marks had equal probability of recapture) for all sites and all months at OB. There was also no significant difference between male and female catchability for the three sites or the three months at OB. Females were significantly more likely to die or emigrate from OB in June ($F_{1,3} = 12.1$, $p < 0.05$, M:F ratio = 1.234) but there was no significant difference in joint residency in July or August or at the small sites. This finding is supported by the low residence time (expected lifespan) for females in June at OB in comparison to males (see Table 6). There is an overall sex ratio bias towards males at all sites for all months, a common finding in MRR studies of butterflies (Gall 1985); however, the proportion of recaptures to captures did not differ between sexes (as expected from results of the equal catchability tests).

Females were significantly larger than males over all sites (Table 1) with the smallest butterflies found at MB ($F_{2,472} = 6.98$, $p < 0.001$, MB = SR & SR = OB, SNK multiple comparisons test). Sexes did not differ in median age (based on wing wear scores, Kruskal-Wallis test, see Table 1); however, a marginal but non-significant difference was found between sites ($F_{2,480} = 2.60$, $p > 0.10$). Older butterflies (i.e., worn and very worn classes) were, on average, significantly smaller than younger butterflies ($F_{4,470} = 4.10$, $p < 0.01$). This variation was more pronounced in males ($F_{4,267} = 5.37$, $p < 0.001$) than in females ($F_{4,208} = 2.51$, $p < 0.05$). The frequency of butterflies in the five age classes at the OB population was similar for all three months (Fig. 4). More than 82% of the butterflies were, on average, less than medium worn (middle-aged). The SR site had proportionately more very fresh (VF) individuals, with greater than 90% of all butterflies being less than medium worn. The MB site had fewer medium worn and a greater percentage of very worn (VW) individuals with only 70% of butterflies less than medium worn (Fig. 4).

Wing damage sustained by butterflies. Thirty-eight percent of all captures exhibited some wing damage at their initial capture and the sex ratio of captures with damage approached unity (0.95 males to each female) despite the overall male-biased sex ratio of all captures (1.3 males to each female). Females were damaged more frequently (46% of females vs. 33% of males, $\chi^2 = 3.84$, $p = 0.05$) and sustained significantly more total damage than males (Table 1) but differences were not significant between sites, and no significant differences were found between months at OB, for either sex. Damaged individuals were consistently assigned to older age-classes, based upon wing wear. A positive correlation

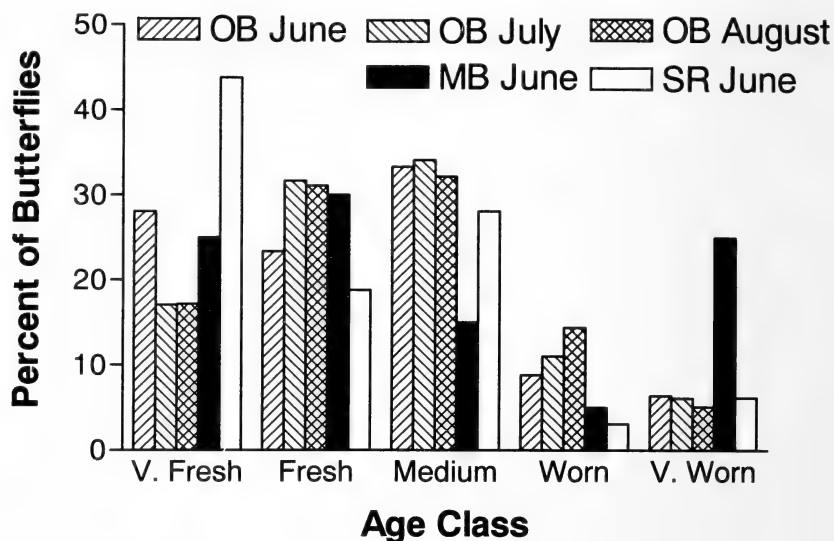


FIG. 4. Comparison of butterfly age structure at one large (OB) and two small (MB & SR) *T. ulmifolia*/*E. hegestia* populations on Jamaica.

between total damage and age explains 36% of the variation ($r_s = 0.63$, $p < 0.001$). Males that were not damaged at their initial capture attained a significantly greater maximum age than those that were damaged at first capture ($F_{1, 270} = 5.30$, $p < 0.05$) and previously undamaged males were recaptured more often than those that were damaged at their initial capture ($F_{1, 270} = 7.37$, $p < 0.01$); however, neither of these was true for females.

Comparison of the frequency, location and type of damage (forewing tip and margin, forewing notch, hindwing margin, hindwing notch) in symmetrical and asymmetrical classes against the capture sex ratio revealed no significant association for any combination except for a significant deviation in the frequency of asymmetric hindwing notches ($\chi^2 = 7.3$, $p < 0.01$, with females receiving disproportionately greater damage). Females had a greater frequency of symmetrical damage (28 vs. 13 males), which is significantly different from the capture sex ratio ($\chi^2 = 9.1$, $p < 0.01$) but not from an expectation of an equal sex ratio. New damage was recorded on second captures for 5 males and 8 females of 26 individuals examined. Comparison of the age (i.e., wing wear) at recapture revealed that females were significantly younger when damage occurred (Table 1).

The 38% of all initial captures from the MRR study, over all months and sites, that exhibited some damage is remarkably similar to the proportion of damaged specimens collected in 1990 and for the three spe-

TABLE 7. Sex ratio and damage frequency in four species of Jamaican butterflies. *E. hegesia*, *A. vanillae* and *A. jatrophae* are sympatric in lowland coastal habitats while *E. claudia* occurs in the Blue Mountains above 1220 m.

Species	Year	Total no. of captures	Damage freq. (% of captures)	Sex ratio (% males)	Damage freq. (% males)
<i>E. hegesia</i>	1990	30	33	63	70
	1991	483	38	55–82	48
	1995	25	32	64	63
<i>A. vanillae</i>	1995	12	42	67	75
<i>A. jatrophae</i>	1995	12	33	83	100
<i>E. claudia</i>	1991	25	12	52	100

cies taken at the OB site in June of 1995 (Table 7). One of the 1990 *E. hegesia* specimens shows evidence (asymmetric hindwing damage) of an attack by a bird (see Fig. 5), one had symmetrical hindwing damage, and six specimens had asymmetrical hindwing damage. One of the 8 damaged *E. hegesia* in the 1995 sample showed evidence of symmetrical hindwing damage (see Fig. 5), one had only forewing damage whereas the remaining six had asymmetrical damage to the hindwings. All of the *Anartia jatrophae* that were damaged had asymmetrical hindwing damage whereas only one half of the damaged *Agraulis vanillae* showed hindwing damage. In comparison, damaged individuals were very infrequent (Table 7) in the sample of *E. claudia* taken in the Blue Mountains in August of 1991 and none of the 3 damaged specimens had hindwing damage.

DISCUSSION

Most studies of the population structure and dynamics of tropical insects have concentrated on rainforest species (Young 1982). The majority of studies on tropical Lepidoptera have been on long-lived or forest inhabitants (Table 8) where hostplant availability (larval or adult resources) and predation (most often by birds) are important as primary and secondary factors determining butterfly population size (Young 1982, Ehrlich 1984, Courtney 1986, Bowers et al. 1987, Quintero 1988, Gilbert 1984, 1991). Few studies of tropical butterflies have been conducted on species that occupy non-forest habitats exclusively—only 5 of the 23 studies (7 of 42 species) in Table 8—or have been conducted on the potential predation pressure exerted by vertebrates other than birds (Boyden 1976, Ehrlich & Ehrlich 1982, Odendaal et al. 1987, Larsen 1992, Sikes & Ivie 1995). Only recently have attempts been made to quantify the selective pressure of aerial and ground-based predators on butterfly ecology and evolution (Robbins 1980, Silberglied et al. 1980, Bowers et al. 1985, 1987, Wourms & Wasserman 1985, Chai 1988, Chai & Srygley 1990, Srygley & Chai 1990, Owen & Smith 1990, Tonner et

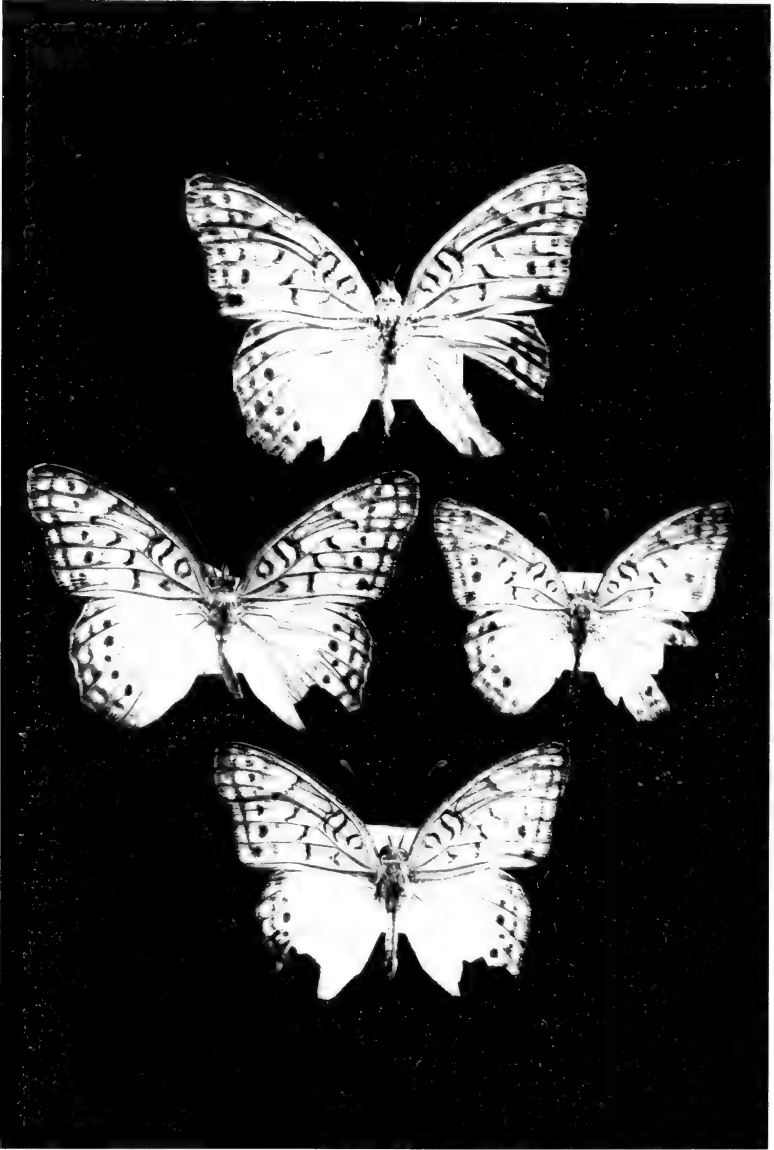


FIG. 5. Types of wing damage sustained by *E. hegesia* that may be attributable to predation. Top: female collected in 1990 with asymmetric hindwing notch thought to be the result of an attack by a bird. Middle: female (left) and male (right) collected in 1995 with asymmetric hindwing damage consistent with an attack by an *Anolis* lizard. Bottom: female collected in 1995 with symmetrical hindwing damage likely due to a single attack by an *Anolis* lizard when the butterflies wings were closed.

TABLE 8. A summary of studies of population structure and dynamics of tropical butterflies. L-P = Lincoln-Peterson, F-F = Fisher-Ford, M-P = Manly-Par, J-S = Jolly-Seber, BTC = Bailey's Triple Catch, sample/census = actual count.

Taxon	Location	Habitat/ area surveyed	Study type	Study duration (days)	Season	Population estimator used	Population size	Sex ratio (% male)	Residence time (days)	Survival rate	Reference
Papilionidae											
<i>Parides</i>											
<i>anchises</i>											
<i>neophilus</i>	Trinidad	scrub	MRR	41		F-F	6-54		6	0.35-0.76 0.76-0.83	Cook et al. 1971
<i>Parides</i>											
<i>pronotus</i>											
<i>bunichus</i>	Brazil	dry forest	MRR	305+	wet/dry	census	756 458 115 90 13	90 106 90 71 275	12 max. 35		Brown et al. 1981
<i>agatrus</i>											
<i>anchises</i>											
<i>neophilus</i>											
<i>Battus</i>											
<i>polydamas</i>							292	72			
Pieridae											
<i>Eurema</i>											
<i>daira</i>	Costa Rica	pasture	MRR	11, 12 42, 111	wet dry	J-S	7-9 25-78	0.60 0.91			Opler 1988
Nymphalidae											
<i>Marpesia</i>											
<i>berania</i>	Costa Rica	wet forest	roost census	180	wet	census	18-68	53	80	0.987	Benson & Emmel 1973
<i>Anartia</i>											
<i>fatima</i>	Costa Rica	fields	MRR/ census	1-7	dry wet	sample sample	36-80 14-539				Emmel 1972
<i>Anartia</i>											
<i>amalthaea</i>	Ecuador	rainforest clearing	MRR	7		L-P/ BTC	78-276	27	7		Fosdick 1973
<i>Hypolimnas</i>											
<i>missippus</i>	Ghana	clearing	MRR	47-92	wet	F-F	60-650	56-86	max. 6.5	0.65	Edmunds 1969

TABLE 8. Continued.

Taxon	Location	Habitat/ area surveyed	Study type	Study duration (days)	Season	Population estimator used	Population size	Sex ratio (% male)	Residence time (days)	Survival rate	Reference
<i>Euptoieta hegesia</i>	Jamaica	coastal scrub	MRR	76	dry	L-P/ BTC	20-400	45-122	6.5-10 max. 14	0.72-0.84	this study
<i>Bematisthes epaea</i>							629	119			
<i>macaria</i>							397	311			
<i>alcinoe</i>	Sierra Leone	wet forest	census	45		census	238	170			Owen 1974
<i>vestalis</i>							26	383			
<i>Pseudacraea eurytus</i>							214	30			
<i>Acraea enceidon</i>	Uganda	savanna	MRR	335	all	L-P	10-1000	2-72	max. 16 (F) to 41 (M)		Owen & Chanter 1969
<i>Acraea enceidon</i>	Ghana		MRR?	730	all	sample	0-160	42			Gordon 1984
<i>Heliconius charitonius</i>	Costa Rica	wet forest	MRR	155	wet/dry	F-F/ J-S/M-P	7-139	48-76	27-42 max. 107	0.88	Cook et al. 1976
<i>Heliconius charitonius</i>	Puerto Rico	wet forest	MRR	300	wet	J-S	146-351	76	26 max. 70		Quintero 1988
<i>Heliconius ethilla</i>	Trinidad	wet forest	MRR	500	wet/dry	M-P	156	59-74	50 max. 162	0.982	Ehrlich & Gilbert 1973
<i>Heliconius erato</i>	Trinidad	coastal scrub	MRR	74	dry/wet	F-F			50 max. 74	0.985	Turner 1971
<i>Placidula euryanassa</i>	Brazil	rainforest	MRR	670	all	J-S	40-1000	42-73	7.5-8.5 max. 43		Freitas 1993

TABLE 8. Continued.

Taxon	Location	Habitat/ area surveyed	Study type	Study duration (days)	Season	Population estimator used	Population size	Sex ratio (% male)	Residence time (days)	Survival rate	Reference
<i>Morpho peleides</i>	Panama?	rainforest	MRR	11	dry	F-F / J-S / M-P	55-105	>50	0.94		Young 1982
<i>Stichopthalma louisa</i>	Burma	rainforest	MRR	32	wet	sample	150-300				Tonner et al. 1993
Satyridae											
<i>Pierella luna</i>	Panama	wet forest	census	146	dry/wet	census	1-7				Aiello 1992
<i>Euptychia hermes</i>	Costa Rica	clearing	MRR	4/5		L-P	140/184	94/70			Emmel 1970
<i>Cissia</i>											
<i>terrestris</i>							1-9				
<i>myncea</i>							2-42				
<i>libye</i>							1-7				
<i>penelope</i>							2-56				
<i>hestione</i>	Trinidad	overgrown plantations	transect	variable	wet/dry	census	1-35				Singer & Ehrlich 1981
<i>renata</i>							2-27				
<i>hermes</i>							7-196				
<i>arnaca</i>							1-21				
<i>junia</i>							5-26				
Danaidae											
<i>Euploea core</i>	Australia	dry forest	MRR	37	winter	L-P	1200-1600	108	10 max. 87	0.90	Kitching & Zahucki 1981
<i>Anaërus nitatus</i>	Sierra Leone	wet forest	census	45		census	63	81			Owen 1974
Riodinidae											
<i>Menander felsina</i>	Brazil	coastal scrub	MRR	120		F-F	20		13 max. 35	0.91	Callaghan 1978

al. 1993). Here we have explored the ecology of a tropical butterfly that occupies open habitats.

Our population size estimates for *E. hegesia* over the three months at OB (approx. 200–400 individuals, Table 6) and the large number of available hosts, both *T. ulmifolia* and *Passiflora* spp., at this site suggests that relatively few plants are being used to sustain the butterfly population. Further, the clumped distribution of larvae on the primary host, *T. ulmifolia* (Table 3), suggests that some hostplants are preferred over others. The hostplants at the two small study sites (MB and SR) are more extensively used, in terms of both adult and larval population sizes, however, larval distribution at these sites is similarly non-random and clumped.

The use of single *T. ulmifolia* plants by three or more larvae, a common finding (see Table 3), is surprising considering that three larvae are capable of defoliating average size plants (Fig. 6). Plants of *T. ulmifolia* most often occur in small aggregations (likely due to limitations imposed on seed dispersal by ants; Barrett 1978), which may allow larvae to find other hosts when necessary; however, plants near to heavily preferred plants are often vacant suggesting that they are for some reason less suitable. For example, a small aggregation of six plants at OB in August contained 0, 6, 12, 12, 14 and an astounding 42 larvae per plant (Table 3) where there were no other potential hosts within 30 m in any direction. It is possible that the clumped distribution of larvae on hostplants coupled with their aposematism (and potential chemical defense based upon sequestration of cyanogenic glycosides) may afford increased protection from predation. Further, the phenotypic similarity between larvae of *E. hegesia* and *A. vanillae* and their sympatric distribution could indicate the operation of larval mimicry (Berenbaum 1995).

The high proportion of recaptures made on subsequent visits to the study sites suggests that individual *E. hegesia* are residents of specific *T. ulmifolia* populations and this appears to be the case for both large and small plant populations. Further support is provided by the lack of recaptures at the plant population just 1 km to the east of the OB site (especially given that inter-plant population movement was looked for in August when the size of the butterfly population appeared to be elevated; Table 6), and by comparison of lifespan estimates (i.e., residence time) with results of captive rearing, which suggest that average residence times span the entire life of individual butterflies. The cyanogenic status and level of intrapopulation variation of these three plant populations is relatively low (Schappert & Shore 1995) and the significance of this finding is that butterfly populations may be limited in their ability to exploit differences in the frequency of cyanogenic plants by "choosing" adjacent plant populations. The highly non-random distribution of larvae on plants also suggests that only relatively few plants in each popu-



FIG. 6. Defoliation of *T. ulmifolia* by three larvae of *E. hegesia* at Duanvale, Jamaica in 1990. Arrows show location of the larvae. Note that all that remains of the leaves are the midribs.

lation are preferred. That is, butterflies exploit differences in host quality within plant populations; however, it is not known what the basis of this choice is. Whether varying levels of cyanogenesis are responsible for this pattern is currently under investigation.

Of the population studies listed in Table 8, the most similar to our studies are those on *Anartia fatima* Godart (Nymphalidae). *Anartia fatima* has a 28–31 day life cycle, a 7–14 day average lifespan in the field (with up to 5 weeks between captures being recorded) and inhabits clearings or open areas away from the forest (Emmel & Leck 1970, Emmel 1972, Young 1972, Aiello 1992, Silberglied et al. 1980). In comparison, our study has shown that *E. hegesia* has a 28–30 day life cycle, a 7–10 day lifespan (with up to 4 weeks recorded in captivity) and similarly inhabits coastal scrub and pasture habitats away from forests. The study by Bowers et al. (1987) of predation on *A. fatima* shows that most predation, likely by birds, occurs while butterflies are at rest and the frequency of damage, interpreted to be the result of predator attack, suggested that the predation rate on adults approached 12%. They reported that males were more likely to show predator damage. Young (1972) reports that mortality in this species is high beyond early adult age classes. Although we have not directly assessed predation rate, we note that 38% of the captures in our population study, and a minimum of 32% of captures of three species of butterflies from this habitat, had sustained damage before their initial capture.

Wing damage frequencies reflect the rate of successful escapes from predators and may not reflect the actual rate of predation (Robbins 1980, Bowers et al. 1985, Owen & Smith 1990). Only if predators are 50% successful will damage or injury rates equal the predation rate. If predators are less successful or if other sources of injury are present then damage frequencies will overestimate the predation rate. Direct assessment of predator efficiency is difficult; however, Schoener (1979) proposed a method for determining predation intensity (or rate) from survival rate and injury frequency. When applied to our data (using the mean of the estimated daily survival rates; 0.632 for males and 0.612 for females) Schoener's method supports our findings that females are under greater predation intensity ($i = 0.68$ for males, $i = 0.91$ for females) and that they are damaged at almost twice the male rate (instantaneous injury rate, $v = 0.22$ for males, $v = 0.42$ for females).

The results of our studies of *E. hegesia* show that: (1) there is pronounced female-biased size dimorphism; (2) butterflies that are smaller attain a significantly greater age; and (3) in contrast to *A. fatima*, females sustain more damage that may be attributable to predators. Together this suggests that females are being removed from the population by predators. Our finding that older age classes consist of significantly smaller

butterflies suggests that selection against large butterflies, likely females, may be occurring. Our finding that females sustain significantly more total damage than males is intriguing. One possible explanation for this is that differences in the habitat where activity occurs (i.e., among vegetation for females and free-flying for males) or the type of activity (i.e., resting vs. flight) influences damage rates. For example, Moore (1987) found that mate location behavior and the activity schedule of male *Euphydryas editha* Boisduval influenced a significant bias towards male mortality for butterflies found in spider webs. Examination of the type of damage found in this study; however, shows that damage to the forewing tips and margins (which would be most expected to occur in the preceding situations) is not associated with sex. In any event, it is unlikely that symmetrical damage to adjacent wing pairs is the result of gradual wear or thrashing around in vegetation (Robbins 1980, Orive & Baughman 1989).

The lack of difference in wear (i.e., age) between sexes in this study indicates that age or "experience" is also not likely to be responsible for sex ratio biases. A capture bias towards adult males is common in butterfly population studies, and the suggestion has been that males are encountered more often and caught more easily because they are more active than females (Gall 1985). For less active females, a second explanation for female-biased damage is that damage is not related to the rate of active encounters with potential predators but to inactive encounters with ground-based predators. Ground-based predators such as *Anolis* spp. lizards may be more important to this species or, more likely, as predators in this type of habitat.

Anolis lizards commonly feed on lepidopteran larvae and adults and these often form the bulk of their diet. Floyd & Jenssen (1983) report that Lepidoptera larvae and adults account for 42% of the volume of prey found in the stomach contents—an average of three larvae or adults per anole—of *A. opalinus* Gosse on Jamaica, while Roughgarden (1995) reports that more than 36% of the volume of prey taken by *A. bimaculatus* Sparrman on St. Eustatius consisted of Lepidoptera larvae and adults. Jamaica has seven species of *Anolis* and one species of *Ameiva* and at least half of these are reported to take Lepidoptera larvae and adults as prey (Williams 1983, Schwartz & Henderson 1991). One of the species found on Jamaica, *Anolis sagrei* Duméril & Bibron, is known to take prey much larger than its body size would suggest (Schoener & Schoener 1980, Schwartz & Henderson 1991) and *A. limifrons* Cope is known to select prey larger than the most commonly available (Sexton et al. 1972).

That anoles are capable of controlling arthropod abundance has been reported by Pacala and Roughgarden (1984) and shown experimentally

by Schoener and Spiller (1987). Exclusion of anoles yielded a 2–3 fold increase in insect abundance and a 20–30 fold increase in the abundance of web-building spiders on St. Eustatius (Pacala & Roughgarden 1984). Interestingly, web-building spiders are themselves predators of butterflies (pers. obs., Moore 1987). Removal of *A. sagrei*, *A. carolinensis* Voigt and *Ameiva festiva* Richtenstien & von Martens from experimental plots in the Bahamas resulted in spider—and spider prey—densities 2–3 times higher than that found in control plots (Schoener & Spiller 1987). Roughgarden (1995) suggests that anoles fill the niche of ground-feeding birds that are absent from the Caribbean islands, and notes that anoles often attain very high densities. Schoener and Schoener (1980) reported densities of *A. sagrei* in the Bahamas approaching 1 per m². Four of the seven species of *Anolis* known from Jamaica occur at OB and if their combined density is 1 anole per m² then some 200,000 anoles may be present at this site.

A few studies have documented the potential importance of lizards as predators of butterflies (Boyden 1976, Ehrlich & Ehrlich 1982, Odenaal et al. 1987, Owen & Smith 1990, Larsen 1992). From our experience with *Anolis lineatopus* Gray preying on captive females in an oviposition enclosure, and experimental presentations of larvae to this species, at Discovery Bay, St. Ann, we would suggest that lizards may be important predators in this system. Despite extensive time in the field we have not seen birds preying on this species, although one specimen of a series of 30 adults taken at OB in June 1990 shows an obvious beak mark (a triangular notch) on the right hindwing (see Fig. 5). Predation by birds is well documented for this and many other species (Bowers et al. 1985, Wourms & Wasserman 1985, Chai & Srygley 1990). Two common species of insectivorous birds occur at OB: the Loggerhead Kingbird, *Tyrannus caudifasciatus* (D'Orbigny) and Northern Mockingbird, *Mimus polyglottos* L.

A variety of other predators are expected, or have been reported, to attack *E. hegesia*. Alonso-Meija and Marquez (1994) report dragonflies preying on various species of butterflies in Costa Rica including *E. hegesia*. Chai and Srygley (1990) reported that 8 of 10 *E. hegesia* offered to a captive bird were attacked and consumed. Interestingly, neither Hallman (1979) nor our studies have found parasitoids in larvae or pupae although Hallman noted their presence in more than 60% of eggs from Colombia. The absence of parasitoids in this species is remarkable; however, our estimate of mortality rate in Jamaican *E. hegesia* is extraordinarily high. Given that the actual sex ratio is 1:1 and that females lay, on average, 27 eggs per day, then 200 females at OB could produce 5400 eggs per day and a stable female population will produce about 37,800 eggs each week. Further, given that the average lifespan in captivity is

about 7 days (and estimates of residence time from this study agree with this figure), and assuming a stable adult population of approximately 400 butterflies, then about 37,400 eggs, larvae, and pupae do not survive to become adults. This suggests that mortality of these stages approaches 99% or more.

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BUTTERFLIES OF THE STATE OF COLIMA, MEXICO

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ABSTRACT. A survey of the butterflies of Colima, Mexico is presented, in which 543 species from 280 genera and 22 subfamilies of Papilionoidea and Hesperioidea are listed. Over 100 species are reported from Colima for the first time. This list was created by reviewing the past Lepidoptera literature, the major collections in the United States and Mexico with Mexican material, as well as by fieldwork at 10 sites carried out by the authors. For each species, capture localities, adult flight dates, and references for the data are provided. An analysis of our knowledge of Colima's butterfly fauna is presented, and comparisons with equivalent faunal works on Jalisco and Michoacán are made. About 78% of the species known from Colima are also known from Michoacán, while about 88% of the species reported from Colima are also known from Jalisco. There are 31 species that have been reported from Colima but not from Michoacán or Jalisco, and for most of these, we have no explanation for such an exclusive distribution, except the need for more fieldwork in all three states. Only one species, *Zobera albopunctata*, appears to be endemic to Colima.

Additional key words: biogeography, conservation, distribution, Hesperioidea, Papilionoidea.

RESUMEN. Se integró la lista de los Rhopalocera del estado de Colima, México, que consta de 543 especies, pertenecientes a 280 géneros, 22 subfamilias y cinco familias. Se mencionan mas de 100 nuevos registros para Colima. Esta lista se formó a partir de la revisión detallada de la literatura publicada sobre Lepidoptera y de las principales colecciones de los Estados Unidos y México con ejemplares de México, así como del trabajo de campo efectuado por los autores en diez sitios en el estado. Para cada especie se presentan las localidades de ocurrencia, los meses y la colección donde están depositados los ejemplares o la cita bibliográfica de la cual fue tomado el dato. Se presenta un análisis sobre el conocimiento de los papilionoideos del estado de Colima y se compara con trabajos equivalentes en los estados de Jalisco y Michoacán; se advirtió que el 78% de las especies que se conocen para Colima también se encuentran en Michoacán y el 88% en el estado de Jalisco. Se determinó que existen 31 especies exclusivas a Colima, aunque para algunas de ellas no tenemos explicación por tal exclusividad, excepto la necesidad de más trabajo de campo formal en los tres estados. Una especie parece ser endémica a Colima, *Zobera albopunctata*.

Palabras clave adicionales: biogeografía, conservación, distribución, Hesperioidea, Papilionoidea.

In order to improve our knowledge of the distribution and diversity of the butterfly species of Mexico's Pacific coast, lists of the butterflies of the state of Jalisco were recently published (Llorente et al. 1995, Vargas et al. 1996, Warren et al. 1996). To further our objective, we present an equivalent list of the butterflies of the state of Colima, and compare our

results with the Jalisco list and a preliminary list of the species known from Michoacán being prepared by the authors, in order to analyze overall distributions of butterflies in this western Mexican region.

ANTECEDENTS

There has been little research on the butterflies of the state of Colima. There are no regional lists of butterflies from any locality in Colima in the literature, and there are no published reports of extensive exploratory fieldwork in the state. The data on Colima butterflies in the literature is in the form of scattered records, which have never represented the true diversity of butterflies present in the state. The first published records of butterflies from Colima are in the *Biologia Centrali Americana* by Godman and Salvin (1878–1901). The *Biologia* gives distributional records for most species treated, citing localities, and in some cases, elevation, vegetation, and other ecological conditions where the species were found. Only 14 species were cited in the *Biologia* from the state of Colima, from only two localities: Colima (city) and Manzanillo. The comprehensive work by Seitz (1924), which treated all the known butterfly species of the Americas, made explicit mention of only one species from the state of Colima: *Papilio eracon* Godman & Salvin (listed herein as *Battus eracon*). In 1940–1941, Carlos Christian Hoffmann, in his *Catálogo Sistemático y Zoogeográfico de los Lepidópteros Mexicanos*, listed 1240 species of butterflies from Mexico, of which 105 species were reported from the state of Colima, although no localities in Colima were listed for any species.

In the Lepidoptera literature we have identified over forty works that cite distributional records from Colima, and these are listed below under Materials and Methods. The studies by Vázquez (1957, 1958) and Brown (1990) include descriptions of new taxa from the Revillagigedo Islands, which are part of the state of Colima. The most recent publication for our purposes is *Mariposas Mexicanas* by De la Maza (1987), which cites 58 species of butterflies from ten localities in the state of Colima, including: Armería, Colima, Comala, El Jabalí, La Salada, Madrid, Manzanillo, San Antonio, Suchitlán, and Tecomán.

During this century, some of the principal collections of Mexican butterflies, including those made by Hoffmann and Escalante were sold to museums in the United States. Additionally, the majority of foreign collectors deposit their material in collections in the United States. We have recorded data from the majority of the Mexican specimens deposited in foreign collections, and have formed a computerized database with the information. Table 1 lists some of the foreign museums that house specimens from Colima. For example, the San Diego Natural History Museum contains more than 1700 specimens from over 20 lo-

TABLE 1. Eight collections in the United States and Europe with material from the state of Colima, including numbers of species and specimens, as well as names of collectors and localities represented in each collection. Collection abbreviations are listed in the Materials and Methods section. Single asterisk = all butterfly families except Hesperidae included in numbers; double asterisks = numbers refer to Hesperidae only.

Collection	No. Specimens	No. Species	Localities	Collectors
AME*	169	64	La Salada, Colima, Comala, Manzanillo	R. Wind
AMNH	964	282	Colima, La Salada, Manzanillo	C. Hoffmann, R. Wind, P. Hubbell
CAS	15	11	Ameria Bridge	
CMNH	446	130	Comala, Colima	R. Wind
LACM*	176	54	Isla Clarion, Isla Socorro, Manzanillo	Y. Dawson, J. A. Comstock
SDNHM	1733	186	Colima, Madrid, La Salada, Tamala, Queseria, Pueblo Juarez	R. Spade
USNM	266	40	Colima, Manzanillo	S. S. Nicolay
BMNH**	41	19	Colima	Draudt collection

calities, taken by Paul Spade, who collected for five years (1980–1984) in the state of Colima.

During the 1970s and part of the 1980s, Sergio Hernández Tobías, a resident of the city of Colima accumulated a collection of butterflies from the state, which was well preserved for several years, but was greatly reduced in the late 1980's due to a lack of maintenance. In 1990, his family donated a portion of the remaining collection to the "Alfonso L. Herrera" Zoology Museum at U.N.A.M.'s Facultad de Ciencias (MZFC), which contained about 300 specimens of 166 species. Some material from the original collection remains under the custody of Hernández' family (mostly various Theclinae), and was not examined during this study.

For the past five years, as part of a study on the distribution of the butterflies of Mexico's Pacific coast, the MZFC has been carrying out a faunal inventory of the Sierra de Manantlán (Jalisco-Colima). During this study, two localities in Colima were studied intensively (Agua Dulce, Mpio. Villa de Álvarez; Platanarillos, Mpio. Minatitlán), which has resulted in the collection of about 2800 specimens of 216 and 241 species, respectively. Additionally, during 1995–1996, six localities surrounding Manzanillo were studied. At four of the localities, we recorded more than one hundred species in a day, with three to four researchers in the field daily. The diversity of species found at these localities demonstrates that previous collecting efforts in Colima have been very incomplete, since in this list we record 50 localities (48% of all the localities) from which only one or two species are known.

STUDY AREA

The state of Colima is situated in the southwestern part of the Mexican Republic, between the parallels of 19°31'N and 18°41'N, and 103°29'W and 104°35'W. Colima occupies 5191 km², and represents only 0.3% of Mexico's total surface area. The highest elevations in the state are the Volcán de Colima, at 3820 m, the Sierra de Manantlán at 2420 m, and Cerro Grande at 2200 m. Geologically, Colima consists of the Neovolcanic Chain (18%), and the Sierra Madre del Sur (82%). The climate in Colima is mostly hot and humid, except in mountainous areas above 1000 m.

The Inventario Nacional Forestal de Gran Visión (SARH 1992) records seven types of vegetational life-zones in Colima, with tropical semi-deciduous forest occupying one-third of the land area (31%). Tropical deciduous forest and thorn forest combined make up an additional 11% of the area. About 36% of the land surface has been altered for agricultural use. The flora of the state is well studied, with 7500 species recorded and an endemism rate of only 1%. The fauna of the state is not as well known. The state has four protected areas (Flores & Gerez 1994).

MATERIALS AND METHODS

Literature and collections. This list was compiled by consulting the computerized database at the MZFC, which includes the data from all the Mexican butterfly specimens examined in foreign and Mexican museums and collections, as well as data from the past Lepidoptera literature. Sources for Colima butterfly records, and sources relating to the nomenclature used in the species list include: Bauer (1960, 1961), Beutelspacher (1976, 1984), Beutelspacher and Brailovsky (1979), Brown (1990), Burns (1994, 1996), Clench (1946, 1972, 1975, 1981), Comstock (1953, 1954, 1955), D'Almeida (1966), R. E. De la Maza (1980), R. E. De la Maza & R. Turrent (1985), R. R. De la Maza (1987), Domínguez & Carrillo (1976), Field (1967), Freeman (1969, 1970, and unpubl. data), Hernández et al. (1981), Jenkins (1983, 1984, 1985, 1986, 1990), Johnson (1989a, 1989b, 1991), Jurado (1990), Kendall and McGuire (1984), Lamas et al. (1995), Luis et al. (1996), Miller (1974, 1978), Miller & J. De la Maza (1984), Neild (1996), Nicolay (1976, 1979), Robbins (1991), Rothschild & Jordan (1906), Skinner (1919), Spade et al. (1988), Tyler (1975), Tyler et al. (1994), Vázquez (1956, 1957, 1958), Vázquez & Zaragoza (1979), Velázquez (1976), Velázquez, & Velázquez (1975) and Warren (1995, 1996, 1998).

The following is an alphabetical list of the abbreviations used for the museums and collections examined: **ADW** = recorded by Andrew D. Warren; **AME** = Allyn Museum of Entomology (Sarasota, FL); **AMNH**

= American Museum of Natural History (New York, NY); **BMNH** = The Natural History Museum (London, England); **CAS** = California Academy of Sciences (San Francisco, CA); **CIB** = Entomology collection in the Instituto de Biología, U.N.A.M. (Mexico City); **CIPN** = Müller collection at the Instituto Politécnico Nacional, see Vázquez (1956), actually at the Natural History Museum in Mexico City; **CMNH** = Carnegie Museum of Natural History (Pittsburgh, PA); **CUIC** = Cornell University Insect Collection (Ithaca, NY); **DGSV** = Dirección Nacional de Sanidad Vegetal, see Hernández et al. (1981); **DMNH** = Denver Museum of Natural History (Denver, CO); **INIA** = Instituto Nacional de Investigaciones Agrícolas, see Domínguez & Carrillo (1976); **JC** = Collection of Dale and Joanne Jenkins, see Jenkins (1983); **LACM** = Los Angeles County Museum of Natural History (Los Angeles, CA); **MZFC** = "Alfonso L. Herrera" Zoology Museum in the Facultad de Ciencias, U.N.A.M. (Mexico City)—includes part of the Sergio Hernández Tobías collection; **RES** = Collection of Ray E. Stanford (Denver, CO); **SDNHM** = San Diego Natural History Museum (San Diego, CA); **UCR** = University of California (Riverside, CA); **USNM** = United States National Museum of Natural History, Smithsonian Institution (Washington, D.C.); **exCLGC** = González Cota collection, now at the MZFC. The fieldwork carried out in the Sierra de Manantlán and around Manzanillo by the authors provided a considerable number of the records presented in this list (MZFC and ADW).

Species list. This list is structured in the same format as the list on Jalisco butterflies (Vargas et al. 1996). Higher classification in this list follows that of Scott (1985), recognizing five families. Within each family, species are arranged in their approximate phylogenetic order, according to subfamilies. Many sources were consulted in determining the nomenclature used in the species list, including many of the works cited in the Jalisco list for nomenclatural purposes. For Hesperioidea, we have followed the nomenclature used in Warren (1998), which includes some modifications from the nomenclature in previous Jalisco lists (Llorente et al. 1995, Vargas et al. 1996, Warren et al. 1996). Major deviations from names used in the Jalisco lists are explained. For the Eumaeini, we have utilized the nomenclature of Robert K. Robbins (USNM), and in other families, we have often relied on the expert opinion of Gerardo Lamas (Museo de Historia Natural, Universidad Mayor de San Marcos, Lima, Perú). For a detailed description on how to extract information from the species list, see the paragraphs following "Butterflies of Jalisco" in the Jalisco list (Vargas et al. 1996:105). Table 2 lists the abbreviations used in the species list for the 25 most commonly cited localities in Colima. In many cases, where we encountered locality labels on specimens from "Colima," we were unable to tell if the speci-

TABLE 2. Abbreviations used in the species list for the 25 most commonly cited Colima localities, the number of species from each locality, and the species richness of each locality; 1 = locality with the greatest number of recorded species, 25 = locality with the fewest recorded species. Species richness numbers correspond to locality numbers of Fig. 1. Data from 54 species from El Jabali were obtained too late to be included in this Table.

Abbreviation	Locality	No. Species	Species Richness
AD	Agua Dulce, 600 m	216	3
BAG	Barranca de Agua, 1600 m	14	22
CAL	Caleras, 100 m	36	18
CHAN	2 km W Chandiablo, 150 m	113	10
COL	Colima City, 500 m	270	1
"COL"	Colima, general record	84	11
COM	Comala, 600 m	147	4
COSU	Cofradía de Suchitlán, 1300 m	43	16
ESA	El Salto, 200 m	121	7
ETE	El Terrero, 2000 m	11	24
LSA	La Salada, 400 m	144	5
MAD	Madrid, 250 m	42	17
MZO	Manzanillo, 0-30 m	128	6
OJO	Ojo de Agua, Madrid, 250 m	45	15
PA	Paso Ancho, 100 m	116	9
PACA	Punta de Agua de Camotlán, 100 m	117	8
PENU	Pedro Núñez, 200 m	75	12
PJU	Pueblo Juárez, 250 m	22	20
PLAT	Platanarillos, 900 m	241	2
PORO	3-5 km NE Playa de Oro, 60 m	66	13
RI	Revillagigedo Islands	10	25
SUCH	Suchitlán, 1000 m	35	19
TAM	Tamala, 200 m	54	14
TECL	Tecolapa, 220 m	17	21
TECM	Tecomán, 100 m	12	23

mens were collected in the city of Colima, or if they represented general records for the state. For species that are recorded from "Colima" that probably did not come from the city (e.g., high elevation species), we have used the abbreviation "COL." Records for species that were definitely or are likely to have been from around the city of Colima are indicated by the abbreviation COL.

RESULTS

Based on our review of collections, publications, and field work carried out to date, we have obtained a list of 543 species of butterflies from Colima, that includes 280 genera in 22 subfamilies of the five recognized families. Over 50 publications were consulted while forming this list, and over 10,000 pinned specimens were examined from 102 localities. We report over 100 species from Colima for the first time.

Since Colima is completely surrounded by Jalisco, except for where it shares its border with Michoacán to the southeast, and since the butter-

TABLE 3. Distribution of species recorded from Colima (COL) in contiguous states of Jalisco (JAL) and Michoacán (MIC), showing percentages of Colima species (543 total) unique to each listed region. All Colima data are from this paper; Jalisco data are from Vargas et al. (1996); Michoacán data are from a study in preparation by the authors.

COL Total	JAL-COL-MIC	COL-JAL	COL-MIC	COL Only
543	387	89	36	31
100%	71.3%	16.4%	6.6%	5.7%

fly fauna of these three states is being systematically collected and studied (as defined by Luis et al. 1991), we have prepared Table 3, which shows the number of species that are known from Colima, those shared by each of the other states, and the number of species that are known from all three states. Out of the 543 species cited from Colima, 31 (5.7% of Colima total) have been recorded only from Colima, and 512 are shared with the other states (Jalisco and Michoacán). Of the 512 shared species, 89 (16.4% of Colima total) are shared only with Jalisco, and 36 (6.6% of Colima total) are shared only with Michoacán; 387 species (71.3% of Colima total) are known from all three states.

We have taken special notice of the 31 species that are known from Colima and are still unknown from Jalisco or Michoacán, and these are indicated in the species list by a •. We consider the occurrence of 5 of these species in Colima (about 1% of state total) to be based on dubious records, rare strays, or transplants, and are bracketed in the list by {}. Some of the species not shared with Jalisco or Colima, including *Phyciodes phaon* (Edwards), *Cyllopsis windi* Miller, *C. diazi* Miller, *Emesis tegula* Godman & Salvin, and *Theope mania* Godman & Salvin, are known from Nayarit or Sinaloa to the north and Guerrero to the south, indicating the need for more fieldwork in all three states. Some of Colima's 31 "unique" species, including *Aethilla lavochrea* Butler, and *Lassaia sessilis* Schaus, are shared with Guerrero and not Jalisco, Nayarit or Sinaloa, and four of the "unique" species unknown from Jalisco, Michoacán, or Guerrero, are known from Nayarit or Sinaloa, including *Moreris stroma* Evans, *Tromba xanthura* (Godman), *Taygetis virgilia* (Cramer), and *Caerofethra carnica* (Hewitson). Many of the species unknown from Jalisco or Michoacán are not known from western Mexico north of Oaxaca, but are small, fast-flying species (mostly skippers and hairstreaks) that may have been easily overlooked, so are not considered dubious records (although some may be), including: *Staphylus tepeca* (Bell), *Decinea mustea* H. A. Freeman, *Calephelis laverna laverna* (Godman & Salvin), *Calephelis argyrodines* (Bates), *Lemonias agave* Godman & Salvin, *Symbiopsis* aff. *tanais* Godman & Salvin, *Tmolus crolinus* (Butler & Druce), and *Nesiostrymon celona* (Hewitson). The disjunct distributions of these species highlight the need for further

fieldwork throughout western Mexico. One skipper species appears to be endemic to Colima, *Zobera albopunctata* H. A. Freeman. There are few species that we can consider broadly distributed in Colima with the available information, but this is probably the result of the lack of previous fieldwork in Colima and the rest of western Mexico.

Other state lists of butterflies that have recently been completed (Vargas et al. 1991, Luis et al. 1991, Vargas et al. 1996, Luis et al. 1996) are consistent with our data for Colima, in that the majority of the records are from fewer than 10 localities in the two or three faunal regions with the greatest ecological heterogeneity and faunal diversity (Sierra de Atoyac in Guerrero, Sierra de Juarez in Oaxaca, Sierra de Manantlán in Colima and Jalisco, Tecelo-Jalapa and Sierra de los Tuxtlas in Veracruz). Such intensive fieldwork at previously uncollected localities has enabled us to begin to identify certain species as "rare," with very restricted spatial or temporal distributions. However, the empirical species accumulation curves for these localities (as described by Soberón & Llorente 1993) indicate that we should still expect additional species from even the best collected areas, and with future fieldwork in these areas, we will be better prepared to identify potentially "rare" species.

Figure 1 shows the twenty five localities in the state of Colima with the greatest numbers of butterfly species, according to the data in this list. Species from UCR from El Jabali (with 54 species) were examined too late in this study to be included in Fig. 1 or Table 2. Colima (city) appears to host the greatest diversity of butterfly species in the state, even though many of the "Colima" records we have come across probably represent general records for the state, and do not represent the city of Colima, as discussed above (Table 2). The estimated richness of species (excluding Hesperidae) for Agua Dulce and Platanarillos is probably close to the true species richness (for Papilionoidea), because these two localities have been systematically and exhaustively collected for several years, and have been monitored by species accumulation curves. La Salada, Colima, Comala, and Manzanillo are the four localities in the state that have been traditionally collected by Mexicans and Americans, but have never been collected in a systematic manner. The four remaining localities, El Salto, Punta de Agua de Camotlán, Paso Ancho, and 2 km W Chandiablo, were each only collected on one day, by a team of three to four researchers, and the true number of species in these localities is probably much higher; these would be excellent areas to conduct formal studies in the future.

It is necessary to continue the systematic collection and documentation of butterflies in all three states, Jalisco, Colima, and Michoacán, as well as in other northwestern Mexican states, especially Nayarit, Sinaloa, and Sonora. 423 (78%) of the species known from Colima are also

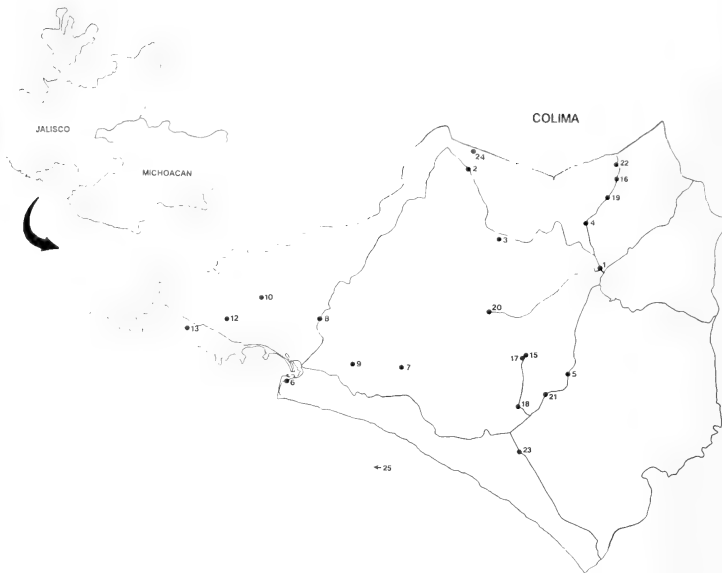


FIG. 1. Areas of greatest species diversity of Rhopalocera in the state of Colima. Major highways in Colima are indicated on the map by solid lines. Numbers correspond to localities listed in Table 2, the 25 localities in the state with the greatest numbers of recorded species (#1 = greatest; #25 = fewest recorded species; #25, Revillagigedo Islands are not shown on the map). Smaller map shows the positions of Jalisco, Colima and Michoacán in western Mexico.

known from Michoacán, and 476 (88%) of the species known from Colima are also known from Jalisco. However, each state still has “exclusive” species, unknown from the other two states, for which we have no ecological, historical, or biogeographical explanation. With Colima only being 6.5% the size of Jalisco (in total surface area), or slightly smaller than the state of Delaware in the United States, 543 species confirmed from Colima suggests that the number of species that actually occur in Jalisco is much higher than has been reported. Vargas et al. (1996) reported 608 species from Jalisco, however the current number of species known from that state is 620 (unpubl. data). The true number of species that occur in Jalisco certainly approaches 700, while Colima is probably home to about 600 species. Only future fieldwork can verify these projected numbers.

BUTTERFLIES OF COLIMA

HESPERIIDAE (221 SPECIES)

- (*Pyrrhopyge crida* (Hewit. [1871])). “COL” (AMNH).
- Pyrrhopyge chloris* Evans 1951. “COL” (CMNH); Río Comala, COM ix (MZFC); San Gerónimo vii (AMNH); SUCH ix (SDNHM).

- Pyrrhopyge araxes araxes* (Hewit. 1867). "COL" xii (AMNH).
- Elbella scylla* (Mén. 1855). "COL" (CMNH); COM iii,iv,ix,x (AMNH); El Jabali viii (UCR); LSA ix (AMNH); PA xii; PACA i (ADW).
- Mysoria amra* (Hewit. [1871]). AD vi (ADW), ix (MZFC); COM X (AMNH); COL v (BMNH); ESA i (ADW); MZO xii (USNM); PACA i (ADW).
- Mysoria affinis* (Herr.-Sch. 1869). AD iv,ix,xii (MZFC); "COL" (CMNH); COL iv,ix; COM iv (AMNH); ESA i (ADW); LSA vi (AMNH); MZO xii (USNM); OJO iii,iv (MZFC); PACA i; PENU i (ADW); PLAT ix (MZFC); Río Comala, COM ix (MZFC).
- Myscelus amystis hages* Godm. & Sal. 1893. LSA xi (AMNH).
- Phocides belus* Godm. & Sal. 1893. "COL" (AMNH, CMNH); COL ix (MZFC), X (SDNHM).
- Phocides pigmalion pigmalion* (Cr. [1779]). "COL" (AMNH).
- Phocides palemon lilea* (Reak. [1867]). "COL" (AMNH, CMNH).
- Proteides mercurius mercurius* (Fabr. 1787). CHAN i (ADW); LSA viii (MZFC); PACA i; PORO xii (ADW).
- Epargyreus exadeus cruza* Evans 1952. COL iii (MZFC); COM v,x; LSA iv-vi,ix (AMNH), viii; PLAT ix (MZFC).
- Epargyreus windi* H. A. Freeman 1969. COSU vii (MZFC); LSA v-vii (AMNH); OJO vi; PLAT ix (MZFC).
- Epargyreus spina* Evans 1952. COM viii; LSA v,vi,viii (AMNH).
- Epargyreus aspina* Evans 1952. COM x; LSA vi (AMNH); PLAT ix (MZFC); PORO xii (ADW).
- Epargyreus spinosa* Evans 1952. AD vi (ADW).
- Polygonus leo arizonensis* (Skinner 1911). CHAN i (ADW); "COL" (CMNH); COM x; LSA ix (SDNHM), X (AMNH).
- Polygonus manueli* Bell & Comstock 1948. TAM viii,ix (MZFC).
- Chioides zilpa* (Butl. 1872). CHAN i (ADW); "COL" (CMNH); El Jabali viii (UCR); ESA i (ADW); LSA ix (MZFC, SDNHM), v (AMNH); OJO iii (MZFC); PA xii; PACA i; PORO xii (ADW); TAM xi (MZFC).
- Chioides catillus albofasciatus* (Hewit. 1867). COL viii (MZFC); El Jabali viii (UCR); ESA i (ADW); MZO xii (USNM); PA xii; PACA i (ADW); PLAT ix,xii (MZFC); PORO xii (ADW).
- Aguna asander asander* (Hewit. 1867). AD vi (ADW); "COL" (CMNH); COL i (AMNH); MZO i,xii (USNM); OJO iii (MZFC); PENU i (ADW).
- Aguna metophis* (Latr. [1824]). COM (Freeman unpublished).
- Typhedanus undulatus* (Hewit. 1867). AD ix (MZFC); COL ii; COM iii; Cuyutlán i (AMNH); El Jabali viii (UCR); MZO xii (USNM); PA xii (ADW).
- Typhedanus ampyx* (Godm. & Sal. 1893). AD vi (ADW), xii (MZFC); LSA ix (SDNHM); OJO v (MZFC); PLAT xii (MZFC).
- Polythrix octomaculata* (Sepp 1848). CHAN i (ADW); COM iii (AMNH); ESA i (ADW); LSA X (AMNH); PACA i (ADW); TAM viii (MZFC).
- Polythrix asine* (Hewit. 1867). CHAN i (ADW); COL i (BMNH); COM iv (AMNH); ESA i (ADW); LSA v,vi,xi (AMNH), ix (SDNHM); MZO i (ADW), xii (USNM); PA xii; PENU i (ADW); PLAT iii (MZFC); PORO xii (ADW).
- Codatractus sallyae* A. D. Warren 1995. AD vi (ADW; Warren 1995).
- Codatractus melon* (Godm. & Sal. 1893). AD vi (ADW); "COL" (CMNH); LSA v,vi (AMNH), viii, ix (SDNHM); OJO viii; TAM ix (MZFC).
- Codatractus bryaxis* (Hewit. 1867). PLAT ix (MZFC).
- Codatractus uvydixa* (Dyar 1914). LSA v,vi (USNM). See Burns (1996).
- "*Codatractus*" *hyster* (Dyar 1916). LSA viii (MZFC); PLAT vi (ADW). See Burns (1996).
- Urbanus proteus proteus* (L. [1758]). "COL" (CMNH); COSU xi (MZFC); COM vii (AMNH); ESA i; MZO i,xii; PA xii; PORO xii (ADW).
- Urbanus belli* (Hayward 1935). CHAN i; ESA i (ADW); Hacienda San Antonio xi (MZFC); PLAT vi (ADW).
- Urbanus pronta* Evans 1952. CHAN i (ADW); COL v (BMNH).
- *Urbanus* sp. undescribed. COSU xi (MZFC).

- Urbanus esmeraldus* (Butl. 1877). COM iii-v,vii,ix,x (AMNH); MZO i (ADW); San Gerónimo xi (AMNH).
- Urbanus evona* Evans 1952. COL ii (AMNH).
- Urbanus prodictus* Bell 1956. COL iii (MZFC).
- Urbanus esta* Evans 1952. COM iv,xi (AMNH); San Gerónimo xi (Freeman unpublished).
- Urbanus dorantes dorantes* (Stoll 1790). AD vi (ADW), ix,xii (MZFC); CHAN i (ADW); "COL" (CMNH); COL vii (MZFC), xii (BMNH); COL, 5 mi SW vii (AMNH); COSU iv (MZFC); ESA i; MZO i,xii (ADW), xi (AMNH); OJO xii (MZFC); PA xii; PACA i; PENU i; PLAT vi (ADW), iv,ix,xii (MZFC); PORO xii (ADW).
- Urbanus teleus* (Hübner 1821). COSU iv (MZFC); COL iii (AMNH); PA xii (ADW); PLAT iii,ix (MZFC).
- Urbanus procne* (Plötz 1881). AD ix (MZFC); "COL" (CMNH); COL i,v (BMNH), viii (MZFC); MZO xii (USNM); PA xii; PORO xii (ADW).
- Urbanus simplicius* (Stoll 1790). "COL" (CMNH); COL ii,iii (AMNH), v (BMNH); ESA i; MZO i (ADW), xii (USNM); PA xii; PACA i (ADW); PLAT ix (MZFC).
- Urbanus doryssus chales* (Godm. & Sal. 1893). CAL ii; COL v (MZFC); COM iv,v,x (AMNH); OJO v (MZFC).
- Astraptus fulgerator azul* (Reak. [1867]). CAL X (MZFC); CHAN i (ADW); "COL" (CMNH); COL iii,v (MZFC); COM iv (AMNH); COSU x,xii; ESA i (ADW); MZO (AMNH), i (ADW); OJO i (MZFC); PA xii; PACA i; PORO xii (ADW); TECL viii (SDNHM).
- Astraptus alector hopfferi* (Plötz 1882). AD iv,xii; CAL X (MZFC); CHAN i; ESA i (ADW); LSA ix (MZFC, SDNHM), X (AMNH); MZO i (ADW); OJO i,iv (MZFC); PACA i; PENU i (ADW); PLAT ix,xii (MZFC); PORO xii (ADW); Volcanillos xi (MZFC).
- Astraptus anaphus annetta* Evans 1952. CAL ii,x (MZFC); CHAN i (ADW); COL ii (AMNH); ESA i; MZO i (ADW); OJO i,v (MZFC); PA xii; PACA i; PENU i (ADW); PLAT iii,ix (MZFC); PORO xii (ADW).
- Astraptus egregius* (Butl. 1870). CAL i; COL X (MZFC), ii; COM iv (AMNH); ESA i (ADW); OJO v; PLAT iv (MZFC).
- Narcosius parisi helen* (Evans 1952). PA xii (ADW).
- Autochton cincta* (Plötz 1882). "COL" xii (AMNH).
- Autochton neis* (Geyer [1832]). "COL" (CMNH); COM viii (AMNH); ESA i (ADW); SUCH X (MZFC, SDNHM).
- Achalarus casica* (Herr.-Sch. 1869). LSA v (AMNH).
- Achalarus toxeus* (Plötz 1882). AD ix (MZFC); CHAN i (ADW); COL i (BMNH), viii (MZFC), ii,iii,v; COM iii,iv,vi,x (AMNH); ESA i (ADW); LSA v (AMNH); Las Conchas, Ixtlahuacán vii (MZFC), X (SDNHM); MZO i (ADW); OJO v (MZFC); PA xii; PACA i (ADW); PLAT iv (MZFC); Río Comala, COM X (MZFC).
- Thorybes pylades* (Scudder 1870). "COL" xii (AMNH). While this species probably does not occur in the city of Colima, it probably does occur at high elevations on the Nevado de Colima.
- Thorybes drusius* (W. H. Edw. [1884]). "COL" xii (AMNH).
- Thorybes mexicana mexicana* (Herr.-Sch. 1869). "COL" i (AMNH).
- Cabares potrillo* (Lucas 1857). AD vi (ADW); CAL ii (MZFC, SDNHM); CHAN i (ADW); COL i-iv,xii (AMNH), X (SDNHM); COSU xii (MZFC); ESA i; MZO i,xii; PA xii; PACA i; PENU i; PLAT vi (ADW).
- Ocyba calathana calanus* (Godm. & Sal. 1894). AD vi; CHAN i (ADW); "COL" (CMNH).
- Celaenorrhinus stola* Evans 1952. AD xii (MZFC).
- Celaenorrhinus fritzgaertneri* (Bailey 1880). Alvarez i,ii (AMNH); "COL" (CMNH); COL v (BMNH); El Cobano, 15 mi S Río Salado i (ADW); MAD v (MZFC).
- Spathilepia clonius* (Cr. [1775]). CHAN i (ADW); COL iii; COM iii,v (AMNH); El Jabali viii (UCR); ESA i (ADW); LSA ix (SDNHM); OJO viii (MZFC); PACA i (ADW); PLAT i,ix (MZFC), vi (ADW).
- Cogia hippalus hippalus* (W. H. Edw. 1882). COL (Godman & Salvin 1887-1901); OJO v (MZFC).

- Cogia calchas* (Herr.-Sch. 1869). "COL" (CMNH); LSA vi (AMNH); TAM viii (MZFC).
- Cogia cajeta eluina* Godm. & Sal. 1894. PENU i (ADW); Tinajas vii (SDNHM), ix (MZFC).
- Cogia aventinus* (Godm. & Sal. 1894). "COL" (AMNH).
- Polyctor cleta* Evans 1953. CHAN i (ADW); LSA v,ix,x (AMNH); PA xii; PACA i (ADW).
- Nisoniades rubescens* (Möschler 1876). AD xii; CAL i (MZFC); "COL" (CMNH); PA xii; PACA i (ADW).
- Nisoniades ephora* Herr.-Sch. 1870. LSA xi (AMNH).
- Pellicia arina* Evans 1953. LSA v,xi (AMNH); PACA i (ADW).
- Pellicia dimidiata* Herr.-Sch. 1870. CHAN i (ADW); COL ii (AMNH); ESA i (ADW); LSA ix (MZFC, SDNHM); PA xii; PACA i; PENU i (ADW).
- Noctuana stator* (Godm. & Sal. 1899). El Jabali viii (UCR).
- Windia windi* H. A. Freeman 1969. LSA [Type Locality] vi,ix (AMNH), ix (MZFC).
- Bolla subapicatus* (Schaus 1902). COSU viii,ix (MZFC); El Jabali viii (UCR); LSA viii (AMNH); SUCH viii,x (SDNHM), X (MZFC).
- Bolla orsines* (Godm. & Sal. 1896). COL i (BMNH); LSA vi (AMNH), ix (MZFC).
- Bolla guerra* Evans 1953. COL vi,xii (AMNH).
- Bolla eusebius* (Plötz 1884). El Jabali viii (UCR); PLAT vi (ADW).
- Bolla ecippe* (Godm. & Sal. 1896). PLAT vi (ADW); SUCH X (MZFC, ADW).
- Bolla clytius* (Godm. & Sal. 1897). COL (USNM).
- Bolla litus* (Dyar 1912). "COL" (CMNH); COL, 5 mi SW vii; LSA vi (AMNH), ix (MZFC, SDNHM).
- Staphylus tierra* Evans 1953. AD iv (MZFC); CHAN i (ADW); "COL" (CMNH); COL ii-iv,xii (AMNH), xii (BMNH); El Jabali viii (UCR); ESA i; PA xii; PACA i; PENU i; PLAT iii,iv,vi,ix; PORO xii (ADW); Quesería X (MZFC); SUCH X (SDNHM); Volcán de Colima xii (AMNH).
- Staphylus azteca* (Scudder 1872). CHAN i (ADW); COL i-v,xii (AMNH), viii (MZFC); COM iii-v (AMNH); ESA i (ADW); PACA i (ADW); Puente Miramar iii (AMNH).
- Staphylus iguala* (Williams & Bell 1940). COM X (AMNH).
- Staphylus vulgata* (Möschler, 1878). CHAN i (ADW); COL iii (AMNH).
- *Staphylus tepeca* (Bell 1942). "COL" iii (AMNH).
- Staphylus* sp. undescribed. CHAN i; PORO xii (ADW); MZO i (USNM).
- Gorgythion begga pyralina* (Möschler 1876). AD vi (ADW); BAG i (MZFC); CHAN i; ESA i; PENU i (ADW); PLAT iii,iv,ix (MZFC), vi; PORO xii (ADW); TAM ix (MZFC).
- Zera hyacinthinus* (Mab. 1877). COL ii,xii (AMNH), X (SDNHM).
- Quadrus cerialis* (Stoll [1782]). San Francisco i (AMNH).
- Quadrus lugubris* (R. Feld. 1869). CHAN i (ADW); COL i-iv; COM X (AMNH); PLAT vi (ADW).
- Sostrata nordica* Evans 1953. COL i (AMNH); PLAT i (MZFC).
- Paches polla* (Mab. 1888). ESA i (ADW); SUCH X (MZFC).
- Atarnes sallei* (C. Feld. & R. Feld. [1867]). AD xii (MZFC); CHAN i (ADW); "COL" (CMNH); COL i,iv (AMNH), v (BMNH); ESA i; PACA i (ADW).
- Carrhenes canescens canescens* (R. Feld. 1869). COL i-iv (AMNH); PENU i (ADW).
- Carrhenes fuscescens* (Mab. 1891). AD vi (ADW); "COL" (CMNH); LSA v,vii,viii (AMNH).
- *Zobera albopunctata* H. A. Freeman, 1970. LSA [Type Locality] vi (AMNH), ix (MZFC).
- Mylon lassia* (Hewit. [1868]). COL i (BMNH); San Gerónimo xi (AMNH).
- Mylon pelopidas* (Fabr. 1793). AD iv,ix (MZFC); CHAN i (ADW); COL vi (BMNH); Lagunita de Ticusitán vii; LSA ix (MZFC), v-x (AMNH); PA xii (ADW); TAM viii (MZFC).
- Xenophanes tryxus* (Stoll [1780]). CHAN i (ADW); COL i (BMNH), iii; OJO ix,xii (MZFC).
- Antigonus nearchus* (Latr. [1817]). CHAN i; ESA i (ADW); LSA (De la Maza 1987); TAM viii (MZFC).
- Antigonus erosus* (Hübner [1812]). AD i,iv,ix (MZFC), vi; CHAN i (ADW); COL iii

- (MZFC); ii,iv (AMNH), X (SDNHM); COM iv (DMNH); ESA i (ADW); OJO iv (MZFC); PA xii; PACA i; PENU i; PLAT vi (ADW), ix (MZFC); SUCH ix (SDNHM); TAM viii (MZFC).
- Antigonus emorsa** (R. Feld. 1869). "COL" (AMNH, CMNH); LSA viii (SDNHM).
- Antigonus funebris** (R. Feld. 1869). AD vi (ADW); "COL" (CMNH); COM v,vi (AMNH); El Jabali viii (UCR); LSA ix (MZFC), v,vi (AMNH); PLAT vi (ADW), ix; Tinajas ix (MZFC).
- Systasea pulverulenta** (R. Feld. 1869). AD xii; BAG ix (MZFC); "COL" (CMNH); COM iii-v; LSA v (AMNH); PACA i; PORO xii (ADW); Tinajas ix (MZFC).
- Zopyrion sandace** Godm. & Sal. 1896. AD ix (MZFC), vi; CHAN i (ADW); "COL" (CMNH); ESA i (ADW); LSA v,vi (AMNH), viii (SDNHM); PA xii; PACA i; PENU i; PLAT vi (ADW); TECL vii (SDNHM).
- **Aethilla lavochrea** Butl. 1872. "COL" (AMNH).
- Achlyodes busirus heros** Ehrm. 1909. LSA xi (AMNH).
- Achlyodes selva** Evans 1953. COSU vi,vii,x (MZFC), X (SDNHM); COL v,xii (AMNH).
- Eantis tamenund** (W. H. Edw. [1871]). AD i,xii (MZFC); CHAN i; ESA i (ADW); LSA ix (MZFC); MZO xii (USNM); TAM viii (MZFC).
- Grais stigmaticus stigmaticus** (Mab. 1883). "COL" (CMNH); PENU i (ADW).
- Timochares trifasciata trifasciata** (Hewit. 1868). AD xii (MZFC); "COL" (CMNH); LSA ix (MZFC); MZO i (ADW).
- Timochares ruptifasciata ruptifasciata** (Plötz 1884). LSA ix (MZFC); MZO xi-xii (Comstock 1953).
- Anastrus sempiternus sempiternus** (Butl. & Druce, 1872). COL iii (MZFC); viii (AMNH); ; COM viii (AMNH).
- Anastrus robigus** (Plötz 1884). CHAN i (ADW); "COL" (CMNH); ESA i; PA xii; PACA i; PENU i (ADW).
- Ebrietas acreon** (Staud. 1876). CHAN i (ADW); "COL" (CMNH); COM iv (AMNH).
- Cycloglypha thrasibulus** (Fabr. 1793). "COL" (CMNH); COL iii (MZFC); El Jabali viii (UCR); ESA i (ADW); TAM iii (MZFC).
- Chiomara mithrax** (Möschler 1878). AD ix (MZFC); COL vii; COM viii (AMNH).
- Chiomara georgina** (Reak. 1868). AD iv; Laguna Amela, TECM vii; LSA ix; OJO v,viii (MZFC); PORO xii (ADW); TAM viii (MZFC).
- Gesta invisus** (Butl. & Druce 1872). AD i,xii (MZFC); Arteaga xii (AMNH); CHAN i (ADW); COL i,ii,iv (AMNH); ESA i (ADW); LSA vii,xii (MZFC); MZO v (AMNH), xii; PA xii; PACA i; PENU i (ADW); PLAT iii (MZFC); PORO xii (ADW); SUCH X (SDNHM).
- Erynnis funeralis** (Scudder & Burgess 1870). Clarión Is., RI ii-v (CAS), XII (BMNH); COL v (AMNH); COSU X (SDNHM); LSA v (AMNH).
- Erynnis scudderi** (Skinner 1914). "COL" xii (AMNH).
- Erynnis juvenalis clitus** (W. H. Edw. 1883). "COL" (Freeman unpublished).
- Erynnis tristis tatus** (W. H. Edw. 1883). "COL" xii (AMNH).
- Pyrgus albescens** Plötz 1884. "COL" (CMNH); COL iv (BMNH), viii (MZFC); El Jabali viii (UCR); Laguna las Cuatas vii (SDNHM); MZO i (ADW), v (AMNH); PA xii (ADW).
- Pyrgus adepta** Plötz 1884. MZO (AMNH).
- Pyrgus oileus** (L. 1767). AD vi (ADW), i,iv,xii (MZFC); CHAN i (ADW); "COL" (CMNH); COL iii,viii (MZFC), ii,iv,v,ix (AMNH); ESA i; MZO i (ADW), v (AMNH); PA xii; PENU i (ADW); PLAT i,iii,iv,ix,xii (MZFC); PORO xii; PACA i (ADW); SUCH X (SDNHM).
- Pyrgus philetas** W. H. Edw. 1881. MZO v (AMNH).
- Helipetes domicella domicella** (Erichson 1848). CHAN i (ADW); PLAT iv (MZFC).
- Helipetes macaira** (Reak. [1867]). AD ix (MZFC); CHAN i (ADW); "COL" (CMNH); COL iii,v (AMNH), vii (BMNH); COM iv (AMNH); ESA i (ADW); Laguna Amela, MZO I; PA xii; PACA i; PENU i (ADW); PLAT iv (MZFC); PORO xii; (ADW); TECM vii (MZFC).
- Helipetes laviana laviana** (Hewit. [1868]). CHAN i (ADW); COL iii (MZFC), iii,v (AMNH); ESA i; PA xii; PACA i (ADW); TAM X (MZFC).

- Helioptetes arsalte* (L. 1758). CHAN i (ADW); COL ii,iv (AMNH); Laguna Amela, TECM vii (MZFC); PA xii (ADW).
- Helioptetes alana* (Reak. 1868). CHAN i (ADW); COL iii (AMNH); ESA i (ADW); PLAT ix; Río Comala, COM i (MZFC).
- *Pholisora catullus* (Fabr. 1793). "COL" (CMNH).
- Piruna penaea* (Dyar 1918). COL ix; COM X (AMNH); LSA ix (ADW, SDNMH).
- Piruna aea aea* (Dyar 1912). "COL" (AME); LSA viii,ix (AMNH).
- Piruna ajjiciensis* H. A. Freeman 1970. El Jabali viii (UCR).
- Piruna* sp. undescribed. COSU vii (MZFC), X (SDNHM); COM viii (AMNH).
- Dardarina dardaris* (Hewit. 1877). AD ix (MZFC); COL i (BMNH); LSA vii,viii,x (AMNH), ix (MZFC).
- Dalla bubobon* (Dyar 1921). El Jabali viii (UCR).
- Dalla faula* (Godm. 1900). El Jabali viii (UCR); LSA vii (AMNH); PLAT ix (MZFC).
- Dalla dividuum* (Dyar 1913). El Jabali viii (UCR); LSA v,vi,ix (AMNH), ix (SDNHM), ix; PLAT ix (MZFC), vi (ADW).
- Synapte syracus* (Godm. 1901). AD iv (MZFC), vi (ADW); COL vii,viii,xii; COM xii (AMNH); PACA i (ADW); PLAT iv (MZFC); SUCH X (SDNHM); Volcán de Colima xii (AMNH).
- Synapte shiva* Evans 1955. COSU ix (MZFC); COL ix; COM vii,viii,x (AMNH); El Jabali viii (UCR); PLAT xii (MZFC).
- Synapte pecta* Evans 1955. ESA i; MZO i; PA xii; PACA i; PENU i; PORO xii (ADW).
- Zariaspes mytheus* (Godm. 1900). AD iv; CAL i (MZFC); CHAN i (ADW); COL ii,iii; COM viii,x,xi (AMNH); ESA i (ADW); LSA xi (AMNH); MZO i (USNM); PA xii; PACA i; PENU I; PORO xii (ADW).
- Anthoptus insignis* (Plötz 1882). COL i,iii; COM iii,viii (AMNH); El Jabali viii (UCR); PLAT xii (MZFC).
- Corticea corticea* (Plötz 1883). CHAN i (ADW); "COL" (CMNH); COL i-iii,xii (AMNH), ix (MZFC), X (SDNHM, USNM); COM iii,vii; El Cintinella iii (AMNH); El Jabali viii (UCR); ESA i (ADW); MZO i (USNM), xii; PA xii; PACA i; PENU i (ADW).
- Callimormus saturnus* (Herr.-Sch. 1869). AD iv (MZFC); "COL" (CMNH); COL i,ii,iv,v,viii (AMNH), i,iii (BMNH), X (SDNHM); ESA i; MZO xii; PACA i (ADW).
- Eprius veleda* (Godm. [1901]). COM X (AMNH).
- *Mnasicles hicetaon* Godman 1901. COL i,iii (AMNH).
- Methionopsis ina* (Plötz 1882). AD ix,xii (MZFC); CHAN i (ADW); COL i-iii,v,xii (AMNH), iii (MZFC), ix,xii (USNM); COM iii,ix,xi (AMNH); ESA i; PACA i; PENU i (ADW); PLAT xii (MZFC).
- Repens florus* (Godm. 1900). COM viii,x (AMNH).
- Phanes aletes* (Geyer [1832]). COL ii (AMNH).
- Vidius perigenes* (Godm. 1900). AD iv (MZFC), vi (ADW).
- Monca tyrtaeus* (Plötz 1883). COL i,ii,iv (AMNH), ix (USNM); MZO xii; PACA i (ADW).
- Nastra julia* (H. A. Freeman 1945). COL X (SDNHM).
- *Nastra hoffmanni* (Bell 1947). COL [Type Locality] iii,vi (AMNH). The status of this taxon is uncertain.
- Cymaenes trebius* (Mab. 1891). COL i-iv (AMNH), iv,vi (USNM), X (SDNHM); COM iv (AMNH); ESA I; MZO xii (ADW); PLAT xii (MZFC).
- Vehilius inca* (Scudder 1872). "COL" (CMNH); COL iii,xii; COM viii (AMNH); MZO i (USNM), xii (ADW); Volcán de Colima xii (AMNH).
- Vehilius illudens* (Mab. 1891). COL i-iii (AMNH).
- Mnasilus allubita* (Butl. 1877). COL ii (AMNH).
- Remella remus* (Fabr. 1798). COL iii; COM iv,x,xi (AMNH); ESA i (ADW); MZO i (USNM); PACA I; PENU i (ADW).
- Remella rita* (Evans 1955). COL iii (AMNH); El Jabali i (RES).
- Remella duena* Evans 1955. COL i (AMNH); El Jabali viii (UCR).
- *Moeris stroma* Evans 1955. COM ix,x (AMNH).
- Lerema accius* (J. E. Smith 1797). AD iv (MZFC); CHAN i (ADW); "COL" (CMNH);

- COL i-iv (AMNH), X (SDNHM); COM X (AMNH); ESA i; MZO i,xii (ADW), xii (USNM); PA xii; PENU I; PORO xii (ADW); Río América, COM xii (AMNH); SUCH X (SDNHM).
- Lerema liris** Evans 1955. "COL" (CMNH); COM vii (AMNH).
- Morys valda** Evans 1955. AD iv (MZFC); COM viii (AMNH).
- Morys micythus** (Godm. 1900). COM X (Freeman unpublished).
- Vettius fantasos** (Stoll [1780]). COL ix (USNM); ESA i (ADW); MZO i (ADW, USNM); PA xii; PACA I; PENU i PLAT vi (ADW).
- **Tromba xanthura** (Godm. 1901). COM iii,viii,x (AMNH); MZO xii (ADW); OJO v,vi (MZFC).
- Carystoides abrahami** H. A. Freeman, 1969. COL i (AMNH), ii (USNM).
- Perichares philetes adela** (Hewit. [1867]). "COL" (CMNH); COL ii,iv,v,xii (AMNH), iv,v (MZFC); PA xii; PORO xii (ADW).
- Lycas argentea** (Hewit. [1866]). COM x,xi (AMNH).
- Quinta cannae** (Herr.-Sch. 1869). COL iii,iv,xii; COM v (AMNH).
- Rhinthon osca** (Plötz 1883). COM viii; MZO xi (AMNH).
- Conga chydaea** (Butl. 1877). COM viii (AMNH); MZO i (ADW).
- **Decinea mustea** H. A. Freeman, 1979. PORO xii (ADW).
- Ancylorhynpha arene** (W. H. Edw. [1871]). AD vi (ADW); "COL" (CMNH); COL (Godman & Salvin, 1887-1901), v (AMNH), iii (MZFC); El Jabali viii (UCR); ESA i (ADW); PLAT i,iii (MZFC).
- Copaeodes minima** (W. H. Edw. 1870). COL iii (BMNH), v (AMNH); El Jabali viii (UCR); MZO xii (ADW).
- Hylephila phyleus phyleus** (Drury [1773]). COL iv,xii (AMNH), viii (MZFC); MZO i (ADW).
- Polites vibex praeceps** (Scudder 1872). COL i,iii (AMNH); El Jabali viii (UCR); ESA i (ADW).
- Polites pupillus** (Plötz 1883). "COL" (Burns 1994).
- Polites subreticulata** (Plötz 1883). "COL" (Burns 1994).
- Pseudocopaeodes eunus chromis** (Skinner 1919). "COL" [Type locality] (Skinner 1919).
- Wallengrenia otho otho** (J. E. Smith 1797). Alvarez i (AMNH); COL iii; COM iv,v (Freeman unpublished); MZO i (ADW).
- Pompeius pompeius** (Latr. [1824]). CHAN i (ADW); "COL" (CMNH); COL i-iii,xii (AMNH), v (USNM), viii (MZFC), X (SDNHM); COL, 5 mi SW vii (AMNH); El Jabali viii (UCR); ESA i; MZO i (ADW), viii (UCR), xii (USNM); PA xii; PLAT vi (ADW).
- Anatrytone mazai** (H. A. Freeman 1969). LSA ix (AMNH).
- Ochlodes samenta** Dyar 1914. El Jabali viii (UCR); LSA viii (AMNH).
- Poanes zabulon** (Boisd. & LeC. [1837]). El Jabali viii (UCR); ETE vi (ADW).
- Poanes inimica** (Butl. & Druce 1872). El Cobano i (RES).
- "Poanes" **benito** H. A. Freeman 1979. BAG X (MZFC).
- Quasimellana aurora** (Bell 1942). El Jabali viii (UCR); LSA iv (USNM).
- Quasimellana balsae** (Bell 1942). El Jabali viii (UCR); LSA v,viii (AMNH).
- Quasimellana eulogius** (Plötz 1883). CAL i (MZFC).
- Quasimellana agnesae** (Bell 1959). MZO xii (USNM).
- Quasimellana mulleri** (Bell 1942). COM iii; LSA ix (AMNH); SUCH X (MZFC).
- Halotus jonaveriorum** Burns 1992. El Jabali viii (UCR); PLAT i (MZFC).
- Amblyscirtes folia** Godm. [1900]. AD ix (MZFC); COM viii (AMNH); El Jabali viii (UCR); LSA vi (AMNH).
- Amblyscirtes patriciae** (Bell 1959). LSA vi,viii (AMNH); PLAT vi (ADW, CUIC), ix (MZFC) (See Warren 1996).
- Amblyscirtes raphaeli** H. A. Freeman 1973. PLAT ix (MZFC).
- Amblyscirtes fluonia** Godm. [1900]. COL vi (AMNH); El Jabali viii (UCR).
- Amblyscirtes tolteca tolteca** Scudder 1872. AD vi (ADW); COL vi (AMNH); PLAT vi (ADW).
- Amblyscirtes fimbriata pallida** H. A. Freeman 1993. ETE vi (ADW).
- Lerodea arabus** (W. H. Edw. 1882). COL iii; COM iv (AMNH).

- Calpodus ethlius* (Stoll [1782]). COL viii (USNM), X (SDNHM).
Panoquina errans (Skinner 1892). MZO xii (ADW).
Panoquina ocola (W. H. Edw. 1863). AD ix (MZFC); "COL" (CMNH); COL i,ii,vii (AMNH), vi (USNM), X (SDNHM); ESA i (ADW); OJO X (AMNH); PA xii (ADW).
Panoquina hecebolus (Scudder 1872). El Jabali viii (UCR).
Panoquina leucas (Fab. 1793). "COL" (Freeman unpublished).
Panoquina evansi (H. A. Freeman 1946). COL ii; LSA ix (AMNH); MZO i (ADW); OJO iv,ix (MZFC).
Nyctelius nyctelius nyctelius (Latr. [1824]). "COL" (CMNH); COL vii,x (SDNHM).
Thespies macareus (Herr.-Sch. 1869). Rancho San Antonio xi (SDNHM).
Thespies dalman (Latr. [1824]). LSA v (AMNH). The subspecific name *guerreronis* Dyar, 1913 is apparently a synonym of *dalman*.
Vacerra litana (Hewit. [1866]). "COL" (CMNH). *Vacerra aeas* (Plotz 1882) as cited in the Jalisco list (Vargas et al. 1996) is apparently a synonym of *litana*.
Vacerra gayra (Dyar 1918). PLAT ix (MZFC).
Niconiades incomptus Austin 1997. COL ii (AMNH).
Aides dysoni Godm. 1900. MZO xii (USNM); PA xii (ADW).
Saliana esperi Evans 1955. "COL" (Freeman unpublished).
Saliana longirostris (Sepp 1840). COL ii (AMNH).
Thracides phidon (Cr. [1779]). COM ix (AMNH).
Agathymus rethon (Dyar 1913). COL iii (AMNH).

PAPILIONIDAE (29 SPECIES)

- Baronia brevicornis brevicornis* Sal. 1893. Armería (De la Maza 1987); LSA v,vi (ex-CLGC); Santiago (Beutelspacher 1984); TAM vi (exCLGC).
Battus philenor philenor (L. 1771). COL (Spade, Hamilton & Brown 1988), v,xi (SDNHM), viii (CIB); ETE vi (MZFC); MAD iv,vi,vii (SDNHM); MZO ix (AME); OJO viii; PLAT iv,vi,xii (MZFC); TECL viii (SDNHM).
Battus philenor orsua (Godm. & Sal. 1889). Clarión Is., RI (Brown 1990, CIB; Vázquez 1956), xii (Rothschild & Jordan 1906).
Battus polydamas polydamas (L. 1758). AD i,iv,vi-xii (MZFC); Armería Bridge ix (CAS); CAL X (SDNHM); CHAN i (ADW, MZFC); COSU (Spade, Hamilton & Brown 1988); COL (AMNH), i-iii,x,xi (SDNHM); ESA i (ADW, MZFC); Guatimoc (AMNH); LSA vi,viii (AME, De la Maza 1987); MZO (Beutelspacher 1984), i,xii (ADW, LACM), ix (AME), xii (CIB); PA xii; PACA i (ADW, MZFC); PLAT i,iv,vi,xii; PORO xii (MZFC).
Battus laodamas iopas (Godm. & Sal. 1897). AD iv,viii-xi (MZFC); Armería Bridge ix (CAS); COL iv,v,x (SDNHM), vi (AME); COM vi (AME); Coquimatlán viii (CIB); LSA (Beutelspacher 1984), viii (CIB); MAD v (SDNHM, De la Maza 1987); PLAT iv,ix,x,xii (MZFC); TAM ix (CIB).
Battus eracon (Godm. & Sal. 1897). AD ii,iv,vi,viii-x,xii (MZFC); Cerro de la Vieja, nr. Coquimatlán (Spade, Hamilton & Brown 1988); COL iii (SDNHM, D'Almeida 1966), viii (CIB); COM vi (AME, Tyler 1975); MAD xi (SDNHM, De la Maza 1987); MZO ix (AME); PA xii; PENU i; PLAT iv (MZFC); Santiago X (CIB); TAM ix-xi (SDNHM), X (exCLGC); Tepames (Spade, Hamilton & Brown 1988).
Parides photinus photinus (Doubleday 1844). AD iv,vi,ix,x,xii (MZFC); Alvarez iii,xii (AMNH); CAL ix,xi (SDNHM); CHAN i (MZFC); COSU X (SDNHM); COL (Rothschild & Jordan 1906), iii-vi (SDNHM); COM (De la Maza 1987), vii,x (AME); ESA i (ADW, MZFC); ETE vi (MZFC); MAD viii,xii (SDNHM); MZO (Beutelspacher 1984), xii (AME), i,xii (LACM), v,ix,xii (CIB); PA xii (ADW); PACA i; PENU i (ADW, MZFC); PLAT iv,xii (MZFC).
Parides montezuma montezuma (Westw. 1842). AD i,ii,vi-xi (MZFC); Armería Bridge ix (CAS); CAL x,xi (SDNHM); COSU (Spade, Hamilton & Brown 1988), xi (SDNHM); COL (Beutelspacher 1984), x-xii (AMNH), ix (CIB); ESA i (ADW, MZFC); Lagunas Las Cuatas ix (MZFC, SDNHM); LSA; Los Mezcales ix (Beu-

- telspacher 1984); MAD vi,vii (SDNHM); PLAT vii,ix,x (MZFC); PJU ix (SDNHM); TAM vii (exCLGC); TECL vi-ix; Yerbabuena vi (SDNHM).
- *Parides eurimedes mylotes* (Bates 1861)). Guatimoc-Guatimotzin vii (AMNH).
- Parides erithalion trichopus* (Rothschild & Jordan 1906). AD i,vi-xii (MZFC); Alvarez iii (AMNH); CAL x,xi; COSU X (SDNHM); COL ii,iv,vii,xi,xii (AMNH); COM (Tyler 1975), vii (AME); LSA (Beutelspacher 1984), X (CIB); MAD v (SDNHM); PLAT v,viii,ix,xii (MZFC); PJU X (SDNHM); San Isidro ix (De la Maza 1980); SUCH ix; TAM x; Tinajas ix; Yerbabuena vi (SDNHM).
- Protographium epidaus tepicus* (Rothschild & Jordan 1906). AD vi-viii (MZFC); COL (Tyler 1975, Beutelspacher 1984, Jurado 1990, AMNH), ii-v (SDNHM); LSA (Velázquez & Velázquez 1975, Beutelspacher 1984), iv (AME), viii (De la Maza 1987), ix (CIB); MAD iv,v,viii (SDNHM).
- Protographium philolaus philolaus* (Boisd. 1836). AD vi,vii,ix (MZFC); COL (AMNH, Beutelspacher 1984), iv,vii (SDNHM); LSA (Velázquez & Velázquez 1975, Beutelspacher 1984), vi (exCLGC, AME), vii (AMNH), viii (SDNHM); MZO (Godman & Salvin 1878-1901), vii (SDNHM); PA xii (MZFC); Peña Colorada vii; PJU ix; Río Naranjo iv (SDNHM), vii (AMNH); TAM vii (exCLGC), viii; TECL vii,viii (SDNHM).
- Protographium agesilaus fortis* (Rothschild & Jordan 1906). AD viii (MZFC); LSA (Velázquez & Velázquez 1975, Beutelspacher 1984), vi (AME), viii (CIB); MZO xii (AME); PJU ix; TAM vii (exCLGC), viii (SDNHM).
- *Protesilaus macrosilaus penthesilaus* (C. Feld. & R. Feld. 1865)). "COL" v (AME).
- Mimoides thymbraeus aconophos* (Gray [1853]). AD ii,vi,viii,ix (MZFC); LSA (Velázquez & Velázquez 1975, Beutelspacher 1984), v (AME); PLAT iv,x (MZFC); TAM vii (exCLGC).
- Mimoides ilus occiduus* (Vázquez 1957). AD viii (MZFC); COL (CIPN: Vázquez 1956); LSA (Velázquez & Velázquez 1975, Beutelspacher 1984), viii (SDNHM).
- Priamides pharnaces* (Doubleday 1846). AD ix,x (MZFC); COL (AMNH), i-iv,x (SDNHM), vi (AME); LSA (Velázquez & Velázquez 1975, Beutelspacher 1984); MAD v (SDNHM); MZO i (LACM); PLAT iv,vii,viii,x (MZFC).
- Priamides erostratus vazquezae* (Beutelspacher 1986). LSA (Beutelspacher 1984), viii (AME); PLAT viii (MZFC).
- Priamides anchisiades idaeus* (Fabr. 1793). AD X (MZFC); Armeria Bridge ix (CAS); LSA (Velázquez & Velázquez 1975, Beutelspacher 1984); OJO xi; PA xii (MZFC); PACA i (ADW); PLAT x,xii (MZFC); TAM ix (CIB).
- Troilides torquatus mazai* (Beutelspacher 1974). "COL" (Tyler 1975, Beutelspacher 1984).
- Calaides ornithion* ssp. AD vi,vii (MZFC); COM (CIB); LSA (Beutelspacher 1984).
- Calaides astygalus bajaensis* (Brown & Faulkner 1992). COL (AMNH), vi,vii (SDNHM); LSA (Velázquez & Velázquez 1975), vi (exCLGC), ix (SDNHM); MAD v; TECL vi,viii (SDNHM).
- Calaides androgeus* ssp. AD vi (ADW), vii,ix,x (MZFC); COM (De la Maza 1987); LSA (Velázquez & Velázquez 1975, Beutelspacher 1984), v (exCLGC), viii (SDNHM), viii (CIB), ix (Velázquez 1976); Los Mezcales ix (CIB).
- Heracides thoas autocles* (Rothschild & Jordan 1906). AD vi-xi (MZFC); COL (AMNH), ii,iv,vii,x (SDNHM); COM vii; Coquimatlán viii (SDNHM); LSA viii (SDNHM, Velázquez & Velázquez 1975, Beutelspacher 1984); MAD iv (SDNHM); MZO (Beutelspacher 1984), xii (CIB); OJO xii (SDNHM); PLAT ix (MZFC); TAM viii; TECL viii (SDNHM).
- Heracides crespontes* (Cr. 1777). AD vi,vii,ix,x,xii (MZFC); Armeria Bridge ix (CAS); COL (AMNH), ii-iii,x (SDNHM), vii,viii (MZFC); LSA (Velázquez & Velázquez 1975, Beutelspacher 1984); MAD iv (SDNHM); PA xii (ADW); PLAT X (MZFC); TAM vii (exCLGC), viii (SDNHM).
- Papilio polyxenes asterius* Stoll 1782. AD xi (MZFC); COL x,xi (SDNHM); LSA (AMNH, Velázquez & Velázquez 1975), viii (CIB, SDNHM); PLAT vii,ix,x,xii (MZFC); TAM vii (exCLGC); Quisería x; TECL vii (SDNHM).
- Pterourus pilumnus* (Boisd. 1836). COM (De la Maza 1987).

Pterourus multicaudatus (Kirby 1884). PLAT x,xii (MZFC).

Pyrrhosticta garamas garamas (Geyer [1829]). COSU iii,vii,viii,x; SUCH vii (SDNHM).

Pyrrhosticta victorinus morelius (Rothschild & Jordan 1906). COL (Beutelspacher 1984), ii–viii,x,xi (SDNHM); COM iv; LSA iv (AME); Tepames X (SDNHM).

PIERIDAE (34 SPECIES)

Enantia mazai diazi Llorente 1984. COSU x–xii; COL xi (SDNHM); PLAT X (MZFC); Quisería X (SDNHM).

Dismorphia amphiona lupita Lamas 1979. COL (AMNH); PLAT iv,ix,xii (MZFC); Quisería x; SUCH X (SDNHM).

Zerene cesonia cesonia (Stoll 1791). AD i,vii–xii (MZFC); COL ix (AME), X (SDNHM); COL, 7 mi SW vii (AMNH); COL-Coquimatlán ix (CIB); COL-Tonila ix (CIB); Coquimatlán ix (CIB); Esperanza X (USNM); LSA vi (exCLGC), ix (SDNHM), X (Beutelspacher & Brailovsky 1979); PLAT i,ii,ix,x,xii (MZFC); Tonila ix (CIB).

Anteos clorinde nivifera (Frühstorfer 1907). AD i,iv,vi–ix,xii (MZFC); CHAN i (ADW); COL ii,vii (SDNHM), ix (AME); LSA vii (AMNH); MZO ix (AME), viii (CIB); PA xii (ADW); PENU I; Perian ix (CIB); PLAT iv,vi,xii (MZFC).

Anteos maerula lacordairei (Boisd. 1836). AD iv,vi–ix,xii (MZFC); Bahía Santiago; COL (AMNH), ii,x,xi (SDNHM), ix (AME); LSA (AMNH); MAD viii; MZO i (LACM), viii (SDNHM); PA xii (ADW); PACA i (MZFC); PENU i (ADW); PLAT i,iv,vi (MZFC); PORO xii (ADW).

Phoebis agarithe agarithe (Boisd. 1836). AD vi,vii,ix (MZFC); Bahía Braithwaite, Socorro Is. RI iv (SDNHM: Brown 1990); CHAN i (ADW); COL (AMNH), ii,iv,vii,x,xi (SDNHM), X (CIB); COM X (CIB); ESA i (ADW, MZFC); LSA v (SDNHM); MZO (AMNH), ii (CIB), ix (AME), xii (CIB, LACM); MZO, 5 mi SW (AMNH); PA xii; PACA i; PENU i (ADW, MZFC); PLAT ix (MZFC); Socorro Is., RI vii,viii,ix,xii (CIB).

Phoebis argante argante (Fabr. 1775). AD vii,ix,x (MZFC); COL (AMNH); PLAT i,vi,vii,ix,xii (MZFC).

Phoebis neocypris virgo (Butl. 1870). AD vi,vii,ix (MZFC); COL ix (CIB); COSU ix,xii (SDNHM); LSA vii (AME); PLAT i,iv,vi,vii,ix (MZFC).

Phoebis philea philea (L. 1763). AD vi–xii (MZFC); Camino COL-Tonila ix (CIB); CHAN i (ADW, MZFC); COL v,vi (LACM), vii,viii,x,xi (SDNHM); ESA i (ADW, MZFC); MZO vii,xii (LACM), i (ADW); PA xii (ADW, MZFC); PACA i (MZFC); PENU i; PLAT iv,vi,viii,ix,xii (MZFC); TAM (exCLGC).

Phoebis sennae marcellina (Cr. 1777). AD i,iv,vi–ix,xi (MZFC); Bahía Braithwaite, Socorro Is., RI iv (SDNHM: Brown 1990); CHAN i (ADW, MZFC); COL ii,vii,ix,xi (SDNHM); COM X (CIB); Coquimatlán ix (CIB); ESA i (ADW, MZFC); LSA (AMNH); MAD v (SDNHM); MZO i (ADW), ix (AME), xii (CIB, LACM); PA xii (ADW, MZFC); PACA i (ADW); PENU i (ADW, MZFC); Perian ix (CIB); PLAT i,ii,iv,vi–x,xii (MZFC); PORO xii (ADW, MZFC); TECL vii,ix (SDNHM); TECM (AMNH); Tonila ix (CIB).

Rhabdodryas trite trite (L. 1758). PA xii (MZFC).

Aphrissa satira jada (Butl. 1870). AD iv,vii–ix (MZFC); CHAN i (ADW); LSA iv (AME); PLAT iv,xi (MZFC); PA xii (ADW, MZFC); PACA i (ADW).

Abaeis nicippe (Cr. 1780). AD ii,vii,ix (MZFC); CHAN i (ADW, MZFC); COL x,xi (SDNHM); COL, 5 mi SW; MZO (AMNH); PA xii; PLAT ii,xii (MZFC); PJU x; Río Naranjo iv (SDNHM).

Pyrisitia dina westwoodi (Boisd. 1836). AD i,ii,iv,vi–xii (MZFC); CHAN i (ADW, MZFC); COL ii,iii,x; COM ix (SDNHM); LSA vii (AMNH); OJO ix (SDNHM); PACA i; PLAT i,ii,iv,vi,vii–x,xii (MZFC).

Pyrisitia lisa centralis (Herr.-Sch. 1864). AD vi (MZFC); COL-Coquimatlán ix (CIB); ESA i (ADW, MZFC); MAD ix; MZO viii (SDNHM), ix (AME); PA xii; PLAT vi (MZFC); TECM, 3 mi E vii (AMNH).

Pyrisitia nise nelphe (R. Feld. 1869). AD i,vi–xi (MZFC); COL (CIB, AMNH),

- i,ii,iv,v,ix-xii; COM ix,x (SDNHM); ESA i (ADW); Esperanza X (USNM); LSA (AMNH); MAD ix (SDNHM); MZO ii (CIB); PLAT ii,iv,vii,ix,x (MZFC).
- Pyrisitia proterpia proterpia*** (Fabr. 1775). AD vii-xii (MZFC); Armería ix (CIB); COL (AMNH), i,viii (CIB), x,xi (SDNHM); COL, 5 mi SW (AMNH); COL-Tonila ix (CIB); COM X (CIB); El Mezquite viii (CIB); ESA i; LSA X (CIB); PENU i (ADW, MZFC); PLAT i,iv,vi,vii,ix-xii (MZFC); TECM, 3 mi E (AMNH); Tonila ix (CIB).
- Eurema albula celata*** (R. Feld. 1869). COL (AMNH); PLAT i,iv,vi,viii-xii (MZFC).
- Eurema boisduvaliana*** (C. Feld. & R. Feld. 1865). AD i,ii,vi-xii (MZFC); CHAN i (ADW, MZFC); COSU xii (SDNHM); COL (AMNH), iv,x,xi (SDNHM), ix (AME); COL-Coquimatlán ix (CIB); COL-Tonila ix (CIB); COM ix,x (SDNHM); ESA i (ADW, MZFC); Hacienda San Antonio xi; Laguna Las Cuatas ix (SDNHM); Los Mezcales ix (CIB); LSA X (CIB); MZO (AMNH), xii (CIB); OJO ix (SDNHM); PA xii; PACA i; PENU i (ADW, MZFC); PLAT i,ii,iv,vi,vii,ix,x,xii (MZFC); PORO xii (ADW, MZFC); PJU ix (SDNHM); Rancho San Antonio ix (SDNHM).
- Eurema daira*** (Godart 1819). AD i,ii,iv,vi-x,xii (MZFC); CHAN i (ADW, MZFC); COL (AMNH), i,ii,iv,vii-xii (SDNHM), ii,viii,xii (CIB); COL, 5 mi SW (AMNH); COM ix,xi,x (CIB); Cóbano X (SDNHM); ESA i (ADW, MZFC); El Mezquite viii (CIB); ETE vi (MZFC); Las Conchas, Ixtlahuacán vii (SDNHM); MAD X (CIB); MZO (AMNH), i (ADW), xii (CIB); Nevado de Colima viii (SDNHM); PA xii; PACA i; PENU i (ADW, MZFC); PLAT i,ii,iv-viii,x-xii (MZFC); PORO xii (ADW, MZFC); Quesería xii (SDNHM); SE slope Volcán de Colima, pine zone xii (CAS).
- Eurema mexicana mexicana*** (Boisd. 1836). AD vii-ix; ESA i; LSA X (CIB); PLAT i,ii,iv,vii-x (MZFC); PJU ix; SUCH X (SDNHM).
- Eurema salome jamapa*** (Reak. 1866). COSU xii (SDNHM); COL (AMNH), xi (SDNHM); PLAT ii,iv,ix,x,xii (MZFC).
- Nathalis iole iole*** Boisd. 1836. AD iv,vii,xii (MZFC); Bahía Santiago (AMNH); PLAT iv,x (MZFC).
- Kricogonia lyside*** (Godart 1869). COL iv (AMNH), viii (AME); LSA X (CIB); PLAT xii (MZFC).
- Hesperocharis costaricensis pasion*** (Reak. [1867]). AD xii; PLAT i,ii,xii (MZFC).
- Catasticta flisa flisa*** (Herr-Sch. [1853]). COL xi; El Jabalí (De la Maza 1987).
- Pereute charops leonilae*** Llorente 1986. COSU i,xii; COL xi (SDNHM); Laguna de Carrizalillo xii; PLAT iv,xi,xii (MZFC); Rancho San Antonio xi (SDNHM).
- Melete lycimnia isandra*** (Boisd. 1836). AD i,ii,ix-xii (MZFC); COL i (AMNH), xii (CIB); LSA (De la Maza 1987), vi (exCLGC); MZO ix (AME); PLAT vii; PORO xii (MZFC); TECM (De la Maza 1987).
- Glutophrissa drusilla tenuis*** Lamas 1981. AD viii-xii (MZFC); CHAN i (ADW, MZFC); COL vii (CIB), ix (AME); COM X (CIB); ESA i (ADW, MZFC); Ixtlahuacán xi (ex-CLGC); Los Mezcales ix (CIB); LSA X (CIB); MZO i (LACM), viii (CIB), xi (AME), xii (CIB, AMNH); PA xii; PACA i; PENU i (ADW, MZFC); PLAT vii,xii; PORO xii (MZFC).
- Pontia protodice*** (Boisd. & LeC. 1829). COL V (AMNH).
- Leptophobia aripa elodia*** (Boisd. 1836). AD xi; COSU xii; COL xi; PLAT xi,xii (MZFC).
- Pieriballia viardi laogore*** (Godm. & Sal. 1889). AD x,xi (MZFC); Bahía Santiago xi (AMNH); CAL i (SDNHM); CHAN i (ADW, MZFC); COM vi (AME); ESA i (ADW, MZFC); LSA v (AME); MAD i,iv (SDNHM); MZO vi,xii (CIB), xi,xii (LACM); PA xii (MZFC); PACA i; PENU i (ADW, MZFC); PLAT i,iv,xi,xii (MZFC); PORO xii (ADW, MZFC).
- Ascia monuste monuste*** (L. 1764). AD vii-x,xii (MZFC); CHAN i (ADW, MZFC); COL (CMNH), viii (CIB), xi (exCLGC), ii,iv,v,vii,viii,x,xi (SDNHM); COL-Coquimatlán viii (CIB); COM X (CIB); ESA i (ADW, MZFC); LSA vi (exCLGC), vii; MZO i,ii,xii (CIB), v (AMNH), viii (SDNHM), ix (AME), xi (Comstock 1954), xii (LACM); PA xii; PACA i (ADW, MZFC); PENU i (ADW); PLAT vii,ix,x,xii (MZFC); PORO xii (ADW).
- Ganyra josephina josepha*** (Sal. & Godm. 1868). AD ii,iv,vii-xii (MZFC); Armería Bridge ix (CAS); CHAN i (ADW, MZFC); COL (AMNH), iv,ix (CIB), v (SDNHM), ix (AME), X (SDNHM), xi (exCLGC); ESA i (ADW, MZFC); LSA (De la Maza 1987), vi (exCLGC), vii (AMNH); MAD iv,ix (SDNHM), X (CIB); MZO i (ADW), ix

(AME), xii (LACM); PA xii; PENU i; PORO xii (ADW, MZFC); PJU ix (SDNHM); PACA i (ADW); TAM vi,vii (exCLGC); Tonila ix (CIB).

NYMPHALIDAE (130 SPECIES)

- Dione juno huascuma*** (Reak. 1866). COL (De la Maza 1987), iv,vi,ix,x,xi,xii (SDNHM); ESA i (ADW, MZFC); MZO (Comstock 1955), i (ADW), xii (LACM); MZO, 13 mi N xii (SDNHM); PACA i; PLAT xii (MZFC).
- Dione moneta poeyii*** Butl. 1873. COL xi,xii; COSU xii (SDNHM); PLAT i,xi (MZFC).
- Agraulis vanillae incarnata*** (Riley 1926). AD vii,x,xi (MZFC); COL iv,v (SDNHM); MZO (De la Maza 1987); PA xii; PLAT ix,x (MZFC).
- Dryas iulia moderata*** (Riley 1926). AD i,ii,iv,ix,xi,xii (MZFC); CAL X (SDNHM); CHAN i (ADW, MZFC); COL i,ii,xi (SDNHM); ESA i (ADW); Laguna La Marfa, COM xi (MZFC); MZO (Comstock 1955), i (ADW, LACM), xii (ADW); MZO, 13 mi N xii (SDNHM); PA xii; PACA i; PENU i (ADW, MZFC); PLAT ix,x,xii (MZFC); PORO xii (ADW, MZFC).
- Heliconius charithonia vazquezae*** Comstock & Brown 1950. AD i,iv,vii,ix,xii (MZFC); CHAN i (ADW, MZFC); COL i,xi (MZFC), iv (SDNHM); ESA i (ADW, MZFC); Laguna de Carrizalillo xi (MZFC); MAD v (SDNHM); MZO i (ADW, Comstock 1955), viii (SDNHM), xii (LACM); MZO, 13 mi N i (SDNHM); PA xii; PACA i; PENU i (ADW, MZFC); PLAT i,iv-vii,ix,xii (MZFC); PORO xii (ADW, MZFC).
- Heliconius erato punctata*** Beutelspacher 1992. AD viii,ix (MZFC); MZO i (LACM); PA xii (ADW, MZFC); PACA i (MZFC); PORO xii (ADW, MZFC).
- Heliconius hortense*** Guérin [1844]. BAG xi; COL xi; San Antonio i,x,xi (SDNHM).
- Euptoieta hegesia hoffmanni*** Comstock 1944. AD vi,vi,ix,xi (MZFC); CHAN i (ADW, MZFC); COL iii,x (SDNHM); COL, 15 mi NE, Hwy. 54 xii (LACM); ESA i (MZFC); MZO i (LACM); PA xii; PLAT ii,iv,vii,ix-xi (MZFC); PORO xii (ADW, MZFC).
- Vanessa virginiensis*** (Drury 1773). Rancho San Antonio, COM ix; PLAT i,xi (MZFC).
- Nymphalis antiopa antiopa*** (L. 1758). COSU X (MZFC).
- Hypanartia godmani*** (Bates 1864). PLAT xi (MZFC).
- Anartia amathea colima*** Lamas 1995. AD i,ii,iv,vi-ix,xi,xii (MZFC); Bahía Santiago (AMNH); CAL X (SDNHM); CHAN i (ADW, MZFC); COL (AMNH), i,ii,x (SDNHM), viii (MZFC); ESA i (ADW, MZFC); Huerta El Boliche i (MZFC); LSA (De la Maza 1987); MAD v (SDNHM); MZO xii (LACM, ADW), i (ADW); OJO i (MZFC); PA xii; PACA i; (ADW, MZFC); PLAT i,ii,iv-vii,ix,xii (MZFC); PORO xii (ADW, MZFC); San Francisco (AMNH).
- Anartia jatrophae leuteipicta*** Frühstorfer 1907. AD iv,vii-ix,xii (MZFC); CHAN i (ADW, MZFC); COL (AMNH), i-iii,x; MZO viii (SDNHM), xii (ADW, LACM); PA xii; PACA i (MZFC).
- Siproeta epaphus epaphus*** (Latr. [1813]). AD xii; OJO vi; PLAT i,viii-x,xii; Quesería x; SUCH X (MZFC).
- Siproeta stelenes biplagiata*** (Frühstorfer 1907). AD iii,iv,vi-xii (MZFC); CHAN i (ADW, MZFC); COL (AMNH), i,ii,xi (SDNHM); COL, 5 mi SW (AMNH); ESA i (ADW, MZFC); LSA (AMNH); MAD xi (SDNHM); MZO i,xii (LACM); PA xii; PACA i; PENU i (ADW, MZFC); PLAT ii,iv,vi,xii (MZFC); PORO xii (ADW).
- Junonia coenia*** Hübner [1822]. AD i,iv,vi,viii,xii; COL X (MZFC); LSA (De la Maza 1987); Laguna de Ticusitán vii; PLAT i,ii,iv,vi,ix,xii (MZFC).
- Junonia genoveva nigrosuffusa*** Barnes & McDunnough 1916. COSU xi (MZFC); COL xi (SDNHM); El Jabali viii (UCR); ESA i (ADW, MZFC); Estancia X (MZFC); Quesería xii (SDNHM); PLAT xii (MZFC); Tepames X (SDNHM). It is possible that all western Mexican *Junonia*, including coastal *genoveva*, montane *nigrosuffusa*, and *coenia* really only represent one single species.
- Chlosyne gloriosa*** Bauer 1960. AD ix (MZFC); TAM vi (exCLGC).
- Chlosyne janais*** (Drury 1782). TAM ix (SDNHM).
- Chlosyne hippodrome hippodrome*** (Geyer 1837). AD vii-ix,xi; Aguas Cuatas xi (MZFC); COL x; COM ix (SDNHM); El Jabali viii (UCR); PLAT ix-xii (MZFC); Rancho San Antonio ix (SDNHM); Tinajas ix (MZFC).

- Chlosyne lacinia crocale*** (W. H. Edw. 1874). AD ii,vii-xii; Arroyo de Arquisola, Coquimatlán viii (MZFC); CAL X (SDNHM); COL (USNM), vii (MZFC), ix-xi; COM ix,x (SDNHM); Esperanza X (USNM); LSA viii (MZFC); OJO ix (SDNHM), viii,ix; PLAT ii,ix (MZFC); PJU ix (SDNHM); Río Comala, COM X (MZFC); TAM vi,vii (exCLGC); Tepames, 0.9 mi S ix (SDNHM).
- Chlosyne marianna*** Röber [1914]. PLAT ix (MZFC).
- Chlosyne marina dryope*** (Godm. & Sal. 1894). AD vii-ix,xii (MZFC); COL xi; COM ix (SDNHM); LSA vi (exCLGC); PLAT viii-x (MZFC); PJU ix (SDNHM); TAM vi,vii (exCLGC).
- Chlosyne riobalsensis*** Bauer 1961. AD ii,vii,ix (MZFC); COL i (AMNH); PLAT ix (MZFC).
- Anemeca ehrenbergii*** (Geyer [1833]). COSU vi,vii,ix,x (SDNHM); COL (Kendall & McGuire 1984), iv,xi (SDNHM, CMNH); LSA (De la Maza 1987); Quesería xii (SDNHM); Río Naranjo iv (SDNHM); PLAT viii,xii (MZFC).
- Thessalia theona*** ssp. AD ii,iv,vii-xii; Cerro de la Media Luna, Coquimatlán ix; CHAN i (MZFC); COL iv,v,x,xi (exCLGC), iii (SDNHM); LSA vi (exCLGC), ix; MZO viii (SDNHM), xii (ADW); OJO ix (SDNHM); PA xii (ADW); PLAT i,ii,vii-ix,xi,xii (MZFC); PJU ix (SDNHM); San Francisco i,xii (AMNH); SUCH X (MZFC); TAM (exCLGC).
- Texola anomalus anomalus*** (Godm. & Sal. 1897). AD vii,ix-xi (MZFC); COL (AMNH); LSA (De la Maza 1987); PLAT vii; TECL vii (MZFC).
- Texola elada elada*** (Hewit. 1868). AD i,vii,ix,xi; COSU xii (MZFC); COL viii; COL, 5 mi SW vii (AMNH); El Jabali viii (UCR); PLAT i,ii,iv,vii-x,xii (MZFC); Quesería xii (SDNHM); SUCH X (MZFC); TAM vi (exCLGC).
- Microtia elva elva*** Bates 1864. AD ii,vii-xii (MZFC); Bahía Santiago; COL, 5 mi SW (AMNH); CHAN i; ESA i (ADW, MZFC); LSA (De la Maza 1987), v (exCLGC); Laguna de Ticuisitán vii; PA xii; PACA i; PLAT i,ii,vii-xii (MZFC); TECM, 3 mi E (AMNH); Tepames, 0.9 mi S ix (SDNHM).
- ***Phyciodes phaon*** (W. H. Edw. 1863). Alvarez i (AMNH); COL iv,v (SDNHM).
- Phyciodes pallescens*** (R. Feld. 1869). AD vii (MZFC); Laguna las Cuatas vii (SDNHM); MZO i (ADW).
- Phyciodes vesta vesta*** (W. H. Edw. 1869). PLAT i,iv,vii (MZFC).
- Anthanassa alexon alexon*** (Godm. & Sal. 1889). AD i,xi,xii; COSU vii; PLAT i,ii,iv,vii-x,xii; SUCH X (MZFC).
- Anthanassa ardys ardys*** (Hewit. 1864). AD iv,vii; BAG x; COSU vii; PLAT i,ii,iv,vi-ix,xii; SUCH X (MZFC).
- Anthanassa*** sp. AD i; PLAT i; SUCH X (MZFC).
- Anthanassa tulcis*** (Bates 1864). AD i,ii,vii-xi (MZFC); Alvarez i (AMNH); CAL i (MZFC); CHAN i (ADW, MZFC); COSU X (SDNHM); COL (CMNH), i (AMNH), ix (USNM), i,iv,v,vii,xi (SDNHM); ESA i (ADW, MZFC); La Playa, Minatitlán vii (MZFC); Laguna Las Cuatas viii,ix (SDNHM); PA xii; PACA i; PENU i (ADW, MZFC); PLAT ii,vii-xii (MZFC); SUCH X (MZFC).
- Anthanassa ptolyca amator*** (Hall 1929). AD viii,ix,xii; PLAT i,ii,iv,v,ix,x,xii (MZFC).
- Anthanassa sitalces cortes*** (Hall, 1917). PLAT vii (MZFC).
- Anthanassa texana texana*** (W. H. Edw. 1863). Cuyutlán (AMNH).
- ***Tegosa guatemalena*** (Bates 1864). COL X (SDNHM); COM iii,v (CMNH).
- Historis odius odius*** Lamas 1995. AD ii; PLAT vi,ix,x (MZFC).
- Smyrna blomfieldia datis*** Frühstorfer 1908. AD i-iv,vi-x,xii (MZFC); CHAN i (ADW, MZFC); COL i-iii,xi; COM iii (SDNHM); ESA i (ADW, MZFC); LSA (De la Maza 1987); MAD v (SDNHM); MZO i (LACM); OJO XII (MZFC); PA xii; PACA i; PENU i (ADW, MZFC); PLAT ii,iv,vi,ix,x,xii (MZFC); PORO xii (ADW); PJU X (SDNHM); TAM viii (SDNHM); SE slope Volcán de Colima xii (CAS).
- Smyrna karwinski*** Geyer [1833]. AD viii-x; MAD i; PLAT vi,xii (MZFC); PJU X (SDNHM).
- Colobura dirce dirce*** (L. 1758). AD i,iii,viii,ix,xii (MZFC); CHAN i (ADW, MZFC); COL ii (SDNHM); ESA i (ADW, MZFC); MAD (De la Maza 1987); MZO xii (LACM); OJO xii (MZFC); PA xii; PACA I, PENU i (ADW, MZFC); PLAT iv,v,viii-x,xii (MZFC).
- Biblis hyperia aganisa*** Boisdu. 1836. AD i,iv,x,xii; CAL X (MZFC); CHAN i (ADW,

- MZFC); COL (AMNH), iv,x (SDNHM); ESA i (ADW, MZFC); MAD v (SDNHM); MZO i (LACM); PACA i (ADW, MZFC); PENU i (ADW); PLAT i,iv,viii,ix,xi,xii; PORO xii (MZFC); TAM vii (exCLGC).
- Mestra dorcas amygone*** (Mén. 1857). AD i,xii (MZFC); COSU X (SDNHM); Las Conchas, Ixtlahuacán vii (MZFC); MZO i (LACM); PLAT vi (MZFC).
- Myscelia cyananthe cyananthe*** C. Feld. & R. Feld. 1867. AD i,ii,iv,vi-xii (MZFC); CHAN i (ADW, MZFC); Coliquinatlán iii (CMNH); Coliavinatlán (Jenkins 1984); COL (USNM); COM; LSA (Jenkins 1984), vi (exCLGC), viii,ix (SDNHM); MAD v (SDNHM, MZFC); MZO (Jenkins 1984), xi (LACM); OJO iv (SDNHM), v (MZFC); PACA i; PENU i (ADW, MZFC); PLAT i,iv,vi,ix,x,xii (MZFC); PORO xii; TAM vi,vii (exCLGC), viii,ix (SDNHM), viii; TECL viii (SDNHM); Volcanillos xi (MZFC).
- Myscelia cyaniris alvaradia*** R.G. Maza & Díaz 1982. AD iv,vi-ix,xi,xii (MZFC); COL (AMNH); MAD (De la Maza 1987), i,vi,ix (SH; Jenkins 1984), xi (JC; Jenkins 1984); OJO i,xi (MZFC), v (SDNHM); PLAT vi,ix (MZFC).
- Myscelia ethusa ethusa*** (Doyère [1840]). Coquimatlán; LSA; MZO (Jenkins 1984), i,xi (LACM).
- Catonephele cortesi*** R.G. Maza 1982. "COL" (AMNH; Jenkins 1985).
- Eunica alcmena alcmena*** (Doubleday [1847]). AD i (MZFC); COL (Jenkins 1990, AMNH); LSA (Jenkins 1990); TAM vii (exCLGC).
- Eunica monima monima*** (Cr. 1782). AD iv,vi-viii,xi; COL vii (MZFC); Laguna Amela, TECM vii; Laguna La Colorada, COL vii; PLAT vi (ADW), i,iv,vi,xii; TECL vii (MZFC).
- Eunica tatila tatila*** (Herr.-Sch. [1855]). "COL" (AMNH, Jenkins 1990).
- Hamadryas aphimome mazai*** Jenkins 1983. AD iv,viii-x,xii; COL iii (MZFC), ii-v (SDNHM), xi (JC; Jenkins 1983), xi (JC; Jenkins 1983); ESA i (ADW, MZFC); MAD iv (SDNHM); PACA i; PENU i (ADW); PLAT iv,vi,xii (MZFC); TAM viii,ix; TECL vii; Turla X (SDNHM).
- Hamadryas atlantis lelaps*** Godm. & Sal. 1883. AD iii,vi,viii,xii; CAL X (MZFC); CHAN i (ADW); COL (USNM); LSA (Jenkins 1983), vii (MZFC); MAD (Jenkins 1983); PACA i (ADW, MZFC); PENU I; PLAT ii,iv-vi,xii (MZFC).
- Hamadryas februa ferentina*** (Godart [1824]). AD i,ii,iv,vi-ix,xii (MZFC); CAL i (SDNHM), X (MZFC, SDNHM); CHAN i (ADW, MZFC); COL i-v,xi (SDNHM), i,iii (MZFC); ESA i (ADW, MZFC); LSA xi (exCLGC); MAD xii (SDNHM); MZO i (LACM); OJO v,ix (MZFC); PA xii; PACA I; PENU i (ADW, MZFC); PLAT iv,vi (MZFC); PORO xii (ADW, MZFC); San Francisco (Jenkins 1983); TAM ix (SDNHM); TECM (Jenkins 1983).
- Hamadryas feronia farinulenta*** (Frühstorfer 1916). CAL X (SDNHM); MAD iv (SDNHM).
- Hamadryas glauconome grisea*** Jenkins 1983. AD i,ii,iv,vi-x,xii (MZFC); CAL X (SDNHM); COL (Jenkins 1983), X (MZFC); COM (Jenkins 1983); ESA i (ADW, MZFC); LSA (Jenkins 1983), vi (exCLGC); MAD iv (SDNHM); xi (LACM); PA xii; PACA i; PENU i; Peña Colorada, MZO vii (MZFC); TAM vi,vii (exCLGC); TECL vii; Turla X (SDNHM). Jenkins (1983) cites specimens intermediate between *H. glauconome glauconome* and *H. glauconome grisea* from COL, LSA and MAD.
- Hamadryas guatemalena marmorice*** (Frühstorfer 1916). AD vi-x,xii; Cerro de la Media Luna, Coquimatlán ix (MZFC); COL (Jenkins 1983), ii,iii,v (SDNHM), iii (MZFC); ESA i (ADW, MZFC); Juárez (SDNHM); MAD (Jenkins 1983), xii (SDNHM); MZO i (ADW); PA xii (MZFC); PACA i (ADW, MZFC); PLAT x,xii (MZFC); TAM vii (exCLGC); TECL vii; Turla X (SDNHM).
- Pyrrhogyra neareea hypsenor*** Godm. & Sal. 1884. AD vii-ix,xi,xii (MZFC); CHAN i (ADW, MZFC); COL (AMNH), X (SDNHM); COM ix (SDNHM); ESA i (ADW); LSA vi (exCLGC); MAD iv (SDNHM); MZO xii (ADW, LACM); MZO, 5 mi N, on Hwy. to Minatitlán ix (LACM); PA xii (ADW); PACA i (ADW, MZFC); PENU i; PLAT vi (ADW), i,iv,x-xii; PORO xii (MZFC); Río Comala, COM ix (MZFC).
- Temenis laothoe quilapayunia*** R.G. Maza & Turrent 1985. AD i,iv,viii-xi,xii (MZFC); COL (AMNH), iii,iv,x (SDNHM); PACA i; PLAT iv,vi,xi,xii; SUCH ix (MZFC); TAM vii (exCLGC).
- Epiphile adrasta escalantei*** Descimon & Mast 1979. AD i,viii,xi,xii (MZFC); Cofradía

- xi,xii (SH: Jenkins 1986); COSU x,xii (SDNHM, MZFC); COL xi (JC: Jenkins 1986); PLAT ix,x,xii (MZFC).
- Dynamine dyonis** Geyer 1837. AD viii-x (MZFC); COL (AMNH); MZO i (LACM); PACA i (ADW); PLAT xi (MZFC).
- Dynamine postverta mexicana** D'Almeida 1952. AD ii,vii-xi (MZFC); COSU ix; COL ii (SDNHM); ESA i; PENU i (ADW, MZFC).
- Diaethria asteria** (Godm. & Sal. 1894). AD x-xii (MZFC); COSU (De la Maza & Turrent 1985), x,xi,xii (SDNHM), x-xii (MZFC); COL (AMNH); COM (De la Maza & Turrent 1985); LSA iv (AME); PLAT viii-xii (MZFC); SUCH (De la Maza 1987); Volcán de Fuego (De la Maza & Turrent 1985). See Luis et al. (1996).
- Cyclogramma bacchis** (Doubleday [1849]). COL xi,xii (SDNHM); COSU viii,xi,xii (MZFC), X (SDNHM); LSA (De la Maza 1987); PLAT ix-xi (MZFC); Quisería X (SDNHM), xii; SUCH X (MZFC).
- Cyclogramma pandama** (Doubleday [1849]). AD ii; BAG i (MZFC); San Antonio (De la Maza 1987).
- Adelpha basiloides basiloides** (Bates 1865). AD x; Cerro de la Media Luna, Coquimatlán ix (MZFC); COL xi (SDNHM).
- Adelpha celerio diademata** Frühstorfer [1913]. COSU xi (MZFC).
- Adelpha fessonia fessonia** (Hewit. 1847). AD iv,vi,ix (MZFC); CAL xi (SDNHM); CHAN i (MZFC); COL (AMNH), v (SDNHM); COM v (AME); MZO i (LACM); OJO v; PACA i (MZFC); PORO xii (ADW, MZFC); Volcanillos xi (MZFC).
- Adelpha iphicles massilides** Frühstorfer [1916]. AD vii-xi; CAL i,xi; Cerro de la Media Luna, Coquimatlán viii; CHAN i (MZFC); COSU ix (SDNHM); COM i,ix,x (AME); ESA i (ADW); LSA v (Beutelspacher 1976), viii (SDNHM); PA xii; PACA i; PLAT i-iv,viii-xi,xii; PORO xii (MZFC); PJU X (SDNHM); Tepames X (SDNHM).
- Adelpha ixia leucas** Frühstorfer [1916]. PLAT xii (MZFC).
- Adelpha leuceria leuceria** (Druce 1874). "COL" vii (AMNH).
- Adelpha naxia epiphicla** Godm. & Sal. 1884. COM i (AME).
- Adelpha phylaca phylaca** (Bates 1866). AD xi; PLAT vi,xi,xii (MZFC).
- Adelpha serpa massilia** (C. Felder & R. Felder 1867). CHAN i (ADW); COL (AMNH); LSA X (Beutelspacher 1976); MZO i (LACM); PA xii (MZFC); PACA i (ADW); PORO xii (MZFC); Río Las Piedras vii (Beutelspacher 1976).
- Marpesia chiron marius** (Cr. 1780). AD iv,vi,vii,ix-xii (MZFC); CHAN i (ADW); ESA i (ADW, MZFC); Laguna Amela, TECM vii (MZFC); MZO xii (LACM); PACA i (ADW); PLAT i,iv,vi,ix,x,xii (MZFC); TAM viii (SDNHM).
- Marpesia petreus tethys** (Fabr. [1777]). AD vi-ix,xii (MZFC); CHAN i (ADW, MZFC); COSU x; COL iv,ix,x (SDNHM); ESA i (ADW); LSA (De la Maza 1987); MAD i,xii (SDNHM); MZO i (LACM); PA xii (ADW); PACA i; PENU i (ADW, MZFC); PLAT i,iv,x,xii; PORO xii (MZFC); TAM viii (SDNHM), xi (MZFC).
- Archaeoprepona demophon occidentalis** Stoffel & Descimon 1974. AD i,ii,viii-x,xii (MZFC); COL iii (AMNH), i,xi,xii (SDNHM); ESA i (ADW); LSA (De la Maza 1987); PA xii (MZFC); PACA i (ADW, MZFC); PENU i (ADW); PLAT ii,iv (MZFC); PORO xii (ADW, MZFC).
- Archaeoprepona demophon mexicana** Llorente, Descimon & Johnson 1993. AD vi-viii,xii (MZFC); COL xii (AMNH); COSU iv (MZFC); COM (De la Maza 1987); ESA i (ADW); PA xii; PACA i; PLAT xii (MZFC).
- Prepona laertes octavia** Frühstorfer 1905. PA xii (ADW); PLAT x,xii (MZFC).
- Zaretis callidryas** (R. Feld. 1869). LSA (De la Maza 1987); PORO xii (ADW).
- Zaretis ellops anzuletta** Frühstorfer 1909. AD i,ii,iv,vii-x,xii; BAG X (MZFC); COL (AMNH); LSA (De la Maza 1987); MAD v (SDNHM); PACA i; PLAT iv,ix,xii; PJU X (MZFC).
- Siderone galanthis** (Cr. [1775]). AD iv,viii,xii (MZFC); CHAN i (ADW, MZFC); COL (AMNH), v (SDNHM); ESA i (MZFC); LSA (De la Maza 1987); PA xii; PACA i (ADW); PENU i; PLAT xi (MZFC).
- Hypna clytemnestra mexicana** Hall 1917. AD vi (MZFC); Bahía Tangola (AMNH); COL (USNM); LSA (De la Maza 1987); PORO xii; TAM viii (MZFC), viii,ix (SDNHM).
- Anaea aidea** (Guérin [1844]). Agua Amarilla viii (USNM); AD i,ii,iv,vi-x,xii; Cerro de la

- Media Luna, Coquimatlán viii (MZFC); COL (AMNH); LSA (De la Maza 1987); PACA i (ADW); PLAT i,ii,iv,vi,viii,x,xii (MZFC); PJU X (SDNHM); TECL vii; Tepames viii,x (SDNHM).
- Consul fabius cecrops*** (Doubleday [1849]). AD ix (MZFC); CHAN i (ADW, MZFC); MAD (De la Maza 1987), X (SDNHM); PA xii (ADW, MZFC); PACA i; PENU i; PLAT xii; Río Comala, COM ix (MZFC).
- Fountainea euryppyle glanzi*** (Rotger, Escalante & Coronado 1965). AD i,iv,viii (MZFC); COL (AMNH); LSA (De la Maza 1987); PENU i (ADW); PLAT iv,vi,ix,x,xii (MZFC); PACA i (ADW).
- Fountainea glycerium glycerium*** (Doubleday [1849]). AD ii,x; BAG X (MZFC); COL (AMNH); PLAT ix,x,xii (MZFC).
- Fountainea tehuana*** (Hall 1917). PORO xii (ADW, MZFC).
- Memphis forreri*** (Godm. & Sal. 1884). AD iv; CHAN i (MZFC); COL (AMNH); LSA (De la Maza 1987); MAD v (SDNHM); MZO i (ADW); OJO x; PA xii; PENU i (MZFC); PORO xii (ADW, MZFC); PJU x; TAM i,viii,ix,xi (MZFC).
- Memphis pithyusa*** (R. Feld. 1869). AD ix; PA xii; PACA i; PLAT i,x,xii (MZFC); PORO xii (ADW); PJU X (SDNHM); TAM ix (MZFC).
- {***Memphis xenocles carolina*** W.P. Comstock 1961}. "COL" X (AMNH). This is the only record of this species from western Mexico.
- Doxocopa laure acca*** (C. Feld. & R. Feld. 1867). AD ii,vi,vii,ix,xi,xii (MZFC); CHAN i (ADW, MZFC); COL ix (AMNH) iv,v; COM ix (SDNHM); El Chanal vii (MZFC); ESA i (ADW, MZFC); LSA (De la Maza 1987); OJO xii (MZFC); PA xii; PACA i (ADW, MZFC); PLAT vi,xii (ADW), vii,x (MZFC); PORO xii (ADW, MZFC); Río Comala, COM ix (MZFC); TAM vii (exCLGC).
- Doxocopa pavon theodora*** (Lucas 1857). COL iii (AMNH); LSA (De la Maza 1987); MZO xii (LACM).
- Pessonia polyphemus polyphemus*** Westw. 1851. AD i,vi-x,xii (MZFC); Bahía Santiago i (AMNH); CHAN i (ADW, MZFC); COL (AMNH), i,ii,xi (SDNHM); ESA i (ADW, MZFC); MZO (Godman & Salvin 1878-1901), i (ADW, LACM); PA xii; PACA i; PENU i (ADW, MZFC); PLAT iv,vi,ix,x,xii (MZFC); PORO xii (ADW, MZFC); Tonila, 10 mi S vii (AMNH).
- Opsiphanes boisduvalii*** Doubleday [1849]. AD iv,vii-x,xii (MZFC); COL i (MZFC), ii (AME), ii,xi (SDNHM); COM ix (AME); LSA (De la Maza 1987), v (AME); MZO i; PA xii (ADW); PACA i; PLAT x,xii; Río Comala, COM ix (MZFC).
- Opsiphanes invirae fabricii*** (Boisd. 1870). CAL i (SDNHM, MZFC); COL viii (AME), i-iii,v,x,xi (SDNHM), xii (AMNH); Huerta El Boliche, COL ix (MZFC); MZO (De la Maza 1987), i,xii (ADW); San Gerónimo vii (AME).
- Opsiphanes tamarindi*** C. Feld. & R. Feld. 1861. COL i; OJO ix; PJU X (SDNHM); TAM vii (exCLGC).
- Danaus eresimus montezuma*** Talbot 1943. AD vii,viii,x (MZFC); CAL X (SDNHM); CHAN i (ADW, MZFC); COL iv,v (SDNHM); PA xii (MZFC); PACA i (ADW, MZFC); PLAT ii,viii-x,xii (MZFC).
- Danaus gilippus thersippus*** (Bates 1863). AD iv,vi,vii-x,xii (MZFC); Cornwallis Bay Naval Base, Socorro Is., RI xi (LACM: Brown 1990); CHAN i (ADW, MZFC); COL i-v,x,xi (SDNHM); ESA i (MZFC); MZO xii (LACM); PA xii; PACA i; PLAT vi,vii,x,xii (MZFC).
- Danaus plexippus plexippus*** (L. 1758). Buenavista X (DGSV: Hernández, Martínez & Rodríguez 1981); COL i,iii,iv,xi (SDNHM); Esperanza viii (USNM); PACA i (ADW).
- Lycorea halia atergatis*** Doubleday [1847]. AD xii (MZFC); COL (AMNH); PLAT iv,ix (MZFC).
- Melinaea ethra flavicans*** C.C. Hoffmann 1924. COL xi (SDNHM); PLAT iv,vi (MZFC); SUCH (De la Maza 1987), iii (SDNHM); Volcanillos xi (MZFC).
- {***Mechanitis polymnia lycidice*** Bates 1864}. "COL" (CMNH).
- Dircenna klugii klugii*** (Geyer, 1837). SE slope Volcán de Colima xii (CAS).
- Pteronymia cottyto*** (Guérin [1844]). MZO i (LACM).
- Pteronymia rufocincta*** (Sal. 1869). PLAT vi (ADW), ix (MZFC); SUCH (De la Maza 1987).

- Greta morgane morgane*** (Geyer 1837). AD vii,x; BAG x,xi (MZFC); COL xi (SDNHM); COSU vii,ix-xi (SDNHM), viii,x (MZFC); El Jabali viii (UCR); Hacienda San Antonio xi; PLAT vii-xii (MZFC); Rancho San Antonio ix (MZFC), xi (SDNMH); SUCH (De la Maza 1987), iii,viii (SDNHM); Volcanillos xi (MZFC).
- Greta annette moschion*** (Godm. 1901). BAG X (MZFC); COL xi (SDNHM); PLAT X (MZFC); SUCH (De la Maza 1987).
- Libytheana carinenta mexicana*** Michener 1943. AD i,vi,vii,ix,xi (MZFC); CHAN i (ADW); COL x,xi; COM ix (SDNHM); ESA i (ADW); LSA (De la Maza 1987); MAD xi (AME); OJO vii (MZFC), viii (SDNHM); PACA i (MZFC); PENU i (ADW).
- Manataria maculata*** (Hopffer 1874). AD xii (MZFC); COM (De la Maza 1987); PLAT vi (MZFC).
- Cyllopsis caballeri*** Beutelspacher 1982. COL (Miller & De la Maza 1984); Volcanillos xi (MZFC).
- Cyllopsis hedemanni hedemanni*** R. Feld. 1869. SE slope Volcán de Colima xii (CAS).
- ***Cyllopsis windi*** L. Miller 1974. Volcán de Colima xii (AME: Miller 1974).
 - ***Cyllopsis diazi*** L. Miller 1974. ETE vi (ADW).
- Cyllopsis suivalenoides*** L. Miller 1974. COL xi; Yerbabuena vi (SDNHM).
- Dioriste tauropolis*** (Westw. [1850]). BAG x,xi (MZFC).
- Euptychia fetna*** Butl. 1870. AD ix; El Jabali viii (UCR); PLAT viii-x (MZFC).
- Hermeuptychia hermes*** (Fabr. 1775). AD i,ii,iv,vi,vii,ix-xii (MZFC); CHAN i (ADW); COL (AME), i-v,x,xi (SDNHM); COM (AME); El Jabali viii (UCR); ESA i (ADW, MZFC); MZO (AME), i,xii (ADW); OJO viii (MZFC); PA xii; PACA i (ADW, MZFC); PLAT iv,vii,xii (MZFC); TAM vii (exCLGC); Yerbabuena vi (SDNHM).
- Megisto rubricata pseudocleophes*** L. Miller 1976. AD iv,vi,viii (MZFC).
- Paramacera xicaque xicaque*** (Reak. [1867]). Cerro Grande xi; ETE X (MZFC).
- Pindis squamistriga*** R. Feld. 1869. AD i,ii,iv,vii,x,xii; BAG i; El Jabali viii (UCR); PLAT i,ii,iv,vi,viii-xii (MZFC); Rancho San Antonio xi (SDNHM); Río Comala, COM X (MZFC); Tinajas xi (SDNHM); Volcanillos xi (MZFC).
- Taygetis mermeria griseomarginata*** L. Miller 1978. AD iv,vi,xii (MZFC); COL i (AME), viii,x (MZFC); COM i [Type Locality] (Miller 1978), vii,x (AME); ETE vi; PA xii (ADW); PACA i (ADW, MZFC); PLAT iv,vi,x,xii (MZFC); PORO xii (ADW).
- Taygetis uncinata*** Weymer 1907. AD ii,iv,vi,xii; CHAN i (MZFC); COL v,vii,x,xi (AME), iii (SDNHM), viii (MZFC); COM iii,v,vii-x (AME); ESA i (ADW, MZFC); LSA xi (AME); MZO i; PA xii (ADW); PACA i; PENU i (ADW, MZFC); PLAT iii,iv,vi (MZFC); PORO xii (ADW); Rancho San Antonio xi (SDNHM); Río Comala, COM i,ix (MZFC).
- ***Taygetis virgilia*** (Cr. 1776). AD iv,vi,xii (MZFC); CHAN i (ADW); ESA i (ADW, MZFC); PA xii (ADW); PACA i (MZFC); PENU i (ADW, MZFC); PLAT vi (MZFC).
- Taygetis weymeri*** Draudt 1912. AD iv,v,xii (MZFC); COM vi (AME); El Jabali viii (UCR); ETE vi (ADW); PLAT iii,iv,vi,x (MZFC).
- Vareuptychia similis*** (Butl. 1867). COL v (AME), i (SDNHM); COM iii-v,ix,x; LSA X (AME); MAD iv (SDNHM).
- Vareuptychia themis*** (Butl. 1867). AD i,ii,iv,vi,vii,ix,x,xii; BAG i; CAL ii,iii (MZFC), X (SDNHM); CHAN i; ESA i (ADW, MZFC); MZO i; PA xii (ADW); PACA i (ADW, MZFC); PENU I; PLAT i,ii,iv,vi-viii,x,xii (MZFC); PORO xii (ADW, MZFC); Tepames X (SDNHM).
- Vareuptychia undina*** (Butl. 1870). AD vii-x; PLAT vii,viii (MZFC); TAM vii (exCLGC).

LYCAENIDAE (128 SPECIES)

- Euselasia eubule*** (R. Feld. 1869). PLAT xi (MZFC).
- Euselasia aurantiaca*** (Sal. & Godm. 1868). El Jabali viii (UCR).
- Mesosemia lamachus*** (Hewit. 1857). AD xii (MZFC); PENU i (ADW); PLAT i,ii,ix,xi,xii; PACA i (MZFC).
- Napaea umbra umbra*** (Boisd. 1870). BAG x; PLAT iii (MZFC); San Gerónimo vii (CMNH).
- Rhetus arcus beutelspacheri*** Llorente 1988. PLAT viii-x (MZFC).

- *Calephelis argyrodines* (Bates 1866). ESA i (ADW); MZO viii (USNM); PA xii (ADW).
- Calephelis fulmen* Stichel 1910. COL ix (SDNHM); PA xii; PENU i (ADW).
- *Calephelis laverna laverna* (Godm. & Sal. 1886). COM x; LSA viii (AME).
- Calephelis mexicana* McAlpine 1971. COM iii (SDNHM); El Jabali viii (UCR); PA xii; PACA i (ADW); PENU i.
- Calephelis montezuma* McAlpine 1971. CAL i (SDNHM); CHAN i; El Jabali viii (UCR); ESA i; PA xii; PACA i (ADW, MZFC); PENU i; PORO xii (ADW).
- Calephelis nemesis nemesis* (W. H. Edw. 1871). COM i; El Jabali viii (UCR); Tonilita ii (AME).
- Calephelis perditalis perditalis* Barnes & McDunnough 1918. COL viii,x (SDNHM); COM i,viii (AME); El jabali viii (UCR); ESA i; PA xii (ADW); Tonilita ii (AME); Yerbabuena vi (SDNHM). As in the Jalisco butterfly list (Vargas et al. 1996), all *Calephelis* records presented here should be considered tentative, until a new revision of the genus is presented.
- Caria ino ino* Godm. & Sal. 1866. AD viii,x (MZFC); CHAN i (ADW); COM iii,x (AME), vi-ix (CMNH); Coquimatlán v (CMNH); PLAT vi,ix (MZFC).
- Caria stilliticia* Dyar 1912. AD x; El Jabali viii (UCR); PLAT vi (ADW), viii-xi (MZFC).
- Baeotis zonata simbla* (Boisd. 1870). AD vii,viii (MZFC); CHAN i (ADW, MZFC); COL iv,v (AMNH), viii (MZFC), ix (CMNH); COM i,x (AME), iii,vi,vii,x; El Jabali viii (UCR); LSA iv (CMNH), vi (exCLGC); PLAT vii; PORO xii (MZFC).
- Lasia sula sula* Staud. 1888. AD ii,vii-xii (MZFC), vi (ADW); COL (AME: Clench 1972), iv (AMNH), X (MZFC); COM (CMNH: Clench 1972), iii,v,ix,x (CMNH); LSA (AME: Clench 1972), i (AME), xi (MZFC); PLAT ix,x (MZFC); TAM vi (exCLGC), ix (MZFC).
- Lasia agesilas callaina* Clench 1972. AD vii,x (MZFC); COL (AMNH: Clench 1972), X (AMNH); PLAT ix,x (MZFC).
- *Lasia sessilis* Schaus 1890. Tepames, 0.9 mi S ix (SDNHM).
- Lasia maria maria* Clench 1972. AD vii-x (MZFC); COL i (AME); COM v (CMNH); PLAT ix,x (MZFC).
- Exoplisia* aff. *cadmeis* (Hewitt. [1866]). ESA i (ADW, MZFC); PACA i (MZFC).
- Melanis cephise cephise* (Mén. 1855). AD xii (MZFC); COL (De la Maza 1987, USNM), ix,x (AME), v,xii (AMNH), iv,vii (SDNHM); COM ix,x (AME), ix (SDNHM), iii,x (CMNH); Las Conchas, Ixtlahuacán vii (MZFC, SDNHM); MAD iv (SDNHM); MZO i (LACM), xii (ADW); PENU i; PLAT ii,v,viii-x (MZFC); PJU viii (SDNHM), X (LACM); San Gerónimo vii (CMNH); San Francisco i,xii (AMNH); TECM iii,iv (INIA: Domínguez & Carrillo 1976). Two species are apparently represented by these records.
- Melanis pixe sepxunctata* (Seitz 1917). AD iii,viii-xii; CAL i (MZFC), ii,x (SDNHM); CHAN i (ADW, MZFC); COL ii-iv (AMNH); COM x,xi (AME); ESA i (ADW); LSA v (CMNH); MAD v,vi (SDNHM); MZO i (AME, LACM); OJO (SDNHM), i,ix (MZFC); PACA i (ADW, MZFC); PLAT ii,iv-vi,viii-x,xii (MZFC), vi (ADW).
- Anteros carausius carausius* Westw. [1851]. AD i,xi; CAL; COL ix (MZFC), iii,iv (AMNH); COM viii,x (AME); El Jabali viii (UCR); ESA i (MZFC); PA xii (ADW); PACA i; PLAT ii,xi (MZFC); Tepames, 0.9 mi S ix (SDNHM); Tonilita ii (AME).
- Calynda sternula hegias* R. Feld. 1869. El Jabali viii (UCR).
- Emesis ares ares* (W. H. Edw. 1882). El Jabali viii (UCR).
- Emesis mandana furor* Butl. & Druce 1872. AD ix; COSU X (MZFC); COM iv,v (CMNH); ESA i (ADW); Quesería X (MZFC).
- Emesis vulpina* Godm. & Sal. 1886. AD vi (MZFC); CHAN i (ADW); COL viii (CMNH), ix (SDNHM); COM i,vi (AME), ix (SDNHM), iv,v,vii-x,xii; Coquimatlán v (CMNH); ESA i (ADW); LSA v,vi (CMNH); PACA i (ADW, MZFC); PENU i; PLAT vi; PORO xii (ADW).
- Emesis poeas* Godm. & Sal. 1901. AD iv,vi-ix,xi (MZFC); COL (AMNH); COM vii (CMNH); ESA i (ADW); LSA vi (CMNH), viii,ix (SDNHM); PLAT vi (ADW), iv,vii,ix; TECL vii (MZFC).
- Emesis tenedia tenedia* C. Feld. & R. Feld. 1861. AD iii,iv,vi-xii (MZFC); CAL i

- (SDNHM); CHAN i (ADW, MZFC); COL i,iv,x,xi (SDNHM); COM i (AME), iii-x (CMNH), iii (SDNHM); COSU vi,x (SDNHM); ESA i; PACA i (ADW, MZFC); PLAT i-iv,vi,viii-xi (MZFC); Quesería X (MZFC); San Antonio vii (CMNH); SUCH X (MZFC).
- Emesis emesia emesia*** (Hewit. 1867). AD viii,x,xi (MZFC); Bahía Santiago xi (AMNH); CHAN i (ADW, MZFC); COL ix (MZFC); COM iv,v,viii; Coquimatlán v; LSA v (CMNH); MZO i (LACM), vii,viii (SDNHM), viii (UCR); PA xii (ADW); PORO xii (ADW, MZFC).
- ***Emesis tegula*** Godm. & Sal. 1886. CAL i; COL X (MZFC), xi (SDNHM); COM viii (AME); El Jabali viii (UCR); Las Conchas, Ixtlahuacán vii (MZFC).
- Pseudonymphidia clearista*** (Butl. 1871). CAL i (MZFC); COM vi (CMNH); LSA vi (ex-CLGC).
- Apodemia hypoglauca hypoglauca*** (Godm. & Sal. 1878). El Jabali viii (UCR); PLAT vii,x (MZFC).
- Apodemia multiplaga*** Schaus 1902. COL i (AMNH); COM v,x (CMNH); Tepames, 0.9 mi S ix (SDNHM).
- Apodemia walkeri*** Godm. & Sal. 1886. AD viii,ix (MZFC); CHAN i (ADW); COL iii,viii,ix; COM iv vii,x,xi (CMNH), viii (AME), viii-x; El Jabali viii (UCR); PLAT i,ii (MZFC).
- Thisbe lycorias lycorias*** (Hewit. [1853]). AD vi,viii,ix (MZFC); COL iii (CMNH, AMNH), iv (SDNHM); COM vi (AME), vii (CMNH); LSA ix (SDNHM); MZO v (AMNH); PLAT i (MZFC), vi (ADW); PJU ix; Río Naranjo iv (SDNHM); TAM vi (exCLGC), X (LACM).
- ***Lemonias agave*** Godm. & Sal. 1886. "COL" (CMNH).
- Synargis mycone*** (Hewit. 1865). AD vii,viii,xi,xii (MZFC); COL (AMNH); COM iii (CMNH); ESA i (MZFC); PACA i (ADW, MZFC); TAM X (MZFC).
- Calospila zeurippa*** Boisdu. 1836. OJO X (MZFC).
- Pandemos godmanii*** Dewitz 1877. "COL" (AMNH).
- Adelotya eudocia*** (Godm. & Sal. 1897). COM vii,viii (CMNH).
- Theope virgilius virgilius*** (Fabr. 1793). PLAT vi (ADW).
- Theope eupolis*** Schaus 1890. MZO i (USNM).
- Theope diores*** Godm. & Sal. 1897. AD X (MZFC); COM vi,ix,x (AME); LSA (De la Maza 1987); PLAT vi,xi (MZFC). *Theope diores* may be a synonym of *eupolis*, but until the two taxa are reviewed, we have listed them separately.
- Theope publius*** C. Feld. & R. Feld. 1861. COL (AMNH), iii (CMNH), iii,v (AME); CHAN i (ADW); COM iv (CMNH), viii,x (AME), iii; OJO ix; SUCH i (MZFC).
- ***Theope mania*** Godm. & Sal. 1897. PLAT vi (ADW),vii,ix,x (MZFC); SUCH iv (SDNHM), vi,x (MZFC).
 - {***Theope hypoxanthe*** Bates [1868]}. COL ix; COM v (AME).
- Theope pedias isia*** Godm. & Sal. 1878. AD iv (MZFC).
- Calociasma lilina*** (Butl. 1870). MAD (De la Maza 1987).
- Eumaeus toxea*** (Godart 1824). "COL" (AMNH).
- Evenus regalis*** (Cr. 1775). AD xi (MZFC); COL iii (CIB); COM iii,iv (CMNH); MZO, 5 mi N ix (LACM).
- Allosmaitia strophius*** (Godart 1824). El Jabali viii (UCR).
- Pseudolycaena damo*** (Druce 1875). COL ii,iii,ix (CIB); COM iii,iv (CMNH); El Jabali viii (UCR); ESA i; MZO ii (CIB); PA xii (ADW, MZFC); PACA i; PLAT vi,ix (MZFC); TAM vii (exCLGC).
- Arcas cypria*** (Geyer 1837). PLAT xi (MZFC).
- Atlides gaumeri*** (Godm. 1901). COL viii (USNM).
- Atlides carpasia*** (Hewit. 1868). MZO i (ADW).
- Paiwarria umbratus*** (Geyer 1837). AD ix-xi; PLAT iv,ix (MZFC).
- "Thecla" (ligurina group) ligurina** (Hewit. 1874). El Jabali viii (UCR).
- Contrafacia bassania*** (Hewit. 1868). El Jabali viii (UCR).
- Thereus cithonius*** (Godart 1824). "COL" (CMNH; Johnson 1989b); El Jabali viii (UCR).
- Thereus oppia*** (Godm. & Sal. 1887). COL (USNM), iii; COM vii (CMNH); El Jabali viii (UCR).

- Thereus orasus* (Godm. & Sal. 1887). El Jabali viii (UCR).
- Aravacus sito* (Boisd. 1836). AD ii,viii,ix (MZFC); COL ii,iv,xii (CIB); COM iii,iv,ix,xii (CMNH); ESA i (ADW, MZFC); MZO i,xii (USNM), xii (CIB); PENU i (ADW); PLAT iv (MZFC).
- Aravacus jada* (Hewit. 1867). AD vi (ADW); COL iv (CIB), xi (exCLGC); El Jabali viii (UCR); PLAT iv,vi,vii,ix-xi (MZFC).
- Rekoa meton* (Cr. 1780). COM v (Robbins 1991); El Jabali viii (UCR); PLAT vi,ix,xi (MZFC).
- Rekoa palegon* (Cr. 1780). COL iii,iv (CIB), iii,iv,viii,xii (Robbins 1991); El Jabali viii (UCR); PLAT ii,iv (MZFC); ESA i (ADW).
- Rekoa zebina* (Hewit. 1869). COL iii; COM X (Robbins 1991); El Jabali viii (UCR).
- Rekoa marius* (Lucas 1857). AD xi (MZFC); COL iv; COM iv (Robbins 1991); OJO ix (LACM); PACA i; PLAT i (MZFC).
- Rekoa stagira* (Hewit. 1867). COL iii (Robbins 1991); PLAT xi (MZFC).
- Ocaria ocrisia* (Hewit. 1868). AD ix, X (MZFC); COM vii (CMNH); El Jabali viii (UCR); PLAT ix,x (MZFC).
- Chlorostrymon simaethis* (Drury 1773). AD vi (MZFC); COL iv (AMNH: Johnson 1989a); Socorro Is., RI iv (LACM: Brown 1990, LACM); PLAT xi (MZFC).
- Chlorostrymon telea* (Hewit. 1868). COL iii (CMNH, AMNH: Johnson 1989a); COM iv (CMNH); PA xii (ADW); PACA i (MZFC).
- Cyanophrys herodotus* (Fabr. 1793). AD ix (MZFC); CHAN i (ADW); ESA i (ADW, MZFC); PLAT ii,vi,ix-xi (MZFC).
- Cyanophrys miserabilis* (Clench 1946). COL (Clench 1946, BMNH: Clench 1981), ii,iv (USNM); El Jabali viii (UCR); PACA i (ADW, MZFC); PLAT vi (ADW), viii,xi (MZFC); An apparent male hybrid between *C. herodotus* and *C. miserabilis* was taken at PLAT in June by ADW.
- Cyanophrys longula* (Hewit. 1868). "COL" (AMNH); El Jabali viii (UCR).
- Panthiades bitias* (Cr. 1777). COL (AME: Nicolay 1976), ix,x (LACM), ix (USNM); CHAN i (ADW); COM (AME: Nicolay 1976), iii,v,ix (CMNH); PA xii (ADW).
- Panthiades ochus* (Godm. & Sal. 1887). PLAT ix (MZFC).
- Panthiades bathildis* (C. Feld. & R. Feld. 1865). AD iii (MZFC); CAL ii (SDNHM); CHAN i (ADW, MZFC); COL iii-v (CMNH: Nicolay 1976, CMNH), iii,iv (CIB); COM (CMNH: Nicolay 1976); ESA i (ADW, MZFC); MZO (AMNH), xii (ADW, CIB); PLAT vi (ADW), ii,ix (MZFC).
- Oenomaus ortygnus* (Cr. 1779). COL ix (CMNH); PLAT vi (MZFC).
- Parrhasius polibetes* (Cr. 1782). AD xi (MZFC); COL-COM (CMNH: Nicolay 1979); COM iii,iv (CMNH); PLAT ix-xi (MZFC).
- Parrhasius moctezuma* Clench 1971. El Huapuste, ETE X (MZFC); El Jabali viii (UCR).
- Michaelus jebus* (Godart 1824). PLAT vi (ADW).
- Michaelus hecate* (Godm. & Sal. 1887). COL (CMNH: Nicolay 1979), iv (USNM); PLAT vi (ADW).
- Michaelus vibidia* (Hewit. 1869). COL (AMNH: Nicolay 1979), ix (SDNHM).
- Strymon melinus* (Hübner 1813). Clarión Is., RI (CIB, USNM, Brown 1990, Vázquez 1957), i,iii,v (LACM); S side Clarión Is., RI iv (LACM).
- Strymon albata* (C. Feld. & R. Feld. 1865). AD i,iv,vi,viii (MZFC); CAL i (SDNHM); CHAN i; ESA i (MZFC); MZO i (USNM), xii (CIB); PENU i (ADW); PLAT iv (MZFC).
- Strymon rufosusca* (Hewit. 1877). "COL" (AMNH, USNM).
- Strymon bebrycia* (Hewit. 1868). PLAT vi (ADW).
- Strymon bazochii* (Godart, 1824). COL iv (SDNHM).
- Strymon yojoa* (Reak. 1867). AD ix,x (MZFC); El Jabali viii (UCR); PLAT i,vi (MZFC).
- Strymon cestri* (Reak. 1867). COL iii,iv (CMNH); El Jabali viii (UCR).
- Strymon istapa* (Reak. 1867). Clarión Is., RI (Brown 1990), i,v (LACM), v (CIB: Vázquez 1957), viii (CIB: Vázquez & Zaragoza 1979); El Jabali viii (UCR); Laguna Nam (CIB); MZO i (USNM), xii (CIB); PLAT iv (MZFC); PORO xii (ADW); Socorro Is., RI v (CIB: Vázquez 1957), i,v (Vázquez 1958), iv,v (LACM).

- Strymon ziba* (Hewit. 1868). "COL" (USNM).
- Strymon serapio* (Godm. & Sal. 1887). AD xi (MZFC).
- "*Thecla*" (*arza* group) *tarpa* (Godm. & Sal. 1887). PLAT i (MZFC).
- Kisutam ceromia* (Hewit. 1877). COL iii,iv (CIB).
- Electrostrymon mathewi* (Hewit. 1874). AD ii (MZFC).
- Electrostrymon sangala* (Hewit. 1868). AD xi (MZFC); CHAN i (ADW); COL iv (CIB); MZO i; PA xii (ADW).
- Electrostrymon canus* (Druce 1907). COL ii,iii (CIB); PA xii; PACA i (ADW); PLAT ix (MZFC).
- *Symbiopsis* aff. *tanais* (Godm. & Sal. 1887). COL iv (CIB).
- Calycopis demonassa* (Hewit. 1868). COM iv,v (CMNH); LSA (De la Maza 1987).
- Calycopis clarina* (Hewit. 1874). COM iii (CMNH).
- Calycopis isobeon* (Butl. & Druce 1872). AD vi; CHAN i (MZFC); COL iii,iv (CIB); El Jabali viii (UCR); ESA i; PA xii; PACA i (ADW, MZFC); PENU i; PLAT i,iv (MZFC), vi (ADW).
- Calycopis susanna* Field 1967. COL (USNM), ii–iv,xii (Field 1967). This species is apparently a synonym of *C. isobeon*.
- Tmolus echion* (L. 1767). AD vi (MZFC); COL iv (CIB), ix (USNM); MZO i,xii (ADW); El Jabali viii (UCR); PLAT i,ii,v,vi (MZFC).
- *Tmolus crolinus* (Butl. & Druce 1872) "COL" (AMNH).
- "*Thecla*" (*keila* group) *keila* (Hewit. 1869). "COL" (AMNH).
- Theclopsis mycon* (Godm. & Sal. 1887). El Jabali viii (UCR); PLAT X (MZFC).
- Siderus tephraeus* (Geyer 1837). AD xi (MZFC); CHAN i (ADW); El Jabali viii (UCR); ESA i (MZFC); MZO xii; PA xii; PACA i (ADW); PLAT vi (MZFC).
- Ministrymon clytie* (W. H. Edw. 1877). AD xi (MZFC); CHAN i (ADW); COL X (LACM), xi (SDNHM); El Jabali viii (UCR); ESA i (MZFC); PA xii; PENU i (ADW); PLAT ii,vi,ix,x (MZFC).
- Ministrymon phrutus* (Geyer 1832). CHAN i (ADW); El Jabali viii (UCR); PLAT vi,ix (MZFC).
- Ministrymon azia* (Hewit. 1873). AD xi (MZFC); COL X (SDNHM); ESA i (ADW, MZFC); MZO xii (ADW); PENU i; PLAT ii,iv,x (MZFC).
- Ipidecla miadora* Dyar 1916. COM iv,v (CMNH); El Jabali viii (UCR); PLAT vi (MZFC).
- Brangas neora* (Hewit. 1867). COL iv; COM viii (USNM).
- Chalybs hassan* (Stoll 1790). COL X (SDNHM); COM iv (USNM); PA xii (ADW).
- Hypostrymon critola* (Hewit. 1874). COL (CMNH; Clench 1975); COM viii,xi; LSA v (AME; Clench 1975); MZO i (ADW).
- *Nesiostrymon celona* (Hewit. 1874). "COL" (Johnson 1991).
- Erora aura* (Godm. & Sal. 1887). El Jabali viii (UCR).
- Erora carla* (Schaus 1902). COL ix (SDNHM); ESA i (MZFC).
- *Caerofethra carnica* (Hewit. 1873). PLAT ix (MZFC).
- Brephidium exilis exilis* (Boisd. 1852). PLAT vi (MZFC).
- Leptotes cassius striata* (W. H. Edw. 1877). AD i,ii,iv,vi–xii (MZFC); CHAN i (ADW, MZFC); COL iv (SDNHM); COM iv (CMNH); ESA i (ADW, MZFC); MZO i,xii (ADW); PA xii; PACA i; PENU i (ADW, MZFC); PLAT i,ii,iv–xii (MZFC); PORO xii (ADW, MZFC); PJU X (LACM); SUCH viii (SDNHM).
- Leptotes marina* (Reak. 1868). AD i,ii,vii,ix (MZFC); Bahía Braithwaite, Socorro Is., RI iv (SDNHM; Brown 1990); El Jabali viii (UCR); PLAT ii,v,ix,xii (MZFC); SUCH viii (SDNHM).
- Zizula cyna cyna* (W. H. Edw. 1881). AD i,ii,iv,vii,x,xii (MZFC); ESA i (ADW, MZFC); PLAT i,ii,iv,v,viii,xi (MZFC); PACA i (ADW, MZFC).
- Hemiargus ceraunus zachaeina* (Butl. & Druce 1872). AD i,ii,iv,vi,vii,xi,xii (MZFC); CHAN i (ADW, MZFC); COL i,iv,x,xi (SDNHM); COM iii (CMNH); ESA i (ADW, MZFC); Esperanza xi (USNM); MZO i,xii (ADW); PA xii; PACA i; PENU i (ADW, MZFC); PLAT i,ii,iv–ix,xii (MZFC); Socorro Is., RI iv (LACM, LACM; Brown 1990).
- Hemiargus isola isola* (Reak. [1867]). AD i,vi,xii; PLAT i,ii,x,xii (MZFC).
- Celastrina gozora* (Boisd. 1870). ETE vi (ADW, MZFC); PLAT iv,vii,x (MZFC).

Everes comyntas (Godart [1824]). AD ii,xii (MZFC); CHAN i (ADW); COL iii (CMNH); ESA i (ADW, MZFC); MZO i (ADW); PA xii; PACA i; PLAT i,ii,vii,xii (MZFC).

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EFFECTS OF HOSTPLANT SPECIES AND ARTIFICIAL DIET
ON GROWTH OF BUCKEYE (*JUNONIA COENIA*)
AND PAINTED LADY (*VANESSA CARDUI*)
CATERPILLARS (NYMPHALIDAE)

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ABSTRACT. We tested the effect of artificial diets and hostplant species on growth of larvae of the Buckeye (*Junonia coenia*) and the Painted Lady (*Vanessa cardui*) in the laboratory. The two hostplant species, *Plantago lanceolata* and *Plantago major* (Plantaginaceae), both contain a particular class of plant secondary compounds, iridoid glycosides. Two artificial diets were also used, one containing dried, ground *P. lanceolata* leaves and the other containing dried, ground *P. major* leaves. In the laboratory, Buckeye larvae, specialists on plants containing iridoid glycosides, grew best on leaf diets; Painted Ladies, a generalist species, showed the opposite trend, exhibiting a higher growth rate on artificial diets. Pupation and survival rates, used as indicators of larval fitness, were also affected by diet. Buckeye larvae feeding on *Plantago* leaves had higher survival rates and pupated sooner than larvae feeding on artificial diets. Painted Lady caterpillars pupated soonest on the artificial diet with *P. major* and had the lowest survival on the artificial diet with *P. lanceolata*. In a complementary field experiment conducted in an experimental garden with both caterpillar species reared on the two *Plantago* species, Painted Lady larvae grew equally well on the two hostplant species, while Buckeye larvae performed significantly better on *P. lanceolata*. The results of these experiments suggest that, for some caterpillar species, laboratory experiments and field experiments may provide different information about larval performance.

Additional key words: iridoid glycosides, *Junonia coenia*, plant-insect interactions, *Plantago*, *Vanessa cardui*.

Generalist and specialist herbivores have been predicted to have different abilities to utilize particular hostplant species, and the chemical compounds that they contain. Specifically, specialists have been predicted to be more efficient at finding, feeding on, digesting, and detoxifying their hostplant than generalists feeding on the same foods (Feeny 1976, Cates 1980, Fox & Morrow 1981, Wiklund 1982). Tests of this prediction, however, have yielded equivocal results: in some cases specialists do perform better than generalists on a particular hostplant or hostplant chemical (e.g., Blau et al. 1978, Kraft & Denno 1982, Bowers & Puttick 1988, 1989), whereas in other cases this is not so (e.g., Scriber & Feeny 1979, Futuyama & Wasserman 1981).

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To further compare the characteristics of generalist and specialist insect herbivores, we examined the performance of larvae of two nymphalid butterflies, on leaf diets and artificial diets containing ground leaves of the same hostplants. As the specialist, we used larvae of the Buckeye, *Junonia coenia* Hübner, and as the generalist, we used larvae of the Painted Lady, *Vanessa cardui* L. Larvae of *J. coenia* specialize on plants containing iridoid glycosides and have been recorded from plants in five families, Plantaginaceae, Scrophulariaceae, Acanthaceae, Verbenaceae, and Cornaceae (Bowers 1984, Scott 1986), all of which contain iridoid glycosides (Bowers 1984). Although larvae of *V. cardui* are quite general in their feeding habits, using plants in over 20 families (Scott 1986, Garrigan 1994), including the Plantaginaceae and Verbenaceae, they apparently prefer various composite species (Scott 1986). There does not appear to be any particular chemical compound(s) involved in determining this species' hostplant range.

Two common hostplant species that *J. coenia* and *V. cardui* share are narrow-leafed plantain, *Plantago lanceolata* L. and common plantain, *Plantago major* L. (Plantaginaceae) (Bowers 1984, Scott 1986). Both these plant species contain iridoid glycosides: *P. lanceolata* contains aucubin and catalpol (Duff et al. 1965, Bowers & Stamp 1992, 1993, Bowers et al. 1992) and *P. major* contains only aucubin (Duff et al. 1965, Bowers, unpubl. data).

We performed two experiments, one in the lab and one in the field, to determine how these two hostplant species affected growth, survival, and development time of *J. coenia* and *V. cardui*. We also wanted to compare the ability of these two caterpillar species to grow and survive on artificial diets, so we reared larvae on one of two different artificial diets: one containing large amounts of dried, ground leaves of *P. lanceolata*, and thus high in both aucubin and catalpol; the other containing a trace of *P. major*, thus containing small amounts of aucubin.

MATERIALS AND METHODS

Study organisms. The Buckeye is found primarily in the south and west of the U.S. (Scott 1986). Despite the toxicity of iridoids to some insect species (Bowers & Puttick 1988, 1989), iridoids function as feeding and oviposition stimulants for Buckeyes (Bowers 1984, Pereyra & Bowers 1988). In the field, Buckeyes have 1–3 broods per year (Scott 1986). The Painted Lady occurs in many of the same habitats as Buckeyes, but has a more cosmopolitan distribution around the world (Garrigan 1994). Painted Ladies are known to have mass migrations, north in the spring and again south in the late fall (Brown 1974, Tilden 1962, Scott 1986, Shields 1992). During their growing season, they typically produce 2–4 broods per year (Opler & Krizek 1984, Scott 1986).

The caterpillars for both experiments originated from well-established lab colonies. The Painted Ladies were obtained from a commercial colony in North Carolina (Carolina Biological), where they are maintained on an artificial diet that contains primarily ground leaves of mallow (*Malva* sp., Malvaceae), a commonly used hostplant (Scott 1986, Garrigan 1994). The Buckeyes came from a colony maintained at the University of Colorado, and fed on leaves of *P. lanceolata* or on an artificial diet containing ground leaves of *P. lanceolata*.

Plantago lanceolata and *Plantago major* are weedy annuals or short-lived perennials that contain iridoid glycosides in their leaves, stalks, and inflorescences (Bowers & Stamp 1992, Bowers et al. 1992). Iridoids are cyclopentanoid monoterpene-derived plant secondary chemicals that are found in members of more than 50 plant families (Jensen 1991). Iridoid content in these plantain species varies both among plants and among leaves on an individual plant (Bowers & Stamp 1992, 1993). The leaf iridoid content of *Plantago lanceolata* plants varies from 1–12% dry weight of the leaf, with new leaves having a higher concentration than mature leaves (Bowers & Stamp, 1992, Bowers et al. 1992). Aucubin concentrations of *Plantago major* range from 0.28 to 1.03% of the leaf dry weight (Bowers, unpubl. data).

A higher iridoid content of *Plantago* leaves increases its oviposition attractiveness to specialists (Klockars et al. 1993) and might therefore increase herbivory by specialists. However, higher iridoid levels have been shown to be toxic and deterrent to generalists such as the gypsy moth, *Lymantria dispar* L. (Lymantriidae) (Bowers & Puttick 1988). Thus, the iridoid content of these *Plantago* plants may have significant growth and survival implications for both the plants and their insect herbivores.

Laboratory experiment. Painted Ladies and Buckeyes were reared on each of four experimental diets. Two were leaf diets of *Plantago lanceolata* or *Plantago major*, and two were artificial diets. For the leaf diets, leaves were collected weekly from mature plants in the vicinity of the University of Colorado, Boulder campus and refrigerated in a moist bag. All leaves were washed prior to use. The artificial diets were prepared following a basic recipe developed by F. Nijhout (Duke University) (Table 1). The artificial diet was modified by adding either 0.5 g dried, powered *P. major* leaves (AD w/ Pm) or 5.1 g dried, powered *P. lanceolata* leaves (AD w/ Pl). The addition of this small amount of leaf material to the AD w/ Pm was necessary for the specialist species to eat the diet and *P. major* was chosen because its leaves have a lower overall iridoid concentration than *P. lanceolata* (*P. major* leaf iridoid content = 0.55% (± 0.05 SE) dry weight, $n = 15$; Bowers, unpubl. data). The artificial diet with *P. lanceolata* leaves has an iridoid glycoside concentration similar to what might be found in an average plant leaf, albeit rather low (see Bowers & Stamp 1992).

TABLE 1. Components of artificial diets used to feed *J. coenia* and *V. cardui* in the laboratory experiments.

Ingredient	Amount or Volume
Cellulose (alphacel)	1.7 g
Sucrose	6.3 g
Wesson salts	2.5 g
Wheat germ	16.3 g
Cholesterol	0.3 g
Vitamin and inhibitor mix	3.6 g
Linseed oil	1.0 ml
Formalin (10%)	0.5 ml
Agar	4.1 g
Water	227.0 ml
Dried, ground <i>Plantago</i>	
If <i>P. major</i>	0.5 g
If <i>P. lanceolata</i>	5.1 g

Eighty Buckeye and 80 Painted Lady caterpillars were taken from eggs hatched on each of the diets. The caterpillars fed *ad libitum* on their experimental diets from egg hatching and throughout the experiment. As larvae molted to the third instar, 20 caterpillars of each species were weighed and reared through to pupation on each of the four diets. Each larva was kept in a separate 150 mm \times 50 mm petri dish, with humidity maintained by a moist piece of paper towel taped to the lid. They were reared in growth chambers set to a constant 25°C temperature and 15L:9D photoperiod. The caterpillars were weighed every second day throughout their development and until pupation. Mortality and development time were recorded.

Field experiment. The complementary field experiment was carried out in an experimental garden near the University of Colorado, Boulder. Thirty *P. lanceolata* and thirty *P. major* plants were collected in early June 1993, from the Boulder area, potted and allowed to acclimate in the greenhouse. On 2 July, they were transplanted into the experimental garden, 0.5 m apart, in single-species rows of 10 plants each. All plants were surrounded by a ring of 15 cm high aluminum edging with a band of Tanglefoot© to prevent the caterpillars from escaping and terrestrial arthropod predators from entering. In addition, to prevent bird predation and deer herbivory, each row was covered with screening held 32 cm above the plant by wooden stakes. Plants were monitored and watered daily.

On 14 July 1993, after plants had recovered from transplanting, one newly molted third instar Buckeye and one newly molted third instar Painted Lady were placed on each of these 60 plants. Larvae were weighed every other day and reared until they molted to the fifth instar.

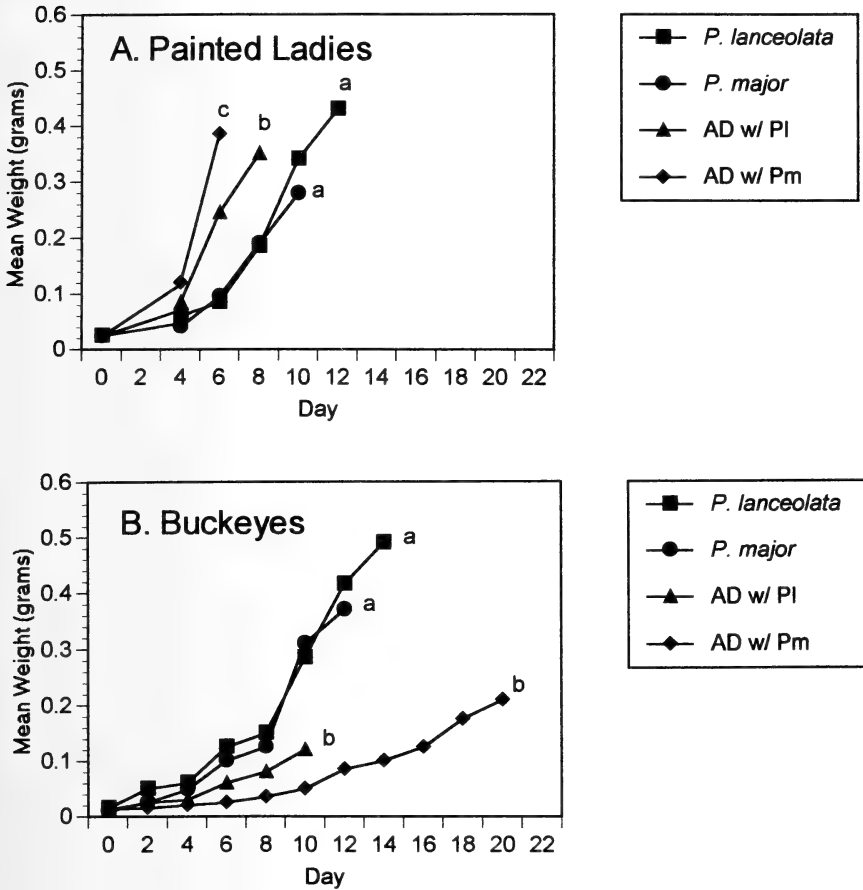


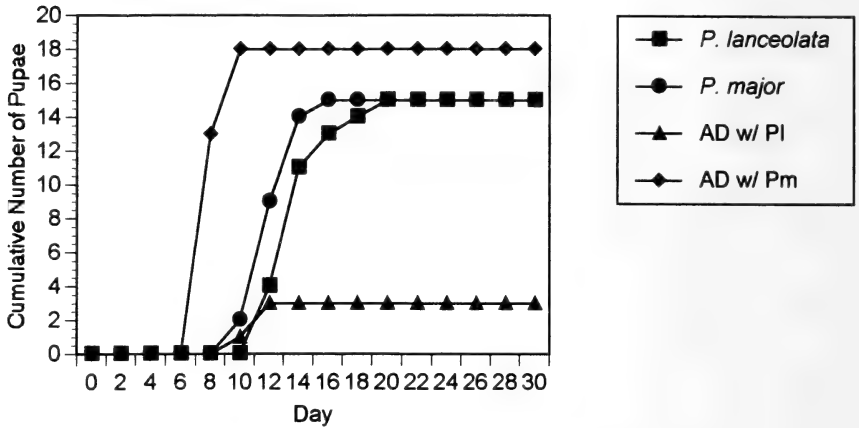
FIG. 1. Growth of the generalist, Painted Ladies (A) and the specialist, Buckeyes (B) on four diets: leaves of *Plantago lanceolata*, leaves of *P. major*, artificial diet with *P. lanceolata* leaves (AD w/ Pl), artificial diet with *P. major* leaves (AD w/ Pm). Lines followed by different letters indicate different growth rates as indicated by Sheffe's post-hoc comparisons.

After weighing, each larva was returned to the plant from which it came. Individuals noted to be missing or dead were not replaced.

RESULTS

Laboratory experiment. The generalist *V. cardui* caterpillars grew two to three times faster than the Buckeyes (Fig. 1A, B). In addition, these *V. cardui* caterpillars grew at different rates on the four diets (Fig. 1A, repeated measures ANOVA, diet factor, $F = 28.43$, $df = 3, 114$, $p < 0.001$) and grew best on the artificial diet with *P. major* (AD w/ Pm)

A. Painted Ladies



B. Buckeyes

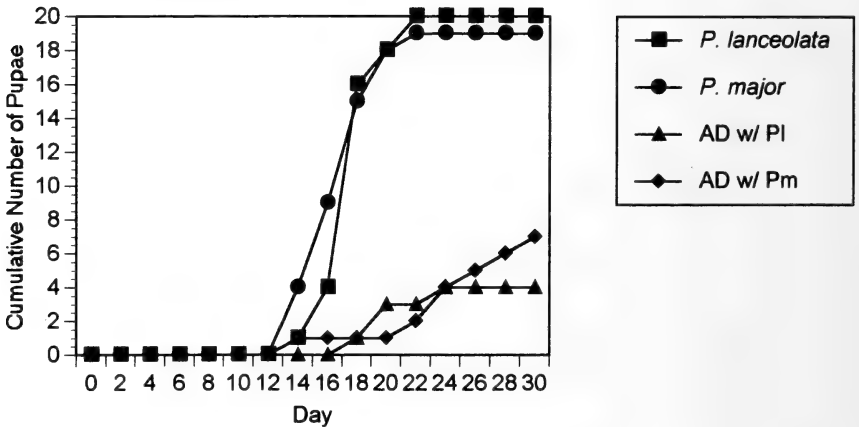


FIG. 2. Time to pupation for the generalist, Painted Ladies (A) and the specialist, Buckeyes (B) on four diets: leaves of *Plantago lanceolata*, leaves of *P. major*; artificial diet with *P. lanceolata* leaves (AD w/ Pl), artificial diet with *P. major* leaves (AD w/ Pm).

(Fig. 1A) and most poorly on the two *Plantago* leaf diets (Fig. 1A). Buckeyes also grew at different rates on the four diets (Fig. 1B, repeated measures ANOVA, diet factor, $F = 24.11$, $df = 3$, 280 , $p < 0.001$), however, they grew best on the leaf diets (Fig. 1B). Sheffe's post-hoc comparisons showed that Painted Lady larvae grew similarly on both *P.*

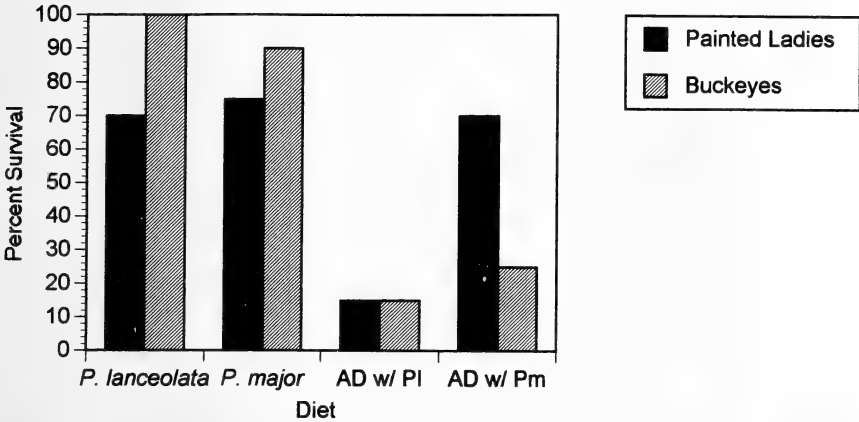


FIG. 3. Survival of Painted Ladies and Buckeyes on four different diets: leaves of *Plantago lanceolata*, leaves of *P. major*, artificial diet with *P. lanceolata* leaves (AD w/ Pl), artificial diet with *P. major* leaves (AD w/ Pm).

lanceolata and *P. major* (Fig. 1A). This was also true for Buckeye larvae (Fig. 1B).

Time to pupation also differed between the two caterpillar species (Fig. 2A, B). The Painted Ladies began to pupate after 8 days, whereas the Buckeyes did not begin to pupate until 14 days (Fig. 2A, B). The diet of the caterpillars also affected time to pupation: Painted Ladies pupated earliest on the artificial diets (Mann-Whitney *U*-test, $z = -2.16$, $p < 0.001$), whereas Buckeyes pupated earliest on the leaf diets (Mann-Whitney *U*-test, $z = -4.44$, $p = 0.003$) (Fig. 2A, B).

Survival of Buckeye larvae varied significantly among diets ($\chi^2 = 9.92$, $df = 3$, $p = 0.025$), but that of Painted Ladies did not ($\chi^2 = 5.94$, $df = 3$, $p > 0.05$) (Fig. 3). Survival of the two caterpillar species differed on two of the diets: *P. lanceolata* leaves ($\chi^2 = 7.06$, $df = 1$, $p > 0.01$) and AD with *P. major* (AD w/ Pm) ($\chi^2 = 8.12$, $df = 1$, $p < 0.005$). However, there was no significant difference in survival of the two caterpillar species on *P. major* leaves ($\chi^2 = 1.56$, $df = 1$, $p > 0.05$) or on the AD w/ Pl, in which both species had mortality of over 80% (Fig. 3).

Field experiment. Painted Ladies grew faster on both *P. lanceolata* and *P. major* than did Buckeyes, as shown by the difference in the log-transformed biomass at eight days for these two caterpillar species (Fig. 4, two-way ANOVA, species, $F = 16.45$, $df = 1, 28$, $p < 0.001$). There was no effect of diet on biomass at eight days (Fig. 4, $F = 2.64$, $df = 1, 28$, $p = 0.115$); but there was a significant interaction (Fig. 4, $F = 4.71$, $df = 1, 28$, $p < 0.05$), indicating that the two caterpillar species responded differently to the two host plant species.

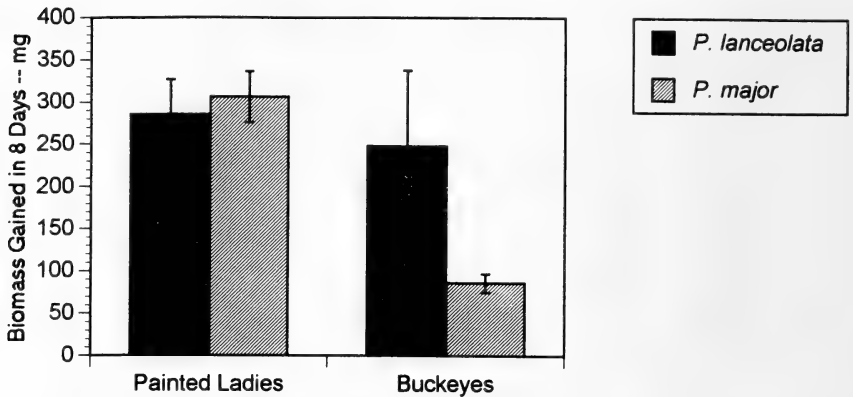


FIG. 4. Biomass gained in eight days by Painted Ladies and Buckeyes fed in the field, on either *P. lanceolata* or *P. major*. Means with standard errors are shown.

DISCUSSION

Explanations for the predominance of specialists among the Lepidoptera (and indeed herbivorous insects in general) have included host availability, predation, and hostplant chemistry (Dethier 1954, Fraenkel 1959, 1969, Ehrlich & Raven 1964, Smiley 1978, Bernays & Graham 1988, Bernays & Chapman 1994). Particularly well-studied is the idea that generalists and specialists may differ in their ability to cope with a particular set of plant chemicals: specialists may be more tolerant of or more efficient at detoxifying or tolerating these chemicals than generalists (Dethier 1954, Ehrlich & Raven 1964, Cates 1980). Our data show that experiments done in the field compared to those done in the laboratory may provide different degrees of support for this idea.

Our data from the laboratory experiments indicate that the specialist, *J. coenia*, grows better and has higher survival when fed on *P. lanceolata* or *P. major* leaf diets, and that the generalist *V. cardui* has reduced growth and fitness on these diets. One reason for this ability of *V. cardui* to perform well on artificial diets is that these larvae were from a colony maintained on artificial diet by Carolina Biological. Although our Buckeye colony was also fed artificial diets during the winter months when plant leaves are not available; they were fed leaves whenever available. Thus in the laboratory experiment, adaptation to artificial diet by *V. cardui* may be an important reason for the differences we observed between the two caterpillar species.

However, the results of the laboratory experiment also revealed that if we consider only the results for larvae reared on plant material (*P. lanceolata* or *P. major*), growth of Painted Lady larvae did not differ on the

two hostplant species (Fig. 1A), nor did that of *J. coenia* (Fig. 1B). However, the data from the field experiments do not confirm these observations: the Painted lady larvae grew faster than the Buckeye larvae on *P. major*, and the two species grew at similar rates on *P. lanceolata*.

Although in the laboratory Buckeye larvae grew equally well on the two different *Plantago* species, their performance in the field was quite different on these two plants: larvae on *P. major* attained approximately one-quarter the mass of larvae on *P. lanceolata*. Reasons for the difference between the laboratory and field experiments are not known, but may be due to a variety of factors. For example, there may have been differences in hostplant quality due to differences in the sources of the plant material fed to the larvae. For the field experiment, larvae were confined to plants grown in our experimental garden, where the plants were watered as necessary, but were not fertilized in any way. Leaves fed to caterpillars in the laboratory experiment were collected from naturally occurring populations located around the University of Colorado campus, usually in lawns that were fertilized and frequently watered. Although we did not measure the iridoid glycoside, water or nitrogen content of plants used in the laboratory or field experiments, differences in these features of plants from these two different sources may have contributed to the differences noted between the laboratory and field experiments.

Another reason for differences between the laboratory and field experiments may be related to the ability of larvae in the field to choose what part of the plant on which to feed. Leaves of *P. lanceolata* vary in their iridoid glycoside content, with newer leaves being high in iridoid glycosides (up to 12% dry weight, Klockars et al. 1993) and older leaves being low (2% to unmeasurable amounts of iridoid glycosides, Klockars et al. 1993). It is likely that a similar pattern occurs in *P. major*. In the field, caterpillars may have been able to choose certain leaves over others, but in the laboratory they were forced to eat the leaves we provided. The potential to choose leaves may have allowed caterpillars in the field to attain more similar growth rates on the two *Plantago* species than would have been predicted from the laboratory experiments.

In conclusion, our data suggest that experiments designed to compare the performance of generalist and specialist insects on particular hostplant species may yield different results when they are performed in the laboratory versus in the field. Although there may be difficulties in conducting field experiments, the use of entire, intact plants growing in relatively natural conditions; the ability of insects to make choices about on what, when and where to feed; and the exposure of both plants and insects to natural fluctuations in temperature, light, humidity, and water, may provide different information about insect performance on hostplants than experiments conducted under laboratory conditions.

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MATE PAIRING PATTERNS OF MONARCH BUTTERFLIES
(*DANAUS PLEXIPPUS* L.) AT A CALIFORNIA
OVERWINTERING SITE

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ABSTRACT. We measured parasitism, size, fluctuating asymmetry, and wing condition of mating and nonmating monarch butterflies at a California overwintering site to document mate pairing patterns and to infer from these patterns some of the behavioral processes involved in pair formation. There was no association between parasitism levels of mating pairs, nor did these levels differ in mating and nonmating individuals. There was size-assortative mating early in the mating season i.e., relatively small males tended to couple with relatively small females and larger males coupled with larger females. Mating females were more asymmetric than nonmating females, and there was a positive assortment based on forewing asymmetry. There was also a negative correlation between size and degree of wing damage in mating females. Females that mated in the afternoon were larger than those that mated in the morning and larger size females tended to be mated less frequently than smaller ones at the end of the mating season. We argue that differences in female ability to resist matings affect pairing patterns. Large symmetrical females are probably more attractive to males, but are better able to control their pairing probability by avoiding or resisting some male mating attempts. Males might prefer large females, or large males may simply be more likely to overcome the resistance of large females.

Additional key words: mating, mate choice, reproductive behavior.

Low temperatures, frequent overcast weather conditions, and day-length regimes restrictive to reproductive development constrain mating activity in monarch butterflies (*Danaus plexippus* L.) at central coastal California overwintering sites to a brief but intense period during the last 4–5 weeks of the overwintering phase (Herman 1973, Hill et al. 1976, Leong et al. 1995). Unlike spring and summer generations, mating by overwintering monarchs is highly localized in both time and space.

At the majority of California overwintering sites, populations have male biased sex ratios (Tuskes & Brower 1978, Sakai 1991, Frey & Leong 1993, 1995, Nagano et al. 1993). This excess of males, plus the likelihood that the optimal number of matings is higher for males than

females, can lead to a condition where the opportunity for sexual selection is stronger on males than on females (Wade & Arnold 1980, Clutton-Brock 1988, Andersson 1994). Females also disperse earlier than males from overwintering sites in California (Hill et al. 1976, Tuskes & Brower 1978, Nagano et al. 1993, Frey & Leong 1995) so that male-male competition must increase over the mating period.

The combination of large aggregations of individuals, a relatively short mating period, a male-biased sex ratio and an early female dispersal, in theory, favors courtship and pairing processes in males that minimize their time-costs and maximize their mating frequency. Under these conditions, pairing processes involving time-extensive choice, preference and/or assessment by males may have been selected against leading to a random mating pattern for a variety of phenotypic characters (Janetos 1980). In other words, males that are too selective or discriminating may miss out on many mating opportunities. On the other hand, because spermatophores represent substantial male investment (Oberhauser 1988, 1989, 1992, Svard & Wiklund 1989) and because of the large number of females at overwintering sites, some form of male choice or preference for specific female phenotypic characters might be expected which may counter tendencies toward random pairing. In addition, the variation in spermatophore mass associated with male age, size, and mating history could make it worthwhile for females to exercise choice, since spermatophore nutrients can affect fecundity (Oberhauser 1989, 1998).

There is little consensus on monarch mating patterns at overwintering sites, or on what determines female mating frequencies. Males actively pursue females and either capture them in rapid flight or "pounce" on them as they roost in the canopy vegetation. In either case, the pair often falls to the ground where the mating attempt continues (Pliske 1975, Hill et al. 1976, pers. obs. by Frey, Leong & Oberhauser). Tuskes and Brower (1978) suggested that pairing among overwintering Californian monarchs was random, while Van Hook (1993), studying overwintering Mexican monarchs, reported that small males and large females were more likely to be in the mating population. On the other hand, Frey (unpubl. data) found that relatively small males tended to couple with relatively small females and larger males coupled with larger females among 100 pairs of mating monarchs during the early stages of the 1992 mating season at a central coastal California overwintering site. Both sexes mate repeatedly, with females and males mating up to 12 and 19 times, respectively, during their lives in captivity (Oberhauser, unpubl. data). Wild captured monarch females contained up to 10 spermatophores (Pliske 1973, Brower 1985, Leong et al. 1995). A prevailing view for their high mating frequency is that it results from the females'

inability to resist male mating attempts (Rothchild 1978, Forsberg & Wiklund 1989, Boppre 1993) and from a male takedown strategy that "apparently precludes precopulatory female choice" (Van Hook 1993). This view holds that female monarch options in mating are limited and dominated by male activity and male decision processes.

We studied pairing of monarch butterflies at a central California overwintering site during their late winter/early spring phase of intense reproductive activity, looking for the effects of four characters on pairing probability and assortative mating. In addition to determining mating patterns, we hoped to be able to infer from these patterns some of the behavioral processes involved.

MATERIALS AND METHODS

Study populations. Our 1.43 ha study site is at the North Beach campground, Pismo Beach, California (35°07'46"N, 120°37'53"W), midway along the California coastline. Dominant vegetation includes blue gum, *Eucalyptus globulus*, with scattered Monterey cypress, *Cupressus macrocarpa*, and Monterey pine, *Pinus radiata*. Another overwintering site occurs 2.0 km to the south. Peak population abundance estimates made during late December by mark-release-recapture studies were 225,000 (1990–1991), 160,000 (1991–1992), and 25,000 (1992–1993) individuals. In 1993, the year mating pairs were collected, the population declined from 22,000 individuals in late January to about 3000 butterflies on March 1 (Frey, unpubl. data). The male sex ratio increased from 56% to 73% during this period.

Data collection and analysis. We measured parasite state (i.e., the neogregarine protozoan *Ophryocystis elektroscirrha*), degree of bilateral wing asymmetry (i.e., fluctuating asymmetry), wing size, and degree of wing damage. The first three characters have figured prominently in recent models on the evolution of mating patterns (e.g., parasitism: Hamilton & Zuk 1982, Zuk 1987, Simmons 1990, Houde & Torio 1992; fluctuating asymmetry: Moller 1990, Thornhill 1992, Liggett et al. 1993, Watson & Thornhill 1994; size: McCauley 1982, Crespi 1989). Since much of monarch courtship activity involves rapid flight (Pliske 1975) and since overwintering females often disperse widely from overwintering mating sites to deposit eggs (Cockrell et al. 1993, Nagano et al. 1993, Riley 1993), wing condition may also be an important factor subject to sexual selection. A total of 141 mating pairs was collected between 0930 and 1600 PST over 30 days from 29 January to 28 February 1993. Fifty-five of these were taken to the laboratory and measured for parasite state, wing damage, wing fluctuating asymmetry, and size. The remaining 86 pairs were measured for all characters except parasitism in the field and subsequently released. Butterflies were

collected from clusters throughout the 1990–1991, 1991–1992, and 1992–1993 overwintering seasons in order to establish trends in size and wing damage. These were measured for wing length and wing damage in the lab. Females were also collected from clusters on 3 February and 3 March 1992 to determine the relationship between female size and prior mating history. Their forewing lengths were measured to the nearest mm and the contents of their bursa copulatrix examined by dissection under 12× magnification.

Ophryocystis elektroscirrha is a tissue-specific neogregarine protozoan parasite of monarchs and the Florida queen butterfly, *D. gilippus berenice* Cramer (McLaughlin & Meyers 1970). Spores of the parasite are located on the scales and other adult integument. We used Leong et al.'s (1992) technique to determine the incidence and level of infection.

Damage to the wings of butterflies occurs as scale loss, membrane tears and torn or missing pieces. Scale loss is difficult to quantify, so wing damage in this study was operationally defined as the number of wings per individual either torn and/or with a portion missing and was scaled from 0 (no wings damaged) to 4 (all four wings damaged).

Because body mass varies greatly with hydration level (Crespi 1989, Leong et al. 1992), lipids (Brower 1985) and recent reproductive history (Oberhauser 1988, 1989, 1992, Jones et al. 1986, Svard & Wiklund 1989), we used forewing length as a measure of size. Forewings were measured to the nearest mm from the base of the discal cell to the furthestmost point in cell R_4 on the wing apex. Body size was defined as the average of the length of both forewings. In cases where the apex of either wing was damaged, size was measured as the length of the intact wing.

Following Leary and Allendorf (1989), Parsons (1992), Thornhill (1992), and Liggett et al. (1993), fluctuating asymmetry was defined as random deviations from perfect bilateral symmetry between right and left-side structures. A measure of fluctuating asymmetry (FA) was derived from wing length measurements. Forewing length FA was computed as the absolute value of the differences between forewing lengths.

RESULTS

***Ophryocystis* parasitism.** Both infection rate (68%) and level (mean \pm SE = 39.6 ± 10.4 spores) for the mating sample and general population butterflies combined were similar to those reported by Leong et al. (1992) for the general population at this site during the 1991 season. To test the null hypothesis of random assortment for pairing based on parasitism, Spearman's test of association was conducted on male parasite infection level versus that of his partner. There was no significant association between the parasite infection level of partners ($r_s = 0.222$, $n = 55$, $p = 0.095$). Neither the incidence ($\chi^2 = 1.05$, $df = 1$, $p =$

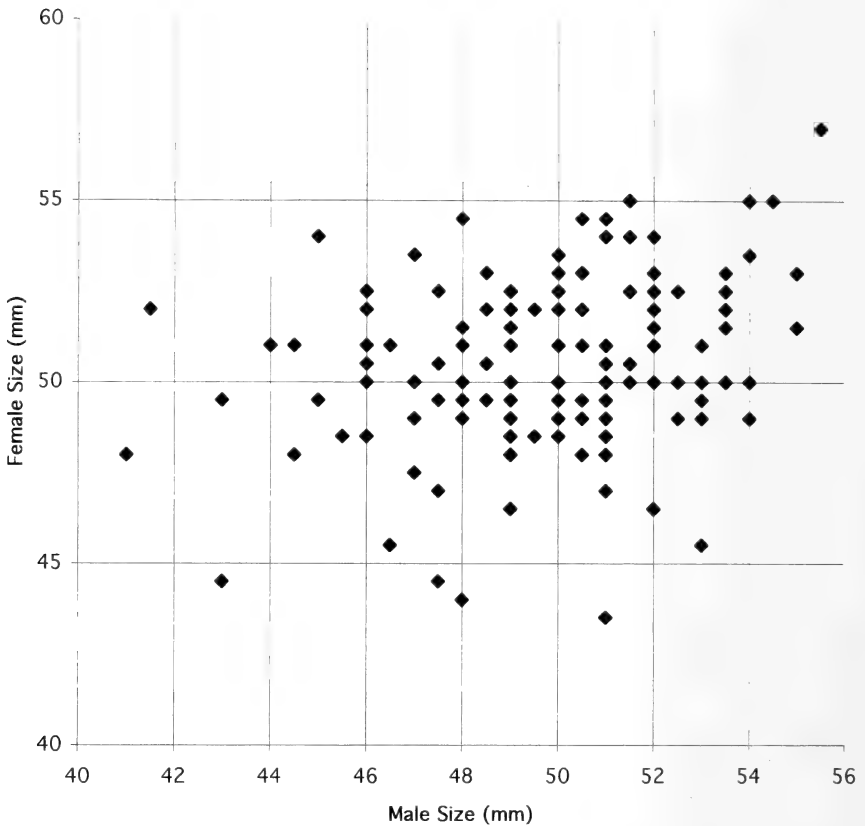


FIG. 1. Wing length association between pairs of mating butterflies. ($r = 0.27$, $F = 10.5$, $df = 1$, 136 , $p < 0.01$).

0.305) nor level of infection (Wilcoxon $z = 0.408$, $p = 0.683$) by *O. elektroscirra* differed between male and female mating partners. Likewise, the distribution of the mating sample infected ($\chi^2 = 1.06$, $df = 1$, $p = 0.303$) and their spore count (Mann-Whitney $z = -1.17$, $p = 0.233$) did not differ from those of the general population.

Size. Fig. 1 shows the relationship between the size of the 1993 mating partners. A significant positive association between forewing length of partners is indicated for the overall season. Size related pairing patterns were also examined for seasonal trends (Table 1). During the early phase (the first two weeks of mating) significant size related assortative pairing occurred, but that trend, while positive, was non-significant during the final two weeks of the study (Table 1a). Neither males nor females of the mating population differed in wing length from their same-sex general population counterparts during early or late 1993 season

TABLE 1. Size relationships for butterflies captured during the 1993 mating season from clusters or from ground pairs: (a) associations between mating partner's wing length using Spearman rank correlation; (b) male forewing length compared using two sample *t*-tests; (c) female forewing length compared using two sample *t*-tests.

Season	Sex	Comparison	Mean (s.e.)	Statistic	p	N
(a)						
early season	males & females	mating partners		$r = 0.34$	0.002	78
late season	males & females	mating partners		$r = 0.21$	0.111	60
(b)						
early season	males	mating vs. clusters	49.4 (0.3) 50.7 (0.5)	$t = 1.84$	0.07	78 20
late season	males	mating vs. clusters	50.5 (0.3) 50.7 (0.4)	$t = 0.34$	0.74	60 22
(c)						
early season	females	mating vs. clusters	50.6 (0.2) 50.0 (0.5)	$t = 1.01$	0.31	81 18
late season	females	mating vs. clusters	50.4 (0.3) 49.2 (0.6)	$t = 1.78$	0.08	60 20

comparisons (Table 1b, c). Butterflies collected from clusters throughout the 1991–1993 overwintering seasons were not sexually dimorphic by size (1991: unpaired $t = 1.53$, $df = 267, 269$, $p = 0.13$; 1992: $t = 0.34$, $df = 83, 67$, $p = 0.74$; 1993: $t = 1.02$, $df = 37, 39$, $p = 0.31$). During the 1993 season, forty two pairs of mating butterflies were collected prior to 1130 PST and 48 pairs collected after 1230 PST: the size of males mating in the morning was not significantly different from males mating in the afternoon (unpaired $t = -1.604$, $p = 0.11$). However, females mating in the afternoon, were significantly larger than females mating in the morning (unpaired $t = -3.126$, $p = 0.0024$) and this pattern was consistent during both the early part of the season as well as during the last two weeks of mating.

Fluctuating Asymmetry (FA). Contingency analysis for incidence of male FA (i.e., presence or absence of asymmetric wings) with that of his partner are given in Table 2a. Positive assortment between partners was indicated for forewing length FA during the first two weeks, but not during late season mating. Cases where both partners were asymmetric or in which neither were asymmetric occurred more frequently than predicted due to chance. The majority of individuals of both the 1993 general population and those captured during mating had symmetrical length forewings (72% and 86% for general population males and females respectively; 56% and 52% for mating males and females respectively). When asymmetry occurred within a group it was balanced i.e., the number with right side bias did not differ significantly ($p > 0.05$) from the number with left side bias. The forewing length asymmetry of

TABLE 2. Fluctuating asymmetry relationships for butterflies captured during the 1993 mating season from clusters or from ground pairs: (a) tests of independence of presence or absence of FA in one mating partner with the other partner using contingency analysis; (b) male forewing length asymmetry compared using Mann-Whitney tests; (c) female forewing length asymmetry compared using Mann-Whitney tests.

Season	Sex	Comparison	Mean (SE)	Statistic	p	N
(a)						
early	males & females	mating partners		$\chi^2 = 6.14, df = 1$	0.013	59
late	males & females	mating partners		$\chi^2 = 0.01, df = 1$	0.938	60
(b)						
early	males	mating vs. clusters	0.68 (0.10) 0.40 (0.16)	$z = 1.75$	0.08	66 22
late	males	matings vs. clusters	0.45 (0.11) 0.21 (0.14)	$z = 1.16$	0.25	60 17
(c)						
early	females	mating vs. clusters	0.76 (0.11) 0.56 (0.06)	$z = 3.31$	0.0009	75 17
late	females	mating vs. clusters	0.46 (0.07) 0.21 (0.09)	$z = 1.94$	0.053	56 19

mating females was greater than that of general population females during the early phase of mating, and differences approached significance during the last two weeks (Table 2c). On the other hand, male FA did not differ significantly between mating and cluster-captured males during either phase of the mating season (Table 2b).

Wing damage. Mating males had greater wing damage scores (males = 1.57) than their partners (females = 0.95). Early season mating males were significantly more damaged than cluster-captured males, but late season differences were not significant (Table 3a). Mating females did not differ from general population females during either mating phase. For mating pairs, the number of damaged wings of one butterfly was independent of the damage status of its partner during both phases of mating (Table 3c).

Interaction between wing damage and size. Table 4 shows associations between size and number of damaged wings of mating individuals and general population butterflies for the overall 1993 season. Mating males showed a positive (but non significant) relationship between size and wing damage, with larger males tending to be more damaged. In contrast, mating female size was inversely related to the amount of wing damage. Among general population butterflies, neither male nor female size was associated with wing damage. Association between wing damage and mating butterfly size was examined for both the first two weeks of the season and the following two weeks. Neither male ($r_s = 0.634, p = 0.5$) nor female ($r_s = -0.829, p = 0.407$) mating individu-

TABLE 3. Wing damage relationships for butterflies captured during the 1993 mating season from clusters or from ground pairs: (a) number of male wings damaged compared using Mann-Whitney tests; (b) number of female wings damaged compared using Mann-Whitney tests; (c) associations between mating partner's wing damage using Spearman rank correlation.

Season	Sex	Comparison	Mean (SE)	Statistic	p	N
(a)	early	males	mating vs.	1.8 (0.1)	z = 2.17	0.03
			clusters	1.1 (0.3)		
late	males	mating vs.	1.3 (0.2)	z = 0.59	0.71	60
			clusters			
(b)	early	females	mating vs.	0.9 (0.1)	z = 1.21	0.23
			clusters	0.6 (0.2)		
late	females	mating vs.	1.0 (0.1)	z = 0.54	0.59	60
			clusters			
(c)	early	males & females	mating partners	r = 0.08	z = 0.72	0.47
				late		

als had a significant relationship between size and wing damage early in the study. However, late season patterns were significant and in opposing directions: larger males had increasing wing damage ($r_s = 2.622$, $p = 0.009$), while female size was inversely related to damage ($r_s = -2.096$, $p = 0.036$).

Mating frequency, female size and fluctuating asymmetry.

Table 5 presents population size, sex ratio and spermatophore data for general population females captured from clusters in 1992. As in the 1993 mating season, the overwintering reproductive phase in 1992 was characterized by a declining population, an increasingly male biased sex ratio, and an increasing proportion of the general population females that were multiply mated. The coefficient of variation for spermatophores per female decreased from 88% to 36% during the 1992 reproductive season, indicating that the mating histories of females became increasingly uniform. Early in the mating phase no relationship existed between female size and number of prior matings (i.e., number of spermatophores present in her bursa copulatrix); toward the end of the mat-

TABLE 4. Association between wing damage and size among mating individuals and members of the general population, 1993, using Spearman rank (see text for seasonal trend).

Group	N	r	p
mating males	138	0.152	0.076
mating females	141	-0.176	0.037
general population males	40	-0.161	0.316
general population females	38	0.059	0.722

TABLE 5. General population demographics, female mating history and Spearman rank correlation between wing length and number of spermatophores for clustering females captured early or late during 1992.

Date	Abundance	Sex ratio (% male)	Spermatophores % female	N	r	p
3 Feb	100,000	65	1.2 ± 0.2	25	0.084	0.68
3 Mar	25,000	85	5.9 ± 0.5	23	-0.496	0.02

ing phase there was a significant inverse relationship between size and mating (cf. Feb 3 and Mar 3, Table 5) and a positive relationship between spermatophore number and female forewing FA ($r_s = 0.325$, $p = 0.028$).

DISCUSSION

Two of the characters we measured, forewing size and fluctuating asymmetry, showed positive assortment between individuals of mating pairs early in the mating season. Larger females also were more likely to mate in the afternoon than in the morning. In addition, by the end of the season a negative relationship existed between female size and spermatophore count, with small females containing more spermatophores. FA was associated with female mating patterns as well: mating females had a greater incidence and degree of FA than cluster-captured females, and females with asymmetric wing lengths had higher spermatophore counts at the end of the season. There was also an interaction between size and wing damage in both sexes among mating butterflies late in the overwintering season, with a positive association between size and wing damage among males and a negative association between female size and wing damage. The level of parasitism was independent among members of mating pairs, and had no effect on mating likelihood.

Adaptive explanations for female multiple mating are varied, and hypotheses that apply to mating patterns in monarch butterflies include: assurance of adequate sperm supply (Gromko et al. 1984), increased genetic quality from later matings (Halliday 1983, Birkhead et al. 1993), increased genetic diversity (Halliday & Arnold 1987), and obtaining male derived nutrients (Oberhauser 1989, Wells et al. 1990, Wells et al. 1993). However, female fitness is negatively impacted in other insects by excessive sexual harassment by males (Odendaal et al. 1989, Cook et al. 1994, Rowe et al. 1994, Stone 1995), and there could be non-trivial costs of mating too frequently in female monarchs. Females mating several times in rapid succession have increased mortality from ruptured bursae copulatrix (Oberhauser 1989). Other potential costs include: (1) wasted time and energy; (2) increased risk of wing damage thus limiting dispersal range; (3) substantial increase in flight load; and (4) delayed dispersal and later initiation of egg laying.

It is likely that female monarchs attempt to minimize costs from excessive male courtship or from mating too many times. Female responses to male harassment in Lepidoptera range from rapid ascending flight as in *Colias* (Rutowski 1978) to elevated abdominal postures in *Anthocharis cardamines* (Wiklund & Fosberg 1985). Female rejection behavior has been thoroughly documented in the Queen butterfly, *Danaus gilippus berenice* (Brower et al. 1965). During ground phase mating activity, female monarchs often exhibit behaviors that make successful coupling difficult: curling the tip of their abdomen forward ventral to their abdomen and clasping it with their legs or sandwiching the tip of their abdomen between tightly closed wings. Most mating attempts are unsuccessful (Frey & Oberhauser, pers. obs).

Our results suggest that larger females more readily avoid or resist excessive mating attempts than do smaller females and that larger males were more successful at overcoming this resistance. The inverse relationship between size and mating frequency in late season general population females in 1992 (Table 5), and the fact that relatively large females in 1993 mating pairs had less wing damage than smaller mating females (Table 4), are each consistent with the hypothesis that relatively large females exercise choice as to when they mate because they are more capable of resisting mating attempts than smaller females. This is not female-choice in the traditional sense (Mason 1969, Phelan & Baker 1986) because females may not actually choose specific males. Rather, they are able to choose whether or not to mate.

Temporal mating data and patterns in FA also support the female choice hypothesis. Females that began mating in the afternoon were larger than those that began in the morning, suggesting that larger females can avoid mating attempts in the morning. Because monarchs remain in copula overnight (Svard & Wiklund 1988, Oberhauser 1989), starting to mate early in the day precludes foraging, rehydration, or other maintenance activities during this time. The fact that mating females were both more likely to be asymmetric than nonmating females and showed a greater degree of asymmetry than nonmating females suggests that symmetrical females are better able to avoid unwanted mating attempts. An alternative explanation is that males prefer small, asymmetric females, but this seems less likely, because fecundity is generally correlated with size in insects (Lederhouse 1981, Jones et al. 1982, Haukioja & Neuvonen 1985). In many taxa there is a positive correlation between the level of FA and environmental stress experienced by individuals during development (Palmer & Strobeck 1986, Hoffman & Parsons 1991). There is also a negative correlation between overall fitness or heterozygosity and FA (e.g., Leary & Allendorf 1989, Leamy 1992, Parsons 1992). These general findings suggest that it is unlikely that

monarch males prefer small asymmetric females. The relatively high frequency of mating pairs in which both partners had forewing FA could indicate reduced ability at partner discrimination in both sexes or that only symmetrical males can overcome symmetrical females.

Many factors influence the evolution and maintenance of mating systems (Clutton-Brock 1988, Andersson 1994). Some of these may operate to favor mate choice by either or both sexes and result in assortative or disassortative pairing. Crespi (1989) pointed out that other factors also produce non random pairing, yet actual choice or preference may not be involved. Additional factors or conditions, e.g., declining female abundance, may favor males that pair randomly and minimize time involvement during the pairing process. For monarch males at California overwintering sites, conditions toward the end of the mating season probably favor random pairing. The general population declined from 20,000 individuals in late January 1993 to less than 2000 butterflies by the first week in March and the population became increasingly male biased. During the last two weeks of the mating period, pairing was random with respect to each of the four variables measured.

Early in the mating season, positive assortative mating based on both size and bilateral wing asymmetry occurred. There is some evidence that males were choosing larger females, and that large males were better able to obtain these preferred mates. Later in the season, two factors could be important in reversing this trend. There was more competition for mates as the sex ratio became more male-biased, and the remaining females were more likely to have mated, and thus more "reluctant" (Sugawara 1979, Oberhauser 1989, but see Rowe et al. 1994). The greater mating frequency for more asymmetric females, as measured by spermatophore counts, and the greater wing damage to smaller mating females support our modified female choice hypothesis that larger females are better able to choose when to mate.

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DISTRIBUTION AND BIOLOGY OF *CHLOSYNE GORGONE CARLOTA* (NYMPHALIDAE) AT ITS NORTHEASTERN LIMIT

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ABSTRACT. During 1996, *Chlosyne gorgone carlota* was found at 13 localities in eastern Ontario. These locations are northeast of historic Ontario and New York sites and 600 miles east of the nearest sites in the midwestern United States. Three broods were evident. First and second instar larvae were found feeding on *Aster lanceolatus*, *Aster novae-angliae*, and *Rudbeckia hirta* var. *pulcherrima*. Older larvae were found eating only *R. hirta*. Habitats in eastern Ontario are open areas including hayfields, abandoned farmlands, road verges, and hydroelectric rights of way. It remains unknown whether *C. g. carlota* has been long established or has recently arrived.

Additional key words: New York, Pennsylvania, prairie, disjunct, biogeography.

In 1996 the Gorgone Checkerspot, *Chlosyne gorgone carlota* (Reakirt) was rediscovered in Ontario after a long period without any reports. While the rediscovery has been briefly noted (Catling & Layberry 1996), there has been no comprehensive summary of the data collected. Here we provide details on flight periods, foodplants, development times, behavior, and distribution.

Field surveys were conducted in 1996 throughout eastern Ontario by driving along roads and checking suitable habitats for both adults and larvae. Voucher specimens were deposited at the Royal Ontario Museum (ROM), University of Guelph, and Agriculture Canada in Ottawa (CNC) and in the private collections of P. M. Catling, A. Wormington, R. H. Curry, J. Crolla, B. Bracken, and R. A. Layberry. Vouchers of larval foodplants were deposited in the DAO (Dept. of Agriculture) collection of Agriculture Canada in Ottawa. Both reared and wild-caught specimens were compared with material from western North America at the CNC to verify subspecific identity. Lists of plants were made for each site with an indication of status as dominant, frequent or rare. Species dominant at 3/4 of the sites were used in the description and restricted native species were noted. The nomenclature for plants follows Morton and Venn (1990).

HISTORICAL RECORDS

Although long known from several localities in Michigan (Moore 1960), *C. g. carlota* has not been seen in that state for approximately 35 years (M. C. Nielsen, pers. comm.). It is not known from Ohio (Iftner et

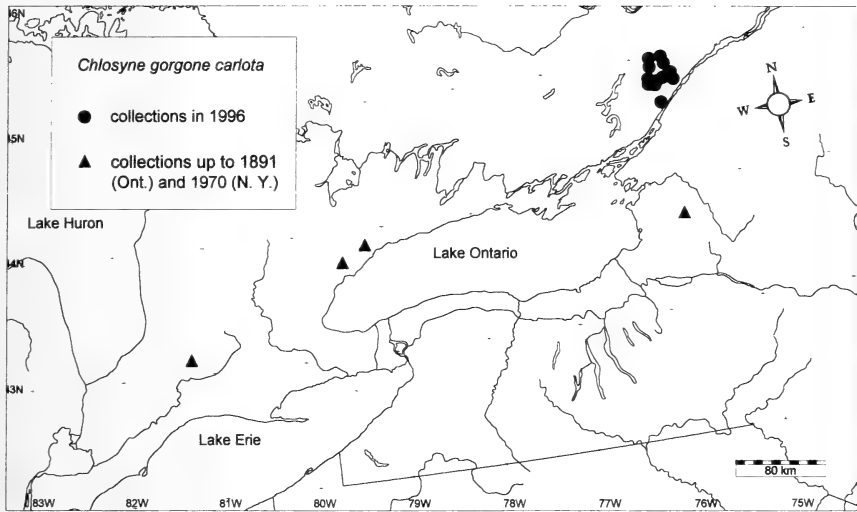


FIG. 1. Geographic distribution of *Chlosyne gorgone carlota* at the northeastern range limit in Ontario and New York. Solid circles, 1996 collections; solid triangles, collections up to 1891 in Ontario and up to 1970 in New York.

al. 1992), has not been observed for 105 years in Ontario (Hanks 1996), and is known from only single occurrences in New York (Shapiro 1974) and Pennsylvania (Davis 1915; there are no recent records, D. Wright, pers. comm.). Major recent texts (e.g., Scott 1986, Opler & Malilik 1992, Opler & Krizek 1984) have mapped these northeastern records.

In Ontario, *C. g. carlota* has been reported previously from London, the Humber valley on the west side of Toronto, and Scarborough east of Toronto (Fig. 1). The report from London is based on a collection by W. E. Saunders (Bethune 1894). The report from the Humber Plains (Riote 1967) or in the Humber valley (Campbell et al. 1990) is based on collections in 1891 by C. W. Nash. The report from Scarborough is based on four specimens collected by G. Geddes on 6 June 1891 (Bethune 1894, Gibson 1910, Holmes et al. 1991). The Royal Ontario Museum once had voucher specimens, now lost, to support these reports (pers. obs., Hess 1979): three from "Humber valley, Toronto, 6 June 1891, C.W. Nash Collection," and one from "Toronto, C.J.S. Bethune collection."

Recently specimens of *C. g. carlota* labelled "White River, Ontario (presumably the White River in Algoma District at 48°33'N, 86°16'W), June 1907, F. Knab" were discovered at NSM (D. Lafontaine, pers. comm.). *Chlosyne g. carlota* was not listed for northern Ontario by Riote (1971), and although the White River location is outside the area he defined as northern Ontario, he would likely have listed it along with the

many other records for adjacent regions if he had a record. This species was treated as a stray in the *Ontario Butterfly Atlas* (Holmes et al. 1991) and Campbell et al. (1990) noted that it may never have bred in Ontario. Gregory (1975) did not list it for Ontario and Sutherland (1994) listed *C. g. carlota* as extirpated.

RECENT ONTARIO RECORDS

During 1996, *C. g. carlota* was collected and observed in the eastern portion of southern Ontario within a 355 square mile area bounded by Kemptville and Merrickville to the north and Brockville and Spencer-ville to the south. Specific sampling included locations near Bishops Mills, Burritt's Rapids, Carley's Corners, Fairfield East, Groveton, Kemptville, Merrickville, McRobert's Corners, North Augusta, Spencerville, Ventnor, and Wolford Centre (Fig. 1). Both reared and wild caught adults from this region proved to be within the normal range of morphological variation exhibited by populations from the prairie provinces of Canada that have been referred to *ssp. carlota*.

The new locations are not only significant records for a species not recorded in Ontario for 105 years, but also represent a range extension 90 miles north of the isolated New York occurrence reported by Shapiro (1974) and ca. 200 miles northeast of the nearest historic Ontario sites at Toronto. The closest extant populations are at least 600 miles to the west, south of Lake Michigan and in Wisconsin (L. A. Ferge, pers. comm.).

There appear to be three broods in eastern Ontario with adults having been seen and/or collected in 1996 from 1–2 June, from 13 July to 7 August and on 3–6 September. In general, the populations appeared to be sparse, with fewer than 3 adults seen at any locality on any day, even during the evident peak flight (the maximum number seen at any site at one time was 10, on 6 September).

LARVAL BIOLOGY

Foodplants. On 5 July 1996 a group of about 200 larvae were found on *Aster lanceolatus* Willd. at the Kemptville site. On 6 July this group had dispersed several feet to another *A. lanceolatus* (52 larvae), an *Aster novae-angliae* L. (40 larvae), and a *Rudbeckia hirta* L. var. *pulcherrima* Farw. (= *R. serotina*) (30 larvae). All of these plants were being eaten. On 6 July at Kemptville another group of 53 younger larvae were found on *Aster novae-angliae* and another group of 30 larvae was found on *R. hirta*. In the same area eight solitary, last instar larvae were found on *R. hirta*.

On 7 July solitary larvae or groups of larvae (2–10) were found 57 times on *Rudbeckia hirta* with 2–15 occurrences at each of seven east-

ern Ontario locations (Bishops Mills, Groveton, Kemptville, North Augusta, Spencerville, Ventnor, and Wolford Centre). At each location there were chewed plants of *R. hirta* with larval skins and frass. At Kemptville groups of smaller larvae were found feeding on both *A. novae-angliae* (8 occurrences) and *A. lanceolatus* (10 occurrences) as well as *R. hirta* (15 occurrences). No large larvae were found on *Aster* and use of these plants was observed only at Kemptville (where *R. hirta* was sparse), by first and second instars. Consequently, the primary foodplant at the new Ontario sites appears to be *R. hirta*.

In captivity, third instar and older larvae refused *Aster lanceolatus*, *A. novae-angliae*, *Helianthus decapetalus*, and *H. divaricatus*, but readily accepted *Rudbeckia hirta* and *Helianthus annuus*. *Helianthus tuberosus* was also accepted, but less readily.

Development and behavior. Rearing of larvae was done indoors under constant light at temperature of 75–85°F. Second to final instar, solitary larvae 2–2.5 cm long found from 6–8 July and from 19–23 August pupated after 2–8 days of feeding on *R. hirta*. The pupal stage required 4–7 days ($n = 13$) with one requiring 10 days. An ichneumon wasp emerged from another pupa after 20 days.

Communal larvae 7–8 mm long collected at the same two sites continued to feed on *R. hirta* for 1–2 weeks, but then hid communally within dry, curled leaves and became inactive. Thus, younger or slowly developing larvae appear to become dormant. *Rudbeckia hirta* grows as scattered plants averaging 1–2 feet tall with 5–7 leaves up to 3 inches long. Plants persist while moist conditions prevail. Completion of flowering is followed by development of new rosettes from the perennial base. Since many of the plants grow in drier sites, summer drought can render them unavailable to *C. g. carlota*, but as soon as moist conditions return, growth resumes. Consequently, the butterfly populations may be able to exploit favorable conditions through three consecutive broods.

Groups of larvae consume whole plants, or most of the leaves on a plant, and then move to new plants. The younger larvae eat the spongy tissue and the upper epidermal layer leaving a whitish, semi-transparent curled leaf. These consumed plants are conspicuous, and along with frass and sometimes shed skins, provide a useful search image for locating larvae. During moves to new plants, larval groups become divided, are more mobile, and frequently do not destroy entire plants. Larvae were found feeding at all times during the day on top of leaves.

HABITATS IN ONTARIO

The area in eastern Ontario where *C. g. carlota* occurs includes extensive marginal farmland that has been largely abandoned and is returning to woody vegetation slowly due to periodic drought, seasonally high wa-

ter table and rugged terrain. It includes sand dunes and sand-covered limestone ridges, as well as gently rolling sandy ground. The open sandy areas were planted with pine and spruce beginning in the 1930's, and few natural openings remain. Granitic, limestone and clay or loam substrates exist to the west, while clay and loam exist to the north and east, but to the east and south of the St. Lawrence River similar isolated areas of sandy substrate are present.

The habitats of *C. g. carlota* include open areas with both wet and dry ground. Some are natural openings with a dominance of native species, but most are intermediate or anthropogenic including road verges, abandoned pastures and hayfields. These latter habitats are dominated by introduced species or contain an admixture of native and introduced species. Three sites are along hydroelectric line rights of way where encroachment of woody plants is actively prevented.

The drier portions of these habitats appear to be preferred, including areas dominated by the shorter grasses, *Danthonia spicata* (L.) P. Beauv. ex Roemer & Schultes and *Poa compressa* L. Characteristic herbs include *Apocynum androsaemifolium* L., *Aster lanceolatus* Willd., *Aster novae-angliae* L., *Bromus inermis* Leysser, *Carex blanda* Dewey, *Carex pensylvanica* Lam., *Carex rugosperma* Mackenzie, *Daucus carota* L., *Fragaria virginiana* L., *Hieracium piloselloides* Villars, *Panicum implicatum* Scribner, *Poa pratensis* L., *Prunella vulgaris* L., *Pteridium aquilinum* (L.) Kuhn, *Rudbeckia hirta* L. var. *pulcherrima* Farw., *Senecio pauperculus* Michaux, *Solidago canadensis* L., *Solidago juncea* Aiton, and *Solidago nemoralis* Aiton. Frequent shrubs and vines include *Juniperus communis* L., *Prunus virginiana* L., *Rhus typhina* L., *Rubus allegheniensis* Porter, and *Vitis riparia* Michaux. Locally restricted native species of dry open habitats include *Carex siccata* Dewey, *Cyperus houghtonii* Torr., *Monarda fistulosa* L., *Polygala verticillata* L., *Pycnanthemum virginianum* (L.) Dur. & Jack., *Potentilla arguta* Pursh, *Selaginella rupestris* (L.) Spring, and *Sporobolus cryptandrus* (Torrey) A. Gray.

Chlosyne g. carlota may have existed in eastern Ontario during pre-settlement times, and become rare partly as a result of the succession of isolated open habitats to dense woody cover as a consequence of restricted fire and changing land use (as appears to be the case with *Plebejus melissa samuelis* (Nabokov) and *Phyciodes batesii batesii* (Reakirt)). Destruction of habitats during intense agricultural use 50–200 years ago may also have contributed to rarity. Since *C. g. carlota* is able to utilize hayfields, recently abandoned agricultural land, and a foodplant that occurs along roadsides, *C. g. calota* may now be expanding its northeastern range. Alternatively *C. g. carlota* may have recently invaded the area, but if this were so, we suspect it would it would have expanded

gradually rather than appearing suddenly in a distant location hundreds of miles from known colonies. It may have moved into eastern Ontario with the cultivation of sunflowers, but such cultivation has been rare over the past few decades.

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THE SPHINGIDAE OF CHAJUL, CHIAPAS, MEXICO

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ABSTRACT. The arthropod fauna of "Selva Lacandona" is poorly studied. Though vertebrate and plant inventories are still in progress, preliminary results indicate these forests are extremely species rich. The information presented here is part of an ongoing inventory of the moth fauna of Estación de Biología Chajul. Eighty-four species of Sphingidae have been documented, and this accounts for nearly half of the fauna of this family for the entire country. Flight periods are presented for most species. Temperature data explain 52% of the variation in monthly species richness.

Additional key words: seasonal patterns, Selva Lacandona, inventory.

The "Selva Lacandona" once was a large forest covering nearly 1.3 million ha (Diechtl 1988 in Dirzo & Miranda 1991). However, within the last 40-50 years it has been reduced to a small fraction of its original area (Dirzo & Miranda, pers. comm.). As a conservation effort, the "Reserva de la Biósfera Montes Azules" was created within the Lacandona's forests in 1978 (Lobato 1981). It encompasses more than 300,000 ha preserving several forest types (SEDUE 1989). Today, large portions remain relatively undisturbed (Dirzo & Miranda 1991). The reserve appears to be the largest tract of northern latitude tropical rain forest (Medellín 1994). However, large portions have been severely disturbed by human activities (Rother 1990).

Though animal and plant inventories are still in progress (Dirzo, pers. comm.) preliminary surveys indicate that "Selva Lacandona" supports a rich biological diversity. For example, within the reserve Medellín (1994) found nearly 100 mammal species and Salgado-Ortiz (1993) found 300 bird species. In addition, within a 2 ha plot, roughly 900 species of flowering plants were found, and at least 200 more are expected (Ramos & Martínez 1993). Information on taxa other than vertebrates and plants is more difficult to obtain, particularly for invertebrates, which are extremely diverse. However, all taxa studied indicate that the area of Chajul supports an unusually high biological diversity. For example, De la Maza and De la Maza (1985a, 1985b) recorded 544 butterfly species within a few hectares, and Morón et al. (1985) identified 110 lamellicornian beetle (Coleoptera) species in three families.

This report is part of an ongoing inventory of the moth fauna of "Selva Lacandona." It represents samples from the forests neighboring "Estación de Biología Chajul," currently administered by Instituto de Ecología, UNAM (EBChajul hereafter), and 160 nights of collecting over three years. We provide a relatively complete checklist of the Sphingidae for EBChajul and neighboring sites, together with information on their phenology.

MATERIALS AND METHODS

Study site. EBChajul was named after Río Chajul, and is located at the southern edge of Montes Azules Biosphere Reserve (Municipio de Ocosingo, Chiapas, México) (16°05'N, 90°56'W), a few miles north of the Guatemala border (Fig. 1). The field station is at the border of the reserve and is accessed through the Lacantún River. This river serves as a natural limit for the reserve and today virtually separates the well preserved forests from a devastated area occupied by numerous villages across the river, altogether called the "Marqués de Comillas" zone (Lobato 1981). The Lacantún has several tributaries: Lacanja, San Pedro, Tzendales, Negro, Jatate, Santo Domingo, Ixcan and Chajul. Geologically, the area is mostly middle and upper Cretaceous with Cenozoic outcroppings. Representative soils are luvisols and Acrisols with a superficial lithology of sandstone, shale and clays (García 1985).

The closest climatic records for EBChajul are from "Estación Lacantún," 4 km downstream from the field station. These records include nearly 10 years of data, indicating a four-month dry season and an average annual rainfall of nearly 3000 mm. September has the highest rainfall (Fig. 2a). Average maximum and minimum temperatures are 34.5°C and 16.4°C respectively. The highest temperatures occur in May–June and the lowest temperatures in December–January.

Tropical rain forest is the main forest type at EBChajul (Rzedowski 1978), although other forest types are present throughout the reserve, including pines, oaks and grasslands (SEDUE 1989). In the vicinity of EBChajul are grasslands associated with the hilltops where two trees, *Brysonima crassifolia* (Malpigiaceae) and *Curatella americana* (Dilleniaceae) and several shrubby species, *Climedia* spp. (Melastomataceae), *Rourea* spp. (Connaraceae) and *Sabicea villosa* (Rubiaceae) are common. The forest canopy comprises 3 to 4 strata. The upper canopy, consisting of trees greater than 25 m in height, includes: *Licania platypus* (Chrysobalanaceae), *Virola coshunii*, (Myristicaceae), *Luehea semanii* (Tiliaceae), *Dialium guianense* (Leguminosae), *Ceiba pentandra* (Bombacaceae), *Ficus* spp. (Moraceae), and *Swietenia macrophylla* (Meliaceae). The middle canopy, consisting of trees of up to 25 m in height, includes: *Bursera simarouba* (Burseraceae), *Brosimum* spp. (Moraceae),

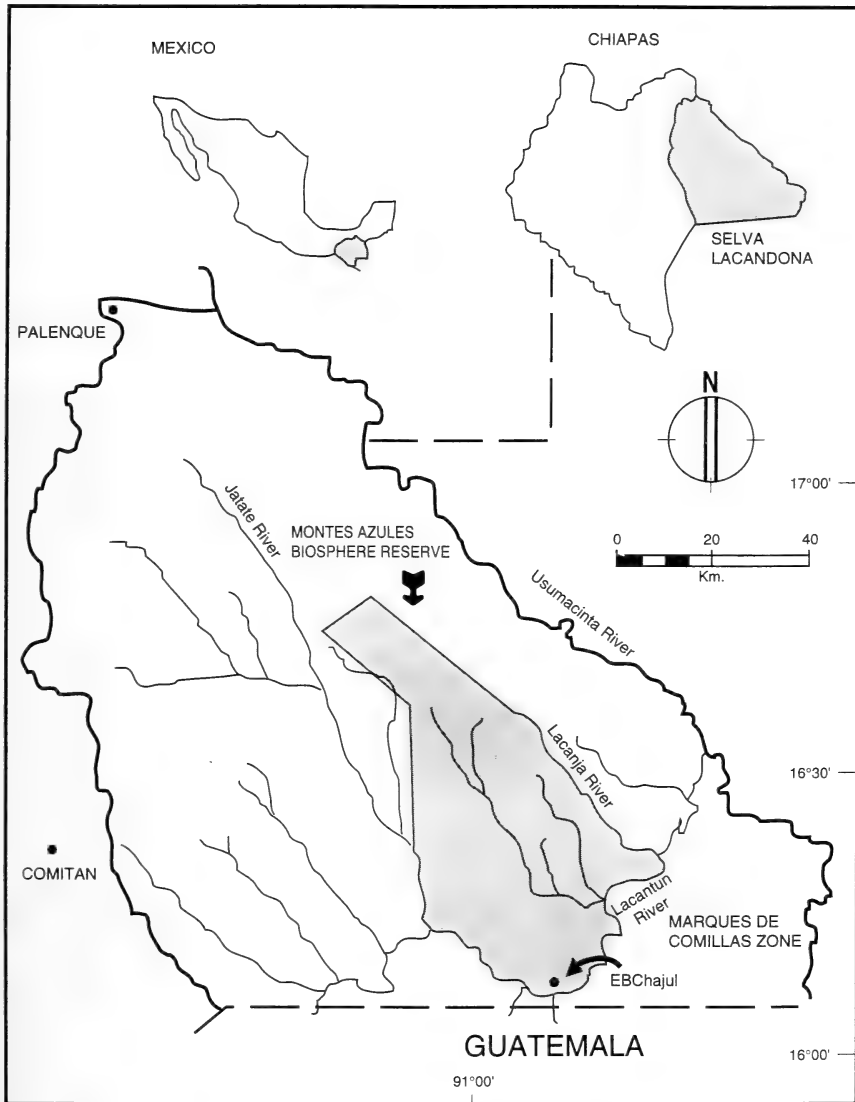


FIG. 1. Location of Estación de Biología Chajul within the Reserva de la Biosfera Montes Azules, Chiapas, México (modified after Medellín 1994).

Zanthoxylum spp. (Rutaceae), *Pterocarpus rohrii* (Leguminosae), *Taluma mexicana* (Magnoliaceae), *Schizolubium parahybum* (Leguminosae), and *Bravaisia integrerrima* (Acanthaceae). The lower canopy, consisting of trees less than 10 m in height, includes: *Cymbopetalum penduliflorum* (Annonaceae), *Guarea glabra* (Meliaceae), *Quararibea*

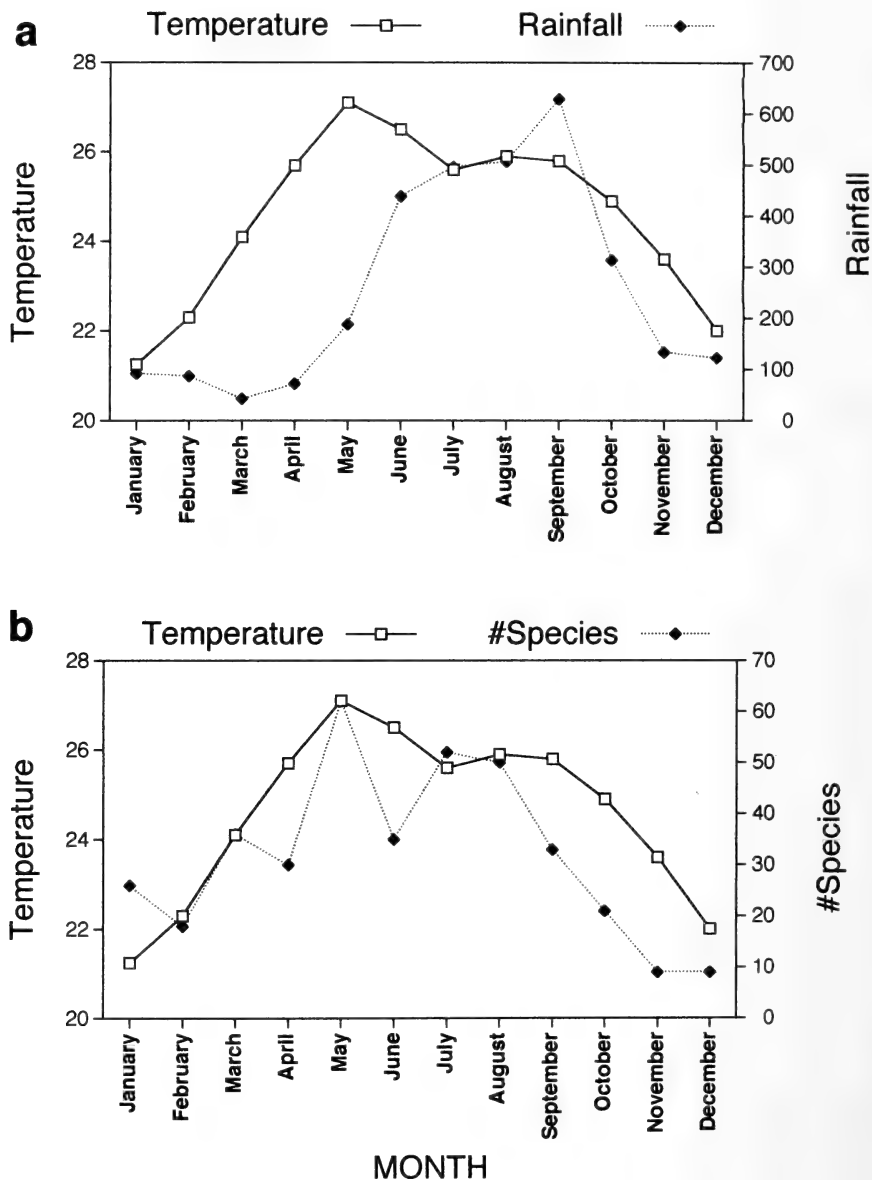


FIG. 2. **a**, Ten year (1980–1990) mean monthly temperature and mean monthly rainfall at “Lacantún” climatological station. **b**, Total number of sphinx moth species captured per month, compared to the ten year mean monthly temperature at the “Lacantún” climatological station.

funebri (Bombacaceae), *Ampelocera hottlei* (Ulmaceae), *Pachira acutata* (Bombacaceae), *Rheedia edulis* (Guttiferae), and *Posoqueira latifolia* (Rubiaceae). In addition, there is an understory rich in palm species, including *Chamaedora tepejilote*, *Bactris* spp. and *Reinhardtia gracilis* (Ramos & Martínez 1993, G. Domínguez, pers. comm.).

Sampling protocol. The inventory effort started July 1991 and ended November 1992; additional collections occurred in January, March and July 1993. We used two 15 watt fluorescent lights powered by a car battery; both were placed 20–30 cm in front of a white sheet measuring 3 m². In each of two settings we used both a black-blue and a day-light bulb. Every night we collected from 1800 h to 0500–0600 h the following morning. Each month our sampling effort lasted approximately two weeks, all days spread evenly around the new moon. Sampling sites were within walking distance of EBChajul. In addition to our own records, we consulted private collections for species not captured by us.

Specimen preparation. All collected specimens were spread to facilitate identification, oven-dried and labeled for permanent storage. Hodges (1971), D'Abbrera (1986) and Janzen (1984, 1986) were our main sources for identifying the collection. However, we also consulted the entomological inventory at Instituto Nacional de Biodiversidad (INBio), Costa Rica, and its curators. Specimens of the collection including Sphingidae and other moth families are currently stored at: Estación de Biología Chamela, Jalisco, Instituto de Biología, Universidad Nacional Autónoma de México; Centro Universitario de Investigación y Desarrollo Agropecuario, Universidad de Colima; El Colegio de la Frontera Sur, San Cristobal de las Casas, Chiapas. Duplicate specimens were deposited provisionally at INBio, Costa Rica.

Data analysis. We compiled information on months of capture for each species along with an analysis relating the number of species collected each month to the average monthly rainfall and temperature. As a way to check the adequacy of our inventory, we generated a species accumulation curve by plotting the number of species collected as a function of the number of nights we spent collecting. We assumed the shape of the curve can serve as a descriptive tool of sampling adequacy.

RESULTS AND DISCUSSION

We collected a total of 84 species of sphinx moths (Table 1; taxonomic arrangement follows Hodges 1971) representing nearly half the Sphingidae known from México (White et al. 1991). The species belong to 25 genera in five tribes and two subfamilies. *Xylophanes* was the most species rich genus with 16 species (19%) followed by *Manduca* with 13 species (15.5%), *Eumorpha* with 8 species (9.5%), and *Erinnyis* with 6 species (7%). Together these genera comprise 51.2% of all species at

TABLE I. Checklist of the Sphingidae of Estación de Biología Chajul. Species marked by asterisks were collected recently by other workers (J. de la Maza, personal collection), and phenological data may be incomplete. Roman numbers indicate months of the year, and each X the presence of that species in that month.

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Subfamily Sphinginae												
Tribe Sphingini												
<i>Agrius cingulata</i> (Fabricius 1775)	X	X		X	X	X	X	X	X	X		
<i>Cocytius antaeus</i> Drury 1773	X	X						X	X			
<i>Cocytius duponchel</i> (Poey 1832)	X	X	X	X	X		X	X		X		
<i>Neococytius cluentius</i> (Cramer 1775)					X		X	X		X		
<i>Manduca sexta</i> (Linnaeus 1763)	X	X	X	X	X	X	X	X				X
<i>Manduca dilucida</i> Edwards 1887					X							
<i>Manduca occulta</i> Rothschild & Jordan 1903	X	X	X	X	X	X	X	X	X	X		
<i>Manduca hannibal</i> Cramer 1779	X	X	X	X	X	X	X	X	X			X
<i>Manduca pellenia</i> (Herrich-Schaffer 1854)			X	X	X							
<i>Manduca lefeburei</i> (Guerin 1844)					X		X		X			
<i>Manduca ochus</i> (Klug 1836)							X	X				
<i>Manduca rustica</i> (Fabricius 1775)	X	X	X	X	X	X	X	X	X	X		
<i>Manduca albiplaga</i> (Walker 1856)					X	X						
<i>Manduca muscosa</i> (Rothschild & Jordan 1903)					X		X	X	X			
<i>Manduca corallina</i> (Druce 1883)	X	X		X	X							
<i>Manduca lichenea</i> (Burmeister 1856)										X	X	
<i>Manduca florestan</i> Cramer 1782				X	X	X	X	X				
<i>Manduca lanuginosa</i> (Edwards 1884)					X	X						
<i>Sphinx merops</i> Boisduval 1870		X		X		X	X	X	X	X		
Tribe Smerinthini												
<i>Protambulyx xanthus</i> Rothschild & Jordan 1906								X				
<i>Protambulyx strigilis</i> (Linnaeus 1771)	X		X	X	X	X	X	X	X	X		
<i>Adhemarius gannascus</i> (Stoll 1790)	X	X	X		X		X	X	X	X	X	X
<i>Adhemarius ypsilon</i> Rothschild & Jordan 1903	X	X	X	X	X	X	X	X	X	X	X	X
Subfamily Macroglossinae												
Tribe Dilophonotini												
<i>Pseudosphinx tetrio</i> (Linnaeus 1771)	X		X	X			X	X	X	X	X	X
<i>Isognathus rimosus</i> Grote 1865						X		X				
<i>Erinnyis yucatanana</i> (Druce 1888)					X							
<i>Erinnyis alope</i> (Drury 1770)					X	X			X			X
<i>Erinnyis lassauxi</i> (Boisduval 1859)	X	X	X	X	X	X	X	X	X			
<i>Erinnyis ello</i> (Linnaeus 1758)	X	X	X	X	X	X						
<i>Erinnyis oenotrus</i> (Cramer 1782)	X	X	X	X	X	X	X	X	X			
<i>Erinnyis obscura</i> (Fabricius 1775)					X	X						
<i>Pachylia ficus</i> (Linnaeus 1758)				X	X	X	X	X				
<i>Pachylia syces</i> (Hübner 1822)					X	X	X	X				
<i>Pachylioides resumens</i> (Walker 1856)		X	X	X	X	X	X	X	X	X	X	X
<i>Kloneus babayaga</i> Skinner 1923*								X	X			
<i>Hemeroplanes triptolemus</i> (Cramer 1779)		X	X		X	X						
<i>Hemeroplanes ornatus</i> (Rothschild 1894)				X								
<i>Madoryx oiclus</i> (Cramer 1779)				X	X							X

TABLE I. continued.

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
<i>Madoryx bubastus</i> Cramer 1777					X		X					
<i>Madoryx pluto</i> Cramer 1779	X	X	X	X	X	X	X	X				
<i>Callionima denticulata</i> Schaus 1895						X						
<i>Callionima inuus</i> (Rothschild & Jordan 1903)				X	X	X	X	X	X			X
<i>Callionima parce</i> Fabricius 1775	X				X		X	X	X			
<i>Callionima falcifera</i> (Gehlen 1943)	X	X	X	X	X	X	X	X	X	X	X	
<i>Callionima nomius</i> (Walker 1856)					X	X	X	X	X			
<i>Callionima neivai</i> Oiticica 1940										X		
<i>Aleuron carinata</i> Walker 1856						X						
<i>Aleuron chloroptera</i> Boisduval 1870							X	X				
<i>Unzela japix</i> (Cramer 1776)									X			
<i>Enyo lugubris</i> (Linnaeus 1777)				X	X							
<i>Enyo ocypete</i> (Linnaeus 1758)		X			X		X	X		X		
<i>Enyo gorgon</i> (Cramer 1777)					X	X		X				
<i>Enyo taedium</i> (Schaus 1890)			X									
<i>Enyo cavifer</i> (Rothschild & Jordan 1903)									X			
<i>Pachygonidia drucei</i> Rothschild & Jordan 1903							X	X	X			
<i>Perigonia lusca</i> Fabricius 1777				X								
<i>Aellopos ceculus</i> (Cramer 1777)*					X		X		X			
<i>Aellopos clavipes</i> (Rothschild & Jordan 1903)								X				
<i>Aellopos fadus</i> (Cramer 1776)*										X		
Tribe Philampelini												
<i>Eumorpha anchemola</i> (Cramer 1780)			X	X	X		X	X	X	X		
<i>Eumorpha triangulum</i> Rothschild & Jordan 1903	X				X	X		X	X	X		
<i>Eumorpha obliquus</i> Rothschild & Jordan 1903					X							
<i>Eumorpha satellitia</i> Linnaeus 1771			X	X	X	X	X	X				
<i>Eumorpha vitis</i> (Linnaeus 1758)		X			X	X	X	X	X			
<i>Eumorpha fasciatus</i> (Sulzer 1776)		X										
<i>Eumorpha labruscae</i> (Linnaeus 1758)					X		X					
<i>Eumorpha phorbas</i> (Cramer 1775)		X		X	X		X					
Tribe Macroglosini												
<i>Xylophanes pluto</i> (Fabricius 1777)	X	X	X		X	X	X	X	X			
<i>Xylophanes tyndarus</i> (Boisduval 1875)		X	X	X	X	X	X					
<i>Xylophanes pistacina</i> (Boisduval 1877)			X	X	X							
<i>Xylophanes porcus</i> (Hubner 1829)					X							
<i>Xylophanes ceratomioides</i> (Grote & Robinson 1867)	X	X	X	X	X	X	X	X	X	X	X	X
<i>Xylophanes anubus</i> (Cramer 1777)	X	X	X	X	X	X	X	X				
<i>Xylophanes amadis cyrene</i> Stoll 1782					X	X						
<i>Xylophanes belti</i> (Druce 1878)					X		X	X				
<i>Xylophanes chiron</i> Drury 1770	X	X	X	X	X	X	X	X	X	X		X
<i>Xylophanes titana</i> Druce 1878			X					X	X			
<i>Xylophanes tersa</i> Drury 1770				X	X		X	X	X			
<i>Xylophanes maculator</i> (Boisduval 1875)				X								
<i>Xylophanes libya</i> (Druce 1878)	X	X	X	X	X	X	X	X	X	X		
<i>Xylophanes neoptolemus</i> (Stoll 1782)	X	X	X	X	X	X	X	X	X	X		X
<i>Xylophanes thyelia</i> Linnaeus 1758	X	X	X	X	X	X	X		X	X	X	
<i>Xylophanes zurcheri</i> (Druce 1894)					X	X		X				
<i>Hyles lineata</i> (Fabricius 1775)					X		X					

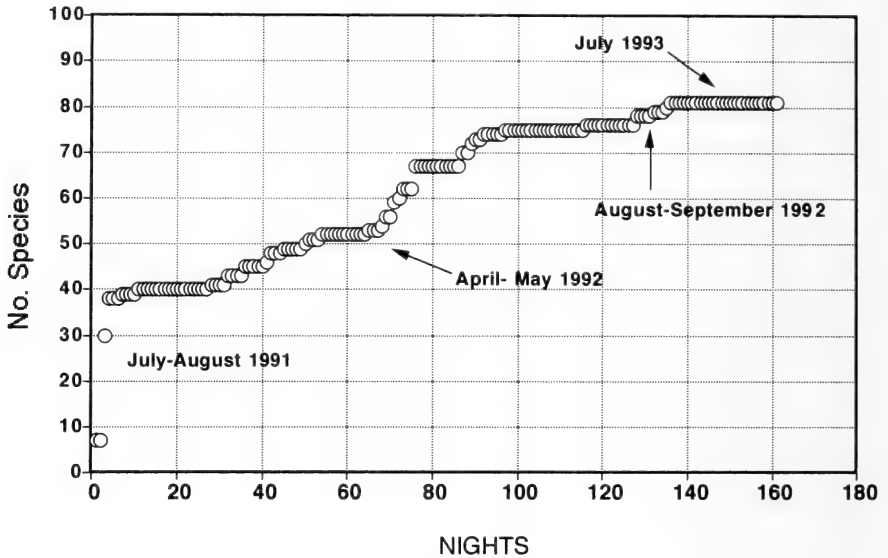


Fig. 3. Sphinx moth species accumulation curve at EBChajul compared to the number of nights of field work.

EBChajul. This pattern appears to be a common feature among sphingid assemblages in tropical forests across tropical America (León-Cortés & Pescador, unpubl. data).

Our sampling effort included 161 nights representing more than 1600 hours of field work. Of the 84 species, 81 were captured by us; 3 additional species had been found in previous years (J. De la Maza, personal collection). Within the first three months after the beginning of the rainy season 87.6% of the total number of species was caught (cf. May–July; Fig. 3, Table 1). However, 62 (76.5%) of all was present in May, the month when the rainy season begins (Fig. 2a, Table 1).

Fifteen species (17.6%) were collected at EBChajul for nine or more months during the year. However, rainfall in May apparently cued the emergence of 24 (28%) sphingid species (Table 1). In addition, photoperiod and/or temperature also appeared to have a strong effect on the phenology of many species; 20 (23.5%) initiated their flying season in March–April, when temperature is rising, two months before the onset of the rainy season (Fig. 2a, Table 1). This pattern (Fig. 2b) suggested a correlation between sphinx moth monthly richness and mean monthly temperature. A regression analysis of species richness versus temperature (log-log scale) indicated that 52.4% of sphingid monthly richness variability was explained by temperature ($MS_{err} = 145.85$, $df = 10$, $F = 11.01$, $p < 0.01$; $\ln(S) = -124.275 + 6.352 \times \ln(\text{temperature})$). In

contrast, rainfall, even when it had a major influence on the start of the flying season for many species in May, apparently had no other effect on subsequent dates.

These patterns are only an approximation of the actual phenologies of the sphingid fauna of EBChajul. Janzen (1983, 1986) has stressed that captures at light sources are only a partial view of sphingid populations. One of the reasons for this is that we do not completely understand why insects are attracted to light (see Janzen 1984 for a review). For example, some species (commonly captured at lights) may be found in large numbers in the forest while foraging for nectar and pollen without reaching the lights (Janzen 1983, Pescador, unpubl. data). Most sphingids collected at lights are in good condition, suggesting they reach the lights soon after emergence (Janzen 1983, 1984).

The shape of the species accumulation curve suggests we collected nearly all the Sphingidae at EBChajul that are attracted to light (Fig. 3). However, given the proximity of EBChajul to Central America and its similarity in floral composition, Janzen (pers. comm.) suggests the following species probably will be added to our list: *Cocytius beelzebuth* (Boisduval), *C. lucifer* (Rothschild & Jordan), *Unzela pronoe* (Druce), *Nyceryx coffeae* (Walker), *N. tacita* (Druce), *Eupyrrhoglossum sagra* (Poey). Moreover, J. M. Cadiou (pers. comm.), who has extensive knowledge of the Sphingidae in the neotropics, suggests that we could expect 12 additional species in this area. Therefore, based on the intensity of our collecting we assume that nearly all the breeding species in the vicinity of EBChajul have been documented. However, a larger effort should be made to explore the rest of the reserve.

A comparison with other published checklists of Sphingidae in the neotropics, particularly in Mexico, is clearly possible. We abstain from doing so here because the results of this study indicate that variation in sampling effort has a substantial effect on the size of a checklist. Variation in sampling effort may be accounted for in various ways, however, those analyses are still in progress (León-Cortés, unpubl. data).

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could be found at EBChajul. J. M. Cadiou commented on the checklist and provided insights into other species that may be found at Chajul. We also thank J. de La Maza for allowing us access to his private sphinx moth collection, and E. Martínez and G. Domínguez for allowing us to use information on plant species richness and forest plant composition respectively. R. Medellín and J. Soberón made constructive comments on the manuscript. Also, we thank Alex Zacarías for his highly professional and patient work during the long night hours of field work. Finally, we are indebted to H. Chacón-Sol, A. Locht-Moisen, M. Yáñez-Rivera, M. Barrios-Herrera, O. Gómez-Nucamendi, D. Figueroa-Castro and E. Saborío for their patient and careful curatorial work.

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GENERAL NOTES

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NOTES ON *PARNASSIUS SMINTHEUS* DOUBLEDAY (PAPILIONIDAE) ON VANCOUVER ISLAND

Additional key words: British Columbia, Canada.

Parnassius phoebus guppyi was described by Wyatt (1969) with the type locality Mt. Arrowsmith, Vancouver Island, British Columbia, Canada. Since its description *P. phoebus guppyi* has been treated in the North American literature as a synonym of *P. phoebus olympianus* Burdick 1941, type locality Hurricane Hill, Olympic Peninsula, Washington, USA. I follow this treatment. Shepard and Manley (1998) have since demonstrated that the correct species name for most non-arctic North American “*phoebus*” populations is *Parnassius smintheus* Doubleday, the name used in this paper.

Only a small number of *Parnassius smintheus olympianus* have been collected on Vancouver Island, from a total of five populations. Additional specimens and habitat information will probably not be acquired rapidly because of the difficult access to the rugged mountains of northern Vancouver Island. All known localities, except the type locality, are within Strathcona Provincial Park (Fig. 1) where a collecting permit from BC Parks is required for any sampling.

The type series of *guppyi* consists of nine males and five females labeled as collected by Richard Guppy on Mt. Arrowsmith, Vancouver Island, British Columbia, Canada, 1500 m, 22 July to 31 August, 1961 to 1967 (Wyatt 1969). Richard Guppy, a few years before his death, told me that he had collected all of Wyatt's specimens on Mount Cokely rather than Mount Arrowsmith. Mount Cokely is frequently called “Mount Arrowsmith” in error, because it is the first summit on both trails to Mount Arrowsmith, and because hikers frequently end their walk at the summit of Mount Cokely rather than completing the strenuous ascent of the bedrock peak of Mount Arrowsmith. The type locality of *Parnassius smintheus guppyi* Wyatt is here corrected to Mount Cokely, elevation 1500–1600 m, Vancouver Island, British Columbia, Canada (49°14'30"N, 124°35'10"W). My own specimens were also all collected on Mount Cokely, and I suspect that most, if not all other, existing specimens are from Mount Cokely.

The summit of Mount Cokely (elev. 1630 m) is 1.8 air km north of the summit of Mount Arrowsmith (elev. 1819 m). A saddle (elevation 1500 m) connects the two mountains. Richard Guppy told me that the majority of the specimens came from the top of the west ridge of Mount Cokely immediately above the saddle connecting the mountains, and a few came from the south slope of the ridge down to the saddle. None came from Mount Arrowsmith itself, although *P. smintheus* occurs there. Richard Guppy said that at least one, and possibly two (he could not remember exactly), specimens of the type series were reared from nearly mature larvae found feeding on *Sedum divergens* Wats. (Crassulaceae). This is significant because the developmental environment of *Parnassius smintheus* can affect the adult phenotype (Guppy 1989). The *P. smintheus* on Mount Cokely and Mount Arrowsmith apparently comprise a single population, because I have observed females flying on the saddle (unsuitable habitat) between the two peaks.

The habitat of *Parnassius smintheus* on Mount Cokely and Mount Arrowsmith consists of barren rounded bedrock ridges and cliffs, with small ledges and slopes of scree. *Sedum divergens* grows in cracks in the bedrock and in the scree, and is the only *Sedum* species on Mount Arrowsmith and Mount Cokely. The saddle between the two peaks is gravel and dirt dominated by heather (*Cassiope* sp.) and lacks *Sedum*. *P. smintheus* is likely to occur on two western ridges of Mount Arrowsmith down to 1400 m, which is as far down as un-forested habitats and *Sedum divergens* occur, but I have not visited those ridges at the appropriate time of year. The habitat is subalpine to the summit of the mountains, with the lack of forest being the result of lack of soil on the bedrock areas rather than elevation.

Male *P. smintheus* patrol up and down the cliffs, and are easily netted when they reach the flat top of the west ridge of Mount Cokely. Females spend most of their time on the ledges of the cliffs where they are difficult to approach, and only rarely are found on the



FIG. 1. Known populations of *Parnassius smintheus* on Vancouver Island. 1, Hurricane Ridge, type locality of *P. smintheus olympianus* Burdick. 2, Mount Cokely, type locality of *P. phoebus guppyi* Wyatt. 3, Cream Lake, Flower Ridge, Hope Lake & Mount Albert Edward, and Mount Becher (west to east). SPP, Strathcona Provincial Park. VI, location of Vancouver Island.

flat ridge top because *Sedum* is sparse there. The flight period is from mid-July to mid-September, with yearly variation depending on weather and melting of the snowpack.

Strathcona Provincial Park contains the other four known populations of *P. smintheus* on Vancouver Island. Three of the populations are connected by continuous alpine habitats. The distance between Mount Albert Edward and Cream Lake is about 21 air km, with a main alpine ridge running between the two sites. Flower Ridge is a spur ridge to the west of this main ridge. Mount Becher is to the east of Mount Albert Edward, with about 10 km of subalpine meadow and forest (unsuitable habitat) between. I estimate the flight period for these populations to be from late July to late September, with the exact period dependant on weather and the melting of the snowpack.

The habitat at Cream Lake is a small recent glacial moraine of hard packed gravel, and is steep and difficult to collect. The remainder of the area around Cream Lake is either bedrock, forest or subalpine heath. *Sedum divergens* is the only *Sedum* species present and is abundant, and I assume it is the larval hostplant. Most specimens collected at Cream Lake were fresh but a few were very worn, suggesting that a lower elevation popu-

lation with an earlier flight season is nearby. A likely location for such a population is southeast of Cream Lake on the south slopes of Mount Septimus and Mount Rosseau above Love Lake (el. 1231 m).

The habitat on Flower Ridge where I collected the one specimen was unsuitable sub-alpine heath. I assumed that the specimen came from the inaccessible slope below, which was a steep east-facing slope with abundant herbaceous vegetation. I did not see any *Sedum* species, but the habitat on the slope below appeared suitable for *Sedum divergens*.

The habitat on the east ridge of Mount Albert Edward is volcanic rock and pumice rubble and scree, with the south side of the ridge being a cliff with talus slopes at the bottom around Hope Lake. The *P. smintheus* on the ridge top and those near Hope Lake are undoubtedly one population, with movement up and down the cliff. The only *Sedum* present on the ridge and on the talus slopes around Hope Lake is *Sedum divergens*, which I presume to be the larval hostplant.

Mount Cokely/Arrowsmith is about 70 km southeast of Cream Lake, with no suitable habitat directly between until a few km south of Cream Lake. To the west the closest suitable elevation is Klitsa Mountain, which lacks *P. smintheus* and has only a small *Sedum divergens* population. The next closest mountain to the west is Nahmint Mountain (unsampled), 40 km from Mount Arrowsmith. A few unsampled summits south of Mount Cokely/Arrowsmith may have *P. smintheus* populations, but most of Vancouver Island south of Mount Arrowsmith is too low to include suitable habitat. The Mount Cokely/Arrowsmith population is therefore isolated from the populations to the north.

There are many other peaks in Strathcona Park which are likely to have populations of *P. smintheus*, and additional mountains occur further north on Vancouver Island. I believe that additional, undiscovered *P. smintheus* populations occur in Strathcona Park and the other mountains of Vancouver Island, but the total number of populations is likely less than fifty. The known populations and specimens are: **Mount Cokely, 1500–1600 m, 49°14'30"N 124°35'10"W**: Mt. Cokeley, 5000 ft, 22 July 1951, J. R. L. Jones; UBC; 5 ♂. Mt. Cokeley, 5000 ft, 30 July 1950, J. R. L. Jones; UBC; 1 ♂. Mt. Cokely, 1600 m, 13 August 1975, C. S. Guppy; JHS & CSG; 4 ♂, 1 ♀. Mt. Cokely, 1600 m, 12 August 1978; CSG; 4 ♂. Mt. Cokeley, 11 August 1952, G. A. Hardy; RBCM; 1 ♂, 2 ♀. Mt. Arrowsmith, 1 August 1970, R. Guppy; CDF; 1 ♂. Mt. Arrowsmith, 17 August 1974, R. Guppy; CDF; 1 ♂. Mt. Arrowsmith, 29 July 1962; AMNH ex dos Passos Collection; 2 ♂. Mt. Arrowsmith, 22 July 1961, R. Guppy; AMNH ex dos Passos Collection; 1 ♂. Mt. Arrowsmith, Vancouver Island, British Columbia, Canada, 1500 m, 22 July to 31 August, 1961 to 1967, R. Guppy (Wyatt 1969). **Strathcona Provincial Park, Mount Becher on Forbidden Plateau, 1385 m, 49°39'00"N 125°13'30"W**: Forbidden Plateau, Courtenay, 20 August 1931, J. D. Gregson; AMNH ex dos Passos Collection; 1 ♂. Mt. Becher, 28 August 1957, G. A. Hardy; RBCM; 2 ♂. Mt. Becher, 10 August 1961, G. A. Hardy; RBCM; 2 ♂, 1 ♀. **Strathcona Provincial Park, Mount Albert Edward, east ridge, 1920–2094 m, 49°40'30"N 125°25'30"W and Hope Lake, west and north sides, 1530 m, 49°40'15"N 125°25'30"W**: Forbidden Plateau, Mt. Albert Edwards, 7000', 26 July 1931 (Gregson); AMNH ex dos Passos Collection; 1 ♀. Strathcona Provincial Park, Hope Lake, west and north sides, el. 1530 m 4 August 1989, C. S. Guppy (several males collected, specimens since misplaced). One female was observed flying on the top of the east ridge of Mount Albert Edward, el. 1920 m (above Hope Lake) on the same date. Mt. Albert [Edward?], August 23, 1953, L. S. Clark; RBCM; 1 ♂. **Strathcona Provincial Park, Flower Ridge, 1400m, 49°32'N 125°31'W**: Strathcona Provincial Park, Flower Ridge, central part, elev. 1400 m, 23 August 1987, C. S. Guppy; CSG; 1 ♂. Approximately 10 males were also observed flying on an inaccessible slope on the north side of the ridge at this location. **Strathcona Provincial Park, Cream Lake, 1400 m, 49°29'02"N 125°31'20"W**: Strathcona Provincial Park, Cream Lake, southeast corner of the lake, el. 1400 m, 22 August 1988, C.S. Guppy; RBCM & McKinnon; 13 ♂.

Acronyms used above include: AMNH = American Museum of Natural History; CDF = Clifford D. Ferris; CSG = the present author; JHS = Jon H. Shepard; McKinnon = Betty McKinnon, deceased, location of her one specimen unknown; RBCM = Royal British Columbia Museum (all RBCM specimens except Cream Lake were apparently part of two drawers of *Parnassius* destroyed by dermestids in the late 1970s (R. A. Can-

nings, pers. comm.), and the data are from Jon H. Shepard's files); UBC = University of British Columbia. One male *P. smintheus* in the Canadian National Collection I consider to be erroneously labelled, "Victoria, BC, June 26, 1925, R.W. Hall."

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MISPLACED HOLOTYPE FROM THE A. E. BROWER COLLECTION

Additional keywords: *Catocala*, type specimens.

The A. E. Brower collection was acquired by the National Museum of Natural History, Smithsonian Institution, Washington, D.C. from 1981–1994 (Davis & Hevel 1995). The last portion of this collection to arrive at the museum was that of the Nearctic *Catocala* (Noctuidae). The museum's *Catocala* collection (including Brower's material) has been curated and recorded in a database and is currently housed at the Museum Support Center in Suitland, Maryland.

Brower's collection was housed in a number of makeshift drawers and various sized cigar boxes. Nancy E. Adams (Dept. Entomology, Smithsonian Institution) found five of Brower's (1976) holotypes in one of these numerous cigar boxes, and brought this to my attention. I compared these specimens with the data and figures of the holotypes in the original publication and they all match. The data for these specimens are presented below, with each line of label data separated by a semicolon:

Catocala texarkana, Forestburg, Tex. 10–12 V 1940; L.H. Bridwell [hand written in india ink]. HOLOTYPE USNM; *Catocala texarkana* Brower [red printed label with black line border, species name hand written in india ink].

Catocala lincolnana, Lincoln Co. Ark.; 1 June 1937; L.H. Bridwell [hand written in india ink]. HOLOTYPE USNM; *Catocala lincolnana* Brower [red printed label with black line border, species name hand written in india ink].

Catocala erichi, Green Valley Creek, San Bernardino Mts.; emgd. 19–V-1966 Calif. [hand written in india ink]. HOLOTYPE USNM; *Catocala erichi* Brower [red printed label with black line border, species name hand written in india ink].

Catocala johnsoniana, Kernville Kern Co.; Calif. 17 June 1905; Erich Walter [hand written in india ink]. HOLOTYPE USNM; *Catocala johnsoniana* Brower [red printed label with black line border, species name hand written in india ink].

Catocala californiensis, Valyermo, L.A. Co.; 27 June 1957 Calif.; Noel McFarland [hand written in india ink]. HOLOTYPE USNM; *Catocala californiensis* Brower [red printed label with black line border, species name hand written in india ink].

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BOOK REVIEW

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HELICONIUS AND RELATED GENERA, by Helmuth and Ruth Holzinger. 1994. Sciences Nat, Vennete, France. 328 pp. English text, 57 figures, 41 color maps, 51 color plates. Available from BioQuip for U.S. \$399.00 (hardcover).

Heliconius and Related Genera comprehensively describes the taxonomy and superficial diagnostic features of the 37 species, 369 described "subspecies" and myriad "forms" of *Heliconius* Kluk, *Neruda* Turner and *Eueides* Hübner. This big, expensive book is oriented solely towards collections of pinned specimens, and contains little evidence to suggest the authors have studied morphological features aside from the extensive wing pattern variation. Nor is there indication that the authors examined material from anywhere other than Vienna, München, and a few private collections. Although the book provides many color illustrations of named *Heliconius* taxa for the first time, I was disappointed by almost every other aspect of the material presented.

1. *What's missing.* The fascinating natural history of *Heliconius* is dismissed in 1/3 of a page, without a single full citation. The reader is referred to "the detailed works of Brown, Gilbert, Turner and Mallet," but no papers are cited, and none of Gilbert's or Mallet's work is listed in the bibliography. Morphology of larvae and pupae are not illustrated or discussed in any useful detail, nor are references provided to the literature on host plant associations (the relationship between *Passiflora* and *Heliconius* is touted as one of the premier examples of herbivore-host plant coevolution). Neither is the extensive work on the genetics and evolution of mimicry within and among *Heliconius* species discussed. The major paper of Sheppard et al. (1985, *Phil. Trans. R. Soc. B* 308:433–613) summarizing these ideas is not cited, and there is no mention of evolutionary hypotheses that explain the dramatic diversity of the group.

The book also fails to offer any inkling of the hypothesized phylogenetic relationships among heliconiines, beyond a dendrogram produced by the authors without any evident character support or a formal methodology. This figure (p. 9) is based primarily on a graphical representation of taxonomic hierarchy, and is not even used as a basis for the taxonomic ranking presented in the book. Although the authors did not have access to recent cladistic work, it is shocking that the authors should choose to ignore the phylogenetic hypotheses of Emsley (1965, *Zoologica* 50:191–254) and Brown (1981, *Ann. Rev. Entomol.* 26:427–456) in favor of their own unsupported dendrogram.

There is no key presented to any level of diversity, because "the reader could be somewhat confused by the superficial resemblances and lose the feeling for the systematic relationships" (p. 7). It is not clear how the reader is supposed to gain this feeling in the first place. *Heliconius* is one of the most difficult butterfly genera, and even the experts cannot agree on the boundaries of its taxa. I suspect most users of this book will be forced to pigeonhole their specimens by comparing them to the plates, the same way we have always used the Seitz and D'Abbrera books.

2. *Quality and Originality of Illustrations and Maps.* The 51 plates contain 765 watercolor sketches of museum specimens with one pair of wings omitted (mostly dorsal surfaces, ventral surfaces for some taxa when they exhibit diagnostic features). Although they will probably be useful for sorting specimens in a collection, these imprecise, artistically rendered figures cannot be considered good scientific illustrations in any sense, when compared to either classical lithographs, modern photographic techniques or modern technical paintings.

The line "drawings" of morphological features are mostly of poor quality and are evidently not drawn from biological material. The abdominal processes in Figs. 4 and 7 were clearly copied (without attribution) from Emsley's (1965) figures, and many of the the valvae and signa bursarum appear to have been redrawn from that work as well. Most of Figs. 9–57 are mechanically enlarged versions of the valvae illustrated in Figs. 2 and 5. Only figure 8 is useful, but even this is misleadingly entitled "elements of the colour pattern" although it is a diagram of wing vein nomenclature, rather than color pattern (this figure is

modified with half-tone shaded areas to illustrate "typical" color pattern elements of various species groups in Figs. 33, 40, and 44).

The species distribution maps are attractively produced outlines of South America showing major river systems and various colored symbols that presumably indicate localities where geographical races or forms have been collected. No labels or legends are provided beyond the association of names with the colored symbols. There is no associated information on specimens or localities, such as Brown (1979, *Ecologia Geográfica e Evolução nas Florestas Neotropicais*, Universidade Estadual de Campinas, Campinas, São Paulo, Brasil) provided for his maps, so it is impossible to determine the precision or accuracy of these "data points." Some of the disjunct distributions on some maps (e. g. *H. wallacei* on Rio Tocantins, Map 14; *H. besckei* on Rio Mamoré, Map 27) are strikingly similar to distributions of the same taxa illustrated in Brown (1979, Figs. 16 and 23, respectively). This could be because Brown and the authors examined the same material or material collected at the same sites, because Brown gave the authors his data, or because the authors copied Brown's maps. There is no way to tell how these maps were made, but the description of numerous "subspecies" in the text with no corresponding distribution on the maps (e.g., *H. melpomene intersectus*, *H. m. ecuadorensis*, *H. m. malleti*) suggests that they are not based on primary observation of specimens. The maps' scientific value is thus heuristic, at best.

3. *Organization and Quality of Systematic Information.* The text is composed of three main sections: a "systematical" checklist, individual taxon accounts, and an annotated, alphabetical list of names. As mentioned above, there is no key. A new catalogue would also have been useful (the last being Neustetter, 1929, Lepid. Cat. 36, W. Junk, Berlin), but this is not provided, either. The checklist and the alphabetical list should have been combined, as it is annoying to flip back and forth between them to check references, and there are an index of names and a bibliography section that repeat most of the information in the two lists. Figures and maps are cited in taxon accounts, but neither figures nor maps contain reciprocal references to the text, again making the book difficult to use.

Characteristics of the taxon descriptions are as follows. The genus *Neruda* is diagnosed, but *Heliconius* and *Eueides* are not. Subgeneric species groups are identified and briefly discussed, with perfunctory character lists based on Emsley (1965). Descriptions of monotypic species consist of a type locality (no other specimen information is included), a reference to geographical distribution by country or region. There is extensive description of wing patterns, in my view the best aspect of the entire book (although better illustrations would eliminate the need for verbal description, except to emphasize key characters). Descriptions correspond reasonably well to original descriptions for the cases I checked. Description of wings is followed by a brief description of "genitalia," comprised only of male valvae and female abdominal processes and signae bursarum (the unacknowledged debt to Emsley is again revealed by occasional statements that descriptions of genitalia "were never published," indicating the authors' failure to make original observations of morphological features). A section on variability includes distributions and descriptions of infrasubspecific forms. Last, a similar species section lists names of other taxa involved in Batesian or Müllerian mimicry with the taxon in question. Polytypic species include descriptions of the above categories under each separate subspecies.

4. *Systematic Rationale.* One would suppose that to address a complex group like *Heliconius* with rampant geographical polymorphism and interracial hybridization, one would need to articulate a taxonomic philosophy allowing consistent interpretation of patterns. Even D'Abrebra's book (1984, *The Butterflies of the Neotropical Region, Part II*, Hill House, Victoria), which emphasized illustrations and minimized text, contains a statement of his views on this issue at the head of the genus. There is no such statement in this book—no species concept, no criterion for differentiating subspecies from forms, and no stated basis for determinations of synonymy. The authors make autocratic taxonomic decisions without justification, such as the reduction of *H. elevatus schmidt-mummi* Takahashi to infrasubspecific rank, while at the same time perpetuating nomenclatorial errors, such as including their own infrasubspecific names, (e.g., *H. cydno weymeri* f. *gerstneri* Holzinger & Holzinger, and *E. eanes koenigi* f. *felicittatis* Holzinger & Holzinger) that are formally unavailable under the ICZN code.

The only way to guarantee the accuracy of taxonomic descriptions is to base them on type material, but only thirty holotypes and thirty four other types are illustrated among the 765 figures in the plates. There is no indication that the authors examined any types except those immediately available to them in the Vienna Natural History Museum and their own collection. Twenty five types from the Natural History Museum in London are illustrated, but it is likely that these were drawn from photographs in the illustrated list of the BMNH's heliconiine types (Ackery & Smiles, 1976, Bull. Brit. Mus. Nat. Hist. Ent. 32:171-214), rather than from the specimens themselves (in every case, the same specimen illustrated in Ackery and Smiles is illustrated in the book, a less than 1 in 25 probability if specimens were chosen at random from syntype series). The figures I compared to photographs in Ackery and Smiles matched reasonably well, although the forewing of *H. cydno galanthus* f. *diotrepes* (Plate 35, Fig. 2c) looks more like the ventral surface of the specimen than the dorsal surface it is purported to be. It is not clear why only twenty five types from the BM(NH) were illustrated when Ackery and Smiles' list illustrated 376.

In summary, it would be wonderful to have a book that described the biology and natural history of these remarkable and attractive butterflies. It would also be wonderful to have a book that provided an authoritative systematic guide for curating a collection of *Heliconius*, including useful plates, empirical data on geographical distribution, complete information on types, a review of phylogenetic relationships, and a thorough bibliographical catalog. Unfortunately, the Holzingers have not written either of these books. At best, their product provides a more-or-less comprehensive, more-or-less accurate source to connect names with phenotypes. The very fact that it is impossible to determine how accurate it is, condemns the book as a nonscientific work. *Heliconius and Related Genera* simply fails to meet the standard of systematic scholarship one expects from a \$400 monograph.

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MANUSCRIPT REVIEWERS, 1997

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LIFE HISTORY OF THE BOG BUCK MOTH (SATURNIIDAE: *HEMILEUCA*) IN NEW YORK STATE

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ABSTRACT. The Bog Buck Moth (Saturniidae: *Hemileuca* sp.) occurs in wetland habitats in the Great Lakes region of North America and has been documented in fewer than 10 sites globally, of which 6 are in Oswego County, New York. The larvae feed on at least 10 species of plants at these sites, including the novel hostplants buckbean (*Menyanthes trifoliata* (Menyanthaceae)) and cranberry (*Vaccinium macrocarpon* (Ericaceae)). Details of the Bog Buck Moth's larval development, pupation, eclosion, flight behavior, and oviposition are presented. A censusing method tailored for the flight period is described.

Additional key words: Cryan's Buck Moth, Menyanthaceae, *Menyanthes trifoliata*.

In central and eastern North America, buck moths (Saturniidae: *Hemileuca*) occupy habitats ranging from pine barrens to wetlands (Ferguson 1971, Cryan 1985, Scholtens & Wagner 1994, Tuskes et al. 1996); presumably, glacial retreat left populations of buck moths in disjunct habitats throughout the Great Lakes region. While some of these populations have long been considered isolates of *Hemileuca maia* (Drury), others appear to be more like *H. lucina* Hy. Edwards or *H. nevadensis* Stretch, and their taxonomy remains enigmatic due to morphological, ecological, and behavioral variation (Ferguson 1971, Scholtens & Wagner 1994, Tuskes et al. 1996).

The Great Lakes populations of buck moths have adapted to wetland habitats. In fens around Ottawa (Ontario), in Oswego County (New York), and in Ozaukee County (Wisconsin), buck moth larvae feed on *Menyanthes trifoliata* L. (Menyanthaceae), an aquatic herb unrelated to other *Hemileuca* hostplants (Scholtens & Wagner 1994, Tuskes et al. 1996). Furthermore, the ability to feed on *M. trifoliata* appears to be limited to these scattered populations of *Hemileuca* (Scholtens & Wagner 1994, Legge et al. 1996, Tuskes et al. 1996). Although *M. trifoliata* occurs in more than half of the counties in New York State (New York Flora Association 1990), the Bog Buck Moth (BBM) only occurs in 6

sites in Oswego County (of 10 sites globally; Fig. 1). Two New York BBM populations were discovered in 1977 by John Cryan and Robert Dirig, hence their alternate common name, Cryan's Buck Moth (Legge et al. 1996).

Previous studies of the New York populations have included laboratory investigations of genetic traits and hostplant performance (Legge et al. 1996), preliminary surveys of potential habitats and captive rearing and cross-breeding experiments (Tuskes et al. 1996, J. Tuttle & D. Schweitzer, unpubl. data). However, little has been published on the BBM's natural history. Here I present details of its life history, feeding ecology, development, and oviposition behavior. I also provide data on egg rings, larvae, pupae, and adults, and describe a censusing method for monitoring these populations.

MATERIALS AND METHODS

I surveyed 6 BBM sites in Oswego County, New York from 4 May to 13 October 1995, and 1 May to 29 June 1996. The sites varied from rich shrub fens to a bog-like poor fen (Reschke 1990). Egg rings were found at 4 sites, larvae at 3 sites, and adult BBMs at 4 sites.

Egg ring data were recorded in May and early June 1995. Data included descriptions of the host plants (species, total height, stem diameter at height of egg ring), the egg rings (length, height from substrate, number of eggs per ring), and microhabitats (nearby plant species, microtopography, amount of water). Each egg ring was individually numbered and flagged.

Data were collected on larval behavior (feeding, moving, or stationary; response to conspecifics; relative position on vegetation), food plants, and larval lengths. If the larvae were clustered, the cluster size was recorded. In an attempt to document pupation and eclosion (i.e., to measure depth in substrate, pupa dimensions, microhabitat of pupation site, time required for pupation), and to collect a series of adult BBMs, I reared 100 larvae to pupation in the field. The larvae were reared in vertical sleeves placed around woody stems of *Spiraea alba* Duroi (Rosaceae). Occasionally I moved the larvae as a group to a fresh plant—approximately 25 larvae in each of 4 sleeves. Upon reaching late instar length (45–60 mm), larvae were placed in a fine mesh enclosure measuring 1 m × 1 m × 15 m. The enclosure transected open fen habitat which included the food plants *M. trifoliata* and *Vaccinium macrocarpon* Aiton (Ericaceae). The area inside the enclosure was cleaned of existing larvae before introducing the sleeve-reared larvae. By comparing the number of moths that emerged to the number of larvae that pupated, I intended to determine whether overwintering pupation occurs

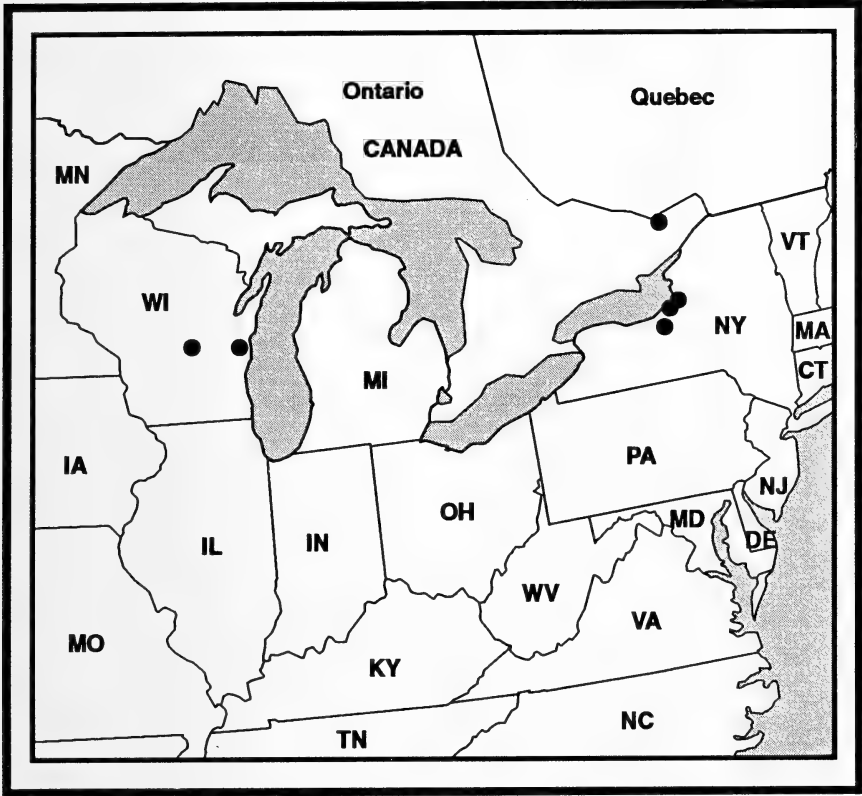


FIG. 1. Distribution of the Bog Buck Moth (*Hemileuca* sp.): populations that feed upon *Menyanthes trifoliata* and occur in fen habitats.

in this taxon, and if so, in what proportion. However, all pupae within the enclosure apparently were preyed upon (see Results).

In 1995, adult BBMs were first observed flying on 11 September, and the last were observed on 11 October. The flight period allowed censusing adult BBMs. I first determined the peak flight time for male moths i.e., between 1100 and 1400 h EST. I then determined the average "circling time" (the time required for a male to circle the fen once in search of females) i.e., approximately 10 min. Positioned at the center of the fen and looking outwards in one direction (along a radius), I then counted all moths that flew past that radius for 10 min. At each site, such a 10-minute count was made while looking north, followed by one looking south, then one looking east, and one looking west. The four 10-min counts were then averaged for an estimate of the number of moths

TABLE 1. Bog Buck Moth (*Hemileuca* sp.) egg ring data, collected spring 1995 from 3 sites in Oswego County, New York. Data expressed as mean with SD. Means followed by different letters are significantly different ($p < 0.05$) by Tukey HSD multiple comparisons.

Site	n	Egg ring height (cm)	Host height (cm)	Stem diameter (mm)	Ring length (mm)	Eggs/ring
A	10	17.9 (9.6) a	37.6 (16.7) a	3.8 (1.5) a	20.4 (3.8) a	142 (32) a
B	85	11.4 (6.1) b	35.1 (18.1) a	3.5 (1.2) a	19.1 (5.7) a	142 (44) a
C	7	27.0 (14.7) c	47.2 (15.2) a	2.7 (1.2) a	19.9 (4.5) a	131 (30) a

flying at that site during the peak flight period for that day. Several sites could be censused each day.

RESULTS

Egg rings. Although egg rings were found at 4 sites, data from only 3 sites were analyzed due to low sample size ($n = 2$) at one of the sites. There were no significant differences in mean stem diameters, egg ring lengths, oviposition plant heights, or numbers of eggs per egg ring between the 3 sites (ANOVA, $p < 0.05$, Table 1). Mean egg ring height from the substrate differed among sites ($F_{2,99} = 17.3$, $p < 0.001$), particularly between sites A and C (Tukey HSD, $p < 0.001$; this was likely due to differences in microhabitat and dominant oviposition plant species). At site C, a rich shrub fen, all recorded egg rings were oviposited on *Myrica gale* L. (Myricaceae), a tall, woody plant that was sparse at sites A and B. Accordingly, the mean egg ring height was greatest at site C (27.0 ± 14.7 cm). At site B, a bog-like, open fen, most of the egg rings were oviposited on short, broken stems of *Anchistea virginica* (L.) J. E. Smith (Blechnaceae) and at the bases of *Alnus incana* ssp. *rugosa* (L.) Moench (Betulaceae). Thus, the mean egg ring height was lowest at site B (11.4 ± 6.1 cm). Egg rings from site A were found in a microhabitat that shared characteristics of sites B and C (i.e., site A egg rings were found in open, sedgy fen habitat, similar to site B, but most egg rings were on *M. gale*, the dominant oviposition shrub at site C). Furthermore, mean *M. gale* heights at sites A and C (35.8 and 47.2 cm, respectively) were not significantly different ($p = 0.220$), while the mean heights of egg rings deposited on *M. gale* were different between sites A and C (lower to the substrate at site A). The *M. gale* that bore egg rings at site C formed dense stands, whereas those at site A were isolated, individual plants in open habitat. Therefore, differences in habitat type and plant structure, not oviposition plant species *per se*, seem to explain the observed differences in oviposition sites.

Egg rings were found on 9 plant species: *Acer rubrum* L. (Aceraceae), *A. incana* ssp. *rugosa*, *A. virginica*, *Carex* sp. L. (Cyperaceae), *Chamaedaphne calyculata* (L.) Moench (Ericaceae), *M. gale*, *Salix pedicellaris*

TABLE 2. Bog Buck Moth (*Hemileuca* sp.) egg ring data, according to hostplant species. Data collected spring 1995 from Oswego County, New York, and expressed as mean with SD. Means followed by different letters are significantly different ($p < 0.05$) by Tukey HSD multiple comparisons.

<i>Myrica gale</i>	15	22.8 (12.4) a	42.5 (17.1) a	3.4 (1.6)	19.6 (3.8) a	132 (27) a
<i>Chamaedaphne calyculata</i>	18	13.5 (8.5) b	30.0 (12.2) a	2.9 (0.7)	21.0 (5.1) a	152 (42) a
<i>Alnus incana</i> ssp. <i>rugosa</i>	42	12.0 (4.6) b	40.6 (19.4) a	3.8 (1.4)	17.9 (5.9) a	136 (41) a
<i>Anchistea virginica</i>	20	6.9 (1.9) c	28.0 (18.2) a	3.6 (0.7)	19.1 (5.4) a	141 (50) a

Pursh (Salicaceae), *Spiraea alba* Duroi (Rosaceae), and *Cornus sericea* L. (Cornaceae). There were no significant differences among sites in mean number of eggs per egg ring or mean oviposition plant heights (Table 2). There were, however, significant differences in mean stem diameters of two plant species oviposited on, the mean egg ring lengths on the same two plant species, and the mean egg ring heights among all of the plant species oviposited on. Data for egg rings oviposited on *A. rubrum*, *Carex* sp., *S. pedicellaris*, *S. alba*, and *C. stolonifera* were not used in statistical analyses because of low sample size.

Mean stem diameter of *C. calyculata* at the height of oviposition was significantly smaller (Tukey HSD, $p = 0.03$) than that of *A. incana* ssp. *rugosa* (2.9 ± 0.7 mm vs. 3.8 ± 1.4 mm). Generally, *C. calyculata* stems were thinner than those of *Alnus*. While the length of the egg ring changed with differences in stem diameter, the number of eggs per egg ring did not ($t = 2.04$, $p < 0.05$). Thus, it appears that the BBM lays an egg ring normally consisting of 100–180 eggs, and that the egg ring will be longer if the oviposition plant stem is thinner. This was supported by an isolated observation of oviposition on a slender stem of *Carex* sp. (1.8 mm diam.), in which the length of the egg ring (28 mm) was greater than the average on other oviposition plants (mean = 19.4 mm, $N = 95$).

Height of oviposition differed significantly among the hostplant species. Although egg rings were found on plants that ranged from 28 cm to >40 cm height, height of the plant did not appear to determine oviposition height. Differences in the height of the egg rings were attributed to differences in plant structure at the mean heights of oviposition (approximately 10–40 cm from the substrate). The density of foliage varied among the four main oviposition plants (*A. incana* ssp. *rugosa*, *A. virginica*, *C. calyculata*, and *M. gale*) at the time of oviposition. *Chamaedaphne calyculata* formed short, dense clumps of evergreen foliage on slender stems. *Alnus incana* ssp. *rugosa* exhibited thick, bare stems up to its sparse, wide leaves, which began at about 15 cm high. *Myrica gale* was sparsely-foliated with exposed stems its entire height, especially in

fall when the leaves began to curl and brown. *Anchistea virginica* died back with the first frost and essentially existed as a vertical stalk with some curled-up foliage. Often, this fern was broken off at a short height, and many old, broken stems bore egg rings. Thus, it appears that structural requisites (e.g., stem diameter, density of foliage), not oviposition plant species preference *per se*, determine the location and the height of egg rings in the field.

Larvae. BBM larvae hatched between 12 May and 14 June 1995. The side of the egg ring facing the sun tended to hatch before the opposite side. Upon hatching, the larvae (<4 mm long) circled the egg rings horizontally and joined into a cluster. The cluster then climbed the oviposition plant stem in a single travel line, investigated any foliage (and briefly consumed small portions of leaves such as *A. rubrum*), remained in the foliage feeding (especially *C. calyculata*, *Alnus*, and *Salix*), or returned down the stem if the oviposition plant was unacceptable. The larvae then formed a traveling line that fed mainly on *V. macrocarpon*, until approximately 12 days after the first egg ring hatched, at which point the leafing of *M. trifoliata* stimulated a switch in primary foodplants.

Throughout the summer, I observed the larvae feeding on *A. incana* ssp. *rugosa*, *Aronia melanocarpa* (Michx.) Elliott (Rosaceae), *Carex* sp., *C. calyculata*, *Ilex verticillata* (L.) A. Gray (Aquifoliaceae), *M. trifoliata*, *Quercus* sp., *S. pedicellaris*, *S. alba*, and *V. macrocarpon*. On 2 June 1995, 72% of feeding early instar larvae were eating *M. trifoliata*, 14% were feeding on *S. alba*, 6% were eating *A. incana* ssp. *rugosa*, 4% were feeding on *V. macrocarpon*, and 4% were eating *C. calyculata*. In contrast, on 5 July, at the same site, 54% of feeding late instar larvae were eating *V. macrocarpon*, 25% were feeding on *M. trifoliata*, 16% were eating *Carex* spp., 3% were feeding on *C. calyculata*, and 2% were eating *A. melanocarpa*. Thus, although *Menyanthes* appears to be the primary foodplant at earlier instars (Legge et al. 1996, Tuskes et al. 1996, pers. obs.), other foodplants are fed upon more heavily by mature larvae.

The number of larvae per cluster declined as larvae grew. Final instar larvae were typically seen alone, whereas solitary first instar larvae were seen only infrequently. On 2 June 1995, for example, the mean number of larvae per cluster was 23 ± 17 ($N = 175$ clusters). On 14 June, at the same site, the mean number of larvae per cluster was 7 ± 9 ($N = 36$ clusters). No significant differences in cluster sizes among 7 different host species were found. Larvae of different instars were sometimes in the same feeding cluster, suggesting that not all larvae in a feeding cluster were from the same egg ring, or that larvae developed at different rates.

Mature larvae reached a maximum length of approximately 60 mm before pupation (Fig. 2). On 11 July 1995 the mean length of larvae before pupating was 49 mm ($N = 60$ larvae). Many late instar larvae were

found dead on the surface of the sphagnum in July. While hot summer temperatures (maximum recorded surface sphagnum temperatures exceeded 38°C on several days in July) might have caused some larval mortality, NPV (nuclear polyhedrosis virus) should also be considered (Mitchell et al. 1985).

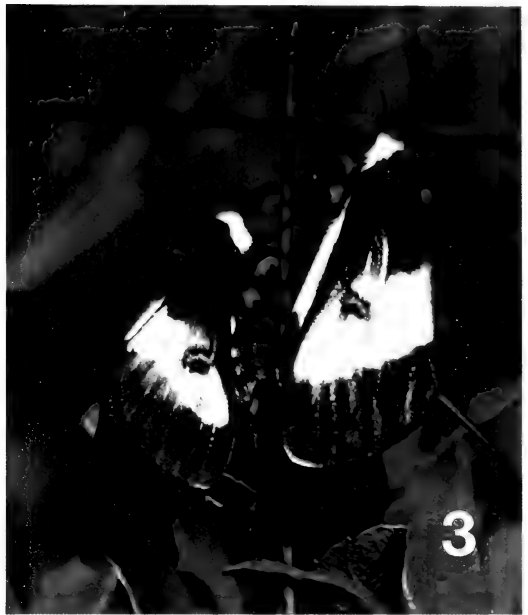
Pupae. Larvae fed throughout the summer and passed through six instars before pupating. Only 10 pupae were discovered within the experimental enclosure, all of which had been bored into and hollowed out. After two exhaustive searches, no other pupae were found in the enclosure. No adult moths emerged within the enclosure. Outside the enclosure, pupae were found that had been preyed upon in similar fashion. Some pupae that had been preyed upon were found under 5 cm of sphagnum. Although predation of the pupae was not directly observed, damage to the buck moth pupae and the conditions of attack match descriptions of predation by beetles (Carabidae, Staphylinidae, and Elatidae) on pupae of the winter moth (*Operophtera brumata* (L.) Hydriomenidae) (Frank 1967; also J. Frank, pers. comm.).

Mean lengths of captive-reared BBM pupae (26.8 ± 2.6 mm, $N = 5$) were significantly different ($t = 2.97$, $p < 0.03$) from pupae discovered in the field (23.0 ± 1.2 mm, $N = 5$). However, mean widths of captive (9.2 ± 0.8 mm, $N = 5$) and wild (8.8 ± 0.4 mm, $N = 5$) pupae did not differ significantly ($t = 0.94$, $p > 0.5$). Significant differences in pupal lengths but not widths might be due to the relatively smaller size of the width measurements, or a small sample size. Mean depths of pupation in sphagnum were not significantly different between captive and field populations (4.3 ± 0.8 cm and 4.5 ± 0.4 cm, respectively).

Adult flight behavior. Upon eclosion, adult BBMs climb up the nearby vegetation to harden their wings. The moths were observed quivering their wings for short periods of time while grasping the vegetation. Presumably, this allows their flight muscles to warm up for the initial flight and for each subsequent flight after periods of inactivity. Flight records of BBMs at four sites are provided in Fig. 6. The total number of moths observed flying at each site during the fall 1995 flight season were: site A = 304, site B = 802, site C = 1369, and site D = 3.

No moths were observed flying during rainstorms, on cold days (temperatures $< 12^\circ\text{C}$), or during high winds. On such days, moths were dormant and clung to vegetation. Mean resting height for moths was not significantly ($t = -1.49$, $p > 0.05$) closer to the substrate in open fen habitat (35.2 ± 15.1 cm, $N = 16$) than in shrubby edge habitat (56.5 ± 39.0 cm, $N = 8$). However, resting height differed among plant species ($F_{7,16} = 5.09$, $p < 0.005$); these differences were attributed to differences in the heights and vegetative structure of the plants.

If approached or handled, moths were reluctant to fly and curled into



a defensive posture: wings extended outward dorsally, and the bright orange abdomen exposed and arched inward ventrally. When disturbed, the BBMs did not fall freely to the ground, as is described for other *Hemileuca* (Tuskes et al. 1996), but rather held tight to the vegetation (it was difficult to remove the moths without injuring them) or flew away.

Both sexes of BBMs flew early in the day (0900 h), but peak flights occurred between 1100 and 1400 h. Males and females were observed flying and resting throughout the day. Although I remained in the fens until dark on several occasions, the latest flight that I observed was just after 1600 h (moths were reported flying at 1830 h during the previous flight season; S. Bonanno, pers. comm.). Most moths flying during the peak hours were males, whereas most moths flying after 1400 h were females. Ovipositions occurred primarily in the afternoon hours from 1300 to after 1600 h.

Males and females differed in flight patterns and behaviors. Males flew in large, circular flight paths, covering the entire open area of the fen in about ten minutes. They flew for longer periods of time than females, which usually flew for only a matter of seconds (females made short but frequent flights in preovipositional searches). Males often flew around in small circles or even backtracked, while females beelined clumsily just above the vegetation. The weaving flights of the males indicated their characteristic search pattern: downwind approaches to pheromone trails and concentric circular flights that tightened around the calling and receptive females.

Often, males circled within a meter of the female for several minutes, then landed nearby and walked around. Failing to locate the female, they eventually flew away. The females were usually well-hidden in vegetation while releasing pheromones. When discovered by a male, the female would sometimes climb up out of the foliage to an exposed stem where copulation proceeded (Fig. 3). Staying concealed may reduce exposure to predators, but often appeared to reduce the success of enticing a male. Mate-finding in the BBM appears to be based mainly on pheromone attraction rather than visual cues. For example, when I enticed males in the field with captively-reared females, the males rapidly swarmed about, but could not readily find the females' cage. Instead,

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FIGS. 2–5. **2**, Late instar Bog Buck Moth larva (*Hemileuca* sp.) feeding on *Menyanthes trifoliata*. Its red head capsule resembles the caranberries (*Vaccinium macrocarpon*) that abound in its habitat. **3**, Male (left) and female (right) *Hemileuca* mating on exposed stem of *Myrica gale*. **4**, Two seamlessly joined *Hemileuca* egg rings on a single stem of *Anchistea virginica*; unhatched, recently oviposited eggs (above, darker) and hatched egg ring from the previous year (below). **5**, Spider (*Argiope aurantia*) predation on *Hemileuca*.

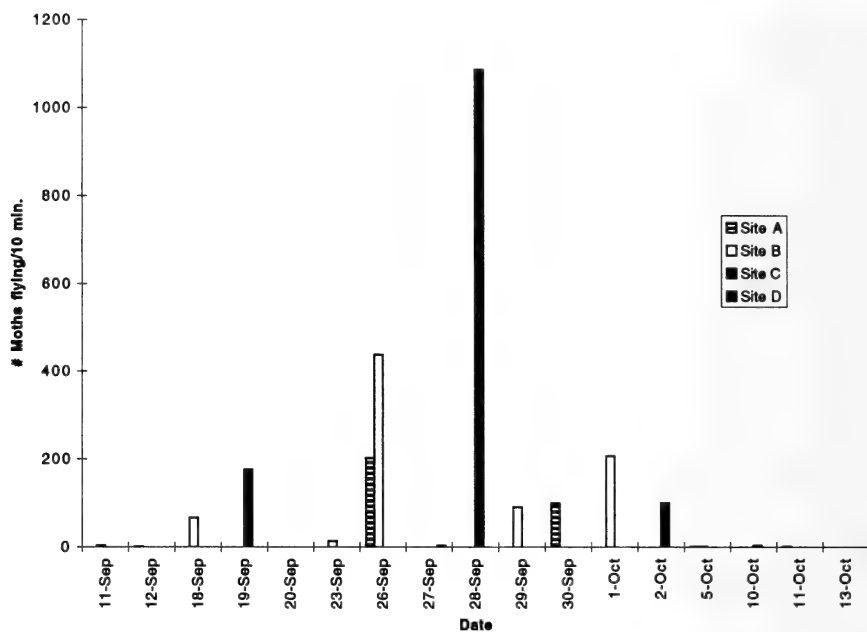


FIG. 6. Flight records of the Bog Buck Moth (*Hemileuca* sp.) from 4 sites in Oswego County, New York, fall 1995.

the males would alight on my head or body, then walk around until locating pheromone on my hand or on the cage.

Both sexes usually flew with the abdomen hanging straight down or curved slightly inward (ventrally). Males tended to fly with the abdomen arched up and back (dorsally) when homing in on the females' pheromones.

No migration between sites was observed, although the presence of a few adult moths in one submerged fen (in which no egg rings or larvae, and only sparse food plants were found) indicated this possibility. Four of the 6 documented sites were completely surrounded by upland deciduous forests. The other 2 sites were separated from each other by a creek and were buffered from surrounding forests by marshes. No moths were seen flying above the treeline surrounding their respective fen. Most moths flew lower than 1 m above the vegetation, although some individuals were observed flying up to 2 m above the fens.

Oviposition. Female BBMs flew hastily and awkwardly, low against the shrubs and open fen habitats. The females landed in clumps of shrubby vegetation (as opposed to the open fen), where they backed down each of the stems around them. The moths fluttered their wings while climbing up and down the stems. At each descent, a female flew

briefly to another stem or crawled across to another plant. Usually only a few centimeters were tested per stem. Occasionally the females flew a few meters away to repeat the process.

The females seemed to choose stems of a particular diameter by using their ovipositor and legs. The chosen site for oviposition tended to be unobstructed by leaves or adjacent stems. The height of oviposition generally was low and probably dictated by low oviposition plant height and the low heights of available, unobstructed stems. Oviposition plant species did not seem to matter *per se*, other than an aversion to the aromatic *Larix laricina* (Duroi) K. Koch (Pinaceae).

Upon choosing a stem, females promptly began laying eggs: facing the stem, they curled their abdomens in towards the stem, felt for a site with the ovipositor, and deposited a single egg perpendicular to the stem. The eggs were grey-brown when deposited and turned light green in about a minute. After laying an egg, the abdomen returned to a relaxed, hanging position (parallel to the stem). The female remained in this position until ready to lay another egg, from a few seconds to a few minutes later. The eggs were not always laid immediately next to another. The females laid eggs in empty spaces, between two eggs, or next to a single egg. One row usually was completed before eggs were laid in the next row up on the stem. Oviposition proceeded in all cases from the bottom up. All observed females laid egg rings with their backs to the sun. Oviposition was concealed by downfolded wings, but the females would respond with the typical defense posture if handled.

One female failed to successfully adhere her initial eggs to an *Aronia* stem. The first three eggs stuck to each other and then came off the stem, attached to her abdomen. She proceeded to lay eggs, and the initial clump of eggs fell to the ground. All subsequently laid eggs adhered to the stem.

Another female was interrupted while laying an egg ring on an *Aronia* stem. A small (approx. 5 mm long) jumping spider (Salticidae) moved up the stem and investigated the freshly-laid eggs. The spider then jumped onto the moth's wing, whereupon the moth twitched her wings and the spider fell. After laying approximately 25 eggs, a male BBM then located the same female moth and proceeded to copulate (at 1515 h). After copulation, the female laid another distinct egg ring of about 30 eggs, 3 cm above the first. Five days later the stem was chewed off less than 2 mm above the upper egg ring, and scattered droppings and a neat trail of nipped-off chokeberry stems suggested feeding by an eastern cottontail rabbit (*Sylvilagus floridanus*) (J. A. Allen).

One fresh egg ring was discovered on *A. virginica* immediately above a hatched egg ring from the previous season. The two egg rings were adjacent and seamlessly joined; the only observable differences were the

color and the hatched/unhatched status of the rings (Fig. 4). I observed old egg rings immediately beneath new egg rings, and instances where the two occurred nearby on the same stem. Bog Buck Moth egg rings are clustered at each site, sometimes 8 on a single shrub. Frequently, old egg rings are found within a meter of new egg rings. I also discovered an egg ring on a stem of *S. alba* that was sleeved off and held larvae for captive rearing experiments in the field. No other egg rings were deposited on the abundant nearby *S. alba* that had not harbored larvae. Some conspecific frass remained attached to this particular stem. Presumably, conspecific larval silk also remained on this stem.

Oviposition did not appear to be cued by proximity to *Menyanthes trifoliata*. Egg rings were found that >20 m from the nearest *M. trifoliata* plant. Some egg rings hatched a week or more before the emergence of *M. trifoliata*, and upon hatching those larvae fed upon *V. macrocarpon*. In September and October 1995, when female moths oviposited, *M. trifoliata* was uncommon or senesced in areas where it was abundant during the summer months.

Predation. Egg rings are susceptible to a variety of predators, including small mammals and invertebrates, and they may accidentally be ingested by white-tailed deer (*Odocoileus virginianus* (E. A. W. Von Zimmermann)) and rabbits (*Sylvilagus floridanus*) that consume the host plant stems. I observed predation on eggs by velvet mites (Trombididae) in spring and fall (12 May and 13 October at site A). An unhatched egg ring that I collected on 24 June 1996 subsequently yielded Hymenoptera (Chalcidoidea: Eupelmidae) from each of the 200 or so eggs in the ring. Buck moth larvae were preyed upon by true bugs (Hemiptera). Other parasitoid Hymenoptera and Diptera surely occur in these sites and also parasitize the larvae. As described earlier, beetles and their larvae (Carabidae, Staphylinidae, and Elatidae) may have been responsible for heavy predation of BBM pupae.

Adult BBMs were also subject to predation. Three paper wasps (Vespidae) were observed stinging a male buck moth in flight and devouring it alive, from the thorax out, once it fell to the sphagnum. Paper wasps had nests in at least four of the sites, and preyed in similar fashion upon migrating Monarchs (*Danaus plexippus* L.) that flew over the fens.

Two species of araneid spiders, *Araneus diadematus* Clerk and *Argiope aurantia* Lucas, preyed upon adult buck moths (Fig. 5). Webs from both spider species were common in the fens and stretched across the shrubby peripheries. Several silk-wrapped BBM bodies were found below the web of one *A. aurantia*, and the spider was eating another.

On 23 September 1995 a Solitary Vireo, *Vireo solitarius* (Wilson) (Vireonidae), took a male BBM in flight, landed in a nearby *Larix laricina*, and ate the body of the moth after discarding the wings. Many in-

sectivorous birds, migrating south in the fall and abundant in the fens, are potential predators of BBMs. Eastern Phoebes, *Sayornis phoebe* (Latham) (Tyrannidae), and other birds were observed feeding in the fens on other insects, and are possible predators of BBMs. Also, dragonflies (Aeshnidae) are potential aerial predators of buck moths, as reported by Scholtens and Wagner (1994).

DISCUSSION

The BBM has adapted to life in wetland habitats. Their reluctance to fall to the ground when disturbed, unlike other populations of *Hemileuca* (Tuskes et al. 1996), appears to be a unique behavior and may prevent them from falling into standing water.

The apparent annual clustering of egg rings strongly suggests that an ovipositional cue is present. Since the herbaceous hostplant *M. trifoliata* dies back in late summer, the moths must oviposit on other plants. As the BBMs oviposited so frequently on the dried, broken stems of *A. virginica* at one bog-like site, I believe the ovipositional cues are structural (correct diameter and height) and perhaps chemical. An oviposition-stimulating, egg-isolated or larval silk-isolated semiochemical might account for the clustered distribution of egg rings year after year. Such a chemical cue might also explain the seamless joining of two egg rings laid in different seasons on the same stem (Fig. 4).

The possibility of oviposition on slender, upper stems of plants over a meter high is unlikely due to the low flight behavior of the female moths; I doubt that a heavily-laden female would fly up into a small tree or shrub when faced with abundant stems of suitable diameter at lower levels. The question thus arises: Why are the egg rings deposited so low in fen habitats, where flooding is a potential threat? Perhaps the low egg ring height may be advantageous for overwintering success. Rabbits and deer would browse on stems above the level of snow. Mice might feed on the egg rings that are not buried in snow, as has been reported in some New Jersey populations of *Hemileuca* (D. Schweitzer, pers. comm.). Also, temperatures under a blanket of snow fluctuate less than air temperatures, thus egg rings would be at less risk of over-freezing or premature warming. Larvae can tolerate some inundation; Legge et al. (1996) observed that larvae swim or walk on the surface tension of water for short periods of time.

Experimental transect sampling of egg rings and larvae did not provide consistent or reliable results for a censusing technique. The censusing method which I developed for this study provides a population estimate that can be compared with future census results for conservation and monitoring purposes. Based on my field observations, one cannot assume at any time that only males are flying, and that an equal number

of females are hidden in the vegetation (or vice versa). Therefore, doubling the census results would not provide an estimate of the overall population, as otherwise might be expected.

Adult BBMs focus their behavior on reproduction, not dispersal. However, I believe it is possible that an adult moth could disperse to a nearby site via strong updrafts or powered flight if the surrounding vegetation did not impede them. The present distribution of the BBM may thus be the remnants of a buck moth expansion from western North America following the last glacial retreat in the Northeast. As the forests reclaimed the wetland habitats, the BBM may have been confined to the remaining fens and bogs.

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TEMPORAL AND SPATIAL DISTRIBUTION OF THE RARE,
MYRMECOPHAGOUS ILLIDGE'S ANT-BLUE BUTTERFLY,
ACRODIPSAS ILLIDGEI (LYCAENIDAE)

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ABSTRACT. A survey of 591 branch sections containing arboreal ant colonies on 197 trees was undertaken over four consecutive seasons for the presence of immature *Acrodipsas illidgei* (Waterhouse and Lyell) in and adjacent to mangroves at Mary River Heads, Queensland, Australia. *A. illidgei* was found in 1.7% of ant colony sections sampled (i.e., 10 colony sections on five *Avicennia marina* (Forssk.) trees). Despite the small number of immatures discovered, *A. illidgei* showed a strong tendency to occur in specific ant colonies over time. The host ant, *Crematogaster* sp. (*laeviceps* group F. Smith) (Formicidae: Myrmicinae), was common and widespread within the survey area. The mean seasonal level of adult ant activity outside the nest positively correlated to mean seasonal ant brood levels within nests but were significantly linked only in spring and autumn. New information supports the hypothesis that ant colony odour selection by ovipositing female *A. illidgei* is the prime influence on this butterfly's localized distribution.

Additional key words: localized distribution, conservation, mangrove, *Crematogaster*, Australia.

The genus *Acrodipsas* Sands (Lycaenidae: Theclinae) is unique to Australia and contains eight described and at least one undescribed species (Sands et al. 1997, Sands, pers. comm.). All *Acrodipsas* species are known or suspected to have larvae that feed on ants (Sands 1979, Common & Waterhouse 1981). *Acrodipsas illidgei* (Waterhouse & Lyell) has an obligate, myrmecophagous relationship with the arboreal ant, *Crematogaster* sp. (*laeviceps* group F. Smith) (Formicidae: Myrmicinae), in or adjacent to mangrove habitats (Smales & Ledward 1942, Samson 1987, Beale & Zalucki 1995).

Ant-attended lycaenids such as *Acrodipsas* species in Australia (Common & Waterhouse 1981) and *Maculinea* species in Europe (Thomas et al. 1989, Thomas & Wardlaw 1990) often occur naturally at low abundance (Pierce et al. 1987, see also review in Walter & Zalucki 1998) in small, semi-isolated demes (Pierce 1984). Curiously, *A. illidgei* does not appear to have specific requirements restricting it to its known habitat, though it depends directly on the presence of its host ant species, which may be found in greatest abundance in and around mangrove environments. Although distribution is not restricted by plant species associations (immatures have been found in ant colonies on grey mangrove, *Avicennia marina* (Forssk.) Vierh. (Avicenniaceae) in mangroves, and on swamp oak, *Allocasuarina glauca* (Sieger ex Sprengal) (Casuarinaceae), and *Eucalyptus* sp. (Myrtaceae) adjacent to mangroves) and its host ant is widespread and abundant, its low relative abundance seems to be maintained primarily by regular bouts of host ant aggression and the carrying capacity of colonies (Beale & Zalucki 1995).

Except for host ant induced mortality, the larval and pupal stages occupy an 'enemy-free' space (see Lawton 1978, Atsatt 1981a) once neonates are carried back to the nest. Unlike some myrmecophagous lycaenids such as *Liphyra brassolis major* Rothchild (Dodd 1902), and myrmecophilous species (Malicky 1970), larvae of *A. illidgei* have an epidermis containing numerous glands (Samson 1989, see also review by Fiedler et al. 1996), which is easily pierced by its small, aggressive host species. According to Malicky (1970), a thick cuticle of the larval integument is a typical lycaenid adaptation against ant mandible damage, yet even mature *A. illidgei* larvae apparently lack this defence against an ant species with which it shares a highly specific relationship. The nature of this ant/butterfly relationship raises the question: are immature *A. illidgei* completely reliant upon chemical mimicry for survival, and if so, are females selecting local 'home' ant colonies because of 'host conditioning' or 'adult emergence experience' (Hopkins 1917, see review by Mackenzie 1992)?

The purpose of this study is to determine the distribution of *A. illidgei* host ant colonies over time and assess whether *A. illidgei* is host ant colony specific. The relevance of the findings to the conservation status of *A. illidgei* is discussed.

STUDY SITES AND METHODS

Sections of *Crematogaster* sp. (*laeviceps* group) colonies in branches (one branch/tree sampled) of grey mangrove, *A. marina*, and non-mangrove species were sampled at the site of a recently discovered population of *A. illidgei* (Manskie & Manskie 1989), Mary River Heads (25°38'S, 152°38'E) in south-east Queensland, over a 10 month period beginning in August 1994 (see Figs. 1, 2). Field trips were made to Mary River Heads on 19–20 September 1994 (winter), 16–19 November 1994 (spring), 21–23 February 1995 (summer), and 15–19 May 1995 (autumn). The first survey included tagging, mapping and data collection from 183 *A. marina* and 14 landward *A. glauca* and *Eucalyptus* species. Sampling was carried out in four sectors, two on the eastern side and two on the western side of the River Heads peninsula (Fig. 2).

A subset of trees were selectively sampled in a haphazard manner for chambered branches of a minimum thickness (≥ 10 mm) containing a section of *Crematogaster* ant nest to maximize chances of encountering *A. illidgei*. Previous studies (Beale & Zalucki 1995) indicated that branches below a minimum thickness were unlikely to possess chambers suitable for *Crematogaster* ants and therefore even less likely to contain *A. illidgei*. Most *A. marina* trees were located on or just inside the seaward edge beyond large stands of red mangrove, *Rhizophora stylosa* Griff., and yellow mangrove, *Cerriops* sp. (both Rhizophoraceae), and

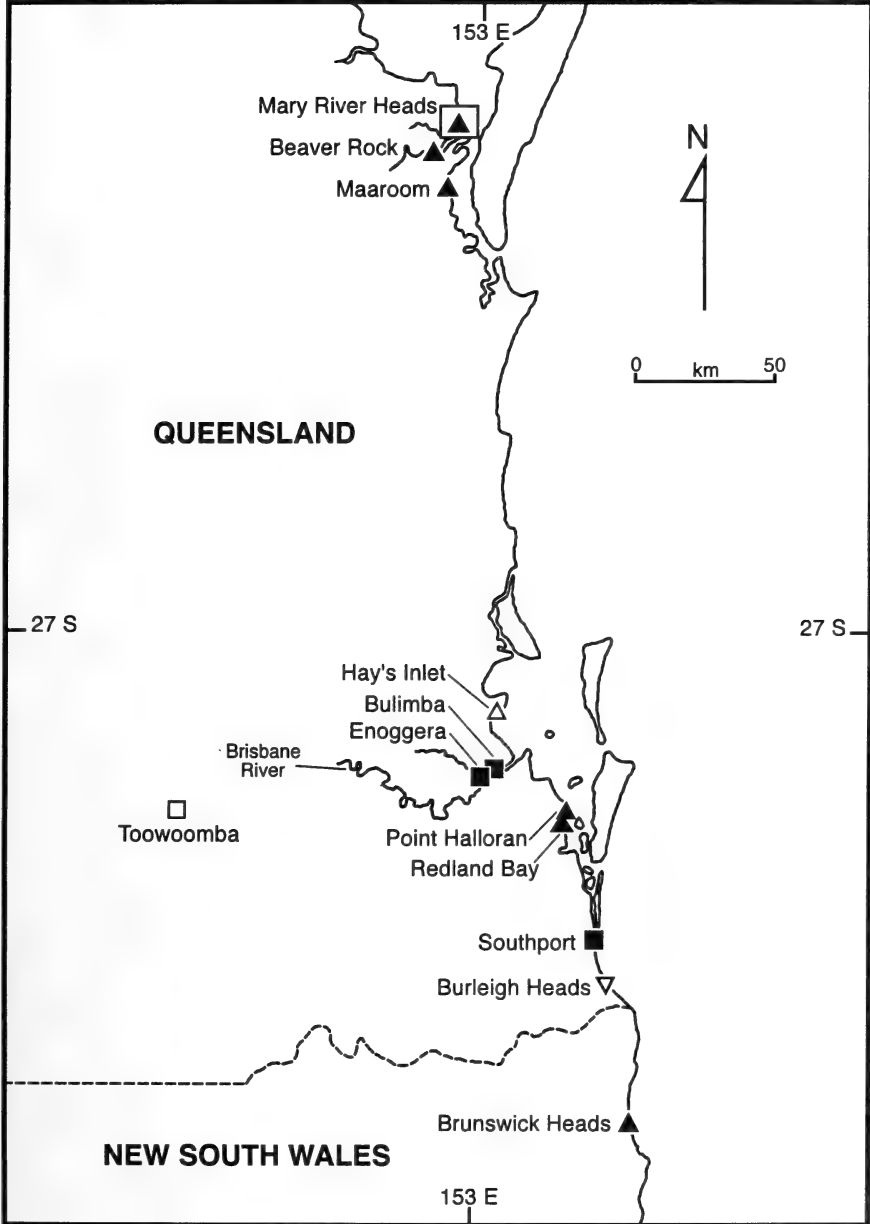


FIG. 1. Status of historical populations of *Acrodipsas illidgei*: filled upward triangle = recorded since 1985, habitat largely intact; open upward triangle = recorded before 1985, habitat largely intact; open square = requires confirmation; filled square = population almost certainly extinct; open downward triangle = status unclear, threatened or extinct. Boxed area at Mary River Heads is location of study area in Fig. 2.

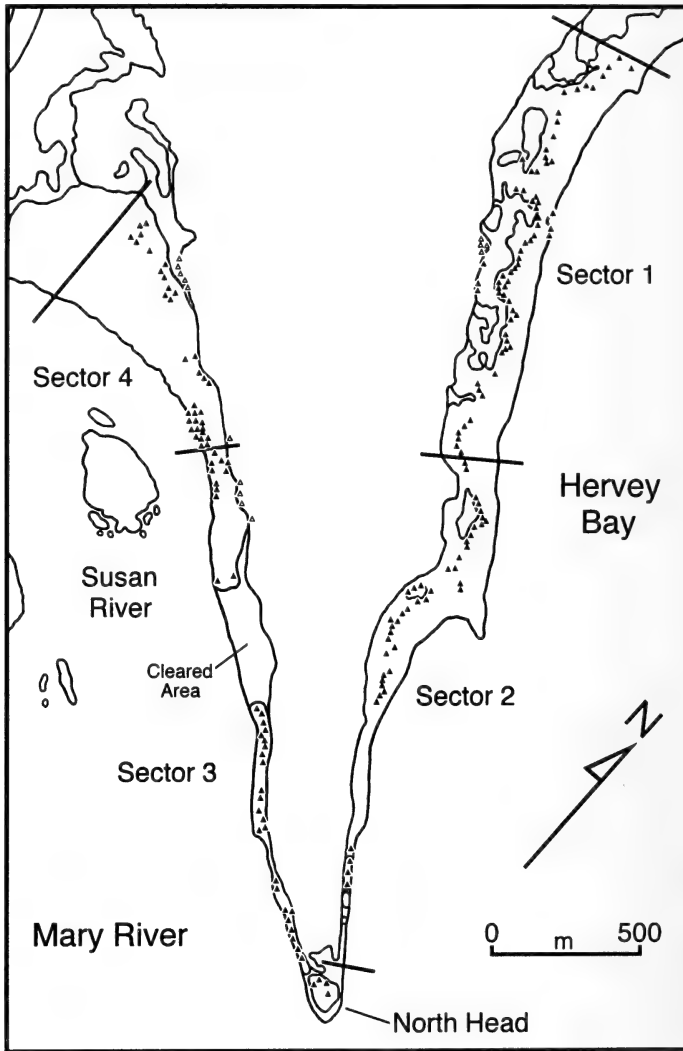


FIG. 2. Map of Mary River Heads field site showing distribution of sampled *Avicennia marina* trees (filled triangles) and non-mangrove tree species including *Allocasuarina* sp. and *Eucalyptus* sp. (open triangles).

river mangrove, *Aegiceras corniculatum* (L.) Blanco (Myrsinaceae). Sampled trees were mapped onto enlarged aerial photographs.

Data collected from each tree included tree height, number of chambered branches/tree, position of tree (edge/non-edge, where edge = at least one side of a tree is facing a clearing, landward or seaward edge),

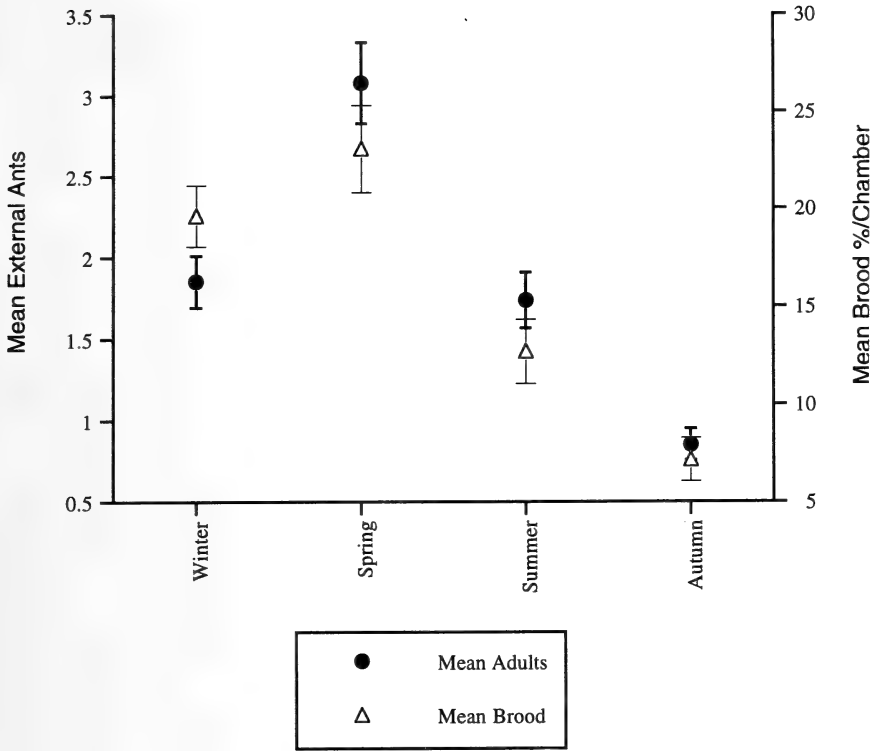


FIG. 3. Graphs showing mean number of external ants and mean ant brood percent per brood chamber in each season at Mary River Heads.

the height of the sampled chambered branch, and the external ant activity adjacent to sampled chambered branch (ants/10 cm of ant trail) (Fig. 3). Chambered branches were split and examined *in situ* for about 5 to 10 minutes each. Chambered branch measurements included length and diameter; the presence or absence of *A. illidgei* immatures and stage present; the presence of other lycaenid butterfly immatures; and amount of ant brood as a volume/chambers in chambered branches as a percentage. Ant specimens were identified and compared by S. O. Shattuck (Australian National Insect Collection, CSIRO, Canberra). Many sampled branches ($n = 153$) were repaired up to three times each with wire and re-attached to the tree close to where they had been removed. Fourteen landward trees (13 *Allocasuarina glauca*, 1 *Eucalyptus* sp.) were sampled and mapped in the same manner as mangrove trees although their position (i.e., edge/non-edge) was not recorded. The probability of host trees possessing *A. illidgei* immatures in recorded se-

quences was calculated. Summary statistics of the complete dataset for adult ant activity and percentage ant brood per chamber are presented as means \pm standard errors with analysis of data using ANOVA and graphed. Data from trees which were sampled in every season was categorized and tested for independence using chi-square (i.e., categories of adult ants: 0, 1, 2, $\geq 3/10$ cm; categories for percentage ant brood/ sampled chambers: low < 10%, medium = 10–40%; high > 40%).

RESULTS

The total number of samples taken from the 183 *A. marina* trees over each season was 554 (many repaired branches resampled up to three times) while 14 non-mangrove species were sampled a total of 37 times. Trees sampled in all four seasons totalled 87. Immature stages of *A. illidgei* occurred in only 10 ant colony sections on five *A. marina* trees among 197 trees sampled (1.7%, Table 1). Four ant colony sections containing immatures were found in both winter and spring, while one was discovered in summer and again in autumn. Sector 1 had immatures in a single landward edge tree in every season, and this same colony possessed two larvae in 1992 (Beale & Zalucki 1995). One tree in Sector 3 possessed immatures in winter and spring only. A single tree in Sector 3 possessed an empty pupal case in winter and a fifth instar larva in spring. Another tree in Sector 4 contained one third instar larva in both winter and spring. No *A. illidgei* immatures were discovered in Sector 2 (Fig. 2). The particular immature stages or instars present in subsequent samples on the same trees indicated that they represented separate generations. There was a tendency for immatures to occur in the same ant colonies over time (Table 1). Cumulative sampling impact meant that only one in five branch sections could be expected to contain ants after four (i.e., three repairs) consecutive samples (Beale & Seeman, unpubl. data).

Although only five trees contained *A. illidgei*, they displayed variation of attribute measurements consistent within the overall sample. For example, host trees in Sectors 3 (host tree heights = 390 cm, 410 cm, 560 cm) and Sector 4 (650 cm) (Fig. 2) were of taller and denser habit than the host tree found in Sector 1 (250 cm). The mean and range of host tree attributes included; a height of 452 cm (250–650 cm); sampled branch height of 164 cm (120–220 cm); sampled branch length of 52 cm (27–120 cm); sampled branch diameter of 22 mm (15–28 mm); and four (1–7) chambered branches per tree. Sixty percent (i.e., three out of five) of host trees were situated on the edge of mangrove vegetation.

Ant specimens from Mary River Heads and Redland Bay proved to be morphologically indistinguishable (S. O. Shattuck, pers. comm.). External ant activity on tree trunks adjacent to sampled colonies varied significantly between all seasons (summer and autumn, $p = 0.0016$; winter

TABLE 1. Persistence of immature stages of *Acrodipsas illidgei* in sampled sections of *Crematogaster* sp. (*laeviceps* group) colonies in *Avicennia marina*. Dashes in table indicate no ant colony section accessible and therefore no sample able to be taken from tree at this time. *p* refers to probability of host tree being positive for *A. illidgei* in the listed sequence over all seasons (except where not sampled) assuming that each sample is independent.

Host tree #	Season				<i>p</i>
	Winter	Spring	Summer	Autumn	
1	1	1	1	1	<0.0001
2	1	—	—	—	0.0219
3	1	1	0	—	0.0007
4	1	1	0	0	0.0007
5	0	1	0	0	0.0320
Total host trees	4	4	1	1	0.0553
Total trees sampled	183	120	112	129	—

and spring, spring and summer, $p < 0.0001$) except summer and winter ($p = 0.58$). A prominent peak in external ant activity on trees was noticed during the spring (mean = 3.1, SE = 0.26, $n = 120$) as compared to winter (mean = 1.9, SE = 0.16, $n = 183$), summer (mean = 1.7, SE = 0.171, $n = 112$) and autumn (mean = 0.9, SE = 0.1, $n = 106$). Similarly, percentage ant brood/chamber occupied varied seasonally ($p < 0.03$) except between winter and spring ($p = 0.108$) (Fig. 3). The spring peak ($\chi^2 = 14.02$, $df = 6$, $p < 0.03$) and autumn level ($\chi^2 = 17.236$, $df = 6$, $p < 0.01$) in external ant numbers corresponded to percentage ant brood in chambered branches during the same seasons but this was not the case in winter ($\chi^2 = 2.965$, $df = 6$, $p > 0.8$) and summer ($\chi^2 = 6.246$, $df = 6$, $p = 0.39$).

DISCUSSION

Localized distributions are common among myrmecophilous lycenids but these are thought to be largely dependent on the overlapping distributions of the attending ant and host plant species (e.g., Smiley et al. 1988, Seufert & Fiedler 1996), the presence of conspecifics or other species (e.g., Webster & Nielsen 1984) or a combination of factors including plant quality (i.e., nitrogen content) (e.g., Pierce 1984, Thomas 1985, Baylis & Pierce 1991). Superficially, the life history of *A. illidgei* seems uncomplicated, with its larvae predominantly feeding upon the immature stages of a common mangrove ant. However, individuals are extremely difficult to locate during any part of their life cycle, are found in extremely low densities during all stages of their development, and seem to be almost certainly restricted to specific host ant colonies. The distribution of ant colonies harbouring *A. illidgei* could be the result of a specific colony recognition by ovipositing females or reflect a high mortality rate in most potential colonies.

Sampling effects were minimized as much as possible during this study but reduced the chances of encountering immature stages in the same ant colony sections during follow up re-samples. The impact of sampling for *A. illidgei* immatures made whole ant colony investigations not only impractical, but undesirable. Cumulative damage to ant colony sections in winter and spring may account for three positive colony sections (i.e., host trees) subsequently becoming negative in the summer sample (Table 1). Despite this impact, consecutive positive samples (up to four after a positive sample two years earlier) indicate a strong persistence of *A. illidgei* in particular host colonies.

Data obtained from host colony sections and trees displayed variation consistent with that found in the overall sample and suggests that despite most trees appearing to be potential hosts for *A. illidgei*, this is rarely the case. A comparison of the two most 'successful' host ant colonies shows that one tree (in Sector 1) occurred in a less densely vegetated area and possessed a smaller, more spindly growth habit (i.e., more branches of smaller dimensions) when compared to the other (Sector 4) in an *A. marina* dominated zone. Similarly, the few positive samples suggest that host colonies are not necessarily confined to trees on the edge of the mangrove forest (where mean ant colony brood volume was significantly higher at Redland Bay) as previously supposed (Beale & Zalucki 1995, see also descriptions of 'edge effects' in Courtney & Courtney 1982).

The only obvious habitat requirement restricting *A. illidgei* appears to be the host ant, *Crematogaster* sp. (*laeviceps* group), a common and dominant taxonomic (i.e., morphological) species at least in surveyed mangrove forests. At Redland Bay, for example, 85% ($n = 93$) of grey mangrove harboured *Crematogaster* sp. (*laeviceps* group) ants (Beale, unpubl. data). The presence of cryptic (refer to Paterson 1991) *Crematogaster* species has not been ruled out but it seems unlikely that the presence of such a cryptic species could explain the butterfly's persistence in a handful of colonies, unless of course the ant species was similarly rare and localized.

Females of *A. illidgei* may require highly specific (i.e., chemical) oviposition cues or alternatively have a tendency not to be 'choosy' when selecting ant inhabited oviposition sites, resulting in a small proportion of individuals surviving in specific, accommodating ant colonies. The presence of a highly specific oviposition system seems most likely. Other (phytophagous) myrmecophilous species are known to select oviposition sites by using the correct ant species as a cue (Atsatt 1981b, Pierce & Elgar 1985, Fiedler & Maschwitz 1989). A highly specific and obligatory relationship with an ant species is typically associated with a highly specialized larval communication system (Fiedler et al. 1996) and this

would be expected to be most pronounced in a species like *A. illidgei*. It is reasonable to suggest that a highly specific larval/ant communication system would be initiated by a comparative level of chemical identification during oviposition, because when a 'good' choice is made, the host colony then becomes more of an enemy-free space (see below). This is not unlike conspecific *Crematogaster* sp. (*laeviceps* group) ants readily differentiating members of the same and different colonies, and behaving accordingly (Beale & Zalucki 1995). Although not direct evidence for specific colony selection behaviour, Samson (1989) observed that most trees harbouring the host ant did not possess eggs of *A. illidgei*, but aggregations of eggs (up to 25 eggs) were present on a few. Oviposition behaviour may be influenced by larval experience and conditioning (e.g., Schweissing & Wilde 1979) or 'adult emergence experience' or initial adult experience (Jaenike 1983, Papaj 1986, Prokopy & Fletcher 1987, Firempong & Zalucki 1991, Cunningham et al. 1998) because adults emerge from within the colony.

The nature of Illidge's ant-blue's/ant relationship is relevant to its overall mortality and therefore colony selection, because it requires either the chemical assimilation of larvae and/or the provision of much sought after bribes for ants, since parasitic larvae possess little physical defence against attack from a typically aggressive ant species. Furthermore, the loss of ant brood is unlikely to be offset by the potential for non-essential chemical benefits provided by *A. illidgei* larvae, if larvae are primarily myrmecophagous as they appear to be. Crypsis can be ruled out since the host ants actively carry neonates back to the colony where they are placed in among the ant's brood (Samson 1989); a very different behaviour to that exhibited towards the phytophagous lycaenid, *Ogyris amaryllis*, which provides the same ants with sugar secretions away from the nest. Colony carrying capacity (i.e., brood volume), although seemingly of great importance to butterfly survival, may not be relevant to colony selection because it cannot be accurately determined from outside the nest, although seasonally (i.e., in spring and autumn) external adult ant activity does appear to be linked to ant brood volume.

CONSERVATION OF *ACRODIPSAS ILLIDGEI*

Illidge's ant-blue provides an example of the dilemma facing researchers studying hard-to-find and potentially threatened insect species. Because only a few specimens at most are likely to be discovered during even a large study, it is difficult to justify the expenditure of resources for further research, relegating unusual species like *A. illidgei* to relative scientific obscurity. Transect counts for *A. illidgei* are likely to record many zeros and only occasional suspected sightings, and would be difficult to implement due to the inaccessibility of much of the dense,

mangrove vegetation. Furthermore, overestimates of distribution and density may occur if the status of *A. illidgei* is based principally upon a census of apparently abundant habitat resources. Hence, it is impractical to accurately monitor *A. illidgei* for anything other than its presence and even then, it can be easily overlooked.

Butterfly monitoring schemes in the United Kingdom have revealed that it is usually the localized species that experience the most severe declines over time (Pollard & Eversham 1995). Even minor damage to Illidge's ant-blue's habitat may in fact seriously threaten a localized population when their host colony specificity is taken into account (and this is even more pronounced in small remnant populations). It is likely that *A. illidgei*, with its relatively weak flight, its tendencies to remain settled for long periods punctuated by short flights, and for the female to emerge with a fully developed egg load (Sands 1979), would have difficulty in colonizing other habitat patches.

Recent efforts to preserve habitat of the Eltham copper, *Paralucia pyrodiscus lucida* Crosby, at Eltham in Victoria (Braby 1987) and *A. illidgei* at Redland Bay and Mary River Heads (Fig. 1) have indicated that public interest in conservation of invertebrates has not necessarily relied upon the economic (e.g., tourism, trading) or aesthetic value of a given species. Exceptions to this include *Ornithoptera* from New Guinea, but even then, commercial value has been used as a means to a conservation end (Cherfas 1979, Pyle et al. 1981). Once the public at Redland Bay and Maryborough and Hervey Bay (both near Mary River Heads) had been made aware of the fascinating biology of the drab, rarely seen *Acrodipsas illidgei*, it then became the driving force behind the species' prominence and habitat preservation efforts. Consequently, an important initial step in insect and habitat conservation should be the elucidation of the biology of rare and threatened species, with the subsequent dissemination of such information in a digestible form to the community at large. This is especially relevant if government insect preservation policy, in effect, relies heavily upon the prohibition of collecting (see e.g., Beale 1998).

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CHANGES IN BUTTERFLY DIVERSITY IN THREE REFORESTED AREAS IN SPAIN

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ABSTRACT. Changes in butterfly diversity induced by reforestation were detected at three areas in central Spain with autochthonous forests and adjacent pine reforestations. The natural areas were pyrenean oak (*Quercus pyrenaica*) and holm oak (*Q. ilex*) forests, and the reforested areas were, respectively, stone pine (*Pinus pinea*), cluster pine (*P. pinaster*) and scots pine (*P. sylvestris*), and subject to different forestry management regimes. Reforestation with alien species causes a decrease in the number of butterfly specimens, the number of species, and the diversity index. These losses are minimal when the management of reforestations allows the recovery of undergrowth.

Additional keywords: conservation, diversity indices, forest management.

When comparing areas of natural vegetation to areas reforested with tree species differing from those previously present, it is generally assumed that the former are always richer in faunal diversity. Reforestations can be considered as rejuvenating elements for the ecosystems (Margalef 1980) and therefore as diversity simplifiers. However in spite of the great extent and importance of reforestations in many areas, studies on their actual influence are relatively scarce.

Reforestations are complex: many factors influence them, including site selection, local conditions or the plant species to be planted, the planting techniques used, and the subsequent utilization of the territory and its management and exploitation. According to studies made on this topic, decreases of diversity have been observed in microflora (Lozano & Velasco 1972), and in forest grassy plants, the number of individuals and species decreases compared to areas still retaining natural vegetation (Magurran 1988). In the soil fauna, diversity decreases in areas reforested with species different from those of the original forest, and is higher in the autochthonous forest (Bonnet et al. 1976, 1979, Arbea & Jordana 1985, Arbea 1987). Bird diversity is also greater in areas with natural vegetation than in reforestations (Batten 1976, Bongiorno 1982, Potti 1986, Avery & Leslie 1990), and these results agree with studies on rove beetles (Staphylinidae) (Buse & Good 1993) and large moths (Magurran 1985).

Planting with conifers has also affected butterflies, which are excellent bioindicators (Erhardt 1985, 1995, Erhardt & Thomas 1991) and a suitable group for exploring diversity topics. Although young conifer planta-

tions can provide suitable habitat for many early successional species, the butterfly communities rapidly deteriorate after canopy closure. Allowing the canopy to close in the native British hardwood forest was extremely detrimental to woodland species (Robertson et al. 1995), and in blocks of mature conifers Robertson et al. (1988) found only five butterflies per km walked. The objective of this paper is to evaluate the effect on butterfly communities of the substitution of autochthonous species by pine plantations.

MATERIALS AND METHODS

Study sites. Three areas in Spain that maintained their autochthonous tree vegetation and were adjacent to areas where the original vegetation had been replaced by pine reforestation were chosen for study: Valdelatas, Soto del Real, and Valsaín (see Table 1). The three areas with natural vegetation have well developed trees and nearly 100% tree cover. Although these forest areas are fragmented and altered, they can be considered, by their aspect and management, as representative of what is left of natural forest in flat or low mountain areas in the center of the Iberian Peninsula. Reforested areas also have mature trees, with a well developed canopy, although forest management is different in each one of them.

Valdelatas: This site is located near Madrid at an altitude of approximately 700 m, UTM (Universal Transverse Mercator) coordinates 30TVK48. According to Rivas-Martínez (1987), the climax vegetation of this area consists mainly of holm oaks, *Quercus ilex ballota* (Desf.) Samp. in Bol. and lusitanian oaks, *Q. faginea* Lam. There are some tall holm oaks (6–8 m), but part of the holm oaks are reduced to a bushy state (3–4 m tall) and constitute an impervious thicket at certain points. Lusitanian oaks are less numerous and scattered among the holm oaks. In this area there is a cleared reforestation of stone pine, *Pinus pinea* L. This reforestation is more than 60 years old, and though it was extensive many years ago, at present it is reduced due to roads and buildings. The total forested area is 250 ha, one half of which is covered by natural vegetation (*Q. ilex ballota*) and the other half by a reforestation with *P. pinea*. In the latter the trees are very separated from one another, have bulky trunks and great size (10–15 m tall). The canopy is closed, with little undergrowth. Both the natural and reforested areas are used periodically for sheep grazing.

Soto del Real: This site is located in Madrid, on the southern slope of the Sierra de Guadarrama, at an average altitude of 1200 m, UTM coordinates 30TVL31, and lies inside the Parque Regional de la Cuenca Alta del Manzanares. The original vegetation is a pyrenean oak forest (*Quercus pyrenaica* Willd.). The area is cleared as a result of extracting

TABLE 1. Characteristics of the sampled natural (NAT) and reforested (REF) areas.

	Valdelatas		Soto del Real		Valsain	
	NAT	REF	NAT	REF	NAT	REF
Altitude	700 m	700 m	1200 m	1200 m	1300 m	1300 m
Vegetation						
tree species	<i>Q. ilex</i>	<i>P. pinea</i>	<i>Q. pirenaica</i>	<i>P. pinaster</i>	<i>Q. pirenaica</i>	<i>P. sylvestris</i>
tree height	6–8 m	10–15 m	8–12 m	10–12 m	10–14 m	6–8 m
plantation age		>60 yr		ca. 40 yr		ca. 30 yr
understory density	+++	++	+	++	+++	+
Management						
cattle grazing	—	—	+++	+	+++	++
goats grazing	—	—	++	—	—	—
sheep grazing	++	++	—	—	—	—
cotting understory	+	++	+++	+	—	++
charcoal production	—	—	++	—	—	—

wood for charcoal production, leaving a mosaic of relatively open areas and closed thickets. Closed areas have young and large sized (8–12 m tall) trees and vegetation in the undergrowth, and the open areas have large trees and pastures. Most of the areas belonging to the pyrenean oak bioclimatic stage have been reforested with cluster pine *Pinus pinaster* Aiton. In adjacent zones, at higher levels than those of the sampling site, reforestations are made with scots pine, *P. sylvestris* L. Both the oak and pine forest are grazed at Soto del Real. In the oak forest, grazing is somewhat more intensive. The pine reforestation conserves more scrub than the adjacent natural zone of pyrenean oaks. Pine trees are quite near one another and they are very tall (10–12 m).

Valsain: This site is located in the province of Segovia, on the northern slope of the Sierra de Guadarrama, at an altitude of 1300 m, UTM coordinates 30TVL12. This area also belongs to the pyrenean oak forest stage (*Q. pyrenaica*). This zone is grazed, and the pyrenean oak forest forms patches surrounded by pasture. The oaks, some of which are large (10–14 m tall), grow in these patches together with a variety of bushes, lianas and other components of the prickly border. The reforested zone here is a *Pinus sylvestris* forest. It consists of not very tall (6–8 m) pines about 30 years old. It is a closed formation into which daylight rarely penetrates. There is no undergrowth. Because of this management, the area is almost devoid of other vegetation. Cattle wander about the forest and graze in the clearings.

Data recording and analysis. Density of butterfly population was estimated using periodic walks along different previously established

transects (Pollard et al. 1975, Pollard 1977, Rodríguez 1991, Pollard & Yates 1993). Two transects were set in each area: one in the reforested zone and the other in the natural vegetation zone. Transect length was fixed at 700 m, and covered at a slow and constant pace, so that the time spent on each was approximately one hour. Because butterflies typically prefer open areas, the transects were often routed through open areas within the forest. Rocky outcrops, cattle tracks and clearings were chosen in order to observe the highest possible number of butterfly species and individuals. All butterflies seen within 5 m on either side of the path were recorded. The surveyed area was therefore 0.7 ha in each transect. In every case the number and days of transect were the same for the natural and corresponding reforested areas. Recording was only done on sunny, cloudless or almost cloudless days and at temperatures above 18°C. Specimens requiring special study for identification were taken to the laboratory (e.g., *Melitaea athalia*). These specimens are now part of the Autónoma of Madrid University Biology Department collection. Butterfly nomenclature follows Higgins (1975) and Higgins and Riley (1983), with minor changes. Agenjo (1975), Fernández-Rubio (1977) and Higgins (1975) have been followed to identify species by genitalic structure. The references used for plant taxonomy were Castroviejo et al. (1986, 1990).

Diversity was estimated by the Shannon-Weaver information index, H' (Margalef 1980, Magurran 1988) as: $H' = -\sum (p_i \log_2 p_i)$, $\sum p_i = 1$, where p_i is the i th species probability. The Shannon-Weaver information index was chosen because it is one of the most frequently used in ecology (Margalef 1980, Magurran 1988, Krebs 1989) and because its use is widespread in butterfly studies (Pinheiro & Ortiz 1992, Sánchez Rodríguez & Baz 1995). Evenness, J' , was calculated by dividing diversity by maximum diversity (Krebs 1989, Magurran 1988) as: $J' = H'/H'_{\max}$. Maximum diversity was calculated as: $H'_{\max} = \log_2 S$, where S is the number of species. Following Margalef's formula (Margalef 1980, Magurran 1988) richness, R' , was calculated as: $R' = S - 1/\ln(N)$, where S is the number of species and N is the number of specimens. Dominance, D' , was calculated using the Berger-Parker index (Magurran 1988) as: $D' = N_{\max}/N$, where N_{\max} is the number of individuals of the most abundant species.

Two similarity indices were used to measure the similarity between two given samples: the Jaccard index and the Bray-Curtis index (Margalef 1980, Legendre & Legendre 1984, Krebs 1989). The qualitative Jaccard index considers only presence or absence data: $S_j = a/(a + b + c)$, where a is the number of species common to samples 1 and 2, and b and c the exclusive species from samples 1 and 2, respectively. The quantitative Bray-Curtis index takes into account the number of individ-

uals of every species: $S_{BC} = 1 - (\sum |y_{i1} - y_{i2}| / \sum (y_{i1} + y_{i2}))$, where y_{ij} is the number of individuals of species i in sample j . An agglomerate cluster analysis was also made from these indices using the single linkage clustering method (Krebs 1989).

RESULTS

A total of 3033 specimens representing 53 species was recorded. The species and number of specimens of all reforested and natural vegetation areas are shown in Table 2. Figs. 1 and 2 show the variation in the number of species and specimens throughout the season in every sampling area. The largest relative number of butterflies was observed on the pyrenean oak forest in Valsaín (698 specimens in 10 samplings), followed by the pyrenean oak forest and the pine reforestation of Soto del Real (875 and 787 specimens, respectively, in 13 samplings). In Valdelatas, the number of records was much smaller: 319 on the pine reforestation and 212 on the holm oak forest in 11 samplings at each area. The Valsaín reforestation is remarkable for its low number of butterflies (only 142 butterflies in 10 samplings).

Among the 3033 butterflies observed 1785 were found in the natural vegetation zones and 1248 in the reforested areas. In Valsaín, a significant decrease in the number of butterflies on the reforested areas was observed ($p < 0.01$ by chi-square). In Soto del Real, both counts were similar, and the differences between natural and reforested areas were not significant (chi-square). In Valdelatas, more butterflies were found in the reforested area compared to natural area ($p < 0.05$, chi-square).

The highest densities and the greatest number of butterflies flying occurred in July at Valdelatas and Soto del Real (both in the southern slope of the Sierra de Guadarrama) and in August at Valsaín (in the northern slope of the Sierra de Guadarrama). Phenology differences were not found in the reforested areas when compared to those of the natural ones.

The diversity index (H') ranged from 3.91 in the natural zone of Soto del Real, to 2.97 in the reforestation area of Valdelatas. Diversity was higher in the natural vegetation zones than in the reforestations at Valdelatas and Soto del Real, whereas at Valsaín the situation was reversed. Maximum diversity (H'_{max}) was highest in the oak forest of Soto del Real (5.43) and the lowest in the reforestation at Valdelatas (4.32). The three locations had larger index values for natural areas and smaller values for reforestations. R index values followed H'_{max} : the largest, 6.20, in the oak forest of Soto del Real, and the smallest in the pine reforestation of Valdelatas. R values were larger in the natural areas than in the reforestations. Evenness (J') was highest in the holm oak forest at Valdelatas and the pine reforestation at Valsaín, and lowest in the pyrenean

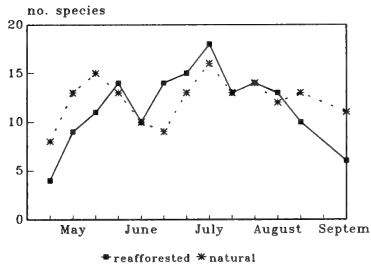
TABLE 2. List of butterfly species recorded in the natural (NAT) and reforested (REF) areas. Sampling intervals: Valdelatas, 11 days; Soto del Real, 13 days; Valsain, 10 days.

	Valdelatas		Soto del Real		Valsain	
	NAT	REF	NAT	REF	NAT	REF
<i>Papilio machaon</i>			1			
<i>Iphiclides podalirius</i>	2		1	4	3	
<i>Zerynthia rumina</i>	3		29	13	4	
<i>Aporia crataegi</i>	6	8	2	7	17	1
<i>Pieris rapae</i>	14	28	15	18	17	3
<i>P. napi</i>				1	3	
<i>Pontia daplidice</i>	11	1	5	11		
<i>Anthocharis cardamines</i>	1		6	20		2
<i>A. euphenoides</i>			1	7		
<i>Colias croceus</i>	4	7	80	40	25	
<i>Gonepteryx rhamni</i>			14	25	14	
<i>G. cleopatra</i>				1		
<i>Callophrys rubi</i>					3	
<i>Lycæna phlaeas</i>	8	11	40	66	5	1
<i>Heodes virgaureae</i>				1		
<i>H. tityrus</i>		2	2	1		
<i>H. alciphron</i>			1	2	2	
<i>Lampides boeticus</i>					1	
<i>Celastrina argiolus</i>			1	1		
<i>Aricia cramera</i>	4	4	11	1		
<i>Polyommatus icarus</i>			6	6	2	
<i>Limenitis reducta</i>			2	1		
<i>Nymphalis antiopa</i>			2	2		
<i>N. polychloros</i>		1	2	1		
<i>Inachis io</i>			2	5	2	
<i>Vanessa atalanta</i>			1		5	
<i>Cynthia cardui</i>			1		6	
<i>Aglais urticae</i>			2			
<i>Polygonia c-album</i>		1	1			
<i>Pandoriana pandora</i>	3	8	16	41	37	23
<i>Argynnis paphia</i>			1	3	1	
<i>Mesoacidalia aglaja</i>			7	7	6	1
<i>Fabriciana adippe</i>			1	7		3
<i>F. niobe</i>	18	25	4	6	1	
<i>Issoria lathonia</i>		2	37	55	38	2
<i>Brenthis ino</i>						1
<i>Melitæa cinxia</i>			3	3		
<i>M. didyma</i>			1	2	1	
<i>M. athalia</i>				6		
<i>Euphydryas aurinia</i>			35	41		2
<i>Hipparchia semele</i>			2			34
<i>Neohipparchia statilinus</i>	8	2	49	7	13	4
<i>Brintesia circe</i>	8	1	75	57	16	6
<i>Pararge aegeria</i>	2	6	6	1	4	1
<i>Maniola jurtina</i>	14	36	43	34	17	13
<i>Hyponphele lycaon</i>			1			
<i>Pyronia cecilia</i>	68	61	105	27	128	17
<i>P. bathseba</i>	6			1		
<i>Coenonympha pamphilus</i>	1	1	51	7	29	14
<i>Lasiommata maera</i>	1				1	
<i>L. megera</i>	6	1	2	5	7	2

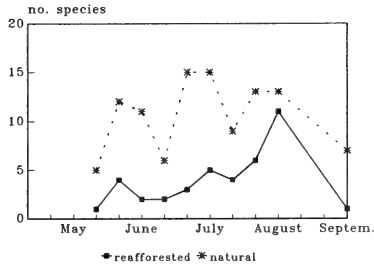
TABLE 2. Continued.

	Valdelatas		Soto del Real		Valsain	
	NAT	REF	NAT	REF	NAT	REF
<i>Melanargia lachesis</i>	11	113	208	243	284	13
<i>M. ines</i>	13					
Abundance (N)	212	319	875	787	698	142
Species (S)	22	20	43	41	32	18
Diversity (H')	3.63	2.97	3.91	3.90	3.21	3.37
Evenness (J')	0.81	0.69	0.72	0.73	0.64	0.81
Richness (R)	3.92	3.30	6.20	6.00	4.73	3.43
Dominance (D')	0.32	0.35	0.23	0.30	0.41	0.23
Max. Diversity (H' _{MAX})	4.46	4.32	5.43	5.36	5.00	4.17

SOTO DEL REAL



VALSAIN



VALDELATAS

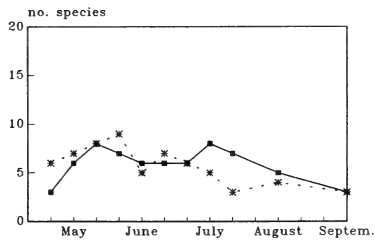
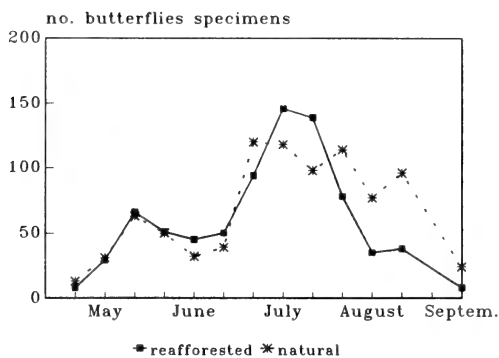
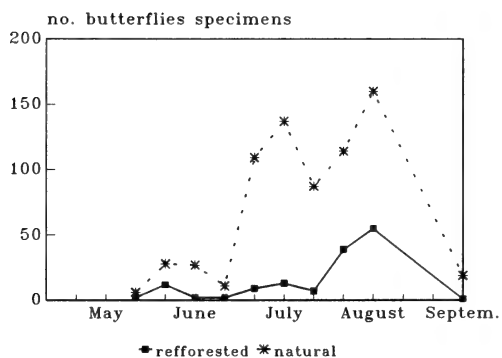


FIG. 1. Variation in the total number of butterfly species at three sites in Spain. Squares and solid lines refer to reforested areas, and stars and dashed lines to natural areas.

SOTO DEL REAL



VALSAIN



VALDELATAS

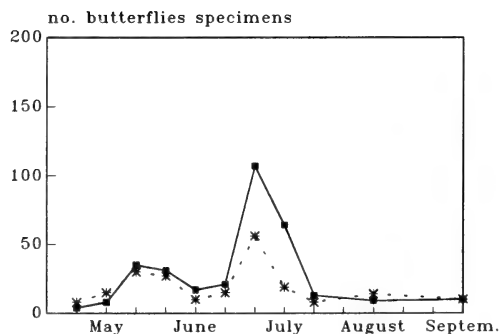


FIG. 2. Variation in the total number of butterfly specimens at three sites in Spain. Squares and solid lines refer to reforested areas, and stars and dashed lines to natural areas.

TABLE 3. Values of the Jaccard and Bray-Curtis similarity indices comparing natural (NAT) and reforested (REF) areas.

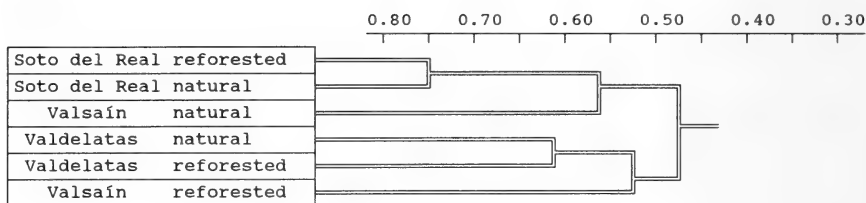
		Valdelatas		Soto del Real		Valsaín	
		NAT	REF	NAT	REF	NAT	REF
Jaccard							
Valdelatas	NAT	1.00					
	REF	0.62	1.00				
Soto del Real	NAT	0.41	0.47	1.00			
	REF	0.47	0.45	0.75	1.00		
Valsaín	NAT	0.46	0.41	0.56	0.52	1.00	
	REF	0.48	0.52	0.42	0.40	0.43	1.00
Bray-Curtis							
Valdelatas	NAT	1.00					
	REF	0.56	1.00				
Soto del Real	NAT	0.29	0.46	1.00			
	REF	0.26	0.43	0.72	1.00		
Valsaín	NAT	0.34	0.48	0.67	0.65	1.00	
	REF	0.36	0.27	0.19	0.21	0.25	1.00

oak forest at Valsaín and the pine reforestation at Valdelatas. The Soto del Real oak wood and pine reforestation had intermediate J' values. Dominance (D') was highest in the pyrenean oak forest at Valsaín and the pine reforestation at Valdelatas, and smallest in the pyrenean oak forest at Soto del Real and the pine reforestation at Valsaín.

Table 3 shows values of the Jaccard and Bray-Curtis indices. The Jaccard index peaked at 0.75 at Soto del Real, so the maximum similarity found is that between the natural and the reforested areas at this location. The next highest value, 0.62, was between the natural and the reforested areas at Valdelatas, and the third highest, 0.56, between the natural areas at Soto del Real and Valsaín. Finally, 0.52 is the value between the reforestations at Valsaín and Valdelatas. Thus, the pine reforestation at Valsaín is not related either to its corresponding natural area nor to the other oak site in Soto del Real, but rather to the poorest area, the pine reforestation of Valdelatas. Similar clusters were obtained by other qualitative indices, like those of Sorensen or Czechanovski, Baroni-Urbani and Busner, which consider double absences (Margalef 1980, Krebs 1989), but these are not presented here.

The quantitative Bray-Curtis index produces similar results to the Jaccard, except for the Valsaín reforestation that is separated from all the other areas (Fig. 3). Figure 4 shows the ordered distribution of butterfly species frequencies in both reforested and natural sites. The lines of the reforested areas are always below those of the natural areas at Valsaín and Valdelatas.

Jaccard:



Bray-Curtis:

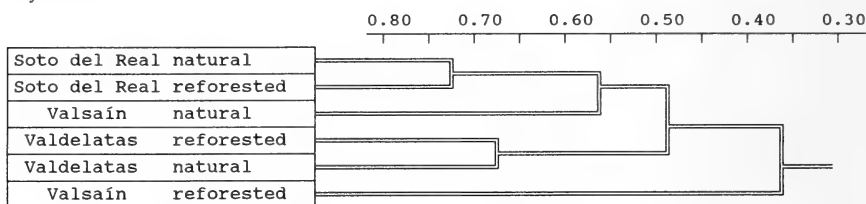


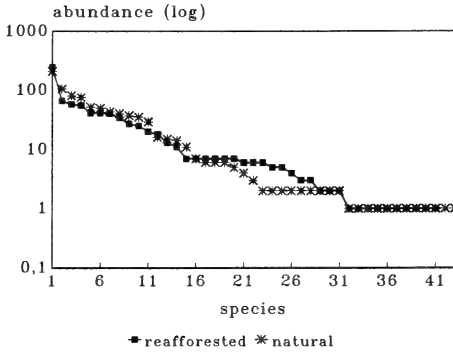
FIG. 3. Tree diagrams obtained from the Jaccard (qualitative) and Bray-Curtis (quantitative) similarity indices. Agglomerate cluster made by single linkage clustering.

DISCUSSION

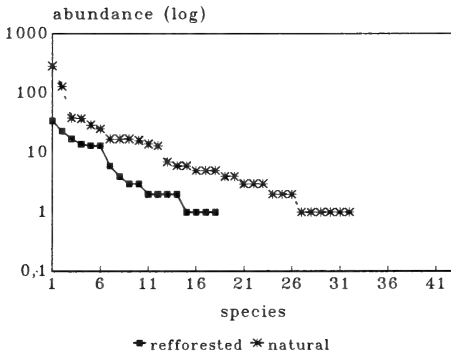
Variation in butterfly density. Among the three study locations, the number of butterflies at Soto del Real is similar in the reforested area in relation to the natural area. This may be because in the reforestation the undergrowth is maintained, and so its floristic richness is similar to that of the oak wood. At Valdelatas, greater butterfly density was observed in the pine reforestation, likely because this is an open area with abundant ruderal vegetation and flowers that are attractive, especially to vagile and opportunistic species such as *Pieris rapae*, *Maniola jurtina* and *Melanargia lachesis* (whose numbers spectacularly increase in the reforested zone). At Valsaín, a typical reforestation, the differences in butterfly densities between the natural and the reforested zones are pronounced, with a large decrease in numbers of individuals. This is reflected in the cluster obtained from the Bray-Curtis index, which takes into account the number of specimens in addition to species, and separates the pine reforestation at Valsaín from its corresponding natural area and from all the other areas. The other reforestations more nearly resemble their respective natural zones. Our results largely agree with those of Avery & Leslie (1990) for birds, Magurran (1985, 1988) for grasses and moths, Buse and Good (1993) for rove beetles (Staphylinidae), and Robertson et al. (1988) for butterflies, in which species numbers decrease in reforested areas.

In most cases, fluctuations in the number of specimens of certain spe-

SOTO DEL REAL



VALSAIN



VALDELATAS

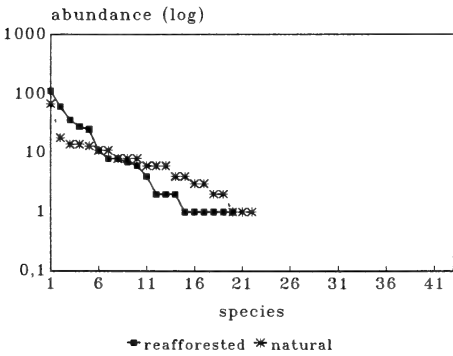


FIG. 4. Abundance plots for butterfly species at three sites in Spain.

cies were not attributable to reforestation. In the most abundant species with high quantitative changes (*Melanargia lachesis*, *Pyronia cecilia*), these can be attributed to the presence of clearings and pastures among the trees, regardless of whether they are autochthonous or reforested.

Changes in number of butterfly species. The autochthonous forests had the largest numbers of species, with a total of 50, compared to 43 in reforestations. The total number of species recorded on all three sampling sites was 53. In Valdelatas, the autochthonous forest had a small number of species even though it is a climax forest. This is because the holm oak forests are poor in understory plants, with only 8 to 10 additional plant species (Izco 1984), and so the number of possible butterfly larval hostplants is diminished.

As with butterfly density, small differences were observed in the number of species in the natural areas compared to the reforestations at Soto del Real and Valdelatas (43 to 41, and 22 to 20, respectively), whereas large differences were seen at Valsaín (32 species in the natural area vs. 18 in the reforestation). This can also be attributed to the fact that the last area is strictly a forest plantation. Similarity clusters show these results graphically: according to the list of species and the Jaccard index, the most typical reforestation (Valsaín) is separated from its natural area, and is placed close to the poorest areas.

These results coincide with those of other authors (García-González 1988, Robertson et al. 1988, Avery & Leslie 1990, Buse & Good 1993). A decrease of the number of species was observed in the reforested areas, probably caused by a simplification and rejuvenation of the ecosystem, as pointed out by Margalef (1980).

Diversity indices as indicators of change. Considering the Shannon-Weaver index, the areas with the greatest diversity belong to Soto del Real, both the autochthonous and the reforested forest. The similar index values for the reforestation and the natural area can be considered normal. We noted earlier that Soto del Real is not used for wood extraction, and is an old pine reforestation. The accompanying vegetation of the pyrenean oak floor has regenerated and supports butterfly species characteristic of such areas. In contrast the pyrenean oak forest is being intensively grazed, and this has led to a convergence in the butterfly faunas of both areas. The sparse undergrowth in the pine reforestation at Valdelatas is probably responsible for decrease in diversity and number of species. At Valsaín, the autochthonous forest is cleared as a result of intensive grazing, and the reforested area is largely a monoculture of *Pinus sylvestris*. Paradoxically, the pine reforestation here shows a greater diversity than in the original oak forest. This is probably because some opportunistic species like *Melanargia lachesis*, whose caterpillars eat grassy plants, are very abundant in the oak forest

clearings: of 698 specimens recorded, 284 were *M. lachesis*, and the H' diversity index reflects this.

The Shannon-Weaver index takes into account the number of species and the relative numbers of each, but if we consider only the number of species, the oak forest has 32 species compared to 18 recorded in the pine reforestation. Likewise, the greatest H'_{\max} values are those of the autochthonous forests. Soto del Real still shows the largest diversity indices and Valdelatas the lowest, due to the scarcity of accompanying plant species in the oak forest. The Margalef returned similar results to H'_{\max} and, in contrast to the Shannon-Weaver index, maxima always corresponded to the natural areas, and the most pronounced differences were observed in the forests at Valsáin.

These results agree with those of Batten (1976), Bongiorno (1982) and Potti (1986) in birds; Bonnet et al. (1976, 1979), Arbea and Jordana (1985) and Arbea (1987) in Collembola; Buse and Good (1993) in rove beetles; and Magurran (1985) in moths. In general, diversity decreases in reforested areas, but such decreases are influenced by use and management subsequent to reforestation (Potti 1986, Avery & Leslie 1990, Buse & Good 1993).

The graphs of species abundances (Fig. 4) illustrate the differences between the three types of reforestation management studied. At Soto del Real, both lines start and end at similar points, and have similar slopes. At Valdelatas, the line corresponding to reforestation starts from a higher point and crosses the line corresponding to the natural zone. In this case, in a reforestation subject to light management there appears to be a decrease in diversity. At Valsáin, the slopes are parallel but the starting and ending points differ. In this reforestation managed to obtain high wood production yields, there is a loss both in the number of butterfly species and abundance.

In conclusion, these reforestations in Spain reduced Lepidoptera diversity compared to areas in which the autochthonous tree vegetation was preserved. The magnitude of the change in diversity depended on the nature of reforestation and on management practices. In reforestations where the undergrowth was conserved, diversities close to those of the original forest were reached.

ACKNOWLEDGMENTS

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HESPERIIDAE OF RONDÔNIA BRAZIL: *RIDENS* AND THE “*PROTEUS*” GROUP OF *URBANUS*, WITH DESCRIPTIONS OF NEW SPECIES (PYRGINAE)

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ABSTRACT. Four new species of HesperIIDae are described from the vicinity of Cacaulândia, Rondônia, Brazil: *Ridens bidens*, *Urbanus villus*, *Urbanus longicaudus*, and *Urbanus parvus*. The phenologies of an additional six species of the “*proteus*” group of *Urbanus* occurring in this area are presented.

Additional key words: genitalia, Neotropics, phenology, South America.

During studies of the butterfly fauna in the vicinity of Cacaulândia in central Rondônia, Brazil (Emmel & Austin 1990, Austin et al. 1993), numerous new species of skippers (HesperIIDae) have been encountered (Austin 1993, 1994, 1995, 1996, Austin & Steinhauser 1996). These samples included a new species of *Ridens* and three new species of the *Urbanus* “*proteus*” group (HesperIIDae: Pyrginae). These are described herein along with information on six additional species of the “*proteus*” group from near Cacaulândia.

Forewing length was measured from base to apex, width was the shortest distance from costa to tornus, and tail length was measured from the end of vein 3A to the end of the tail. All primary types are deposited at the Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil; other vouchers and comparative material are there, at the Nevada State Museum, and at the Allyn Museum of Entomology.

Ridens Evans 1952

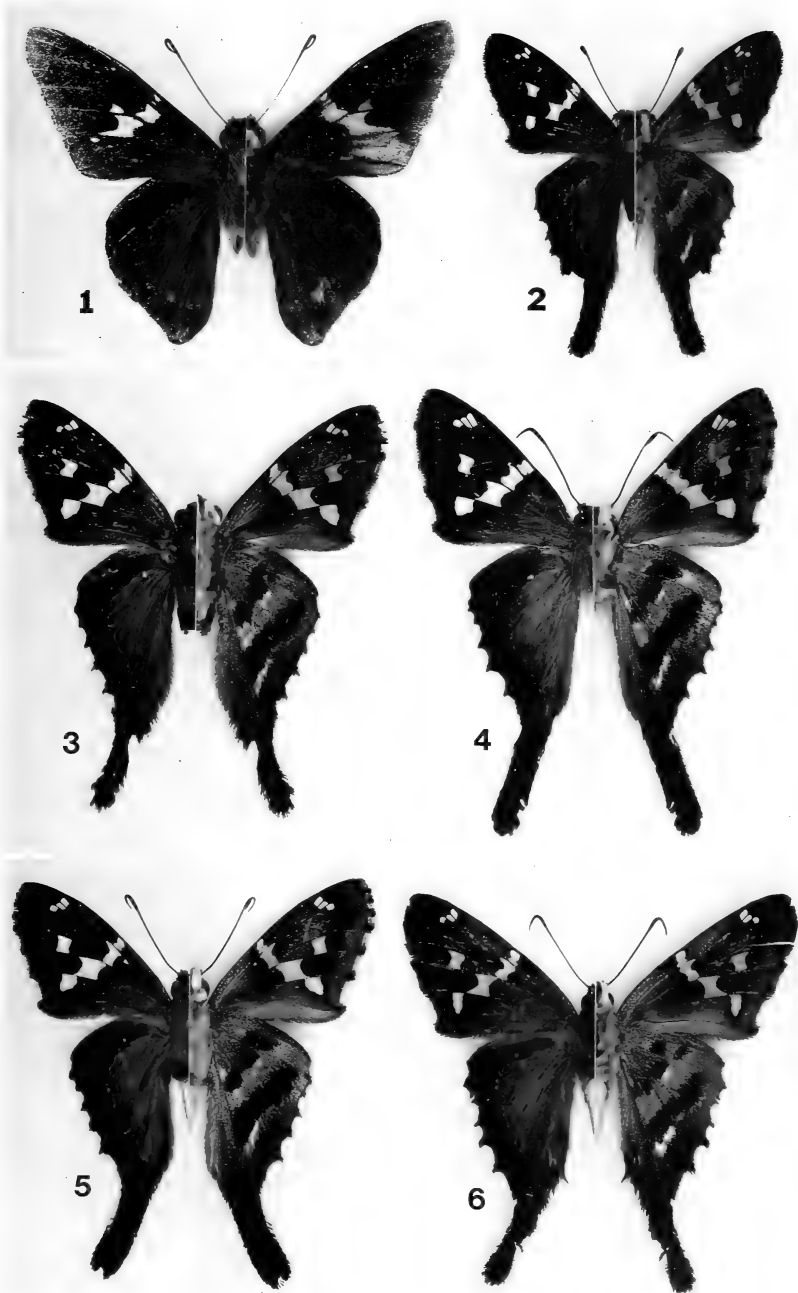
Evans (1952) included thirteen species in this Neotropical genus. Descriptions of four new species (Steinhauser 1974, 1983, Freeman 1979), the raising of a subspecies to specific status (Freeman 1976), and two new combinations (Steinhauser 1983) have increased this to twenty species. A single, previously undescribed, species is known from central Rondônia.

Ridens bidens Austin, new species

(Figs. 1, 7)

Description. *Male* (Fig. 1). Forewing length = 26.4 mm (holotype); forewing produced, with costal fold; hindwing lobed at tornus; dorsum brownish black, basal 1/3 of

FIGS. 1–6. New species of *Ridens* and *Urbanus*. **1**, *Ridens bidens*, holotype male, dorsal and ventral surfaces. **2**, *Urbanus parvus*, holotype male, dorsal and ventral surfaces. **3**, *Urbanus villus*, holotype male, dorsal and ventral surfaces. **4**, *Urbanus villus*, paratype female, BRAZIL: Rondônia; B-80, between C-10 and 15, 17 Nov. 1991, dorsal and ventral



surfaces. **5**, *Urbanus longicaudus*, holotype male, dorsal and ventral surfaces. **6**, *Urbanus longicaudus*, paratype female, BRAZIL: Rondônia; Linha C-20, 7 km E B-65, Fazenda Rancho Grande, 22 Nov. 1992, dorsal and ventral surfaces.

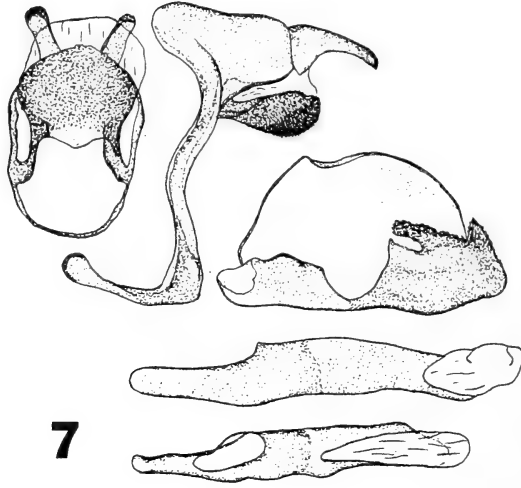


FIG. 7. Male genitalia of *Ridens bidens* (holotype, GTA #3498), including lateral view of tegumen, gnathos, uncus, and associated structures; ventral views of uncus, gnathos, and tegumen; interior view of right valva; left lateral and dorsal views of aedeagus.

forewing and basal 2/3 of hindwing dull blue-green; forewing with white hyaline macules as follows: discal cell, more or less quadrate, slightly excavate on distal edge; CuA_1-CuA_2 , large, overlapping distal 2/3 of discal cell macule, excavate on proximal edge and prominently on distal edge, posterior edge longer than anterior; M_3-CuA_1 , small, triangular at base of cell, proximal 2/3 overlapping macule in CuA_1-CuA_2 ; CuA_2-2A , very small, oval, at postero-distal corner of macule in CuA_1-CuA_2 ; R_1-Sc , minute, very thin, over distal end of discal cell macule; costal cell, larger than macule in R_1-Sc and anterior to it; fringes very worn, brown anteriorly, appearing white posteriorly to CuA_2 ; hindwing unmarked; fringes worn, apparently brown and unchecked. Ventral forewing dull blackish, brown along anal margin; hyaline macules repeated from dorsum; most of distal end of cell CuA_2-2A opaque white from just proximal to macule in CuA_1-CuA_2 to outer margin except anterior half of cell where blackish distad of hyaline macule in same cell; hindwing glossy dull green; white submarginal scaling posterior to CuA_1 , this as relatively distinct patch in CuA_2-2A . Dorsal head and thorax dull blue-green; palpi mixed whitish and gray; white beneath eyes; antennae black, slight yellow distad beneath including club, nudum red-brown, 34 segments; thorax gray-green on sides beneath wings, pectus gray with pale yellow cephalad, legs gray, tibiae not spined, mid tibia with single pair of spurs, hind tibia with 2 pairs of spurs, back of hind tibia with sparse row of hairlike scales; dorsal abdomen blackish, white at anterior segments and indistinct gray at last four, ventral abdomen white with medium width blackish bands. *Male genitalia* (Fig. 7). Uncus divided, arms divergent in ventral view; gnathos entire, broader than uncus in ventral view; valva with costa short, ampulla broadly rounded, harpe with relatively broad serrated tooth dorsad and relatively long serrated projection extending dorso-cephalad; aedeagus tubular, longer than valva, no cornutus. *Female*. Unknown.

Type series. Holotype male with the following labels: white, printed - BRASIL: Rondonia / 62 km S Ariqueemes / linea C-20, 7 km E / B-65, Fazenda / Rancho Grande / 17 June 1993 / leg. G. T. Austin / (at paper lures / 1530-1600); white, printed and hand-printed - Genitalia Vial / GTA - 3498; white, printed and handprinted - *Ridens* sp. / nr. pacasa / Det. S. R. Steinhauser; red, printed - HOLOTYPE / *Ridens bidens* / Austin. The holotype will be deposited at the Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil.

Type locality. BRAZIL: Rondônia; 62 kilometers south of Ariquemes, Linha C-20, 7 kilometers (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 having two teeth, referring to the two processes of the harpe, and rhymes nicely with *Ridens*.

Diagnosis and discussion. *Ridens bidens* will key to *Ridens pacasa* (Williams 1927) in Evans (1952); that species is well illustrated in its original description (Williams 1927). *Ridens bidens* differs from *R. pacasa* by having no indication of a checkered fringe on the hindwing, a larger macule in M_3-CuA_1 , a smaller macule in CuA_2-2A , an extensive whitish area in CuA_2-2A on the ventral forewing, no indication of a discal cell macule on the ventral hindwing, and less extensive submarginal white on the ventral hindwing. The genitalia of the new species also differ from those of *R. pacasa* with its costa/ampulla margin more broadly rounded, longer harpe, broader dorsal tooth of the harpe, and longer, more robust anterior process of the harpe which has a slightly dorsal orientation (this appears to angle ventrad on *R. pacasa*).

Distribution and phenology. The species is known only from the holotype.

Urbanus "proteus" group

Steinhauser (1981) reviewed the "proteus" group of *Urbanus* Hübner 1807 in which he recognized sixteen species of these butterflies with long, brown tails and green bodies and wing bases. In practice, the species of this group are difficult to determine even with the excellent keys, descriptions, and illustrations given by Steinhauser (1981); comparative material is very useful to identify certain specimens. Nine species of the "proteus" group were encountered in the Cacaulândia area of which three represented undescribed taxa. The phenology of the Rondônia fauna is discussed herein along with the descriptions of the new species. All species have been found associated with army ants, *Eciton burchelli* (Westwood) (Hymenoptera: Formicidae) and are attracted to paper lures (see Austin et al. 1993). At the study site, a pronounced dry season generally extends from May to September; the peak of the wet season occurs in January.

Urbanus proteus (Linnaeus 1758)

Urbanus proteus is common in central Rondônia with records for March, May, June, August, September, November, and December. The species appears most frequent during the early and late wet season and less common during the dry season.

Urbanus pronta Evans 1952

Urbanus pronta is by far the most abundantly encountered "proteus" group species in the Cacaulândia region with records in March, April, and June through December. Peak abundance appears to be in November during the early wet season.

Urbanus esmeraldus (Butler 1877)

Urbanus esmeraldus is uncommon near Cacaulândia with all records in November.

Urbanus esma Evans 1952

Urbanus esma is an uncommon species in central Rondônia with records in June, September, and November (6 of 9 records). This species seems to be more closely associated with primary growth forests than other species in the region.

Urbanus esta Evans 1952

Urbanus esta is a common species in the Cacaúlândia area and was recorded in March to June and August to December with most records in the early wet season.

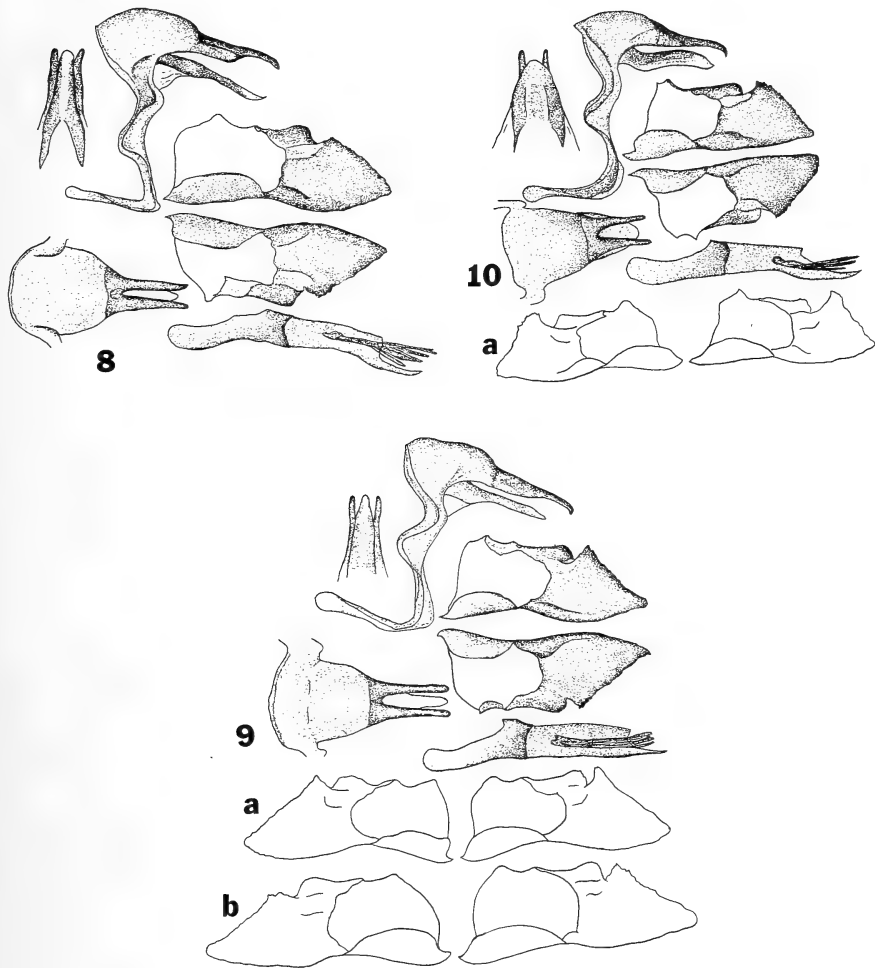
Urbanus velinus (Plötz 1880)

This species, until recently known as the synonymous *Urbanus acawoios* (Williams 1926) (see Robbins et al. 1996), is relatively uncommon near Cacaúlândia with records in May to December. Unlike other "proteus" group species in the region, this was encountered most frequently during the dry season.

***Urbanus villus* Austin, new species**

(Figs. 3, 4, 8, 11)

Description. *Male* (Fig. 3). Forewing length = 22.2 mm (21.2–23.2, N = 5), width = 12.0 mm (11.7–12.4, N = 5), tail length = 12.3 mm (11.2–13.3, N = 3); forewing with costal fold not quite to distal edge of costal macule; apex rounded; hindwing with outer margin slightly convex, curved posteriorly to long tail; forewing with usual hyaline macules present, white, that in CuA_1 – CuA_2 the largest, partially to completely overlapping discal cell macule, macule in lower M_2 – M_3 (3 of 5 individuals), no macule in M_1 – M_2 ; wing bases dull green with slight blue tinge, this not reaching macules on forewing and sharply defined distad on hindwing, 4–5 mm from margin; fringe of forewing gray-brown except whitish in CuA_2 –2A, of hindwing white of moderate width, checkered with dark brown at veins. Venter brown; forewing with macules of dorsum repeated; submargin with distinct blackish brown band distad of macules; ventral hindwing overscaled with whitish; central band entire, including a pair of closely spaced smaller macules in $Sc+R_1$ – Rs , proximal adjoined with macule in discal cell, discal cell macule edged with white distad; postdiscal band entire, extending to vein Rs , subterminal macule prominently edged distad with white. Antennal club yellow-orange on the venter with black center, nudum = 21–23 segments, dorsal head and thorax green scaled, palpi black above, white beneath; dorsal abdomen brown with scattered green scales, gray at segments, white on venter with very broad central band of dark brown. *Male genitalia* (Fig. 8). Tegumen short, stout, somewhat dome-shaped in lateral view, more or less oval in dorsal view; uncus slender, moderately long and divided, arms very slightly divergent in dorsal view; gnathos entire, long and narrow in lateral and ventral views; valvae long, symmetrical, costa/ampulla margin undulate, ampulla with rounded shoulder, harpe relatively short, triangular with dorsal ridge dentate cephalad where at about the same height as or shorter than shoulder of ampulla; aedeagus of typical form for genus; cornuti as typical (for the "proteus" group) cluster of long bristles. *Female* (Fig. 4). Forewing length = 23.9 mm (23.3–24.2, N = 3), width = 13.2 mm (13.2–13.3, N = 3), tail length = 16.4 mm (16.2–16.6, N = 2); very similar to male, wings slightly more rounded. *Female genitalia* (Fig. 11). Papillae anales with nearly straight caudal margin; lamella postvaginalis relatively short and broad, more or less concave with a moderate central indentation on caudal edge; lamella antevaginalis thin, weakly sclerotized centrally, somewhat sinuous cephalad margin; ductus bursae narrow throughout; corpus bursae elongate, narrow, somewhat bent in middle.



FIGS. 8–10. Male genitalia of new species of *Urbanus* from Rondônia, Brazil, including lateral view of tegumen, gnathos, uncus, and associated structures; ventral views of uncus, gnathos, and posterior tegumen; dorsal view of uncus, gnathos and tegumen; interior view of right and left valvae; left lateral view of aedeagus. **8**, *U. villus*, paratype, BRAZIL: Rondônia; Linha C-20, 10 km E B-65, lot 18, 22 Nov. 1992 (GTA #2815). **9**, *U. longicaudus*, paratype, BRAZIL: Rondônia; Linha C-20, 7 km E B-65, Fazenda Rancho Grande, 19 Nov. 1992 (GTA #5097) with valvae of two additional paratypes showing variation: **9a**, BRAZIL: Rondônia; Linha C-20, 7 km E B-65, Fazenda Rancho Grande, 16 Nov. 1992 (GTA #2780); and **9b**, BRAZIL: Rondônia; Linha C-20, 10 km E B-65, lot 18, 18 Nov. 1992 (GTA #2834). **10**, *U. parvus*, holotype (GTA #5123) with valvae of a paratype showing variation: **10a**, BRAZIL: Rondônia; Linha C-20, 7 km E B-65, Fazenda Rancho Grande, 12 June 1993 (GTA #5121).

Type series. Holotype male with the following labels: white, printed - BRASIL: Rondonia / 62 km S Ariquemes / linha C-20, 7 km E / B-65, Fazenda / Rancho Grande / 24 April 1991 / leg. G. T. Austin; white, printed and handprinted - Genitalia Vial / GTA - 1347; yellow, printed - photographed / G. T. Austin & / J. P. Brock / March 1992; red, printed - HOLOTYPE / *Urbanus villus* / Austin. Paratypes: same location as holotype, 9 Nov. 1991 (♀), 15 Nov. 1992 (♂); BRAZIL: Rondônia; 65 km S Ariquemes, Linha C-20, 10 km E B-65, 3 km E Fazenda Rancho Grande, lot 18, 15 Nov. 1992 (♂), 22 Nov. 1992 (2 ♂); BRAZIL: Rondônia, road B-80 between linhas C-10 and C-15, 17 Nov. 1991 (2 ♀). The holotype and a female paratype will be deposited at the Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil.

Type locality. BRAZIL: Rondônia; 62 kilometers south of Ariquemes, Linha C-20, 7 kilometers (by road) east of route B-65, Fazenda Rancho Grande, 180 meters. This is approximately 5 km northeast of Cacauplandia in typical lowland tropical rainforest.

Etymology. The name represents a meaningless combination of parts of the names of similar species (see below): *Urbanus viterboana* (Ehrmann, 1907), *Urbanus belli* (Hayward, 1935), and *Urbanus dubius* Steinhauser, 1981.

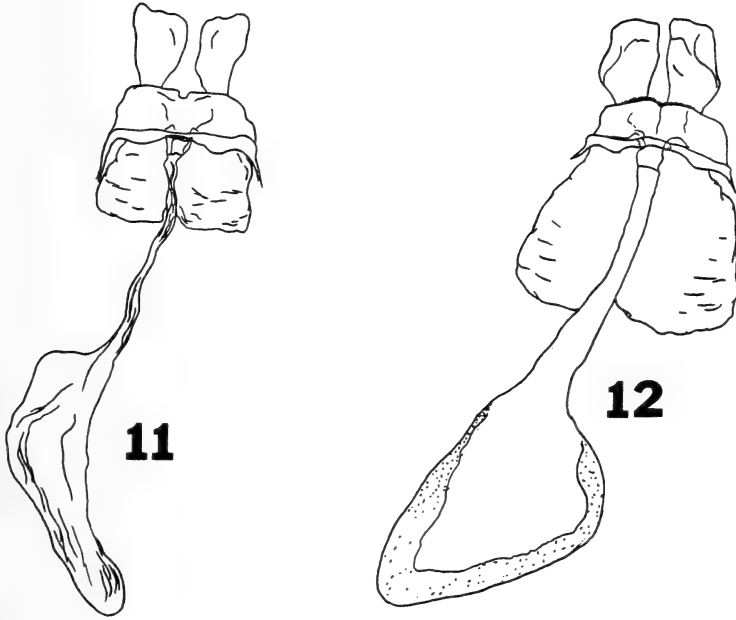
Diagnosis and discussion. This species was an enigma. It was originally identified as *U. belli* with Steinhauser's (1981) superficial key; yet the ventral surface does not resemble his figure and description or other material determined as *U. belli*, especially in the presence of distinct white edging to the subternal macule. The genitalia are different, particularly those of females. Compared to *U. belli*, the male genitalia of *U. villus* have a shorter and broader tegumen and the cephalad end of the harpe is distinctly shorter than the caudal end of the ampulla; the female genitalia have a shallow notch on the lamella postvaginalis and the corpus bursae is not "J"-shaped. The same specimens were closest to *U. viterboana* using the genitalic key of Steinhauser (1981). The wings somewhat resemble *U. dubius*, but the dorsal color of *U. villus* is not blue, the postdiscal band on the ventral hindwing does not extend to vein Sc+R₁, and the genitalia differ. Male genitalia of *U. dubius* have a narrower tegumen and a more elongate harpe than do those of *U. villus* and female genitalia have a more deeply notched lamella postvaginalis and a broader lamella antevaginalis. Essentially, *U. villus* is a green species like *U. belli*, with relatively prominent edging to the ventral hindwing subternal macule like *U. dubius*, and genitalia somewhat like *U. viterboana*. Of these three species, *U. belli* was reported from much of Central and South America south to Bolivia and Argentina (but unrecorded for Brazil), *U. dubius* is known from Colombia and Ecuador, and *U. viterboana* is known from Mexico south to Colombia and Ecuador (Steinhauser 1981).

Distribution and phenology. This species is known only from the types taken in April and November and a female (not seen) recorded from the type locality in August (*vide* A. D. Warren).

Urbanus longicaudus Austin, new species

(Figs. 5, 6, 9, 12)

Description. *Male* (Fig. 5). Forewing length = 22.6 mm (21.7–23.0, N = 10), width = 12.5 mm (11.9–13.1, N = 10), tail length = 14.8 mm (13.2–16.8 mm, N = 10); forewing with costal fold to proximal edge or middle of costal macule; apex broadly rounded; hindwing with outer margin slightly convex, curved posteriorly to long and relatively broad tail; forewing with usual hyaline macules present, pale yellow, that in CuA₁-CuA₂ the largest, partially or entirely overlapping discal cell macule, macule in CuA₂-2A relatively large, slightly overlapping to widely separated from macule in CuA₁-CuA₂, usually (9 of 13 specimens) minute macule in M₂-M₃, but none in M₁-M₂; wing bases blue-green, usually not reaching macules on forewing and sharply defined distad on hindwing, 3–5 mm from margin; fringe of forewing pale brown vaguely checkered with dark brown at veins, of hindwing broadly white with slight yellow cast, conspicuously checkered with dark brown at veins. Venter brown; forewing with macules of dorsum repeated; submargin with distinct blackish brown band distad of macules; fringe pale gray often becoming browner towards apex, entirely checkered with dark brown at veins, most prominent posteriad; ventral hindwing heavily overscaled with pale ochreous, some specimens with violet cast; central



FIGS. 11–12. Female genitalia of new species of *Urbanus* from Rondônia, Brazil, ventral view. **11**, *U. villus*, paratype, BRAZIL: Rondônia; Linha C-20, 7 km E B-65, Fazenda Rancho Grande, 9 Nov. 1991 (GTA #1716). **12**, *U. longicaudus*, paratype, BRAZIL: Rondônia; Linha C-20, 7 km E B-65, Fazenda Rancho Grande, 22 Nov. 1992 (GTA #5099).

band of separate macules, including a pair of closely spaced smaller macules in Sc+R₁-Rs, one (usually that basad) or both adjoined with macule in discal cell, discal cell macule faintly edged with white distad; postdiscal band macules partially or completely separated by paler ground color along veins, this most often involving anterior 1–3 macules of band, entire band vaguely outlined distad with pale ochreous, subternal macule prominently edged distad with narrow line of white. Antennal club yellow-orange beneath with central black, nudum = 20–22 segments; dorsal head and thorax green, palpi mixed pale yellow and gray. *Male genitalia* (Fig. 9). Tegumen somewhat elongate, slightly constricted in middle in dorsal view; uncus long and slender, deeply divided, arms slightly divergent at tips in dorsal view; gnathos entire, long and narrow in lateral and ventral views; valva long, symmetrical, costa/ampulla margin sinuate, ampulla with rounded caudal shoulder slightly serrate, harpe relatively long, triangular with dorsal ridge slightly irregular and dentate cephalad where about the same height as or slightly higher than shoulder of ampulla; aedeagus of typical form for genus, slender; cornuti as typical cluster of long bristles. *Female* (Fig. 6). Forewing length = 23.8 mm (23.3–24.3, N = 3), width = 13.2 mm (12.6–13.7, N = 3), tail length = 16.2 mm (15.8–16.8, N = 3); very similar to male, wings slightly more rounded; antennal nudum = 23–24 segments. *Female genitalia* (Fig. 12). Papillae anales broad with slightly convex caudal margin; lamella postvaginalis relatively short and broad, more or less concave with a slight central indentation on caudal edge; lamella antevaginalis thin, weakly sclerotized centrally, somewhat sinuous on cephalad margin; ductus bursae expanded slightly cephalad; corpus bursae large, more or less triangular.

Type series. Holotype male with the following labels: white, printed - BRASIL: Rondônia / 65 km S Ariquemes / linea C-20, 10 km E / B-65, 3 km E / Fazenda Rancho /

Grande, lot 18 / 15 August 1992 / leg. G. T. Austin / (at paper lures / 1030–1100); white, printed and handprinted - Genitalia Vial / GTA - 5113; red, printed - HOLOTYPE / *Urbanus longicaudus* / Austin. Paratypes (leg. G. T. Austin): same location as holotype, 18 Nov. 1992, associated with *Eciton burchelli*, 1400–1430 (♂), 22 Nov. 1992, leg. G. T. Austin, at paper lures, 1230–1300 (♀), BRAZIL: Rondônia; 62 km S Ariquemes, Linha C-20, 7 km E B-65, Fazenda Rancho Grande, 13 June 1993, assoc. with *E. burchelli*, 1500–1530 (♂), 15 July 1991, leg. G. Bongiorno (♀), 15 Sept. 1992 (♂), 6 Nov. 1991 (♂), 9 Nov. 1992, assoc. with *E. burchelli*, 1000–1030 (♂), 12 Nov. 1992, assoc. with *E. burchelli*, 0900–0930 (♂), 14 Nov. 1992, assoc. with *E. burchelli*, 1330–1400 (♂), 16 Nov. 1992, assoc. with *E. burchelli*, 1300–1330 (♂), 19 Nov. 1992, at paper lures, 1330–1400 (♂), 20 Nov. 1991, assoc. with *E. burchelli* (♂), 20 Nov. 1992, assoc. with *E. burchelli*, 0800–0830 (♂), 21 Nov. 1992, at paper lures, 1100–1130, Linha C-0 off B-65, 15 km S Cacaulândia, 11 Nov. 1990 (♀). The holotype and a female paratype will be deposited at the Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil.

Type locality. BRAZIL: Rondônia; 65 kilometers south of Ariquemes, Linha C-20, 10 kilometers (by road) east of route B-65, Fazenda Rancho Grande, lot 18, 180 meters. This is approximately 7 km northeast of Cacaulândia in typical lowland tropical rainforest.

Etymology. The name refers to the long tail of this species compared with that of its most closely similar species, *U. pronta* (see below).

Diagnosis and discussion. This species is very similar to and was initially determined as *U. pronta*. Fortunately, Steinhauser (1981) illustrated the holotype of *U. pronta* and its genitalia facilitating direct comparisons. The latter differs from *U. longicaudus* by its longer costal fold (to or beyond the distal edge of the costal macule), more acute forewing apex, straighter hindwing termen which is less curved posteriorly before the shorter (10.4 mm [8.7–12.3, N = 10; sample from Rondônia]) and straighter tail. The macule in CuA_2-2A is usually narrower on *U. pronta*, the macule in M_2-M_3 is usually absent (present on only 15 of 40 individuals), the green basal scales usually reach the macules on the forewing and extend to 2–3 mm from the margin on the hindwing, the forewing fringe is dark brown except in CuA_2-2A where it is white and is not obviously checkered, and the hindwing fringe is narrower, white, and less distinctly checkered. On the venter, the forewing dark band is less contrasting on *U. pronta* than on *U. longicaudus*, the forewing fringe is very vaguely or not checkered, the hindwing distal edging to the discal cell macule is more prominent, the postdiscal band macules are more broadly and conspicuously separated along the veins, and the distal white edging to the subterminal macule is broad. The forewing of *U. pronta* in Rondônia is virtually of the same length (22.6 mm [21.9–23.5, N = 10]) as that of *U. longicaudus* but averages somewhat narrower (12.1 mm [11.8–13.0, N = 10]).

The male genitalia of *U. longicaudus* resemble those of *U. pronta*, but the tegumen is longer (shorter and stouter on *U. pronta*); the uncus and gnathos are conspicuously longer and the latter is also narrower; the margin of the ampulla is undulate, much more so than on *U. pronta*; and the dorsal projection of the harpe does not or barely exceeds the height of the shoulder of the ampulla. The female genitalia are also similar to those of *U. pronta*, but the papillae anales of *U. longicaudus* are more massive, the lamellae are shorter and broader, and the corpus bursae appears slightly smaller and more triangular.

Distribution and phenology. The species is known only from the types recorded in June through September and November.

Urbanus parvus Austin, new species

(Figs. 2, 10)

Description. *Male* (Fig. 2). Forewing length = 19.8 mm (19.0–21.1, N = 7), width = 10.7 mm (10.3–11.0, N = 7), tail length = 10.8 mm (10.0–11.3, N = 7); forewing with costal fold not quite to distal edge of costal macule; apex narrowly rounded; hindwing with outer margin relatively straight, curved posteriorly to short and relatively broad tail; forewing with usual hyaline macules present, white, that in CuA_1-CuA_2 the largest, partially overlapping discal cell macule, with or without minute macule in M_2-M_3 , none in M_1-M_2 ; wing bases dull blue-green, not reaching macules on forewing and sharply defined

distad on hindwing, 3 mm from margin; fringe of forewing gray-brown posteriorly where vaguely checkered with dark brown at veins, dark brown anteriorly, of hindwing white of moderate width, checkered with dark brown at veins. Ventral forewing similar to that of *U. longicaudus*, but submarginal dark band less distinct, fringes vaguely checkered to apex; ventral hindwing overscaled with pale ochreous; central band of separate macules, that in Sc+R₁-Rs as a single fused, elongate macule, discal cell macule faintly (but more prominent than on *U. longicaudus*) edged with white distad; postdiscal band macules separated by paler ground color along veins similar to *U. pronta*, subtornal macule prominently edged distad with white. Antennal club pale yellow beneath with black center, nudum = 23, 24 segments; head and body green above, palpi mixed pale yellow and dark gray. *Male genitalia* (Fig. 10). Tegumen short, slender, somewhat dome-shaped in lateral view, more or less trapezoidal in dorsal view; uncus slender, moderately long, deeply divided, arms slightly divergent in dorsal view; gnathos entire, long, and moderately broad in lateral and ventral views; valva rather short, symmetrical, costa/ampulla margin somewhat concave, ampulla with long shoulder, sloping nearly vertically at caudal end, harpe short, triangular with dorsal ridge prominently dentate cephalad where at about same height as shoulder of ampulla; aedeagus of typical form for genus; cornuti as typical cluster of long bristles. *Female*. Unknown.

Type series. Holotype male with the following labels: white, printed - BRASIL: Rondonia / 62 km S Ariquemes / linha C-20, 7 km E / B-65, Fazenda / Rancho Grande / 14 November 1991 / leg. G. T. Austin; white, printed and handprinted - Genitalia Vial / GTA - 5123; red, printed - HOLOTYPE / *Urbanus parvus* / Austin. Paratypes: same location as holotype, leg. G. T. Austin unless noted, 12 June 1993, assoc. with *Eciton burchelli*, 1330-1400 (♂), 12 Nov. 1995, leg. D. & J. Lindsley (♂), 16 Nov. 1994, at paper lures, 1530-1600 (♂), 18 Nov. 1994, at paper lures, 0930-1000 (♂), 18 Nov. 1994, at paper lures, 1100-1130 (♂), 18 Nov. 1994, at paper lures, 1430-1500 (♂). The holotype will be deposited at the Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil.

Type locality. BRAZIL: Rondônia; 62 kilometers south of Ariquemes, Linha C-20, 7 kilometers (by road) east of route B-65, Fazenda Rancho Grande, 180 meters. This is approximately 5 km northeast of Cacaupônia in typical lowland tropical rainforest.

Etymology. The name refers to the relatively small size of this taxon.

Diagnosis and discussion. Superficially, *U. parvus* is distinctive in its small size and continuous bar anterior to the ventral hindwing central band. The male genitalia of *U. parvus*, while resembling those of *U. pronta*, differ in their more slender tegumen which appears trapezoidal in dorsal view (more bulbous on *U. pronta*); and the valvae are more compact with a more highly angular costa, a long and sloping ampulla, and a rather short harpe. The genitalia also resemble those of *U. longicaudus* but differ much as they do from *U. pronta*.

Distribution and phenology. This species is known only from the types taken in June and November.

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A NEW GENUS OF TORTRICID MOTHS FROM CHILE AND
ARGENTINA RELATED TO *VARIFULA* RAZOWSKI
(LEPIDOPTERA: TORTRICIDAE)

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ABSTRACT. *Argentulia*, new genus (Tortricinae: Euliini), is described to accommodate *A. montana* (Bartlett-Calvert 1893), new combination, type species, and *A. gentilii*, new species, from Chile and Argentina. A neotype is designated for *A. montana*. In general facies, members of the new genus are unlike any other species in the tribe Euliini. However, features of the male and female genitalia suggest a close relationship to *Varifula* Razowski from Chile.

Additional key words: phylogeny, neotype, systematics, Euliini, *Proeulia*.

"*Antithesia*" *montana* Bartlett-Calvert, 1893, had a history of taxonomic uncertainty until its mystery was solved by Clarke (1978). The type apparently was lost sometime after the description, leaving a generalized illustration (Bartlett-Calvert 1893:831) as the only permanent record of the moth. In 1922 Meyrick transferred the species to *Hypercallia* (Oecophoridae), apparently based on a misinterpretation of the illustration in which he mistook the antennae for long labial palpi. Based on a single female specimen collected in Argentina in 1974, Clarke (1978) was able to associate the moth convincingly with the illustration and original description. Clarke (1978) provisionally transferred *A. montana* to *Proeulia* Obraztsov, whose included species have similar female genitalia and wing venation.

I recently discovered a small series of *P. montana*, along with an undescribed congener, in the recently acquired Gentili Collection at the National Museum of Natural History, Smithsonian Institution. The availability of both sexes of *P. montana*, along with a closely related second species, allows for a more meaningful generic assignment. The purposes of this paper are to describe *Argentulia*, new genus, and *A. gentilii*, new species, designate a neotype for *A. montana*, and comment on the putative phylogenetic relationship of *Argentulia* to *Varifula* Razowski.

All specimens examined are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Dissection methodology followed that summarized in Brown and Powell (1991). Forewing measurements were made with an ocular micrometer mounted in a dissecting microscope. Terminology for wing venation and genitalic structures follows Horak (1984). Abbreviations are as follows: FW = forewing; HW = hindwing; DC = discal cell.

Argentulia Brown, new genus

Antithesia (in part); Bartlett-Calvert 1893:831.

Hypercallia (in part); Meyrick 1922:163.

Proeulia (in part); Clarke 1978:251; Powell, Razowski & Brown 1995:145; Razowski 1995:278.

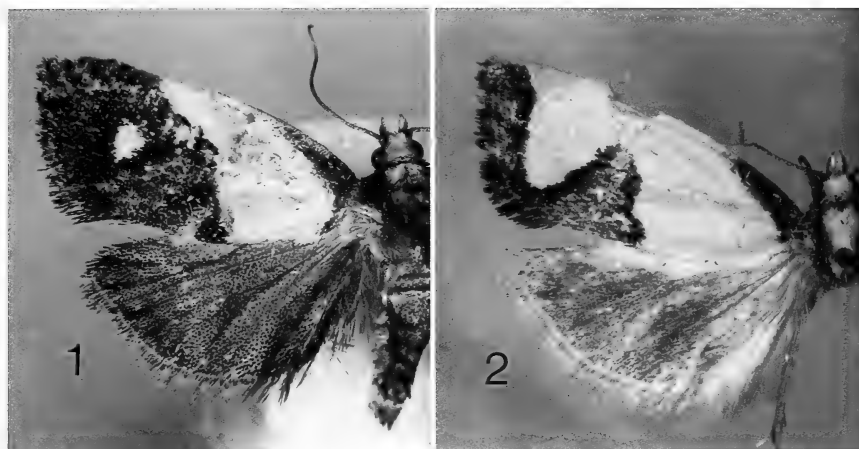
Type species: *Antithesia montana* Bartlett-Calvert, 1893.

Description. *Head:* Antennal cilia in male approximately 0.5–0.6 times flagellar segment diameter; less than 0.1 times flagellar segment diameter in female. Labial palpus 1.0–1.2 times horizontal diameter of eye; segment II weakly upturned, slightly expanded distally by scaling; segment III 0.2–0.3 as long as II, smooth-scaled, exposed. Maxillary palpus rudimentary. Proboscis well developed. Frons with overhanging crown of scales. Ocelli present. Chaetosema present. *Thorax:* Smooth-scaled. Legs unmodified, male foreleg hairpencil absent. Forewing: Length 2.3–2.4 times width; length of DC about 0.60 times FW length; width of DC about 0.20 its length; CuA₂ originates about 0.60 distance along length of DC; all veins separate beyond DC; CuP present; chorda present; M-stem absent. Hindwing: Sc+R and Rs separate; Rs and M₁ connate or extremely short-stalked; M₃ and CuA₁ separate; CuP present; M-stem absent. *Abdomen:* Dorsal pits and specialized scaling absent. *Male genitalia:* Uncus short, stout, with blunt apex. Socius moderately elongate, attenuate distally with curved apical portion; not fused to gnathos. Gnathos simple, non-dentate, arms narrow, joined distally, with fine, spinelike tip. Subscaphium and hami absent. Transtilla a simple, weakly sclerotized band. Valva simple, broadest at base, rounded apically; sacculus weak, confined to basal one-half. Pulvinus absent. Vinculum weak. Juxta a small, sclerotized, undulate plate. Aedeagus simple, somewhat pistol-shaped, attenuate and sclerotized apically; phallobase simple, rounded; vesica with bundle of 12–15 slender cornuti (possibly deciduous). *Female genitalia:* Papillae anales simple. Apophyses anteriores and posteriores stout. Sterigma a simple, weakly sclerotized band; ostium very broad, strongly sclerotized interiorly. Ductus bursae short, undifferentiated from corpus, sclerotized, wrinkly. Corpus bursae oblong, with weak sclerotization caudally; signum lacking. Ductus seminalis from caudal one-third of corpus. Sexual dimorphism (based on *A. montana*) is restricted to the difference in the length of the antennal cilia (longer in male) and slight differences in forewing color.

Diagnosis. Superficially, adults of *Argentulia* are unlike any other genus in the Euliini. Although similar in facies to some Cochylini, the presence of a gnathos excludes the new genus from that tribe. Features of the male and female genitalia of *Argentulia* suggest a close relationship to *Varifula* from Chile (Razowski 1995). The two genera share a remarkably similar aedeagus in which the distal portion is attenuate and highly sclerotized, with a dense patch of 12–15 short, spinelike cornuti (possibly deciduous) in the vesica (Figs. 3, 4). This unique configuration of the aedeagus is considered a synapomorphy for the two genera. The male genitalia of *Argentulia* are distinguished from *Varifula* by a short, stout, blunt uncus, which is long and slender in *Varifula*; a slender thornlike process at the apex of the united gnathos arms, absent in *Varifula*; the attenuate, curved distal portion of the socius, unmodified in *Varifula*; and a markedly reduced transtilla. A broad, spiny transtilla (Razowski 1995:282, fig. 11) is considered an autapomorphy for *Varifula*. Autapomorphies for *Argentulia* include the blunt uncus, the curved distal portion of the socius, and the highly reduced transtilla. Both genera lack the strongly upcurved costa of the valva, the elongate aedeagus with few (1–5) extremely large cornuti, and the male foreleg hairpencil (Brown 1990), which are characteristic of nearly all *Proeulia*. The female genitalia of the two genera, likewise, have many similarities, most of which are symplesiomorphies; both lack the sclerotized, dislike signum of *Proeulia*.

Distribution and biology. *Argentulia* is known from Argentina and Chile. Nothing is known of the early stages, although larvae of the closely related *Proeulia* are mostly polyphagous with many important agricultural pests. Adults of *Argentulia* have been recorded from November through February.

Etymology. The new genus is a combined form of "Argentina" and "Eulia" Hübner, the type genus of the tribe Euliini, to which the new genus belongs.



FIGS. 1-2. Adults of *Argentulia*. 1, Female of *A. montana*. 2, Male of *A. gentilii*.

Argentulia montana (Bartlett-Calvert), **new combination**

Figs. 1, 4, 5

Antithesia montana Bartlett-Calvert 1893:831.

Hypercallia montana; Meyrick 1922:163

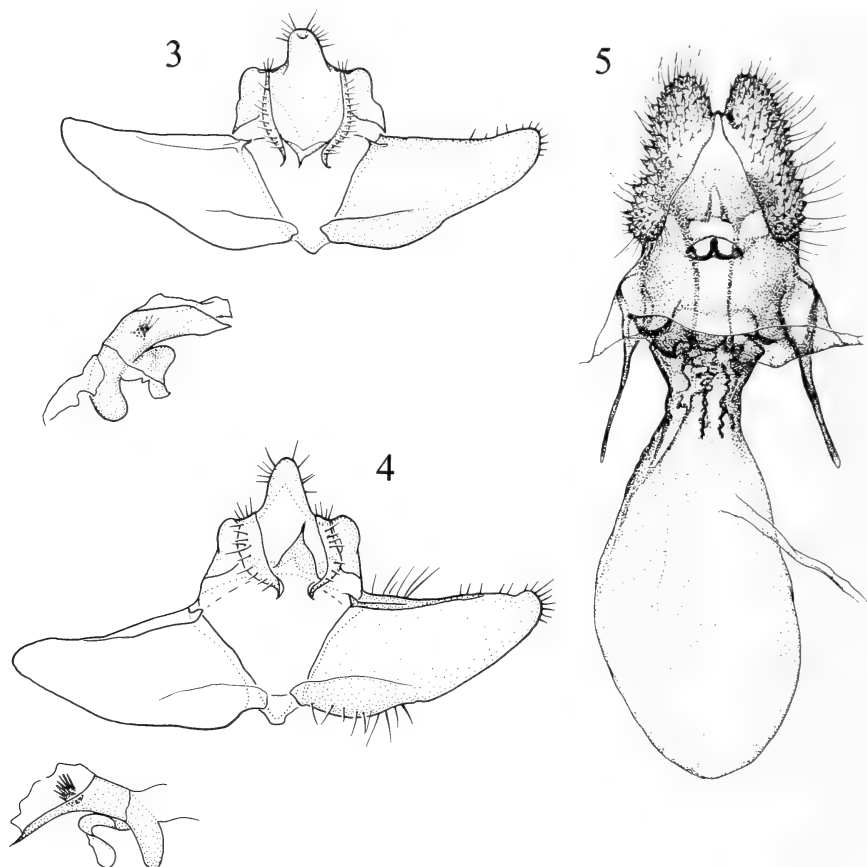
Proeulia montana; Clarke 1978:251; Powell, Razowski & Brown 1995:145; Razowski 1995:278.

Redescription. *Male.* FW length 6.0–8.0 mm (mean = 6.9 mm; n = 4). *Head:* Frons with sparse scaling below mid-eye, brown; roughened above, orange. Labial palpus pale yellowish mesally, light brown laterally. Antenna brown. *Thorax:* Orange; tegula dark brown. *Forewing* (Fig. 1): Distinctly bicolored, yellow-orange in basal one-half, dark brown in distal one-half; brown along base of costal margin; distinct yellow-orange dot near end of DC. *Hindwing:* Uniform brown. *Genitalia:* As in Fig. 4 (drawn from USNM slides 88413 and 88414, Argentina; n = 2). Essentially as described for the genus. *Female.* FW length 7.5–8.5 mm (mean = 7.8 mm; n = 3). FW pattern as in male, but with basal one-half more yellow; distal one-half more orange-brown; yellow-orange dot near end of DC smaller and rounder; and antenna without conspicuous cilia. *Genitalia:* As in Fig. 5 (drawn from USNM slide 24331; Argentina; n = 2). As described for the genus.

Type. The holotype from Lolco, Araucania, Chile, apparently is lost. It is not present in either The Natural History Museum, London, England, or Museo Nacional de Historia Natural, Santiago, Chile, the most likely depositories for types of species described by Bartlett-Calvert (Clarke 1978). The species was described from a single individual, the sex of which was not stated in the original description and cannot be determined from the illustration that accompanied the description. A **NEOTYPE** is designated as follows: male, Chapelco-Techos, 1400 m, Neuquén, Argentina, 24 Jan 1984, Y. P. Gentili (USNM).

Additional specimens examined. ARGENTINA: Río Nonthue, Est. For. Pucara, ♀, 28/31 Jan 1974 (O. S. Flint, USNM); Menendez, L. Verde, Chubut, 560 m, 2 ♀, 4 Nov 1983 (Y. P. Gentili, USNM); San Martín, Andes, Neuquén, 640 m, ♂, 15 Nov 1980 (M. Gentili), ♂, 10 Jan 1982, ♂, 15 Dec 1983 (Y. P. Gentili, USNM).

Diagnosis. *Argentulia montana* is easily distinguished from *A. gentilii* by the forewing pattern (Figs. 1, 2). Differences in the genitalia are considerably more subtle; the transtilla is more narrow with a slender line of sclerotization in *A. montana*.



FIGS. 3-5. Genitalia of *Argentulia*. 3, Male genitalia of *A. gentilii*. 4, Male genitalia of *A. montana*. 5, Female genitalia of *A. montana* (from Clarke 1978).

Argentulia gentilii Brown, new species

Figs. 2, 3

Description. *Male.* FW length 6.0-7.0 mm (=6.5 mm; n = 3). *Head:* Frons with sparse, smooth scaling below mid-eye, brown; roughened above, brown. Labial palpus pale yellow mesally, brown laterally. Antenna brown. *Thorax:* Yellow, with dark brown tegula. *Forewing* (Fig. 2): Yellow, with large, rounded, triangular brown patch from near midpoint of dorsum, extending toward termen, joining a uniform, brown terminal band; brown streak along base of costal margin. *Hindwing:* Uniform gray-brown. *Genitalia:* As in Fig. 3 (drawn from USNM slide 88412; n = 2). Essentially as described for genus, except transtilla slightly broader than in *A. montana*. *Female.* Unknown.

Types. Holotype: Male: Paso Cordoba, 1300 m, Neuquén, Argentina, 20 Nov 1980, M. Gentili, USNM. Paratypes, 2 ♂ as follows: CHILE: Bío-Bío Province: Lag. El Barco, Gualali, Santa Barbara, 1200 m, 25/28 Feb 1981 (L. Pena, USNM).

Diagnosis. As indicated above and illustrated in Figs. 1 and 2, *A. gentilii* is distinguished easily from *A. montana* by forewing pattern. Owing to the similarity of the male

genitalia, it is possible that the two represent forms of the same species; however, such dimorphism within the same sex is unknown for any other Euliini. Although subtle, differences in the transtilla described above are consistent in the material examined and support the separation of the two as species. Some phenotypically distinct species of *Varifula* and *Proeulia* also exhibit only subtle differences in genitalic structures.

Etymology. This species is named in honor of Mario Gentili, noted Argentinian lepidopterist and collector of the holotype.

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PARTIAL GENETIC ISOLATION BETWEEN *PHYCIODES* *THAROS* AND *P. COCYTA* (NYMPHALIDAE)

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ABSTRACT. Systematists have been interested in the *Phyciodes tharos* group since Oliver discovered partial hybrid breakdown in crosses between populations of nominal *P. tharos*. The traits so far identified as diagnostic in the group are difficult to characterize genetically, and there are considerable limitations in using them to ascertain the status of genetic isolation. We searched for genetic markers in *P. tharos* and *P. cocyta* which would make these deductions easier. We found notable frequency differences between the taxa in malate dehydrogenase (MDH) and glutamic-oxaloacetic transaminase (GOT). Though significant statistically, these differences can be maintained by partial genetic isolation and an introgression rate of about 1 genome per generation. A review of the published research on the diagnostic traits is consistent with this interpretation, and we suggest that these taxa be considered as subspecies unless further research turns up evidence of genetic isolation. Previous researchers have invoked strong selection to explain the high similarity among populations in allozyme frequencies of *P. tharos*. We find that such similarity can be maintained by a rate of only 7 individuals exchanged among populations each generation without invoking selection, although very weak selection may also be involved. We found what may be a gene duplication in the phosphoglucumutase (PGM) locus that, if verified, may be useful in phylogenetic studies of *Phyciodes*.

Additional key words: gene flow, genetic population structure, phosphoglucumutase, *Phyciodes pascoensis*, species-level systematics.

Over the last 25 years, the *Phyciodes tharos* species group in eastern North America has attracted the attention of biologists interested in systematics and evolution, and new species-level taxonomic divisions have been proposed. We first review the current status of the taxonomy and its biological basis in light of recent theoretical advances, then present the outcome of a genetic analysis that calls into question the existence of sibling species within the group. We then propose an alternative explanation for the maintenance, in a single polytypic *tharos* species, of apparently adaptive differences in the life-history traits that were originally used to delimit sibling species within the *tharos*-group. Though the available data are best interpreted by a single-species model, it is beyond the scope of this paper to solve the taxonomic problem; for that, a closer look at the contact areas will be required. Throughout, our theme is to draw attention to what we believe is the crux of an old and general problem in species-level systematics, that of inferring underlying biological processes from patterns of differentiation in traits within and among populations. Though the presence of differentiation is widely used to infer reproductive isolation, there are other biological processes that can

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maintain geographic differences in traits we use as diagnostic, even in the face of strong gene exchange. We hope to engender a greater awareness among systematists of new methods available, and problems with established methods, for delimiting reproductively isolated species.

CURRENT TAXONOMY

Nomenclature. Oliver (1972, 1979, 1980) discovered patterns of partial hybrid breakdown in crosses between populations of the widespread butterfly *Phyciodes tharos*, and he initially identified these as Type A and Type B population groups. These groups were subsequently reported to be associated with univoltine (Type B) and multivoltine (Type A) life cycles, adult body size differences, coloration differences in late-instar larvae, and subtle differences in adult wing pattern (Oliver 1980). The taxonomy has since been in a state of confusion and flux. Oliver (1980, 1983) considered the northeastern Type B populations to intergrade continuously with the Rocky Mountain populations, to which the name *P. pascoensis* Wright applies. He therefore classified them into two species, *Phyciodes tharos* Drury (=Type A) and *P. pascoensis* Wright (=Type B) on the basis of these differences and their apparent sympatry in parts of Pennsylvania and West Virginia, as he believed that these differences were evidence of reproductive isolation. Meanwhile, Miller and Brown (1981) suggested in a footnote that the older name *P. selenis* (Kirby 1837) was available for the eastern Canadian populations, and this nomenclature was followed by Opler (1992). Scott (1986a) advocated the name *P. morpheus* (Fabr. 1775) as the oldest and, because its type was lost, he restricted its type locality to Nova Scotia, ensuring its applicability to the univoltine populations. This change was problematic. First, Miller and Brown (1981) considered that type to have probably come from the vicinity of New York City, which is within the range of multivoltine *P. tharos* (Shapiro 1974). Second, Scott (1994) has since reported that Fabricius's name was a junior homonym of a hesperiid described by Pallas in 1771, making *morpheus* unavailable. Scott (1994) also found that the original illustration of *P. cocyta* (Cramer 1777), ostensibly from Surinam, agrees rather well with *tharos*-group individuals from northeastern North America, suggesting *cocyta* as the oldest available name for the northern populations. Scott (1994) has now identified the types or has designated neotypes for all the available names. The neotypes include *P. tharos* (Drury) and *P. euclea* (Bergstraesser 1780) collected near New York City, *P. selenis* (Kirby 1837) from Cumberland House, Saskatchewan, and *P. cocyta* (Cramer 1777) from Cape Breton, Nova Scotia. As Scott's efforts seem the most rigorous and complete, we follow his nomenclature here.

Diagnosis. Though the names now appear sorted out, the diagnos-

tic traits and their underlying biology remain controversial, and there is no trait or trait combination generally agreed to be diagnostic. Oliver (1980, 1983) emphasized the number of annual generations as the primary diagnostic trait, with larval coloration and subtle dorsal wing pattern traits also showing consistent differences. Opler and Krizek (1984) added that *P. tharos* males usually have black antennal clubs whereas those of *P. cocyta* males, and both species' females, are usually orange. Scott (1986a, 1994) indicated that orange antennae are not unusual in male *P. tharos* in the northern and western parts of its range, making this character uninformative there, but he added that minor differences were detectable in the shape of a pair of spines on the male genitalia. For distinguishing *tharos* from *cocyta*, Scott (1994) placed greatest emphasis on the male dorsal hindwing pattern, namely the extent to which the median and postmedian orange bands are fused, although Oliver (1976) showed that this trait was influenced by photoperiod. Scott (1994) considers *cocyta* to have both single- and double-brooded populations. All authors agree that considerable variability and overlap exists in the morphological traits of these taxa (Oliver 1980, Opler & Krizek 1984, Scott 1986a, 1994, Opler 1992), and this ambiguity is compounded by the fact that the wing pattern of *P. tharos* is seasonally polyphenic (Oliver 1976). All agree that putative hybrids exist which defy classification into the two types. Nevertheless, range maps for these taxa have been estimated, mainly from pinned specimens, for use in general butterfly guides (Opler & Krizek 1984, Scott 1986a, Opler 1992).

ASSAYING FOR GENETIC ISOLATION

How useful are the diagnostic traits? It has always been difficult to deduce genetic isolation from a suite of morphological and life-history traits, because no body of theory is yet available that allows us to estimate the rate of gene exchange, a biological process, from geographic variation in such quantitative traits, a statistical pattern. This is partly because quantitative traits are usually influenced by environmental as well as genetic factors, and the relative contributions of each are usually unknown. Patterns of variation may well be due to evolutionarily inconsequential environmental variation, spatial as well as seasonal and annual, particularly where phenotypic plasticity is involved as in *Phyciodes*.

Over the last 20 years, our ability to deduce genetic isolation has been greatly informed by theoretical advances in population genetics. These advances came after it was recognized that it is typological, and misleading, to treat hybridizing systems as comprised of interactions among "pure" forms and "hybrids" (Barton & Hewitt 1985). Rather, such systems are more appropriately reduced to the genetic level and investigated on a gene-by-gene and trait-by-trait basis. This approach explicitly accounts for

all degrees of intermediate genotype, yet it still permits taxonomic entities to be reconstructed, tested, and studied empirically when strong and consistent correlations exist among traits (Barton & Hewitt 1985, Barton & Gale 1993). We adopt this perspective throughout.

Three corollaries of this reductionist viewpoint bear further comment. First, the approach permits us to develop quantitative measures of the degree of genetic isolation between taxa (Porter 1990) through models that relate gene flow (or, when taxa are considered, introgression) to degrees of genetic differentiation. This is a significant advance over the qualitative methods used in classical systematics, but it raises a question: How much introgression is enough to qualify two taxa as conspecific? There are three answers plausible along a continuum, one absolute, one practical from a theoretical perspective, and one practical from an operational perspective. One could maintain an absolute criterion that any introgression at all is enough to invalidate a hypothesized species boundary. Porter et al. (1997b) suggest that a low theoretical limit of 10^{-6} individuals per generation might be appropriate, because this is roughly the inverse of the mutation rate, and alleles identical in state might be expected to arise independently in the opposite taxon at about the same rate. However, this is far below the detectable level as measured by current methods, which permit the estimation of introgression levels above only about 10^{-1} genomes per generation (Porter 1990), and this provides a current operational threshold.

As a second corollary, this viewpoint helps to highlight a subtle distinction between the terms genetic isolation and reproductive isolation. Genetic isolation refers simply to the lack of gene exchange and may be directly measured from patterns of genetic differentiation. Reproductive isolation is sometimes used synonymously, but it often contains allusions to reproductive behavior or physiology (cf. Paterson 1993, Lambert & Spencer 1995), and reduced viability or fecundity of hybrids. These mechanisms are a subset of the processes responsible for genetic isolation, but they cannot be quantified from patterns of genetic differentiation. We therefore use genetic isolation as a more precise term for what we believe is appropriate to measure when testing taxonomic hypotheses. Finally, further emphasizing our view that pattern and process should be kept separate in evolutionary studies, we use the terms contact area and hybrid zone in a purely descriptive sense. They are simply places where ranges abut and, in the latter, where hybridization is known to occur, and we include no allusions to the evolutionary processes that produce these geographic patterns. Rather, these processes must be inferred by evolutionary models, preferably made explicit, that relate processes to the genetic and phenotypic patterns we describe.

Abstracted into the mathematics of this gene-by-gene approach is an

important lesson for species-level systematists. It has long been known that natural selection operates to produce local adaptations in ecologically relevant traits, including life-history traits, coloration, etc. These traits are quite likely to be taken as diagnostic at the species- and subspecies-level by systematists, yet such differences are likely to comprise only a small proportion of the genome. Theory shows that it is a mistake to deduce that these differences necessarily indicate genetic isolation in the remainder of the genome (Barton & Bengtsson 1986). The reasoning is subtle, involving quantitative interactions among gene flow, natural selection, and linkage among neutral and selected genes on the same chromosomes. All genes experience the same rate of gene flow because when individuals move among populations, they carry all their genes with them. Complete genetic isolation can result only when neutral genes, themselves unaffected by environmental variation, experience selection barriers indirectly through their correlations with traits under direct selection. These correlations, called linkage disequilibria (though they may arise for reasons other than physical proximity on the chromosome), are strongest for neutral loci closely linked to genes influencing traits under selection, but they are usually negligible for genes on different chromosomes or at opposite ends of the same chromosome. Correlations among all differentiated traits exist in F_1 hybrids from different parental "types," but with further generations of interbreeding, these correlations decay at rates inversely proportional to their linkage to genes influencing selected traits (Wright 1969), and unlinked traits become uncorrelated after about six generations of hybridization (Robbins 1918). It follows that, in order for complete genetic isolation to occur between differentiated, hybridizing populations, either selection must be so strong that the hybrids are completely infertile (or inviable), or a large number of genes under selection must be distributed throughout the genome such that all neutral loci are closely linked to them (Barton and Bengtsson 1986). If these rather stringent criteria are not met, then the initial correlations break down and neutral and adaptive genes will spread via the hybrids to the other taxon. Such genes contribute to the evolutionary history of both taxa, even if strong differentiating selection continues to maintain differences in the diagnostic traits. Such "diagnostic" traits are not markers for genome-wide differentiation, and at best, can be used only for subspecies recognition.

Viewing the current status of the *Phyciodes tharos* and *P. cocyta* problem in this context, several ambiguities arise. The deduction of genetic isolation from the currently available biological information has tacitly entailed the assumptions that: (i) environmental variation has not appreciably influenced the few diagnostic wing pattern traits that have been identified; (ii) the quantitative traits of body size and voltinism, and per-

haps adult wing pattern, larval coloration, male genital morphology, and suspected pheromone differences (Scott 1986b), are influenced by strong selection; and (iii) the genes controlling variation in these traits and any others producing partial hybrid breakdown comprise a large proportion of the genome. The third assumption was partially refuted by Oliver (1979), who concluded that the partial hybrid breakdown was likely to be due to the action of only a small number of loci. Alternatively, it has been suggested that genetic isolation might be enforced by the differing phenologies of these taxa (Scott 1986a), such that they rarely have the opportunity to interbreed. This hypothesis was not supported by the data in Oliver (1980), who showed that when environmental conditions are held constant, as they would be where the two taxa occur sympatrically and have the opportunity to interbreed, the eclosion patterns following larval diapause of the two taxa are quite similar. The current taxonomy clearly stands on a poor foundation and requires, in addition to better data, greater attention to the logic and methods we use as species-level systematists to infer underlying processes from superficial patterns.

In this article, we report the results of an electrophoretic survey of metabolic enzyme variation undertaken to search for single-locus genetic markers which may be useful in the study of genetic isolation in the *Phyciodes tharos* group. The advantage of using such markers is that a considerable body of theory is available with which to estimate the rates of genetic exchange among populations (Slatkin 1987). The estimation of gene exchange rates between *P. tharos* and *P. cocyta* permits an independent empirical test of the hypothesis that these taxa are genetically isolated (Porter 1990, Porter & Geiger 1995). Throughout the article, we adopt the literary convenience and current taxonomic practice of referring to these taxa as *P. tharos* and *P. cocyta*, without implying any conclusion about their actual biological status as species or subspecies. We will address the current status of their taxonomy and its supporting evidence below, after consideration of the available genetic data.

METHODS

Genetic data. Butterflies were netted haphazardly from the locations shown in Fig. 1 (detailed in Table 1), transported alive to the laboratory on ice in individual glassine envelopes within reclosable plastic bags, and stored until analysis at -80°C . Populations were classified to species following the range maps in Opler (1992), Opler and Krizek (1984), and Scott (1986a). We used standard electrophoretic protocols from our laboratory (described in Porter and Mattoon 1989) and stained the following enzyme loci: aldolase (ALDO), adenylate kinase (AK), fumarase (FUM), glutamic-oxaloacetic transaminase (2 loci: GOT-1, GOT-

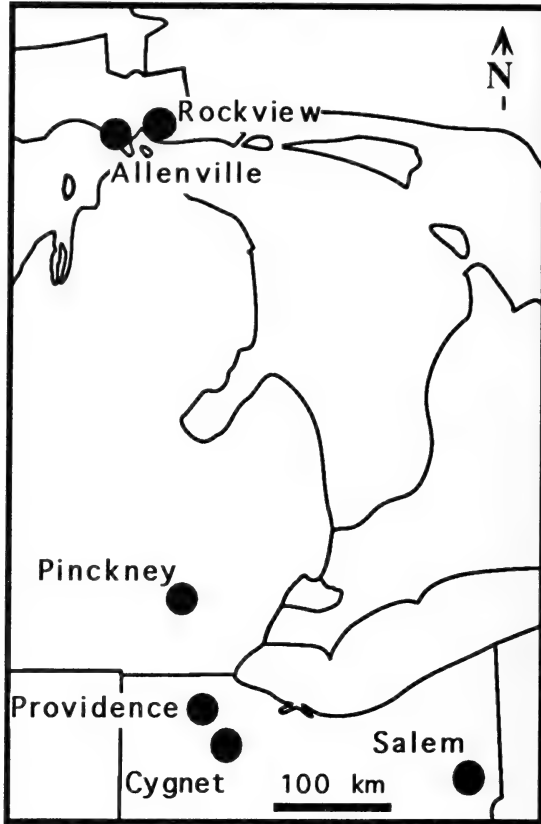


FIG. 1. Sampling localities used in this study. Opler and Krizek (1984) estimates that *tharos* extends to the top of lower Michigan on the eastern half of the state, whereas *cocyta* (nee *selenis*) extends throughout northern Michigan and to the Michigan-Indiana line in western lower Michigan; the two taxa would overlap little in Michigan. Following Opler, the Allenville and Rockview sites are *P. cocyta*, and the remainder are *P. tharos*. However, Scott (1986a) estimates *tharos* to extend north across the middle of lower Michigan and adjacent Ontario, and *cocyta* to extend south throughout southern Ontario and along the Michigan-Ohio line. The Pinkney sample thus falls within his range of overlap.

2), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), α -glycero-phosphate dehydrogenase (aGPDH), isocitrate dehydrogenase (2 loci: IDH-1, IDH-2), malate dehydrogenase (2 loci: MDH-1, MDH-2), malic enzyme (2 loci: ME-1, ME-2), 6-phosphogluconate dehydrogenase (6-PGD), phosphoglucose isomerase (PGI; = PHI in Vawter & Brussard 1975), and phosphoglucosmutase (PGM). Ambiguous alleles were rerun side-by-side on the same gels to confirm scoring. All statistical analyses of the allozyme data were done using a computer program written by AHP.

TABLE 1. Sample localities, capture dates, sample sizes (n), and taxonomic affinities.

#	Population	Date	n	Taxon
1	Cygnets, Wood Co., Ohio	5 Sep 1995	26	<i>P. tharos</i>
2	Providence Metropark, Lucas Co., Ohio	30 Jul 1995	31	<i>P. tharos</i>
3	Salem, Columbiana Co., Ohio	4 Jun 1995	19	<i>P. tharos</i>
4	Pinckney, Washtenaw Co., Michigan	15 Jun 1995	20	<i>P. tharos</i>
5	5 mi S Allenville, Mackinac Co., Michigan	29 Jul 1995	25	<i>P. cocyta</i>
6	10 mi WSW Rockview, Mackinac Co., Michigan	30 Jul 1995	7	<i>P. cocyta</i>

Measurement of genetic isolation. We used hierarchical F statistics (Wright 1969, 1978, Porter 1990, Porter & Geiger 1995) to describe allozyme variation among populations. Unlike standard genetic distance/identity measures, F statistics describe genetic diversity among populations in a way that can be used to estimate underlying rates of genetic exchange (Slatkin 1987, Cockerham & Weir 1993), such that we can legitimately infer process from pattern. At larger geographic scales, they may be used to measure rates of introgression and its complement, genetic isolation, and are valuable tools for testing hypotheses about species status (Porter 1990). As many readers of this journal may not be familiar with this approach, we provide a more detailed description in the Appendix. Further introduction to the population-genetic principles underlying this method may be found in introductory texts (e.g., Hartl & Clark 1997).

It is possible to estimate the rate of gene exchange among subpopulations using $M \approx (1/F_{ST} - 1)/4$ (Slatkin 1987, Cockerham & Weir 1993), where M is the effective number of individuals (or gene copies) exchanged among subpopulations per generation, and F_{ST} describes differentiation among subpopulations. This method extends across hierarchical scales, such that gene exchange may be estimated among demes within subpopulations, or among taxonomic groups (Porter 1990). Here, we use $M \approx (1/F_{GT} - 1)/4$ to estimate the degree of gene exchange between *P. tharos* and *P. cocyta*. It is a basic result of population genetics that a gene exchange rate among populations of about 1 individual (or 2 gene copies) per generation is enough to produce important homogenization of gene frequencies, regardless of population size (Wright 1931, 1969, 1978). For neutral loci, differentiation among subpopulations (F_{ST}) or taxa (F_{GT}) is produced by genetic drift and is counteracted by gene flow. Balancing selection on allozymes probably plays a negligible role in subpopulation differentiation unless the subpopulations are quite large (Porter 1990, Porter & Geiger 1995). Caution must be used in interpreting these estimates because the estimation of gene flow requires that genetic differentiation be near the equilibrium level produced by the opposing effects of gene flow and drift. If it is not, the direction of

the bias depends on whether contact among subpopulations is of primary or secondary origin. When it is out of equilibrium because of the interruption of gene flow, gene flow (M) will be overestimated, and this is especially so in large populations or over geographic regions, because genetic drift will act more slowly therein (Porter & Geiger 1995). In cases where taxon-wide differentiation has not yet equilibrated, hybrid zone analyses may then provide information of value in determining reasons for the deviation from equilibrium (Porter and Geiger 1995). However, if gene flow is estimated to be low (say, $M < 0.1$), then this value has been attained in the face of historical biases, and genetic isolation becomes a plausible explanation (Porter 1990).

Morphological data. Antennal clubs were scored for color (orange or black) and geographic variation assessed using a contingency table test. We scored the color of the ventral medial background, which forms a net-like pattern among the underside pattern elements; this reportedly tends to be black in *P. tharos* and orange in *P. cocyta*. We also scored the color of the ventral hindwing's postmedial crescent mark, which reportedly tends to be white in *P. tharos* and creamy or obscured with brown in *P. cocyta*. Correlations were calculated to confirm the degree of association among these putatively diagnostic traits; strong correlations would confirm the impressions of previous workers and tend to favor a genetic isolation interpretation. More detailed measurements of the complex patterns of wing coloration require breeding in controlled environments for interpretation of the polyphenism involved, and are beyond the scope of this paper. Wings, antennae and genitalia were saved as vouchers and are deposited in the insect collection of the Entomology Department at the University of Massachusetts at Amherst.

RESULTS

Allozyme variation within populations. Allele frequencies for the polymorphic loci are given in Table 2. ALDO, FUM and GAPDH showed no polymorphism and are omitted from the table. PGM, discussed below, was not scorable and omitted from further analyses. 6-PGD showed useful polymorphism but did not resolve in over half the individuals, and did not resolve in any of the seven individuals in population 6. For statistical reasons this locus was omitted from among-population comparisons.

Standard genetic variability scores are given in Table 3. We found high levels of genetic variability at several loci. PGI yielded 16 identifiable alleles with up to 9 alleles in a single population, and both GOT-1 and ME-1 showed 7 distinct alleles. These are higher levels of variability than reported by Vawter and Brussard (1975), though their sample sizes were comparable.

TABLE 2. Allele frequencies (standard errors) of polymorphic loci for all populations. Sample sizes for individual loci are given in brackets if they differ from those in Table 1.

	Cygnets, Ohio	Providence, Ohio	Salem, Ohio	Pinckney, Michigan	Allenville, Michigan	Rockview, Michigan
AK-1						
A		0.016 (0.016)	0.026 (0.026)		0.020 (0.020)	
B	0.981 (0.019)	0.984 (0.016)	0.974 (0.026)	0.975 (0.025)	0.960 (0.028)	1.000 (0.000)
C	0.019 (0.019)			0.025 (0.025)	0.020 (0.020)	
GOT-1						
		[30]			[24]	
A				0.025 (0.025)		
B		0.083 (0.036)	0.026 (0.026)		0.021 (0.021)	
C		0.033 (0.023)		0.050 (0.034)	0.542 (0.072)	0.500 (0.134)
D	0.077 (0.037)				0.021 (0.021)	
E	0.904 (0.041)	0.850 (0.046)	0.947 (0.036)	0.925 (0.042)	0.417 (0.071)	0.500 (0.134)
G	0.019 (0.019)	0.017 (0.017)				
H		0.017 (0.017)	0.026 (0.026)			
GOT-2						
A			0.026 (0.026)	0.025 (0.025)		
C	0.020 (0.020)	0.048 (0.027)	0.026 (0.026)	0.050 (0.034)	0.080 (0.038)	0.143 (0.094)
D	0.920 (0.038)	0.903 (0.038)	0.895 (0.050)	0.825 (0.060)	0.880 (0.046)	0.714 (0.121)
E					0.020 (0.020)	0.143 (0.094)
F	0.060 (0.034)	0.048 (0.027)	0.053 (0.036)	0.100 (0.047)	0.020 (0.020)	

TABLE 2. Continued.

	Cygnets, Ohio	Providence, Ohio	Salem, Ohio	Pinckney, Michigan	Allenville, Michigan	Rockview, Michigan
aGPDH						
A			0.026 (0.026)			
B	1.000 (0.000)	1.000 (0.000)	0.947 (0.036)	1.000 (0.000)	1.000 (0.000)	1.000 (0.000)
C			0.026 (0.026)			
IDH-1						
		[29]				
A					0.020 (0.020)	
B		0.017 (0.017)			0.040 (0.028)	
C		0.017 (0.017)				
D	1.000 (0.000)	0.966 (0.024)	0.974 (0.026)	0.950 (0.034)	0.920 (0.038)	1.000 (0.000)
E			0.026 (0.026)	0.050 (0.034)	0.020 (0.020)	
IDH-2						
	[15]	[18]	[12]	[17]		
A		0.028 (0.027)	0.083 (0.056)	0.059 (0.040)	0.020 (0.020)	0.143 (0.094)
B	0.900 (0.055)	0.889 (0.052)	0.833 (0.076)	0.941 (0.040)	0.960 (0.028)	0.857 (0.094)
C	0.067 (0.046)	0.083 (0.046)				
D	0.033 (0.033)		0.083 (0.056)		0.020 (0.020)	
MDH-1						
				[19]	[24]	
A				0.026 (0.026)	0.021 (0.021)	
B	0.096 (0.041)	0.194 (0.050)	0.158 (0.059)	0.474 (0.081)	0.958 (0.029)	0.929 (0.069)
C	0.865 (0.047)	0.806 (0.050)	0.842 (0.059)	0.500 (0.081)	0.021 (0.021)	0.071 (0.069)

TABLE 2. Continued.

	Cygnets, Ohio	Providence, Ohio	Salem, Ohio	Finckney, Michigan	Allenville, Michigan	Rockview, Michigan
D	0.019 (0.019)					
E	0.019 (0.019)					
MDH-2						
A	1.000 (0.000)	0.984 (0.016)	1.000 (0.000)	1.000 (0.000)	1.000 (0.000)	1.000 (0.000)
B		0.016 (0.016)				
ME-1						
B	0.212 (0.057)	0.419 (0.063)	0.289 (0.074)	0.325 (0.074)	0.440 (0.070)	0.643 (0.128)
C	0.019 (0.019)	0.016 (0.016)	0.053 (0.036)			
D	0.212 (0.057)	0.194 (0.050)	0.211 (0.066)	0.225 (0.066)	0.280 (0.063)	0.143 (0.094)
F	0.288 (0.063)	0.258 (0.056)	0.132 (0.055)	0.200 (0.063)	0.140 (0.049)	0.143 (0.094)
G	0.250 (0.060)	0.081 (0.035)	0.211 (0.066)	0.125 (0.052)	0.140 (0.049)	0.071 (0.069)
H		0.032 (0.022)	0.105 (0.050)	0.100 (0.047)		
I	0.019 (0.019)			0.025 (0.025)		
ME-2	[10]	[21]	[16]	[15]	[20]	
A			0.156 (0.064)	0.333 (0.086)		
B	1.000 (0.000)	1.000 (0.000)	0.812 (0.069)	0.633 (0.088)	1.000 (0.000)	1.000 (0.000)
C			0.031 (0.031)	0.033 (0.033)		
6-PGD	[16]	[15]	[4]	[10]	[9]	[0]
A	0.938 (0.043)	1.000 (0.000)	0.750 (0.153)	0.900 (0.067)	0.889 (0.074)	
B	0.062 (0.043)					

TABLE 2. Continued.

	Cygnat, Ohio	Providence, Ohio	Salem, Ohio	Finckney, Michigan	Allenville, Michigan	Rockview, Michigan
C			0.250 (0.153)		0.111 (0.074)	
D				0.100 (0.067)		
PGI					[24]	
A		0.016 (0.016)				
B	0.019 (0.019)	0.016 (0.016)	0.026 (0.026)			
C	0.231 (0.058)	0.194 (0.050)	0.211 (0.066)	0.200 (0.063)	0.021 (0.021)	
D				0.050 (0.034)	0.021 (0.021)	
E	0.442 (0.069)	0.274 (0.057)	0.342 (0.077)	0.400 (0.077)	0.562 (0.072)	0.429 (0.132)
F	0.058 (0.032)					
G	0.019 (0.019)	0.081 (0.035)	0.053 (0.036)	0.025 (0.025)	0.021 (0.021)	0.071 (0.069)
H	0.154 (0.050)	0.371 (0.061)	0.237 (0.069)	0.250 (0.068)	0.208 (0.059)	0.500 (0.134)
I	0.019 (0.019)	0.032 (0.022)			0.021 (0.021)	
J			0.026 (0.026)		0.062 (0.035)	
K			0.079 (0.044)			
L	0.038 (0.027)			0.025 (0.025)	0.062 (0.035)	
M	0.019 (0.019)					
P			0.026 (0.026)	0.050 (0.034)		
Q		0.016 (0.016)				
W					0.021 (0.021)	

TABLE 3. Genetic variability scores for all populations, averaged over loci. A = mean alleles/locus; %P = percent of loci polymorphic; H_{obs} = proportion of individuals observed to be heterozygous; H_{exp} = proportion of heterozygous individuals expected from allele frequencies, assuming Hardy-Weinberg genotypic proportions. Standard errors, from jack-knife estimates, given in parentheses. 6-PGD variability is not included in the Rockview scores because it did not resolve in those individuals.

#	Population	A	%P	H_{obs}	H_{exp}
1	Cygnets, Ohio	2.85 (0.20)	61.5 (4.2)	0.147 (0.021)	0.184 (0.022)
2	Providence, Ohio	2.92 (0.18)	69.2 (4.0)	0.189 (0.022)	0.196 (0.022)
3	Salem, Ohio	3.08 (0.16)	84.6 (3.1)	0.239 (0.028)	0.255 (0.022)
4	Pinckney, Michigan	2.85 (0.16)	76.9 (3.7)	0.268 (0.026)	0.262 (0.023)
5	Allenville, Michigan	3.08 (0.18)	69.2 (4.0)	0.163 (0.018)	0.204 (0.021)
6	Rockview, Michigan	1.83 (0.09)	50.0 (4.7)	0.190 (0.022)	0.202 (0.022)

A possibility exists that *P. tharos* and *P. cocyta* are truly genetically isolated and that we sampled both taxa in some localities, in which case diagnostic allozyme markers at different loci would be correlated within individuals. As a weak test, we therefore estimated linkage disequilibrium (a correlation coefficient) between GOT-1 and MDH-1, the only partially diagnostic markers we found (see below), in all populations. None differed significantly from zero, giving no evidence that two independent species are inadvertently mingled within our population samples. However, given that the allele frequencies at GOT-1 do not differ profoundly between taxa, this test is only likely to be strong enough to detect samples where the taxa are present in roughly equal numbers.

Variation among populations and genetic isolation. There were no fixed differences among populations at any loci, but two loci showed marked geographic differentiation in frequency. Populations 5 and 6 from Mackinac County, Michigan, in the Upper Peninsula, differed from the remaining populations especially at MDH-1 and GOT-1, with the Pinckney, Michigan, population showing intermediate frequencies at MDH-1. It is perhaps easiest to visualize these patterns using phenograms constructed from genetic distance/identity measures. The overall divergence as estimated from Nei's (1978) unbiased genetic distance and identity measures is shown in Fig. 2a, where the Mackinac Co. Michigan, populations (*P. cocyta*) appear as a distinct group. This pattern is confirmed with a second analysis using Rogers' (1972) genetic distance, and is displayed (Fig. 2b) in a tree built using the distance-Wagner algorithm described in Ferris (1972).

Results of the hierarchical *F*-statistical analysis are shown in Table 4. F_{SC} describes the differentiation among gene frequencies of the populations in Table 2 from the average frequencies of their respective groups, *P. tharos* and *P. cocyta*. The differentiation is low, and may be explained by an average gene exchange rate of $\hat{M} = 7.6$ (95% c.i. 5.2–13) individu-

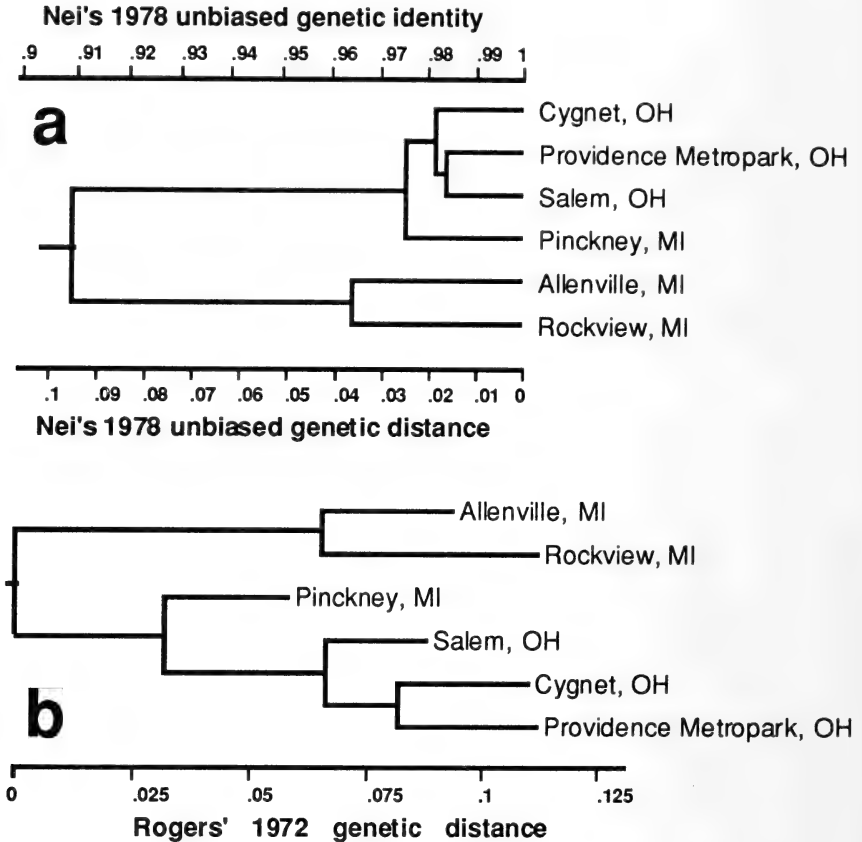


FIG. 2. Phenograms describing genetic differentiation among populations. a, UPGMA (Sokal & Sneath 1963) phenogram based on Nei's (1978) unbiased distance and identity measures. b, Distance-Wagner tree (Ferris 1972) based on Rogers' (1972) genetic distance. *P. cocyta* populations from Mackinac Co., Michigan fall into a distinct group in both measures.

als per generation within these two taxa. F_{CT} describes differentiation of gene frequencies between those population groups designated as *P. tharos* and *P. cocyta*. This differentiation is higher, but still permits a gene exchange rate between these taxa of $\hat{M} = 0.88$ (0.54–1.7) individuals per generation. This value suggests incomplete genetic isolation, particularly in comparison to the high within-taxon values (Porter 1990, Porter & Geiger 1995).

Morphological traits. We found no support for the hypotheses that the antennal club colors, ventral hindwing ground color, or the color of the underside crescent were useful for taxonomic diagnosis of *P. tharos* and *P. cocyta*. There were significant differences among popula-

TABLE 4. *F* statistics describing genetic divergence at different hierarchical levels, and estimates of the rates of genetic exchange (\bar{M}) at these levels. Upper and lower bounds of \bar{M} represent 95% confidence intervals derived from jackknife variance estimates on the *F* statistics, taken over the 11 polymorphic loci (omitting 6-PGD).

Hierarchical level		Value	(SE)	Lower bound	\bar{M}	Upper bound
F_{GT}	between <i>tharos</i> & <i>cocyta</i>	0.221	0.014	0.54	0.88	1.7
F_{ST}	among all populations	0.246	0.015	0.48	0.77	1.4
F_{SG}	among populations within <i>tharos</i> & <i>cocyta</i>	0.0319	0.0021	5.2	7.6	13
F_{IT}	within individuals	0.289	0.015			
F_{IC}	within individuals, within <i>tharos</i> & <i>cocyta</i>	0.0873	0.0038			
F_{IS}	within individuals, within populations	0.0572	0.0043			

tions in the frequencies of black vs. orange antennal color morphs in both males and females (Table 5), but these were not associated with the taxonomic groupings. This supports Scott's (1986a, 1994) observation that the antennal color is ambiguous in the northern part of the range of *P. tharos*. We found what appeared to be continuous variation in the color of the ventral crescent, and also in the degree of black scaling mixed into the ventral ground color. When all populations were pooled, we found an expected correlation between sex and the color of the ventral crescent ($r = -0.53$, $p < 0.001$), but no other significant associations among sex, antennal club color, crescent color, and ventral ground color. When we broke this down by population, we found additional significant ($p < 0.05$) correlations between sex and antennal color in Pinckney and Salem (cf. Table 5), crescent and antennal color at Salem (probably acting through the previous correlation), and antennal and ground color at Pinckney. Within females, we also found significant positive correlations between ventral ground color and crescent color in Pinckney and Al-

TABLE 5. Antennal club color frequencies for each population. For males, significant differences are due to the higher frequency of black-clubbed individuals at Salem, Ohio. For females, significance is due to the higher frequencies of black morphs in Pinckney and Rockview. These do not correlate to the taxonomic affinities.

Color	<i>P. tharos</i>				<i>P. cocyta</i>		G	p <
	Cygneth, Ohio	Providence, Ohio	Salem, Ohio	Pinckney, Michigan	Allenville, Michigan	Rockview, Michigan		
♂								
orange	19	17	4	12	11	2	-49.03	0.001
black	3	4	8	0	1	0		
♀								
orange	4	8	6	4	10	3	-80.47	0.001
black	0	2	1	4	3	2		

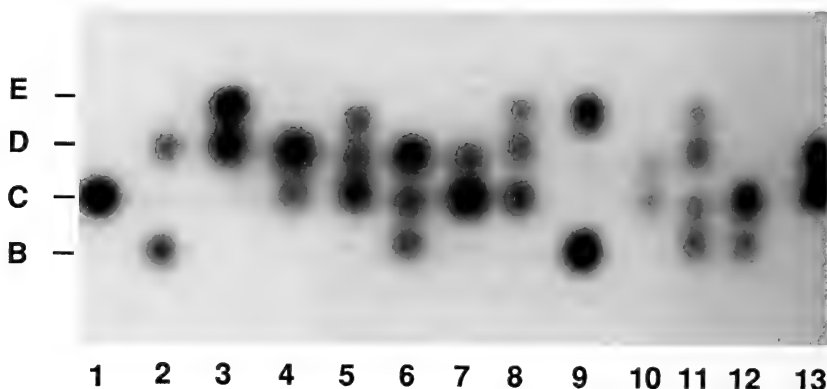


FIG. 3. Representative zymogram showing duplication of the PGM locus. Individuals are numbered and electromorphs are lettered. Alleles of the two loci overlap and cannot be assigned to the separate loci, but the genotypes can be estimated from the relative banding intensity, with relatively darker bands indicating that more than one allele has migrated to that location. The combined 2-locus genotypes seen here are: 1) CCCC, 2) BBDD; 3) DDEE; 4) CDDD; 5) CCDE; 6) BCDD; 7) CCCD; 8) CCDE; 9) BBEE; 10) CCDD; 11) BCDE; 12) BCCC; 13) CCDD. 1-5: Salem, Ohio; 6-10: Pinckney, Michigan; 11-13: Providence, Ohio, all *P. tharos*; similar patterns were found in the *P. cocyta* populations.

lenville, suggesting general ventral melanization effects there. These patterns varied geographically and were not sufficiently strong to form a basis for taxonomic diagnosis. We were not able to confirm Oliver's (1980) qualitative descriptions of differences in dorsal wing pattern traits between *P. tharos* and *P. cocyta*.

The PGM locus. PGM is a monomeric enzyme (comprised of a single protein unit), so heterozygotes are expected to show a pair of bands and homozygotes show a single band. In both *P. tharos* and *P. cocyta*, individuals show up to 4 bands (Fig. 3), suggesting that gene duplication may have occurred. Individuals with 2-3 bands show variation in the relative intensity of those bands, and all individuals with 3 bands show one or another of their bands of greater intensity, in a manner consistent with the interpretation that alleles of two PGM loci migrate to overlapping locations on the gel. These banding patterns are well-resolved, repeatable, and not consistent with simple patterns of secondary banding caused by degradation, sometimes seen in other loci. However, without breeding studies, it is not possible to assign electromorphs to the two PGM loci. Vawter and Brussard (1975) reported only a single PGM locus with typical patterns of variability, and we cannot explain the discrepancy. If verified by breeding and molecular methods, a duplication of PGM would make a good derived trait for phylogenetic studies, as was recognized for the duplicated PGI locus in *Clarkia* (Onagraceae) (Gottlieb & Weeden 1979).

DISCUSSION

One species or two? The allozyme analyses presented here (Table 4) support the interpretation that *P. tharos* and *P. cocyta* are incompletely isolated from one another genetically. Although the amount of genetic differentiation observed between the two taxa is higher than that observed among populations within them, biologically important genetic exchange rates of approximately one genome per generation (Wright 1931, 1969, 1978, Slatkin 1987) across the taxonomic boundary are still consistent with the patterns we observed.

This interpretation is in full agreement with Oliver's breeding data. He found that F_1 hybrid and backcross broods had high fertility and survivorship rates, with developmental incompatibilities accounting for only a 15% reduction in survivorship, a negligible barrier to gene exchange. Scott (1986b) released Rocky Mountain *P. cocyta* females in front of *P. tharos* males and thereby readily obtained natural matings and fertile offspring, indicating that there is presently no evidence for mating barriers between these taxa. All the currently available evidence indicates that when these taxa do come into contact, avenues exist for considerable introgression between them. From this perspective, these taxa might best be considered taxonomically as subspecies, whereupon the name *tharos* is the oldest available.

How then might the putatively diagnostic traits be maintained in the face of homogenizing gene flow? If there are plausible explanations for the maintenance of the differences we observe between taxa in the *Phyciodes tharos* group, then it would be premature to reach the conclusion that genetic isolation is responsible. This is especially so because the putatively diagnostic traits are apparently not correlated with one another (Tables 4, 5).

Within a species, there is a simple adaptive explanation available for the primary diagnostic-trait difference that Oliver (1980, 1983) identified between *tharos* and *cocyta*, namely the association between body size, development time, and the number of annual generations along the geographic line of transition between one generation and two. Roff (1983) developed a general model of these transitional regions in voltinism. He demonstrated that just north of such a line, where a single generation is favored, individuals may increase their fitness by prolonging development. This permits them to reach larger adult body sizes, with concomitant increases in fecundity, without selective pressure to reach the appropriate diapause stage before the season ends. This life-history strategy begins to backfire further northward in the range, where the season ends sooner and selection favors more rapid development in order to simply reach the diapause stage. Just south of the transition line,

two generations are favored, but only for those individuals able to develop fast enough that the second generation is able to diapause. This requires individuals to mature at smaller body sizes, as the fitness advantage of having an additional generation outweighs the costs on individual fecundity of smaller body size. Further south, the time window is longer, and selection favors larger body sizes even with two generations. As these life-history traits are closely tied to fitness, the selection acting upon them is likely to be strong enough to overcome the homogenizing gene flow rates of $M \approx 1$ individual per generation that we observed across the taxonomic boundary. Burns (1985) suggested a similar explanation for the correlation between body size and voltinism in the hesperiid *Wallengrenia egeremet* (Scudder).

Patterns of variation in the remaining traits have not yet been documented well enough quantitatively to be able to determine their contribution to genetic isolation, and the qualitative impressions made "by eye" of population averages, used to date in the taxonomic research of this group, are inadequate to this task. The wing patterns are highly variable within populations and show seasonal adaptations. Given the developmental complexity of pattern elements on the wing surface (Nijhout 1991), adequate statistical description of geographic variation in wing pattern will be a major undertaking, and a quantitative understanding of its genetic basis as it relates to genetic isolation may be formidable. But until the patterns of variation are adequately described, we cannot hope to distinguish among their possible causes. The genitalic differences reported by Scott (1986a, 1994) are subtle, and such differentiation is not necessarily indicative of reproductive isolation (Shapiro & Porter 1989, Porter & Shapiro 1990), a point Scott (1994) acknowledges. They may be maintained, for example, by sexual selection during copulation (Eberhard 1985) or even as neutral traits in an isolation-by-distance population structure (Endler 1977). It is difficult to imagine the larval color patterns contributing in a significant way to genetic isolation. The known level of geographic variation in this suite of diagnostic traits remains consistent with a pattern of partial genetic isolation between *P. tharos* and *P. cocyta*.

Does the differentiation observed to date indicate secondary contact between taxa evolved in allopatry, or simple geographic differentiation without separation? One can only speculate. The geographic location of the contact area in eastern North America was glaciated 18,000 years ago, and is likely to have achieved its present ecosystem (barring very recent human population growth) only in the last 8000 years. Given that the present contact area runs west to east, and glacial recession proceeded from south to north, the biogeography of range changes involving any hypothesized allopatry would have had to be complex. A com-

plex history in this region can be found in genetic patterns from the *Papilio machaon* (L.) group taxa (Sperling 1993), but suitable data are not available to address this issue in *Phyciodes*.

In summary, there is yet no *prima facie* evidence of separate species status for *P. tharos* and *P. cocyta* and it is at best premature to separate them. Field collections yield intermediate specimens, and laboratory studies of the life cycles indicate that the two taxa respond similarly to spring-time conditions that determine the timing of the first adult generation (Oliver 1980), suggesting that the taxa are not temporally isolated in sympatry. For the maintenance of the life-history differences, there is a reasonable, adaptive explanation available that does not require genetic isolation. Several putatively diagnostic morphological differences were not well supported in our correlational analyses. Remaining differences proposed by various workers, and untested by us, require quantitative analysis and more certain evidence of genetic isolation as their cause. The genetic data, for which the best methods are currently available to link patterns of genetic variation to gene flow barriers, do suggest that a weak barrier exists. However, this barrier is analogous more to a sieve than a wall, in that it is too weak to inhibit for more than a few generations neutral and adaptive genetic exchange between the taxa, even when the confidence limits are considered. The genetic analysis too is preliminary: if genetic isolation has in fact evolved only very recently, it remains possible for the regional patterns of differentiation we observed between the taxa to have had insufficient time to drift apart (Porter & Geiger 1995). Therefore, studies of the contact area on a finer scale are needed to test and resolve the results we present here.

The *Phyciodes tharos/cocyta* system is a prime candidate for study using hybrid zone theory (Barton & Gale 1993). The taxa are parapatrically distributed, with a defined region of contact and apparent hybridization in the center. There are ecological conditions capable of producing adaptive differences in the regulation of diapause on either side, and available allozyme markers with which to document cline shape. This body of theory is useful for interpreting the relationships between pattern and underlying evolutionary processes, regardless of whether the taxa are in secondary contact or have reached their present level of differentiation without separation (Harrison 1993), and regardless of the width of the contact region (Barton & Gale 1993). These models permit the estimation of the strength of natural selection acting both in the zone itself and out in the tails of introgression, and permit the estimation of the rate of introgression (Barton & Gale 1993, Porter et al. 1997b). If such introgression resolves to be negligible, this would comprise *prima facie* evidence for genetic isolation and it would be appropriate to reassess the taxonomic status of this group.

Selection, gene flow and allozyme variation. There have been significant advances in our understanding of the causes of geographic patterns of allozyme diversity since the study by Vawter and Brussard (1975). There is no need to invoke strong stabilizing selection for the allozyme similarities in the *P. tharos* system, as gene flow rates of several individuals entering a population each generation are sufficient to maintain the observed levels of variation. Nevertheless, very weak selection may account for high similarity over very large areas, as the effective population sizes are so much higher on regional spatial scales that very weak stabilizing selection (on the order of the mutation rate) can maintain range-wide similarity (Porter & Geiger 1995). Such subtle processes may be unmeasurable in natural populations, where the stochastic effects of genetic drift may overcome the weak deterministic forces of selection at the local spatial and temporal scales to which field biologists, for logistic reasons, are confined.

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APPENDIX

F statistics summarize the extent to which populations deviate from Hardy-Weinberg genotypic proportions. Populations in Hardy-Weinberg equilibrium proportions have $F = 0$. Populations with excesses of homozygotes have $F > 0$ to a maximum of $F = 1$; those with heterozygote excesses have $F < 0$ to a minimum of $F = -1$. A population may be hierarchically organized as a group of subpopulations (the terms 'population' and 'subpopulation' are simply statistical constructs which may or may not be identical to populations in the biological sense), whereupon F in the total population, denoted F_{IT} , may be hierarchically partitioned to describe averages of deviations from Hardy-Weinberg expectations on different geographic scales. The partitioning is $(1 - F_{IT}) = (1 - F_{IS})(1 - F_{ST})$ (Wright 1951, 1978), where F_{IS} describes the average of deviations from Hardy-Weinberg proportions within the subpopulations, and F_{ST} describes the component of overall deviation produced by gene frequency differences among subpopulations. Other hierarchical levels are often inserted, as we describe below. On local scales, within subpopulations, deviations from Hardy-Weinberg expectations arise from nonrandom mating, and F_{IS} may be positive or negative. At larger scales, only positive values (aside from sampling variation) may arise in F_{ST} , when the subpopulations have different allele frequencies. This is easiest to imagine in the extreme case where subpopulations are fixed for different alleles, yielding a complete deficiency of heterozygotes in the total population. As such, F_{ST} is a common statistic describing average differentiation among subpopulations.

F statistics have historically been derived mathematically from three additional perspectives: as the degree to which alleles identical-by-descent are distributed within and among individuals (f of Malécot 1969) and populations (G of Nei 1973); by path analysis as correlations between alleles in uniting gametes (i.e., within diploid individuals) within and among subpopulations (F of Wright 1951, 1978); and from a nested analysis of variance model describing the pattern in which total allelic variation is partitioned among subpopulations, among individuals within subpopulations, and between pairs of alleles within (diploid) individuals (Cockerham 1969, 1973, Weir & Cockerham 1984). Although the derivations yield the same analytical result and their various interpretations are biologically equivalent, the third approach lends itself most readily to statistical treatment of data because degrees of freedom can easily be incorporated at several sampling levels (Weir & Cockerham 1984, Weir 1990).

Because of the hierarchical structure of F -statistics, additional levels may be readily included in analyses, representing, for example, subdivisions of large subpopulations into

demes (Wright 1978) or grouping of subpopulations into intraspecific geographical or taxonomic units (Porter 1990, Porter & Geiger 1995, Porter et al. 1997a). In this study, we investigate differentiation at three hierarchical levels: between taxonomic units (F_{CT}), namely *P. tharos* and *P. cocyta*, among subpopulations within taxonomic units (F_{SG}), and among individuals within subpopulations (F_{IS}). The partitioning is thus $(1-F_{IT}) = (1-F_{IS})(1-F_{SG})(1-F_{CT})$. These hierarchical levels may be collapsed to yield $(1-F_{IT}) = (1-F_{IS})(1-F_{ST})$ and $(1-F_{IT}) = (1-F_{IC})(1-F_{CT})$ as above, and we also draw inferences from F_{ST} . We used Weir and Cockerham's (1984) statistical estimators for F -statistics, derived from the unbiased hierarchical variance components a , b_1 , b_2 , and c , as defined in their paper. These estimators are:

$$F_{IS} = 1 - (c / (b_1 + c))$$

$$F_{IC} = \hat{f} = 1 - (c / (b_1 + b_2 + c))$$

$$F_{IT} = \hat{F} = 1 - (c / (a + b_1 + b_2 + c))$$

$$F_{SG} = 1 - ((b_1 + c) / (b_1 + b_2 + c))$$

$$F_{ST} = \theta_1 = 1 - ((a + b_2) / (a + b_1 + b_2 + c))$$

$$F_{CT} = \theta_2 = 1 - (a / (a + b_1 + b_2 + c))$$

where θ_1 , θ_2 , \hat{F} , and \hat{f} follows their notation; the "hat" indicates that the quantity is being estimated from data. Single-locus estimates were combined over loci and alleles using a weighted average, and error estimates were obtained by the "jackknife" resampling method (Weir & Cockerham 1984).

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GENERAL NOTES

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A RECONSIDERATION OF MIMICRY AND APOSEMATISM IN CATERPILLARS OF THE *PAPILIO MACHAON* GROUP

Additional key words: Papilionidae, *Papilio polyxenes*, warning coloration, adaptation.

Williams (1966) pointed out that adaptation is a special and onerous concept that should only be invoked when other explanations have been ruled out by the evidence. To support a theory of Müllerian mimicry between taxa, the adaptive basis of mimetic resemblance (the color pattern, the defensive mechanisms that result in unpalatability) should be experimentally demonstrated. Correlated character distributions need not imply causal relationships (Miller & Wenzel 1995, Brower 1995), especially if complementary data on behavior and on interactions with predators in the field are subject to alternate interpretations (Lauder 1990). The burden of proof lies upon the advocate of a particular hypothesis of mimicry, because other, simpler explanations must be eliminated prior to acceptance of an adaptive scenario.

Mimicry among butterflies and day-flying moths is common, and its adaptive basis has been theoretically and empirically demonstrated (Bates 1862, Müller 1879, Brower 1958, Fisher 1958). Among lepidopteran larvae, however, the phenomenon is nearly unknown. Berenbaum (1995) recently reviewed three hypotheses to explain its apparent infrequency. First, evolution of larval patterns and colors could be limited by developmental constraints. That idea was rejected because there is genetic evidence for extensive larval pattern lability from the paradigmatic "model" lepidopteran, *Bombyx mori* L. Second, caterpillars may be less able than adults to survive handling by predators, as their bodies are more delicate (Poulton 1885) and they may suffer the additional risk of being knocked off their food plant. However, this hypothesis is not directly relevant to the evolution of mimicry, because it predicts that bright coloration attracting the attention of predators should be less likely to evolve in larvae, irrespective of their palatability or mimetic resemblances. Furthermore, the existence of many gaily-colored and noxious caterpillar species (Slater 1877, Bowers 1993, Sillén-Tullberg 1988) implies that fragility is not a major impediment to the evolution of bright larval color patterns.

A third possibility is that people simply have not noticed mimicry rings among caterpillars because immature Lepidoptera have not been as well studied as adults. We agree with Berenbaum that lack of study may partially explain the apparent rarity of larval mimicry in general, but we feel that an additional hypothesis may be relevant as well. We suggest that caterpillars do not commonly exhibit mimicry because they tend to be associated with particular foodplants which represent an "extended phenotype" (Dawkins 1982) that forms an integral part of potential predators' search image. If the plants look different, predators may be not be fooled by similarities in color pattern between potential models and mimics.

Berenbaum (1995) explored the idea that larvae of *Papilio polyxenes* Fabr. (Papilionidae) are Müllerian mimics with unpalatable larvae of *Danaus plexippus* L. (Nymphalidae). To support this hypothesis, *P. polyxenes* larvae must resemble monarch caterpillars closely enough that potential predators are deceived by their similarity, viewing larvae of both species as representatives of a single, noxious entity (Müller 1879). Additionally, *P. polyxenes* larvae must themselves be aposematic (unpalatable and warningly colored; Bowers 1993). In this note, we reevaluate the evidence supporting these two aspects of the hypothesized adaptive relationship between monarch and black swallowtail larvae. We question the view that larvae of *P. polyxenes* and its relatives are aposematic, and argue that this case of potential larval Müllerian mimicry is poorly supported by available evidence.

Is the larva of *P. polyxenes* unpalatable and warningly-colored? Many authors have contended that *P. polyxenes* (or its close relative *P. machaon*, and by extension, all *machaon*-group larvae) are aposematic. Because prey that are easy to see are more likely to be attacked by predators, aposematism will not evolve unless it confers an advantage greater than the cost of being obvious (Turner 1984). Here, we cast doubt upon the notion that *P. machaon*-group larvae are unpalatable in an ecologically meaningful sense,

contrary to the claims of Järvi et al. (1981), Sillén-Tullberg (1988, 1990), Berenbaum (1995), and others.

Recent support for the idea that these larvae are aposematic stems from a series of laboratory predation experiments testing ideas about kin selection and the evolution of gregariousness. In the first of these (Järvi et al. 1981), wild tits (*Parus*) were given a choice of halved mealworms (*Tenebrio*) and third-instar *P. machaon* larvae, after two initial trials with mealworms only. The birds ate only the mealworms and the authors concluded that the swallowtail larvae are unpalatable and supposed that they are also aposematic. However, as pointed out by Brower (1984), this experiment demonstrated neither unpalatability nor aposematism but simply a preference for familiar, palatable prey over novel, perhaps distinctly-flavored prey. Tinbergen (1960) found a substantial time lag between the advent of a novel prey species in the environment and its acceptance by tits, perhaps due to an innate avoidance of novel visual stimuli (Vaughan 1983) or to a failure to recognize the novel prey as food. The short duration of Järvi et al.'s experimental trials and the continual availability of a preferred alternative food weaken their conclusion that *P. machaon* larvae are unpalatable. However, the aposematism of *P. machaon* larvae was assumed in subsequent papers (e.g., Wiklund & Järvi 1982, Wiklund & Sillén-Tullberg 1985, Sillén-Tullberg 1988, 1990), and additional corroboration came only from indirect and uncontrolled observations, such as the low rate of attack on 6 to 7 cm. caterpillars by small birds (Sillén-Tullberg 1990) which might be frightened by the size of the "prey" alone. Stronger evidence for relative unpalatability among swallowtail larvae was provided by Leslie and Berenbaum (1990), who fed late instars of various species to quails (*Coturnix*) and found that both *P. polyxenes* and the cryptic *P. cresphontes* Cramer were always rejected whereas *P. glaucus* L. was always eaten.

It is likely that palatability of prey varies among predators (Poulton 1887, Brower et al. 1968) and also depends on the particular circumstances of the encounter (e.g., degree of hunger, availability of alternate prey; see Brower 1995). These experiments demonstrated that *P. machaon* and *P. polyxenes* larvae are not accepted by tits and quail under laboratory conditions (or simply that they not as tasty as mealworms or *P. glaucus* larvae). To make a convincing case for aposematism as an adaptive trait, however, experimental observations must be supported by evidence from the field, where the role of selection by birds can be evaluated in an appropriate behavioral and ecological context (Brower 1984, Takagi et al. 1995). Contrary to conclusions from the above experiments, evidence suggests that wild birds are important enemies of *P. machaon* larvae in nature. Dempster et al. (1976) recorded heavy predation by three passerine bird species at one site in Britain, and noted that the rate of bird attack was positively correlated with caterpillar density. This pattern is in accord with the search-image model of birds foraging for cryptic prey (Ruiter 1952, Tinbergen 1960), and would not be expected for an aposematic, unpalatable caterpillar. While comparable field observations have not been made for *P. polyxenes*, the food-plants, habitats, habits, and predator guilds of *P. machaon* and *P. polyxenes* are similar (Dempster et al. 1976, Feeny et al. 1985) and we would not expect these closely related species to differ greatly in susceptibility to birds.

Oviposition by *machaon*-group females and foraging behavior of larvae are also more consistent with their being palatable than aposematic. Nicholls and James (1996) reported relatively dispersed patterns of oviposition, with females often rejecting plants that already bore eggs; Evans (1984) was surprised to discover that supposedly aposematic *P. machaon* larvae are usually solitary (distribution significantly more uniform than a null hypothesis of Poisson distribution). Both observations imply a palatable larval lifestyle, for cryptic species tend to maintain low densities in the field to limit search-image formation by birds (Evans 1984), while many unpalatable larvae (including troidine swallowtails) are gregarious (Sillén-Tullberg 1988; although gregariousness is advantageous to aposematic caterpillars, some unpalatable species may be solitary, and cannibalistic, under certain circumstances, especially if they are competing for small food plants (Benson 1978)). Further, Codella and Lederhouse (1984) reported that *P. polyxenes* feeds so as to enhance crypsis, leaving symmetrical leaf damage and resting away from feeding areas (Heinrich 1979). In contrast, monarch larvae often feed in plain view on the upper surfaces of broad, leathery milkweed leaves.

Do the larvae of *Papilio polyxenes* mimic the larvae of *Danaus plexippus*? The

eight (Sperling 1987) to fourteen (Hancock 1983) species of the *Papilio machaon* group comprise a monophyletic lineage within the large genus *Papilio* (sensu Munroe 1961, Miller 1987, Sperling & Harrison 1994). The group has a Holarctic distribution apart from *P. polyxenes*, whose range extends to Ecuador (Tyler et al. 1994). Larvae feed primarily on the Apiaceae, a habit thought to have originated once, in the ancestor of the clade (Sperling & Feeny 1995). Like many swallowtails, the young larvae are dark with a white band, a pattern that may provide protection via resemblance to bird or lizard droppings (Minno & Emmel 1992). However, the later instars of all species in the *machaon* group share a color pattern not found elsewhere in *Papilio*—a distinctive display of green, black and white transverse annular stripes, some species with small orange or yellow spots scattered in the black (Igarashi 1979, Tyler et al. 1994). Berenbaum (1995) suggested that this pattern mimics the black, yellow and white rings of the unpalatable monarch caterpillar.

Because mimicry can evolve only when predators are exposed to both potential mimics and models (Sheppard 1960, Bowers 1988, Brower 1995), the hypothesis of mimicry between *P. polyxenes* and the monarch can be tested using cladistic and biogeographical evidence: if *machaon*-group larvae mimic *D. plexippus*, then their peculiar coloring must have arisen in sympatry with monarch larvae. Thus, if they are mimics, either *P. polyxenes* or *P. zelicaon* (because they are the only species in the *machaon* group with much geographical and ecological overlap with *D. plexippus*) must be the basal members of the clade, the Eurasian species having evolved later and retaining the mimetic color pattern in the absence of the model. Molecular data (Sperling 1987, Sperling & Harrison 1994), however, suggest that *P. alexanor* (from France, where no danaid species occurs) and *P. indra* (from the North American Great Basin, where the monarch occurs only rarely) are at the base of the *machaon* group. In any case, the conservatism of the pattern within the *machaon* group implies that it is unlikely to have originated via selection for mimetic resemblance to a species with which the majority of the taxa in the clade are largely or entirely allopatric. No alternative model has been suggested.

Monarch larvae could instead be mimics of *machaon*-group larvae, but we dismiss this suggestion because the monarch's larval color pattern occurs throughout *Danaus*. In fact, the details of the color patterns of some of the tropical *Danaus* species appear more similar to those of *P. polyxenes* than to the monarch's (Ackery & Vane-Wright 1984). Because there is even less geographical overlap between them, the chances for larval mimetic co-evolution between species such as *D. erippus* and *D. chryxippus* and *machaon*-group caterpillars are less likely than is Berenbaum's monarch-*polyxenes* hypothesis.

Given these biogeographical arguments against mimicry in *machaon*-group caterpillars, we prefer E. B. Poulton's simpler explanation (1887, p. 240) "that the bright green coloring broken up by black markings is very well adapted for concealment among the much-divided leaves of the Umbelliferae on which the larva feeds." As pointed out by Endler (1978), crypsis does not demand dull coloration, but rather coloration that effectively matches the natural background (Poulton's [1884] "general protective mimicry"). A fat green caterpillar is not well hidden on a thin green leaf. The disruptive contrasting stripes on *machaon*-group caterpillars may be the most cryptic option given the architecture of the food plants and the constraints of body shape and size. An independent case of larval color-pattern change in concert with the host shift from Rutaceae to Apiaceae has been described in the unrelated South African swallowtail *Papilio demodocus* (Clarke et al. 1963). Those authors interpreted the change from a typical solid green and brown *Papilio* caterpillar to a rather unusual and contrasting mottled yellow and brown as being due to selection for crypsis on the new food plant.

Another challenge to the case for mimicry between *D. plexippus* and *P. polyxenes* larvae is suggested by the study of Heinrich and Collins (1983). Chickadees (*Parus atricapillus*) in an experimental aviary were able to recognize differences among plant species and to concentrate their search for prey on "host" plants while avoiding plant species that harbored no potential prey. We suggest that this sort of hierarchical searching in the wild may represent an integral part of the predator-prey signal system for aposematic larvae, and that birds are likely to learn not only the color pattern of the caterpillar, but also the architecture of its foodplant, as elements of the aposeme. If such discrimination among hunting sites is typical of foraging wild birds, then the chances of birds' mistaking a swallowtail

caterpillar on an umbellifer for a monarch caterpillar on a milkweed seem rather small, especially given the behavioral differences noted above. Mimicry between aposematic caterpillars sharing the same food plant (e.g., *Meris alticola* and *Neoterpes graefiaria* on *Penstemon* (Poole 1970, Stermitz et al. 1988) and *Eueides* and *Heliconius* on *Passiflora* (Brown & Benson 1975)) has a better chance of deceiving birds that use environmental cues to hierarchically focus their foraging behavior.

Although the proponents of the aposematism hypothesis generally concede that *P. polyxenes* and *P. machaon* larvae are extremely difficult to find in the field, many authors rationalize this apparent contradiction with the idea that *machaon*-group larvae are cryptic from a distance but warningly-colored at close range (e.g., Järvi et al. 1981, Lederhuser 1990, Brakefield et al. 1992, Takagi et al. 1995, Berenbaum 1995). This concept is referred to as "dual signals" by Rothschild (1975) and developed at greater length by Brown (1988). Given our hierarchical searching hypothesis, however, we feel that the dual signals concept applies better to aposematic adult butterflies and their mimics than it does to sedentary prey like caterpillars. Butterflies are mobile and may be encountered fortuitously anywhere in their habitat, which makes them relatively unpredictable prey. Predators of flying insects may pursue all of them by default, and rely on visual cues to break off an energetically expensive pursuit when the game is not worth the chase. By contrast, many caterpillars, including *P. machaon* group swallowtails, are sedentary on one or a few related host-plant species, and a fundamental component of finding and recognizing caterpillars as prey is finding their specific habitat. We thus view the dual-signals hypothesis to be less appropriate for larvae, and in particular for *P. machaon* group larvae, given Poulton's alternative explanation for the color pattern discussed above.

In conclusion, distinctive coloration as perceived by the human eye is not adequate evidence for adaptive function to the organism bearing it; aposematic warning is a possible but not necessary function of a color pattern. The monarch is a conspicuous feeder on a broad-leaved plant, suggesting that it maximizes the potential of the banded color pattern to function as a signal to predators. The black swallowtail's similar pattern is not displayed in this way, but instead in a manner consistent with a cryptic habit. This might be expected, because mortality data from the field suggest that the taste of *machaon*-group larvae is not broadly deterrent to avian predators. We consider *P. polyxenes* caterpillars to have the plesiomorphic color pattern for the *machaon* clade, and we consider crypsis the plesiomorphic function of the color pattern, because it evidently evolved along with a transition to herb-feeding. If evidence demonstrated both that *P. polyxenes* caterpillars in nature were unpalatable and that they behaved conspicuously, we would accept that the species had acquired a derived warning function for its larval coloring consistent with aposematism (an exaptation sensu Gould & Vrba 1982; see also Lauder 1990, Wenzel 1992). Were experimental data to show that birds avoid *P. polyxenes* under natural circumstances because it looks like *D. plexippus* (or some other model), only then would we conclude that *P. polyxenes* has gained a derived, adaptive function—mimicry—for its plesiomorphic coloration. We are doubtful that this will be demonstrated, and therefore argue that *P. polyxenes* is neither a Batesian nor a Müllerian mimic, but a relatively palatable caterpillar that relies on crypsis as its main defense from vertebrate predators in nature. The simplest explanation is that its coloring is disruptively cryptic, and that its resemblance to the monarch caterpillar is incidental.

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FIELD OBSERVATIONS ON MATING BEHAVIOR AND PREDATION OF *HEMILEUCA ELECTRA* (SATURNIIDAE)

Additional key words: visual cues, predation, silk moth, mate location, pheromones.

Hemileuca electra (Wright), the Electra Buckmoth, is a widespread inhabitant of xeric habitats in the southwestern United States and northwestern Mexico (Tuskes 1984). Larvae emerge from diapausing egg masses in the spring and feed on Flat-top Buckwheat, *Eriogonum fasciculatum* Benthiam (Polygonaceae) (Stone & Smith 1990). The species is univoltine, flying in autumn, with peak emergence from September through early November (Tuskes & McElfresh 1995). Most adults emerge the same year they pupate; however, reared individuals from San Diego County, California have emerged four and one half years after pupation (pers. obs., Powell 1987). Adults are diurnal, non-feeding, and brightly colored (Ferguson 1971, Tuskes et al. 1996). Mate location is facilitated by an airborne pheromone from 'calling' females, and once a female has mated, she stops releasing the pheromone (Tuskes et al. 1996). While investigating aspects of patch-size distribution of this species in southern California, I observed previously unreported mating behavior, on which I report here.

Field work was conducted between 1030 and 1530 PST, 6–19 October, 1996, at Naval Air Station Miramar (parcel G) in San Diego County, California. 11 mm long rubber lures infused with a chemical blend that replicates the primary components of *Hemileuca electra* female pheromone (Jocelyn Millar & Steve McElfresh, unpubl. data) were deployed to attract conspecific males. The dull red-brown lures were kept in a cooler until trials began. In order to observe male response only to their physical presence, two non-calling, sedentary females that had mated on an earlier day were placed approximately 12 cm from the lures on a flat surface. Fifteen males were allowed to land unmolested on the flat sur-



FIG. 1. Male *Hemileuca electra* attempting copulation with a pheromone-releasing rubber lure within 12 cm of two non-calling female *H. electra*.

face where the lure and two non-calling, mated females were resting, and male behavior was recorded. Observations confirm that males are not attracted to the lures if synthetic pheromone has not been added, and females used had attracted males, prior to mating.

Males were attracted within 1–2 min of deploying lures. Fourteen of the 15 males allowed to land did so within 5 cm of the lures, crawled the remaining distance, and attempted copulation with the lure (Fig. 1). These males apparently were not distracted by the presence of non-calling females less than 12 cm away. One male made incidental contact with one of the females as he approached the lure. After crawling around her, he initiated copulation, which the female accepted. I separated the pair approximately 15 seconds later and released the male. He immediately returned, landed near the lure, and attempted copulation with it, ignoring the female. After a few minutes of attempted copulation with the lure, males departed, as did the male that initially contacted the female.

These observations suggest that visual cues do not play a large role in mate location and initiation of copulation in this species. Males are attracted to the source of the pheromone and attempt to mate on contact. Because males ignored females that were 12 cm away, except when incidental contact resulted in female location, color, pattern, or other visual cues in *H. electra* may not play a large role in facilitating mate location.

During the six days of field work, 497 males of *H. electra* were attracted to lures and captured. Three of these lacked a portion of the abdomen, two of which lacked it entirely. These three males were placed in glassine envelopes where they remained alive for approximately 16 h after capture. It is surprising that these males were able to fly, and lived so long following complete or partial abdominal amputation.

When disturbed, adult *Hemileuca* assume a characteristic defensive posture in which the brightly colored abdomen is curled under the thorax to the head (Tuskes et al. 1996). This posture exposes the abdomen to a predator's attack. However, Steve McElfresh (pers. comm.) has observed the Greater Roadrunner, *Geococcyx californianus* Lesson (Neomorphidae), consuming large numbers of *Hemileuca* males, apparently undaunted by this display.

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NEW DISTRIBUTIONAL AND FOODPLANT RECORDS FOR TWENTY CUBAN MOTHS

Additional key words: distribution, larval sampling, light traps, *Estigmene acrea*.

The most recent treatment of the Cuban insect fauna is that of Bruner et al. (1975), which discussed a number of lepidopteran species of economic interest. The purpose of the present paper is to expand upon this base of knowledge, and provide new distributional and foodplant records for 20 species of Lepidoptera from Cuba. All records discussed in the text and Table 1 derive from field collections made since 1990. Larvae were removed from their wild hosts and reared individually to adults in the laboratory in petri dishes, with fresh pieces of foodplant provided daily. Voucher specimens of adults are deposited in the Entomological Collection of the Centro de Investigaciones de Medio Ambiente (CIMA) in Camagüey, Cuba.

Table 1 summarizes the rearing results for 15 moth species. In addition, foodplant relationships were determined for 4 species for which no previous Cuban data were available. These 4 species are discussed in greater detail below, as is the recent capture of *Estigmene acrea*, apparently a new record for the island of Cuba.

TABLE 1. Foodplant relationships recorded in this study for Cuban Lepidoptera.

Species	Foodplant
Geometridae	
<i>Disclisoprocta stellata</i> (Guenee 1857)	<i>Boerhaavia erecta</i> (Nyctaginaceae)
Noctuidae	
<i>Hypena vetustalis</i> Guenee 1854	<i>Sida rhombifolia</i> (Malvaceae)
<i>Mursa phtisialis</i> (Guenee 1854)	<i>Malva acuta</i> (Malvaceae)
Crambidae	
<i>Hyalorista limasalis</i> (Walker 1886)	<i>Hyptis verticillata</i> (Labiatae)
<i>Ategunia ebulealis</i> (Guenee 1854)	<i>Heterotrichum umbellatum</i> (Melastomataceae)
<i>Arthromastix lauralis</i> (Walker 1859)	<i>Trichostigma octandrum</i> (Phytolacaceae)
<i>Bicilia iarchasalis</i> (Walker 1859)	<i>Rivinia humilis</i> (Phytolacaceae)
<i>Cryptobotys zoilusalis</i> (Walker 1859)	<i>Xanthium struemarium</i> (Asteraceae)
<i>Hileithia ductalis</i> Moschler 1890	<i>Blechum pyramidatum</i> (Acanthaceae)
<i>Lineodes graciealis</i> Herr.-Sch. 1871	<i>Brunfelsia</i> sp. (Solanaceae)
<i>Omiodes cunicularis</i> Guenee 1854	<i>Gliricidia sepium</i> (Leguminosae)
<i>Salbia haemorrhoidalis</i> Guenee 1854	<i>Lantana camara</i> (Verbenaceae)
	<i>Syda nodiflora</i> (Verbenaceae)
	<i>Phyla scaberrima</i> (Verbenaceae)
Pyralidae	
<i>Pococera jovira</i> (Schaus 1922)	<i>Gliricidia sepium</i> (Leguminosae)
Thyrididae	
<i>Banisia myrsusalis</i> (Walker 1859)	<i>Chrysophyllum oliviforme</i> (Sapotaceae)
Tortricidae	
<i>Celostathma parallelana</i> Walsing. 1887	<i>Acacia farnesiana</i> (Leguminosae)

***Estigmene acraea* (Drury).** This polymorphic species has a wide distribution in the New World, from Canada to Colombia (Hampson 1901, Watson & Goodger 1986). One female was collected at Sierra de Najasa Natural Reserve, Camagüey Province, Cuba, on a wall attracted to an incandescent light. *Estigmene acraea* is not known from any of the Antillean islands (J. Rawlins, D. Ferguson, L. Hernández, in litt.) and is likely a recent introduction for Cuba, as such a conspicuous species would not remain unnoticed for very long. The female was kept alive for one day and laid a mass of eggs from which about 20 larvae emerged. These were fed on fresh cabbage leaves but died before pupation. The captured female is the white form as illustrated in Covell (1984, pl. 13, fig. 16).

***Hymenia perspectalis* (Hübner).** Larvae of this species were collected and reared on *Alternanthera pungens* (Amaranthaceae). This species is distributed throughout the Nearctic and Neotropical regions, as well as Australia and Ethiopia (Passoa 1985). Several foodplants are recorded in the literature: *Eclipta prostrata*, *Eleutheranthera ruderalis*, *Melanthera canescens*, *Wedelia trilobata* (Asteraceae); *Amaranthus hybridus*, *A. australis* (Amaranthaceae); and *Rivinia humilis* (Phytolacaceae).

***Lygropia tripunctata* (Fabricius).** This species was collected and reared on *Turbina corymbosa* and *Merremia umbellata* (Convolvulaceae), and is widely distributed from the United States to Brazil, including the Antilles (Passoa 1985). Its larvae feed on plants in the family Convolvulaceae (Bruner et al. 1975, Alayo & Valdés 1982, Passoa 1985).

***Microtyris anormalis* (Guenee).** Larvae of this species were collected and reared on *Ipomoea batatas* and *Turbina corymbosa* (Convolvulaceae). It ranges from the United States to South America, including the Antilles and West Indies (Passoa 1985). The litera-

ture I reviewed only cited convolvulaceous foodplants for this moth, but Silva and d'Araujo (1968) list *Tabemamontana coronaria* (Apocynaceae).

***Pleuroptya silicalis* (Guenee).** Larvae of this species were collected and reared on *Ipomoea batatas*, *I. setifera*, *Merremia umbellata* (Convolvulaceae) and *Rivinia humilis* (Phytolacaceae). The distribution of this species includes Panama, Guyana and Brazil (Druce 1881). Bruner et al. (1975) recorded it from Cuba on *Bougainvillea spectabilis* (Nyctaginaceae) and *Bohemeria nicea* (Urticaceae).

I thank Vitor O. Becker for identifying the Lepidoptera, and Eddy Martínez and Angela Beyra (CIMA, Camagüey, Cuba) for identifying the foodplants.

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NEW ANT ASSOCIATIONS FOR *GLAUCOPSYCHE LYGDAMUS* DOUBLEDAY (LYCAENIDAE)

Additional key words: myrmecophily, silvery blue, *Astragalus*.

Larval myrmecophily among the Lycaenidae is well known and documented. In North America, the silvery blue, *Glaucopsyche lygdamus* Doubleday, and its associated ants have been studied by Pierce and Mead (1981) and Pierce and Eastal (1986). Larvae of *G. lygdamus* secrete substances (e.g., sugars, amino acids) that attract and feed ants, while ants provide protection against predators and parasitoids (Pierce & Eastal 1986).

While collecting in the Ozarks (Christian County, Missouri) in April 1996, we discovered a colony of *G. lygdamus*. We attempted to find its larval host by observing adult females and searching legumes for larvae. We subsequently discovered that most larvae were found on *Astragalus crassicaarpus* var. *trichocalyx* (Nutt.) (Fabaceae); *Vicia caroliniana* Walt. (Fabaceae) was also infrequently used. The larvae often were tended by ants, and we noted size discrepancies among the ants. A few ants were collected for identification purposes. In a return trip to the area in 1997, we decided to look more closely at the ant-larva relationship and collect a larger sample of larvae and their associated ant tenders. We also observed that the larger instars appeared to be tended by larger ants.

Pierce and Esteal (1986) recorded six species of ants that tended *G. lygdamus* in Colorado and Ballmer and Pratt (1991) listed three species in California. We found eight species in Missouri: *Prenolepis imparis* (Say), *Camponotus pennsylvanicus* (De Geer), *Camponotus americanus* Mayr, *Formica schaufussi dolosa* Wheeler, *Tapinoma sessile* (Say), *Monomorium minimum* (Buckley), *Crematogaster punctulata* Emery, and *Leptothorax pergandei* Emery. Of these ants, only *T. sessile* had been previously reported as tending *G. lygdamus*.

We had hypothesized that the smaller species of ants were tending earlier instars, so we grouped ant species into three size categories: large (7.0–9.0 mm; *C. americanus*, *C. pennsylvanicus*, *F. s. dolosa*), small (2.5–4.0 mm; *C. punctulata*, *P. imparis*, *T. sessile*, *L. pergandei*), and minute (<2.0 mm; *M. minimum*). Large ants tended second, third, and fourth instars; small ants tended second and third instars, and minute ants tended first instars. However, larval samples may have been unrepresentative because first and second instars usually burrow into the inflorescence and do not often come in contact with ant tenders (Pierce & Esteal 1986). It also seemed that the number of ant tenders per larva increased as ant size decreased, which would be consistent with Wagner's (1993) observations on *Hemiargus isola* (Reakit). Most larvae we found were feeding on open flowers or buds, with very few on stems or leaves. No statistical testing was attempted due to the small sample sizes.

We thank Leon Higley and Tom Hunt for reviewing an earlier draft of this manuscript, and Gregory Ballmer, Richard Heitzman, and an anonymous reviewer for reviewing the submitted draft. We are grateful to Mark Dubois for ant identifications. Voucher ants have been deposited in the University of Nebraska State Museum and/or in Mark Dubois' personal collection. This is paper number 12085 of the journal series of the Nebraska Agricultural Research Division and contribution number 970 of the Department of Entomology, University of Nebraska.

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ON THE TRUE TYPE LOCALITIES OF *MESOTAENIA VANINKA DELAFUENTEI* NEILD AND *MEMPHIS VILORIAE* PYRCZ & NEILD (NYMPHALIDAE)

Additional key words: butterflies, holotypes, Lepidoptera, Pantepui, Venezuela.

In his recent book on the butterflies of Venezuela, A. Neild (1996) described the new subspecies *Mesotaenia vaninka delafuentei*, apparently based on a color picture made by J. Wojtusiak of the unique female specimen at the Museo del Instituto de Zoología Agrícola, Maracay, Venezuela (MIZA). Neild provided the following in the text: "an extraordi-



FIG. 1. Map of Venezuela showing true type locality (1) of *Mesotaenia vaninka delafuentei* Neild and *Memphis viloriae* Pyrcz and Neild, and the erroneous type locality (2) given in Neild's (1996) book. (1) = Cerro Yutajé, Amazonas state; (2) = Auyán Tepui, Bolívar state.

nary new Venezuelan subspecies . . . also exists on the Auyán Tepui (the source of the Angel Falls), in south-eastern Bolívar state (p. 58) . . . *delafuentei* Neild ssp. n. Auyán Tepui (south-eastern Bolívar state) (p. 59) . . . It was collected on the Auyán Tepui (the source of the Angel Falls), in south-eastern Bolívar state. . . . Type locality Auyán Tepui, south-eastern Bolívar state, in eastern Venezuela." In the Appendices he provided: "Auyán Tepui, Bolívar, Venezuela (full data not recorded) [!] (MIZA) (p. 129) . . . Auyán Tepui, Bolívar, Venezuela, Expedición MIZA (MIZA)" (p. 132). However, the actual data on the label attached to the holotype are: "VENEZ. Amazonas Cerro Yutajé, 1750 m 5°45'N-66°8'W 17-24-II-1995 J. L. García Exp. Terramar." This locality is situated about 380 km to the West of the Auyán Tepui (Fig. 1). We note that this subspecies is dedicated by Neild to Mrs. Alma Torres de la Fuente, and hence the name should be spelled *Mesotaenia vaninka delafuenteae*.

Regarding *Memphis viloriae*, Pyrcz and Neild (p. 114 in Neild 1996) state: "Range . . . presently known only from Venezuela on the Auyán Tepui in eastern Bolívar state . . . Type locality The Auyán Tepui, eastern Bolívar state, in south-eastern Venezuela . . . collected recently at 1700 m elevation, on the slopes of the Auyán Tepui ." In the appendices they state: "Auyán Tepui, Bolívar, Venezuela, 1700 m. Expedición MIZA. Col. J. A. Clavijo (MIZA) (p. 130) . . . Holotype: Auyán Tepui, Bolívar. Coll. J. A. Clavijo (MIZA)" (p. 135). However, the actual data on the two labels attached to the male state: "VENEZ. Amazonas

Cerro Yutajé, 1750 m 5°45'N–66°8'W 12-17-II-1995", and "Col. J. Clavijo A. Exp. Terramar." (see also Fig. 1). This species was dedicated by Pycz and Neild to Angel Viloría and therefore the spelling of the name should be *Memphis viloriai*.

Pantepui is a biogeographic area of high endemism, but even within that area almost every mountain has its own endemic taxa. It is therefore crucial that published locality labels be as exact as possible, especially in original descriptions.

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BOOK REVIEWS

THE WILD SILK MOTHS OF NORTH AMERICA, by Paul M. Tuskes, James P. Tuttle and Michael M. Collins. 1996. Cornell University Press, Sage House, 512 E. State Street, Ithaca, New York 14850. ix + 250 pages, 30 color plates. Hardcover, 22 × 29 cm., ISBN 0-8014-3130-1. \$75 US.

The Saturniidae, or wild silk moths, have historically captured the attention of lepidopterists and others often attracted by the large size and rich colors of many of these moths that number more than 1200–1300 species worldwide. This beautiful book covers about 70 species in 18 genera that occur within the limits of the continental United States and Canada. The authors' many years of experience with these remarkable insects have been condensed and translated into an easily readable tome replete with black and white photographs, maps, and drawings. Thirty fine-quality color plates illustrate in life-size all adult moths treated and smaller photographs illustrate the last instar caterpillars of all but two species. That the authors were able to rear and photograph so many species of moths reveals just part of the dedication, enthusiasm and labor required to produce this outstanding work.

The authors are well known in the United States for their contributions to saturniid research. Paul Tuskes has published numerous papers on the U.S. Saturniidae; James Tuttle, a police detective-lieutenant, has been an officer of the Lepidopterists' Society, and collects, rears and photographs wild silk moths; Michael Collins is a Research Associate with the Carnegie Museum of Natural History, and is especially interested in speciation and natural hybridization.

The text is divided into two main sections in small print, allowing ample information to be packed in: Part One, entitled Behavior and Ecology, discusses topics such as metamorphosis and development, parasitism, diseases, species concepts and taxonomy, collecting, rearing, and silk moth impact on human culture. Part Two, Species Accounts, contains the color plates, and presents a description of each subfamily (three in U.S. and Canada), genus, and species. Each species receives about one or more pages of coverage, including general comments, adult diagnosis, variation and biology, immature stages and rearing notes. I was gratified to see that the striking photographs of caterpillars were presented in the natural "hanging down" position beneath the limb instead of the reverse, as is often done by other authors. Two appendices list host-parasitoid records and saturniid hybrids. An extensive bibliography of cited literature is especially valuable for the student.

However, there is a tendency to overlook or disregard recent taxonomic opinions and conclusions by other U.S. and international saturniologists. An obvious example is the arbitrary decision to reinstate *Sphingicampa* Walsh, 1864 removing all species from *Syssphinx* Hübner, [1819] except *S. molina*, the type species of *Syssphinx*, on the basis that *S. molina* differs morphologically, including differences in the genitalia, from the other species. The authors "feel that the North American species are phylogenetically closer to each other than to *Syssphinx molina*." This is followed by the statement that "The genus *Sphingicampa* is obviously related to *Anisota* and *Dryocampa* and to the tropical genus *Adelocephala*." *Adelocephala* Duponchel, 1841 is not a valid generic name, because it is a junior objective synonym of *Anisota* Hübner [1820] that occurs mainly in North America. Their provincial approach dismisses or ignores the landmark updated revision of Lemaire (*The Saturniidae of America: Ceratocampinae*, 1988, Museo Nacional de Costa Rica, San Jose, 480 pp., 64 plates) who worked with the much greater number of species found throughout the New World, and the work of Fletcher and Nye (*The Generic Names of Moths of the World*, 1982, Vol. 4, Trustees of the British Museum (Natural History), London, 192 pp.) and others. Thus, this otherwise excellent book is a bit weak in its taxonomic treatment, and will perpetuate some confusion among its readers.

The geographical area covered reflects the focus of many U.S. saturniologists, an area limited to North America north of the Mexican border. This political boundary separates a faunistically extremely rich territory to the south from the rest of North America, and hampers or discourages study of these insects by U.S. investigators. But because more than half of North American silk moth species reside there, I would like to see a book in-

tegrating the saturniid fauna of the entire North American continent. Also, a more complete introductory overview of worldwide Saturniidae and recognition of international saturniid researchers would have been welcome. Nevertheless, for areas north of the Mexican border this book represents an impressive reference work that belongs in the library of every serious lepidopterist.

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INDEX OF ECONOMICALLY IMPORTANT LEPIDOPTERA, compiled by Bin-Cheng Zhang. 1994. CAB (Centre for Agriculture and Biosciences) International, North American Office, 8454 North Park Avenue, Tucson, Arizona 85719. 599 pp. Hardcover, 17.5 × 25 cm, ISBN 0-85198-903-9. \$85 US. Also available on diskette (3.5" or 5.25"), MS-DOS only, with access software provided [CD-ROM version was not available to reviewer]; ISBN 0-0000-254-02. Price for book and diskette together: \$119 US.

This book is a reminder that Lepidoptera comprise not only adult forms of spectacular beauty and fascination, but larval ravagers of the land as well. It spotlights pests of agriculture, horticulture, forestry, and environmental management worldwide. In keeping with "economically important" in the title, beneficial species such as silk moths, scale and mealybug predators, and weed feeders are included also.

As traced in the introduction, the book is a result of mergings, branchings, and expansions of previous indexes and databases going back to 1913. (A systematist might be tempted to use an inverted tree to depict this history.) The introduction reflects the tendency for acronyms to proliferate around large databases: ANI for Arthropod Name Index, RAE for Review of Applied (now Agricultural) Entomology, CABI for Centre for Agriculture and Biosciences International, CAB ABSTRACTS for the Centre's bibliographic database, CABPESTCD for the Centre's pest abstracts on compact disk, and more. CABI maintains ANI in electronic form now as a source of preferred insect names for CAB ABSTRACTS, from which RAE and CABPESTCD are produced. The book is a printed version of the Lepidoptera subset of ANI enhanced with annotations.

The book has six sections. It gets to the point promptly; scarcely four pages among its 599 consist of prose, and these are in the opening two sections: Introduction (two pages), and How this Book is Arranged (two pages). The remainder are workhorse sections: List of Common Crop Names Used (three pages), List of Families and Genera (21 pages), Main Index (469 pages), and lastly, Index of Specific and Intraspecific Epithets (97 pages).

List of Common Crop Names Used provides a key so that short and familiar vernacular names can represent many binomial and trinomial host names in the main index. List of Families and Genera is an alphabetical guide to the supraspecific categories in the book with tallies of the number of species in each category covered in the main index. I counted no less than 81 families. The top three in number of species in the main index are, perhaps predictably, Noctuidae with 1034, Pyralidae with 748, and Tortricidae with 687. Butterfly families and their number of main index entries are Nymphalidae 152, Lycaenidae 95, Pieridae 61, Papilionidae 54, and Riordinidae (absent from the book) 0. It is hard to imagine a more authoritative source for ranking the economic importance of lepidopteran families.

Main Index presents the core information by preferred names of the 6000 or so lepidopterans treated in the book. The arrangement is alphabetical by both preferred and nonpreferred genus and species names; author names are included without parentheses. The nonpreferred genus and species names, which also number about 6000, are cross-referenced by "see" to the preferred names. Cross-referencing is a useful and necessary feature because different names have often been used for the same taxa during the history of ANI and RAE, and different names sometimes still prevail in different parts of the

world. Annotations for most species consist of "Common Names," "Host Records," "Geographical Records," and "RAE References." RAE references are to volume number only, thus fostering compactness in the book without greatly hindering retrieval of abstracts and original publications.

Index of Specific and Intraspecific Epithets serves as the book's general index. It is arranged alphabetically by species names, each followed by the preferred generic name in bold italics and any nonpreferred ones in plain italics.

Manufactured at the University Press, Cambridge, the book's print format is comfortably readable, its paper of high quality, and its binding sturdy.

Shortcomings are self-acknowledged. One is that choice of species for inclusion follows from prior inclusion in ANI and RAE. Actually, many included species are of scant economic importance. Some seem present only because important congeners are, or because of a commodity host plant. A few entries lack host records; very few host records mention the plant part affected. It is also stated that expediency prompted assembly of annotations almost entirely from RAE and CAB ABSTRACTS, and therefore the host lists and geographic ranges are not comprehensive. There may be overmodesty in this caveat because RAE covers more than 6200 serials, not to mention annual reports of research and other organizations (Smith, S. [ed.], 1988, *CAB International serial checklist*, 1988 ed., 511 pp.). The annotations for an arbitrary list of species I am familiar with seemed quite adequate. A few synonymies had not caught up with ANI in time to be included in the book. Refreshingly, the book invites readers to suggest improvements to CABI for future editions.

In addition to a source of snapshot information on economic Lepidoptera worldwide, this book improves accessibility to RAE. RAE, an admirable legacy of empire, is the oldest entomological abstract journal, indeed, the only one for more than half a century (Gilbert, P. & C. J. Hamilton, 1990, *Entomology: a guide to information sources*, 2nd edition, Mansell, New York, 259 pp.). It is useful anywhere—in developed countries because it abstracts many obscure publications from the less developed often in languages other than English, and in developing countries because it abstracts expensive publications from the more developed countries. Beginning in 1913 as the Review of Applied Entomology in two series, agricultural (A), and medical (B), RAE was more formally divided in 1990 when the letters began to stand for Review of Agricultural Entomology. Countless professional and student literature reviews have been and still are generated from RAE. ANI and RAE are not only being continued but expanded, references by the thousand being added annually.

The book also aptly identifies its audience, namely people involved in international, national, and local plant quarantine and crop pest management. Journal readers might browse in it for a different or broader spin on their favorite taxa. Anyone who opens it will find it easy to use and informative.

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A MONOGRAPH TO THE NEW WORLD HELIOTHENTINAE (LEPIDOPTERA: NOCTUIDAE), by David F. Hardwick. 1996. Published (apparently) by the author through the Centre for Land and Biological Resources Research, Agriculture Canada, Ottawa, Canada. 281 pages, 24 color plates. 17 × 25 cm, ISBN: None. Soft cover, \$50 US; hardcover, \$70 US, available from the author.

This attractive and potentially useful book is a compilation of Hardwick's extensive work on this widespread, popular subfamily of the Noctuidae. The subfamily Heliiothinae (see below) includes some well-known genera (such as *Heliothis* and *Schinia*) that are brightly colored and can be observed both at lights and on the flowers of the larval foodplants. The

147 species discussed in this book include all apparent known species from Canada, the United States, and Mexico. Hardwick attempts to describe 8 new species and raises a few more to species status. He also attempts to resolve confusing species groups, and in the process synonymizes several species names. This book represents the first major revision of the subfamily, picturing mounted adults of all species as well as the larvae of many, and so is a vital resource for anyone interested in the Heliothinae.

The book is user-friendly in many respects. In the Introduction, Hardwick presents an overview of oviposition behavior and foodplant choice, number of broods and flight periods (in synchrony with the flowering of foodplants), adult behavior and lifespans, and larval feeding habits. He also provides an excellent section on specific rearing techniques for numerous species, as well as general descriptions of all life stages. In the individual species accounts, he presents characteristics of each larval instar and of the pupal stage for those species that have been reared. He includes a larval food plant table for quick reference for those interested in rearing. The color plates depicting the larvae are excellent, providing images that should allow the reader, along with the appropriate sections of text, to make reasonably accurate identifications. The plates of the mounted adults, however, do leave something to be desired. Plates H, J, and L are excessively dark, though are not obscured to the extent where they are virtually useless (Brou, Vernon A., 1997, *A brief critique of "A monograph of the North American Heliothentinae" by David F. Hardwick*, News So. Lepid. Soc. 19:5). Even though the images of many adults are dark (for example those of *Schinia indiana* and *Schinia "conizae"* on plate H are indistinguishable) the images are reasonably accurate and average wingspans are given for each species. Presumably, the individuals who will be using the book will be somewhat familiar with the Heliothinae, and should be able to identify most species through comparisons with the plates.

Although "useful" is a word I used above to describe the monograph, "unsettling" is unfortunately also appropriate as the book experiences a number of shortcomings. The references cited in the book offer an excellent resource of information to anyone interested in heliothine moths, but some extremely important references on noctuid moths are omitted, such as the work on cutworm moths by Rockburne and Lafontaine (1976, *The Cutworm Moths of Ontario and Quebec*, Canada Dept. Agric. Res. Branch Publ. 1593, 164 pp., 613 figs.) and the major work on the owlet moths of Ohio (Rings, Roy W., Eric H. Metzler, Fred J. Arnold, & David H. Harris, 1992, *The Owlet Moths of Ohio (Order: Lepidoptera; Family: Noctuidae)*, Ohio Biol. Surv. Bull. New Series Vol. 9 No. 2, 219 pp., 16 plates). These omitted references provide important information on both flight periods and ranges for several species that would have extended Hardwick's ranges for some species. For example, Hardwick states that *Schinia parmeliana* occurs in the Gulf States, but it has been recorded from Ohio (Rings, et al., *ibid.*), as has what Hardwick calls *Schinia grandimedia* (= *Schinia oleagina* in Ohio in Rings, et al., *ibid.*) that he lists as occurring from Kansas westward. Additionally, although several important institutional and private collections were apparently examined, Hardwick clearly did not examine a number of other collections that would also have filled in or extended the ranges for many species. For instance, Hardwick indicates that he examined specimens of *Schinia bimatrix* "only from the type locality in Texas and from. . . Brandon, Manitoba." Does this mean the species occurs in two very isolated populations, or does the range extend all the way from Manitoba to Texas? The examination of just a few collections from the Great Plains and Rocky Mountain states would have allowed Hardwick to give the range as "sparsely distributed" in much of the Great Plains (as far east as Lawrence, Kansas). Several other ranges are underrepresented: *Schinia ultima* extends north and east of the indicated range into northeastern Kansas and northwestern Missouri; *S. regia* extends north into northwestern Kansas and eastern Colorado; *S. chrysella* is abundant in Missouri and recorded as far east as Kentucky; *S. sexplagiata* extends eastward into west Texas; *Derrima stellata* has been taken many times as far west as Missouri; *Heliocheilus lupatus* extends northward into southern Tennessee; and *H. julia* occurs in the Davis Mountains of west Texas (a locality that is frequented by collectors), not just in Arizona and New Mexico in the United States as listed by Hardwick. I am well aware that the stated ranges/range maps in any book on any group of organisms can never be completely accurate, but the underrepresentations in this book seem a little excessive.

By far the most disturbing aspect of the book are the nomenclatorial problems that have been created in the monograph. Hardwick uses "Heliothentinae" to represent this subfamily, even though the currently approved name (by the International Commission on Zoological Nomenclature [ICZN]) is "Heliothinae." He gives a reasonable argument as to why the name should (probably correctly) be "Heliothentinae," but unfortunately the name currently has no standing. Though the subfamilial name may seem to some to be a minor point, Hardwick's "descriptions" of new species present a major problem to anyone working with heliothines. Hardwick states in his introduction that "... genitalic characters [are not] employed in the treatment of species in the present work." Unfortunately, this practice includes treatment of his "new" species. As indicated by Heppner (1996, *Book review: A monograph to the North American Heliothentinae (Lepidoptera: Noctuidae)*, *Holarctic Lepid.* 3:42), the new species descriptions lack appropriate descriptive information, with no information on or illustrations of genitalia, and very little discussion of important characteristics distinguishing these species from other similar species. It is doubtful that most of the new species are even validly described, as there is not enough diagnostic information presented in the text (according to the appropriate ICZN rules). For instance, Hardwick's "new" species *Schinia blanca*, *S. pulchra*, *S. arizonensis*, and *Heliolonche joaquinensis* are all described solely by the statement "The new species is as illustrated in Figure. . ." (see Brou, 1997, *ibid.*). *Schinia grandimedia*, *S. macneilli*, and *S. subspinosae* are described in a little more detail, but only in comparison to "macular differences" with the close relatives *S. trifascia/oleagina*, *S. persimilis*, and *S. spinosae* respectively. Of all of Hardwick's new species, only the ultimate instar larva of *H. joaquinensis* is described (and illustrated), and the description of the larva is more extensive than that of the adult. *Pyrrhia adela* is also described as new, but the authors of this species (Lafontaine and Mikkola) have used genitalic characters to indicate distinctness from the Old World *Pyrrhia umbra*, the name previously applied to the North American species. Some other "species" have been raised to specific status, including *Schinia conizae* and *S. intermontana*. These two were originally described by Hardwick (1958, *Taxonomy, life history, and habits of the elliptoid-eyed species of Schinia (Lepidoptera: Noctuidae), with notes on the Heliothidinae*, *Can. Entomol. Suppl.* 6:1-116) as subspecies of *S. villosa*, but he now separates them (unfortunately again) on the basis of coloration and macular differences. At least the larval and pupal descriptions of *S. villosa* and *S. intermontana* are detailed and do include some distinct differences. In spite of the problems with the "new" species descriptions, Hardwick has done a respectable job of putting information about heliothine species in one work, though the reader should be aware that there are at least a few species of *Schinia* known to me that are neither pictured nor described in the text (perhaps we should be thankful about this?). As such, not quite the entire fauna is covered in the text, and the reader may, as is always the case, encounter additional undescribed species.

Almost as disturbing as the lack of descriptive information for his "new" species are the numerous synonymies made with an apparent lack of appropriate morphological evidence i.e., he does not discuss what features support the synonymy. Actually, the first major synonymy of *Heliothodes fasciata* and *H. joaquin* with *H. diminutiva* is extensively discussed and well supported. However, virtually every other synonymy lacks credible discussion. Hardwick does indicate where the types are deposited for the synonymized species and whether genitalic preparations have been made. In two cases, types were lacking abdomens, so comparisons of the genitalia of the types was impossible. Hardwick states *Schinia alencis* is a synonym of *S. chrysellae*, explaining that *S. alencis* is a form of *S. chrysellae*, but that the type of *S. alencis* is missing the abdomen. He does not give any indication in the text that other specimens of *S. alencis* have been examined for any unifying characteristics. Hardwick also synonymizes *Schinia ernesta*, *S. baueri*, and *S. sara* with *S. oleagina*, but indicates that the "evident monotype of *S. oleagina*. . . is without abdomen." Some very familiar species, such as *Schinia bifascia* and *S. gloriosa*, have also been synonymized with *S. gracilentae* and *S. sanguinea* respectively, again with no discussion. Even worse, *Schinia ar.*, *S. approximata*, and *S. labe* are all synonymized with *S. sordida*, not only without discussion, but with a statement that "the species [*sordida*] is highly variable in maculation and colouration." An unfortunate side effect of the apparent unsupported synonymies is that the reader will be left unsure as to what species the larval descriptions

and plates may actually represent; thankfully, Hardwick does indicate the source area for all larvae reared. In Hardwick's defense, some of the synonymies are valid. For instance, *Schinia inclara* has been synonymized with *S. siren*; specimens of "*inclara*" I examined are superficially indistinguishable from those of *S. siren*, and the genitalia of the two "species" are virtually identical.

The book, despite all of its shortcomings and uneven as it may be, contains a tremendous amount of useful information. It is the only available compendium of the North American heliothine fauna, and reasonably affordable. Interested workers will find it useful as a visual identification tool, and an excellent resource for adult behavior and larval rearing information for some species. But in many cases the reader is left to wonder what names are actually valid, and some groups are potentially more confusing now (such as the *S. gracilenta/bifascia/oleagina/ernesta/baueri/sarae/grandimedia* [sp. nov.] group) than before the publication of the book. But as is the case with any revisionary work, there is always some debate over nomenclature. There is little doubt that anyone interested in the heliothines will want this book.

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52(2), 1998, 225-226

SUOMEN KIITÄJÄT JA KEHRÄÄJÄT, by Olli Marttila, Kimmo Saarinen, Tari Haahtela and Mika Pajari. 1996. Published by Kirjayhtymä Oy, Helsinki, Finland. 384 pages, 153 color photographs, 3 black and white photographs, 29 color plates, 137 maps. Hardcover, dustjacket, glossy paper, 21.5 × 28.5 cm, ISBN 951-26-4145-3. Available from South Karelia Allergy and Environment Institute (Lääkäritie 15, SF-55330, Tiuruniemi, Finland, e-mail: all.env@inst.inet.fi) for about US \$77.00 (postpaid, airmail).

This team of Finnish authors has again given the lepidopterological community an outstanding book documenting their fauna. As a follow-up to their 1990 book, *Suomen Päiväperhoset*, on the butterflies of Finland (reviewed in 1997 by Warren in the *News of the Lepidopterists' Society*, 39:16-17), the title of this new book roughly translates to mean "Finnish Bombyces and Sphinges," a traditional concept that includes Sphingidae, Lasiocampidae, Saturniidae, Notodontidae, Lymantriidae, Arctiidae, Endromidae, and Lemoniidae. These are the families treated in this volume, and are now all classified in Bombycoidea and Noctuoidea by most taxonomists.

Although the very detailed text is in Finnish, there is an English summary under each species giving basic data on habitat, distribution (with a map of Finland), phenology, and hostplants. A total of 14 excellent illustrations of male and female genitalia are included in the text for similar species that are difficult to distinguish without genital examination. A detailed bibliography on the Scandinavian literature published on these moth groups is of particular value.

The common names of every species covered in the area are given in Finnish, Swedish and English. Swedish is the primary language of about 6% of the Finnish people, but is used regularly by a much larger percentage. While some of us can wade through many foreign language texts using our knowledge of related languages and relying on cognates, this expectation cannot be realized in the case of Finnish, which is neither a Slavic nor Germanic language. We would have liked to see an English version of the table of contents, so that we would not have to guess the topics of the chapters by illustrations alone. These chapters include rearing in captivity, collecting in the field, preparation of specimens for collections, morphology, ecology, and complete species treatments for all 109 species treated, as well as 26 additional species which have not yet been recorded from Finland, but are considered likely to be found in the future. Regarding collecting, imagine collecting moths during the northern summer when the sun never sets!

This book will appeal to book collectors, especially those like us who value books having many color photographs of living caterpillars and adult lepidopterans in their natural habitats. The abundance of stunning and clear photographs with well thought-out compositions (often showing habitat in backgrounds) more than compensates for a text which one may not be able to read. Most of

the moths and many larvae are shown in a natural resting repose. Toward the back of the book is a set of 24 color plates showing all 109 Finnish and 26 hypothetical species pinned and spread. At least one male and one female are illustrated for every species, but many species are represented by up to eight individual specimens to show variation of the species. Additionally, five more color plates show inflated or freeze-dried larvae and pupae and cocoons.

Most of the species covered in this book range throughout much of Europe, and many taxa range across Siberia to the Far East, some even in Japan. Therefore, the coverage of this book should be of interest to lepidopterists in many regions. Lepidoptera conservationists should find the species treatments of endangered fauna such as *Lemonia dumi* (L.), of particular interest.

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MOTHS OF THAILAND, VOLUME 2, SPHINGIDAE, by Hiroshi Inoue, Robert D. Kennett, and Ian J. Kitching, 1997. Published by Chok Chai Press, 45 Soi Isarapab 12, Klong San, Bangkok, 10600 Thailand. vi+149 pages, 44 color plates. Hard cover, 18.5 cm × 26.5 cm, dustjacket. ISBN: none. Available from Brother Amnuay Pinratana, St. Gabriel's College, Bangkok 10300, Thailand. Price US \$35.00.

Several series of works are in progress to cover moths of tropical Asia, including ones for Taiwan, Nepal, Sumatra, Borneo, and China. This is the second volume of the series *Moths of Thailand*, of which volume 1 by A. Pinratana and Rudolf Lampe appeared in 1990 covering Saturniidae. This new volume covering Sphingidae, with 176 species known from Thailand, is more than twice as thick as the one for Saturniidae, with only 29 known species from Thailand. In the volume for Saturniidae, those authors acknowledged that much more collecting needed to be done, especially in southern Thailand. The present volume addresses that issue by bringing together authors from diverse abilities to contribute—one from Japan, one a resident of Thailand who has collected there intensively for more than ten years, and the other at The Natural History Museum (London). Dr. Inoue spent several years dissecting genitalia of Thai sphingids in order to clarify their taxonomy and nomenclature.

The book will serve perfectly to identify specimens collected in Thailand and several neighboring countries, with photographic plates showing all species, subspecies, and color forms. The brief text for each taxon gives the synonymy, key literature references, notes, habitats, flight times, host-plants (cited as genera and families, but not particular plant species), and general distributions. No larvae are figured. There are 50 black and white photographs showing male and female genitalia, conveniently arranged together for easier comparison.

I found only a few typographical errors, and for books cited in the bibliography, the city of the publisher is given, but generally not the publisher's name itself. However, the bibliography appears to be complete and up-to-date, with numerous entries published in the 1990s.

The color plates show how diverse yet uniform the hawk moths can be. Some are obvious bee mimics, and there are large and spectacular species depicted as well, of which some were discovered and named relatively recently like *Rhodambulyx schnitzleri*. The introduced North American *Darapsa myron* is also treated, with the note that its permanent establishment in Thailand remains uncertain (see I. J. Kitching & S. A. Rudge, 1993, *J. Lepid. Soc.* 47:240–242).

With extensive field work by all three authors and taxonomic input by Inoue and Kitching, the nomenclature and systematics in this book are probably highly reliable. As a taxonomist interested in tropical Asian moths, yet one who is not expert on Sphingidae, I question whether the subspecies concept has any validity for such mobile insects, when it is rapidly losing ground among formally trained taxonomists who work with Saturniidae and other lepidopteran families. The other taxonomic question that troubles me is that some of these sphingids appear very similar to ones we have in the New World, yet they are cited under different generic names. I assume that

some generic synonymizing is inevitable as we continue to harmonize the lepidopteran faunas from different continents. However, these taxonomic issues should not be considered deficiencies of the present volume, since they are purely subjective.

The book can be described briefly as having a sturdy physical quality, well organized text, numerous color figures, and very few errors (none of which are serious). Considering these points along with the low price, this book is to be highly recommended to any individual interested in Sphingidae in particular or Asiatic Lepidoptera in general, and it should be added to many libraries around the world. I believe it will stimulate additional field collecting and conservation efforts in Thailand.

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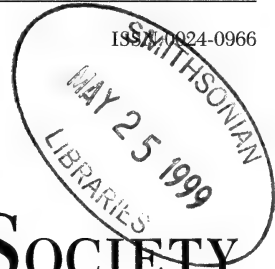
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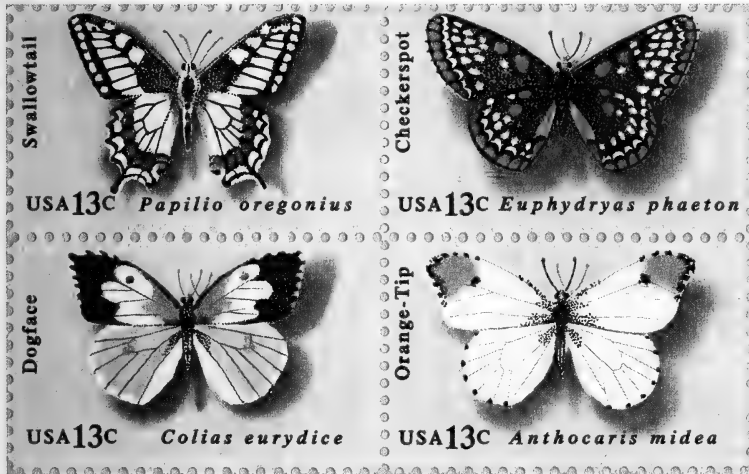
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Cover illustration: Butterfly stamps used for first class mail in the United States. Four species are represented: Swallowtail (*Papilio oregonius*, Papilionidae), Checkerspot (*Euphydryas phaeton*, Nymphalidae), Dogface (labelled as *Colias eurydice* but should be *Zerene eurydice*, Pieridae), Orange-tip (*Anthocaris midea*, Pieridae).

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BUTTERFLIES OF THE UPPER FRIO-SABINAL REGION, CENTRAL TEXAS, AND DISTRIBUTION OF FAUNAL ELEMENTS ACROSS THE EDWARDS PLATEAU

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ABSTRACT. A survey of the butterfly fauna (1988–96) of the upper Frio-Sabinal region of the southern Edwards Plateau, Texas, is presented. Butterflies were observed along transects at five study sites and during repeated opportunistic transects at 12 secondary localities. A total of 28,035 specimens, comprising 100 species was recorded. Another 51 species were reported by other lepidopterists working 15–25 km south of this region during the same period; most were collected from the vicinity of Concan, in north-central Uvalde Co. Twenty-seven species recorded in the upper Frio-Sabinal region were represented by 1–5 specimens only. Simple approximation models were used to estimate the proportion of the theoretical total species collected to date at the upper Frio-Sabinal site. No statistically significant differences were found between the geographical components at the Frio-Upper Sabinal site and two other well-worked sites; Barton Creek (Travis Co.) and Concan (N. Uvalde Co.). Composition and distribution patterns of the butterfly fauna across the Edwards Plateau were examined by analyzing data from 16 reasonably well-collected counties. Geographically, the butterfly fauna across the Edwards Plateau has a strong W/SW trans-Pecos component in Brewster and neighboring counties, which is only weakly represented in the north and east. A S/SE element is significant only along the Balcones fault region from Uvalde to Travis counties, while a NE/E element is numerically important but decreases sharply west of Real and Uvalde counties. Both are associated with the riparian corridors of the southeast. A N/NW element is widespread, but only weakly represented in all counties. Disturbed habitats were dominated by Pieridae (64%). Intergrading dry, subtropical habitats, dry montane woodland areas, coastal woodlands and southern tropical woodlands were dominated by Hesperioidea (45–75%). Richest ecological zones were the south tropical woodlands (49 species), dry subtropical forest and scrub (32 species) and Great Plains savanna habitats (16 species). Other ecological zones were characterized by 12 species or less. The Hesperioidea was the best represented family (97 species) and the Pyrginae the most abundant subfamily (53 species). There is little endemism in the butterfly fauna of Edwards Plateau. The relative species richness (227, with 35 more in Brewster Co. only) can be attributed largely to its strategic geographical position. It is difficult to specify any one element on the Plateau which could truly be said to be characteristic of the butterfly fauna, because so many of these species reach a range limit at some point on the Plateau.

Additional key words: Papilionoidea, Hesperioidea.

¹Deceased

Texas has a diverse butterfly fauna commensurate with its size, wide latitudinal range, topographic variety and complex vegetational zones. The southernmost counties of Texas in particular attract entomologists seeking Neotropical species rarely encountered elsewhere in North America (Opler 1993). Information on the butterflies of Texas is scattered throughout books (e.g., Holland 1930, Klots 1951, Howe 1975, Pyle 1981, Opler & Krizek 1984, Scott 1986, Opler & Malikul 1992, Stanford & Opler 1993, Neck 1996), journal articles (e.g., Freeman 1951, Kendall 1964, 1976, Durden 1982, McGuire 1982, McGuire & Rickard 1974), and annual summary reports of the Lepidopterists' Society. However, only the survey by Durden (1982) treats the south-central region in detail. His decade-long survey concentrated on the butterflies found in the ten counties surrounding Austin, with particular focus on Barton Creek Canyon, a locality at the eastern boundary of the Balcones Fault Zone, and in the transition area of the Edwards Plateau and South Central Vegetational Zones (*sensu* Gould 1969, Ajilvsgi 1984, Amos & Gehlbach 1988, Enquist 1987).

The present paper describes and quantifies the butterfly fauna of the upper Frio-Sabinal region, which encompasses the confluence of the East and West Frio Rivers, in the area where Real, Bandera and Uvalde counties meet. Results are compared with data from two other intensively worked sites, Concan (E. Knudsen 1996, *in litt.*) in central Uvalde Co., 15–25 km south of my Frio-Sabinal sites, and Barton Creek Canyon in the Austin region, 160 km to the northeast (Durden 1982).

Relative distributions of the butterfly fauna across 16 counties of the Edwards Plateau are analyzed by geographic components (5), taxonomic groups (15), habitat types (18) and range position or limit (12), the last two following designations by Durden (1982). Comparisons of species-richness in the counties across the plateau are made with caution. While these can reveal real differences attributable to habitat diversity or differences in magnitude of unit area, they can also be a function of unequal sampling effort. Two approximation models were used to identify under-collecting, and assess the probable level of completeness of the total species counts, for 16 counties across the Edwards Plateau for which reasonable data are available.

MATERIALS AND METHODS

Thirteen expeditions were made to the upper Frio-Sabinal Rivers area of the Edwards Plateau, popularly known as "The Hill Country", between March 1988 and April 1996. The study covered localities in adjacent parts of Real, Bandera and Uvalde counties bounded by 29°25–55'N and 99°20–50'W. Observations were made over 224 h during 160 days at five main study sites (Fig. 1), from 243 linear transects on 15

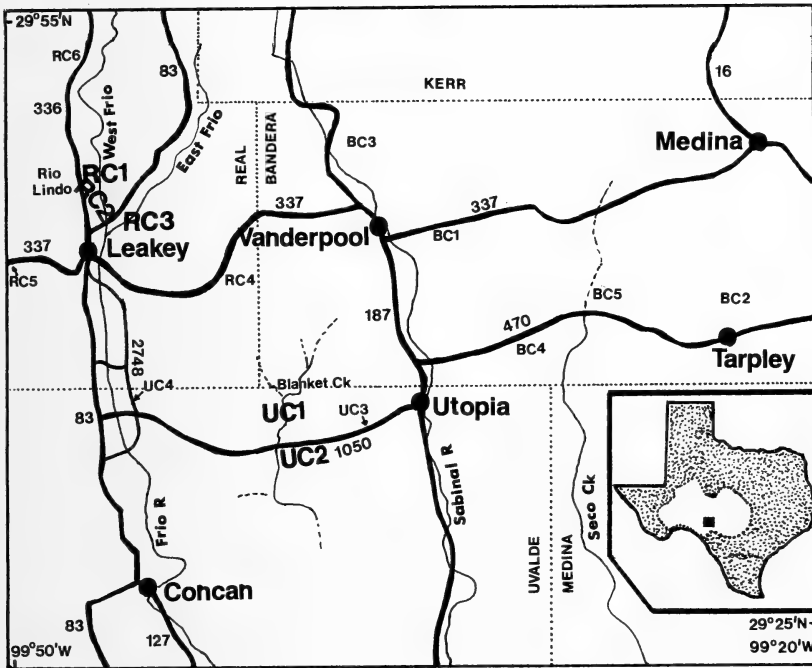


FIG. 1. The upper Frio and Sabinal River region on the south-central Edwards Plateau, Texas. Dotted lines show county boundaries; solid lines state roads (with numbers) and county roads. Study sites have a county abbreviation. The five primary transect sites are in bold.

measured track lines, totaling some 285 km, and an additional 60 h of opportunistic transects at 12 secondary sites (Fig. 1). In both cases, transects were designed, based on initial surveys, to sample all major habitats at each site. Most quantitative observations were collected at sites **RC1-3** near the town of Leakey and **UC1-2** on the Blanket Creek west of Utopia (see below). Transect methodology followed Pollard (1977, 1991), Pollard and Yates (1993), Thomas (1983) and Warren et al. (1984), with minor modifications appropriate to local circumstances.

To facilitate data comparisons, particularly with Durden's detailed butterfly records from Barton Creek, I used species rather than subspecies. Although Durden (1969) argued that "the subspecies is the primary occupant of the niche", the value and definability of either concept is debatable (e.g., Collins 1991, Ehrlich & Murphy 1981a, 1981b, 1982, Hammond 1985, 1990, Kudrna 1986, Miller & Brown 1981, Shapiro 1982), and some of the subspecies listed by Durden have either undergone status changes or are no longer recognized.

Relative abundance of each species was assessed by four categories similar to those used by Durden (1982): **A**, *abundant*—a series of five to ten specimens can be taken in an hour or so; **C**, *common*—such a series can be taken in a day's collecting; **U**, *uncommon*—takes several seasons to collect such a series; **S**, *scarce*—only one to five specimens encountered during the entire study. Durden's category **A** incorporates both my categories **A** and **C**. In my modification, category **A** is reserved only for the handful of species for which well over 1000 specimens were recorded during the survey.

Unlike Durden's semi-quantitative records, results from the time and distance-based transects used in the Frio-Sabinal survey also permit data to be expressed in other ways, such as the logarithmic scaling of numbers per unit search time (see Results), as proposed by Clench (1979).

Butterflies were observed during the following periods: 1988: 16–23 Mar.; 1989: 11–16 May; 1990: 16–21 Sept.; 1991: 6–10 Jul.; 1992: 5–28 May; 5–12 Oct.; 1993: 4–19 May; 1994: 14–24 May; 6–16 Jun.; 8–24 Sep.; 1–7 Nov.; 1995: 12–24 Apr.; 1996: 10–24 Apr. Butterflies were flying on all the days indicated, although in small numbers on two days in March 1988 and two in May 1994.

Several study sites within each of three counties were surveyed (Fig. 1).

NORTHERN UVALDE COUNTY: **UC1.** 547 m. Blanket Creek, on the Indian Blanket Ranch (primary study site subject to periodic minor flooding once or twice each year); **UC2.** 550–580 m. Adjacent section of Ranch Road (RR) 1050 verges (subject to periodic minor flooding); **UC3.** 663 m. Edge of escarpment on RR 1050 about 6 km from Utopia; **UC4.** 540 m. Section of RR 2748, about 1 km from RR 1050 junction.

WESTERN & CENTRAL BANDERA COUNTY: **BC1.** 450 m. Verges of RR 337 about 2 km from junction with HW 187; **BC2.** 520 m. Gun Mountain Ranch near Tarpley; **BC3.** 470 m. Canyon Creek region of Lost Maples State Park (primary study site); **BC4.** 510 m. Verges of RR 470 about 3 km from junction with HW 187; **BC5.** 430 m. On RR 470 about 7 km from Highway (HW) 187.

EASTERN REAL COUNTY: **RC1.** 493 m. "Rio Lindo" property about 3 km N of Leakey, on RR 336 (primary study site subjected to one major flood episode in Dec. 1990); **RC2.** 487 m. West bank of the Rio Frio just E of Rio Lindo (primary study site subject to two major flood episodes, Dec. 1990 & Apr. 1994); **RC3.** 472 m. Twin Forks Estate, about 3 km E of Leakey on RR 337 (primary study site subject to two major flood episodes, Dec. 1990 & Apr. 1994); **RC4.** 450 m. Verges of RR 337 about 5 km E of Leakey; **RC5.** 550 m. Verges of 337 about 5 km W of Leakey on RR 337, towards Camp Wood; **RC6.** 527 m. Verges of RR 336 each side of crossing with Cedar Creek, about 7 km N Leakey (primary study site subject to periodic minor flooding).

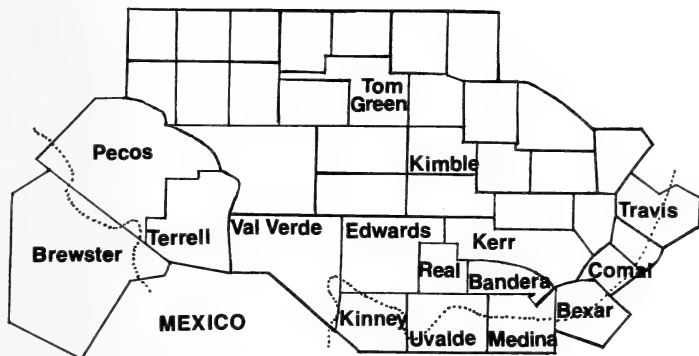


FIG. 2. Schematic map of the southern and central greater Edwards Plateau (after Amos & Gehlbach 1988), showing the 16 counties analyzed. Dotted lines indicate escarpments along the southern edge of the Plateau.

In addition to transect data, records of butterfly species from the 16 counties of Edwards Plateau which have been reasonably well-collected (Fig. 2), were assembled from data points of the maps of Stanford and Opler (1993), their unpublished supplements for 1994 and 1995, annual summaries of the Lepidopterists' Society and unpublished data kindly provided by Mr. E. Knudson, the Zone 6 coordinator for the Society. The data from these two sources showed 227 butterfly species recorded from this area. Each species was categorized by taxon, geographic element, ecological habitat and range limit. Thirty-seven more species were not recorded east of Brewster Co. and are included in comparative totals and calculations only when appropriate.

To compare the species composition of different geographic areas, I used cluster analysis (a program adapted by Dr. Gao Anli of the University Guelph) to calculate dissimilarity coefficients (D) for each pair of taxa. Dissimilarity coefficients (D) are calculated based on the formula $D = 1 - n/N$, where n is the number of areas in which both species occur and N those where either or both occur (Holloway & Jardine 1968, Holloway 1977, 1979). Relationships between all pairs can be displayed as a dendrogram, or in this case, as a compact area dendrogram summarizing average linkage between area groups.

I also assessed the relative completeness of these county species inventories. In such inventories it is important to distinguish real differences among regional faunas from artifacts of unequal collecting effort. Amos and Rowell (1988) faced a similar difficulty during assessments of relatively common species of plants in this region. Three approximation methods were applied to assess the scale of the problem:

1. Records were compared for the 27–33 species of cosmopolitan butterflies with wide ranges through the central and southern United States, most of which should be present in all the 16 counties being assessed on the Edwards Plateau. If less than 24–25 of these had been recorded, then the county was considered as significantly under-collected (see Results).

2. The theoretical maximum number of species of a fauna in a region of known size can be estimated by fitting appropriate field data to one or more asymptotic models. Early examples were given by Fisher et al. (1943), Preston (1948, 1962) and Simpson (1994). Preston (1962) suggested that the numbers of species was an approximate function of the square root of the area in comparable ecological situations. Later models were applied to regional fauna and flora, especially on islands, in various regions of the world by MacArthur (1965, 1972), MacArthur and Wilson (1967), Raven (1967), Robinson (1975), and Holloway (1977, 1979). Whittaker (1972), Poole (1974) and Pielou (1975) provided useful reviews of these techniques.

Preston (1962) and Robinson (1975) demonstrated a linear relationship between plots of log. numbers against log. surface area, for birds of the West Indies, and the Lepidoptera of several South Pacific islands, respectively. This method is applied to the 16 sample counties of the Edwards Plateau in this study (see Results).

3. Clench (1979) found that the number of butterfly species recorded over a period of years at a study site in Pennsylvania followed an asymptotic curve when plotted arithmetically against hours ($\times 100$) spent collecting/observing. He used sequential fits of the constant in the logistic equation to predict the asymptotic value. A similar relationship is shown when the logarithm of species number is plotted against the logarithm of the number of individuals in large samples (Holloway 1979). Frio-Sabinal data were assessed using both these methods (see Results).

RESULTS

Species recorded in the Frio-Sabinal region, measurements of abundance, and new county records. A total of 28,035 specimens representing 100 species was recorded and identified in the upper Frio-Sabinal region during 1988–96 (Table 1). These included eight new records for Bandera County, 10 for Uvalde County and 47 for Real County (indicated by bold initials B, R or U in Table 1). In this context “new county record” is defined as a species not listed for Real, Bandera or Uvalde Counties by Stanford and Opler (1993), or in the 1994 Supplement and Addenda appended to that volume.

Records of 51 more species were accumulated by other lepidopterists during the same period (Table 2). Almost all were from the vicinity of

Concan (387 m) on the south-central edge of the canyon zone of the Plateau, in north-central Uvalde County, about 20 km south of the sites in the present study. Twenty-six of these species have been plotted by Stanford and Opler (1993). The other 25, indicated by bold initials in Table 2, are from annual summaries of the Lepidopterists' Society News (1988–95) and unpublished data (Mr. E. C. Knudson, *in litt.*). A few of these were also briefly noted by Stanford and Opler in the unpublished 1994 supplemental list to their 1993 Atlas.

Species totals for the three upper Frio-Sabinal counties are now: Bandera 86 (77), Real 98 (49) and Uvalde 145 (109). The parentheses show counts given by Stanford and Opler (1993). Numbers for Real and Uvalde also significantly exceed those projected (70 and 110 respectively) by Stanford and Opler in their unpublished 1995 supplemental list to the 1993 Atlas.

Relative abundance and absences in the upper Frio-Sabinal region, 1988–96. The five most abundant butterflies at Frio-Sabinal were *Nathalis iole* Bdv. (7613; 27.15%), *Battus philenor* (L.) (6397; 22.82%), *Colias eurytheme* Bdv. (1654; 5.90%), *Eurema nicippe* (Cram.) (1516; 5.41%) and *Strymon melinus* Hbn. (1062; 3.79%). At the other extreme, 29 species were represented by only 1–5 specimens. A plot of the abundance of each species for the Frio-Sabinal fauna shows a typical monotonically decreasing profile (Fig. 3a), exaggerated by the large proportion comprised of *N. iole* and *B. philenor*. Figure 3b illustrates the profile of the abundance curve when the exaggerated influence of those two species is removed.

A number of species expected for this region were never encountered, despite careful examination of sightings and samples of superficially similar taxa. These include:

1. *Heracles thoas* (L.). I examined the valvae of 43 males netted and released in April–June and September to November. All were *H. cresphontes* Cram. and of these, 15 had the forewing markings similar to those often cited as diagnostic of *thoas*; spot shape seems to be an unreliable criterion for *cresphontes* in this region. The absence of this species in the southern Hill Country is supported by E. K. Knudson (*in litt.*) who had never encountered it during intensive searches and collecting in Uvalde County.

2. Despite the large numbers of small yellows examined, no *Eurema nise* (Cramer) or *E. दौरa* (Godart) were found, only *E. lisa* in various forms and sizes and the seasonal forms of *N. iole*.

3. The presence of the widespread *Phycioides tharos* (Drury) was anticipated, but not recorded; only *P. phaon* (Edw.) and *P. vesta* (Edw.) were moderately common.

4. *Pieris rapae* (L.) was absent from all sites in all years, despite

TABLE 1. Butterfly records from the Frio-Sabinal region of the Edwards Plateau, March 1988 to April 1996. Codes largely follow Durden, 1982 (see text for elaboration): A = abundant, C = common, U = uncommon, S = scarce. Bold letters after species represent new county records: **B**—Bandera; **R**—Real, **U**—Uvalde. Asterisks for *Pyrgus* indicate approximate values based on percent of male genitalia examined in each period. Percentages do not add to 100 due to rounding.

Species	Years												All yrs specimens totals	All yrs percent composition of total	
	1988 Mar.	1989 May	1990 Sep.	1991 Jul.	1992 May	1992 Oct.	1993 May	1994 May	1994 Jun.	1994 Sep.	1994 Nov.	1995 Apr.			1996 Apr.
Hesperioidea															
Hesperitidae															
1. <i>Chiodes zilpa</i> (Butler) R	—	—	S	—	—	—	—	—	—	—	—	—	—	1	<0.01
2. <i>Achalarus toxus</i> (Plötz) R	—	—	—	—	—	—	—	—	S	—	—	—	—	2	<0.01
3. <i>Thorybes bathyllus</i> (Smith) U	—	—	—	—	—	—	—	—	S	—	C	—	—	1	<0.01
4. <i>Thorybes pylades</i> (Scd.) B	—	—	—	S	—	—	—	—	C	—	—	—	U	49	0.17
5. <i>Gorythion begga</i> (Kby) R	—	—	—	—	—	—	—	—	—	S	—	S	—	1	<0.01
6. <i>Systasea pulverulenta</i> (Fid.) R	—	—	—	—	—	—	—	—	—	S	—	—	—	1	<0.01
7. <i>Gesta gesta</i> Evans R	—	—	—	—	—	—	—	—	—	—	—	—	—	1	<0.01
8. <i>Erymnis juvenalis</i> (F.)	S	—	—	—	—	—	—	—	—	—	—	—	—	1	<0.01
9. <i>Erymnis horatius</i> (Scd. & Bg.)	U	C	U	C	A	—	U	C	U	C	—	—	—	723	2.58
10. <i>Erymnis funeralis</i> (Scd. & Bg.) R	—	C	—	—	U	—	U	U	U	—	—	—	—	41	0.15
11. <i>Pyrgus communis</i> (Grote)	U	C	C	U	A	C	U	U	C	U	U	U	U	*206	0.73
12. <i>Pyrgus albescens</i> (Plötz)	—	—	C	—	C	C	—	C	C	U	—	—	S	*242	0.86
13. <i>Pyrgus philetas</i> Edw.	—	—	—	—	—	—	—	—	—	S	—	—	—	13	0.05
14. <i>Calotes nessus</i> (Edw.)	—	—	—	—	—	—	—	—	—	—	—	S	—	1	<0.01
15. <i>Phloxsora cattulus</i> (F.)	—	—	—	—	—	—	—	—	—	S	—	—	—	1	<0.01
16. <i>Nastra julia</i> (Freeman)	—	—	—	—	—	—	—	—	—	—	—	—	—	5	0.02
17. <i>Lerema accius</i> (Smith) R	S	—	—	—	U	S	—	—	U	S	—	—	S	18	0.06
18. <i>Copaecodes aurantiacus</i> (Hew.)	—	S	C	C	C	U	—	—	—	S	S	—	—	41	0.15
19. <i>Copaecodes minimus</i> (Edw.)	—	—	—	C	U	S	—	—	—	U	—	—	S	31	0.11
20. <i>Hylephila phyleus</i> (Drury)	U	C	—	U	U	U	U	C	C	S	C	—	—	53	0.20
21. <i>Hesperia viridis</i> (Edw.)	—	C	—	U	U	U	—	U	S	—	—	S	S	33	0.12
22. <i>Wallengranta otho</i> (Smith)	—	C	—	U	U	—	U	—	—	—	—	S	—	108	0.38
23. <i>Atalopedes campestris</i> (Bdv.) B	—	—	U	—	U	A	S	S	U	—	C	—	U	472	1.68

TABLE I. Continued.

Years Species	1988 Mar.	1989 May	1990 Sep.	1991 Jul.	1992 May	1992 Oct.	1993 May	1994 May	1994 Jun.	1994 Sep.	1994 Nov.	1995 Apr.	1996 Apr.	All yrs species totals	All yrs percent composition of total
24. <i>Anatrytone logan</i> (Edw.) R	—	—	—	—	S	—	S	—	S	—	—	—	—	8	0.03
25. <i>Euphytes vestris</i> (Bdv.) R	—	C	U	C	S	U	U	—	U	A	S	C	U	271	0.97
26. <i>Amblyscirtes njsa</i> Edw.	—	S	—	—	S	S	S	—	—	—	—	—	S	9	0.03
27. <i>Amblyscirtes columbia</i> Skln. R	—	—	—	S	—	S	—	—	—	S	—	—	S	6	0.01
28. <i>Panoquina ocola</i> (Edw.) R	—	—	U	C	U	A	C	U	U	U	C	—	—	29	0.11
29. <i>Lerodea eufala</i> (Edw.)	—	—	—	—	—	U	—	—	—	C	—	—	—	109	0.39
Papilionoidea															
Papilionidae															
30. <i>Battus philenor</i> (L.)	C	A	A	C	A	C	C	C	C	A	U	C	U	6397	22.82
31. <i>Battus polydamas</i> (L.) U	—	—	S	—	—	—	—	—	—	—	—	—	—	1	<0.01
32. <i>Papilio polyxenes</i> F. R	—	—	—	U	C	U	—	U	U	U	—	U	S	82	0.29
33. <i>Heracles cressphontes</i> Gram.	—	C	C	—	U	U	U	U	U	C	U	U	S	103	0.37
34. <i>Heracles ornithion</i> Bdv. U	—	—	S	—	—	—	—	—	—	—	—	—	—	1	<0.01
35. <i>Pterourus glaucus</i> L. B,R,U	S	S	—	—	—	—	—	U	—	—	—	—	S	10	0.03
36. <i>Pterourus multicaudatus</i> Kby.	—	—	—	—	—	—	—	—	—	U	—	—	—	7	0.03
37. <i>Pterourus troilus</i> L. R	—	S	—	—	—	—	—	—	U	—	—	—	—	5	0.02
38. <i>Appias drusilla</i> (Gram.) R,U	—	—	—	—	U	—	—	—	—	—	—	S	—	21	0.08
39. <i>Pontia protodice</i> (Bdv. & Lct.) U	—	—	—	—	C	U	S	S	U	—	S	U	S	118	0.42
40. <i>Ascia monuste</i> (L.) R	—	—	—	—	—	S	—	—	—	—	—	—	—	1	<0.01
41. <i>Colias eurytheme</i> Bdv. R	U	C	U	U	A	C	C	C	U	S	C	A	S	1654	5.90
42. <i>Colias philodice</i> Godt. R	—	—	—	—	—	—	—	—	—	—	S	S	—	5	0.02
43. <i>Zerene cesonia</i> (Stoll.) R	U	A	C	—	C	U	C	U	U	U	C	U	S	243	0.87
44. <i>Phoebis sennae</i> (L.) R	—	U	C	—	S	S	U	S	S	S	S	S	—	47	0.17
45. <i>Phoebis philea</i> (Johansn.) R	—	—	U	U	—	—	S	S	—	S	—	—	—	8	0.03
46. <i>Phoebis agarithe</i> (Bdv.) R	—	A	U	U	—	—	—	S	—	A	S	—	—	61	0.22
47. <i>Kricogonia lyside</i> (Godt.) R	—	C	U	U	A	—	C	C	U	A	—	—	S	704	2.51
48. <i>Eurema lisa</i> Bdv. & Lct.	—	C	C	C	C	C	—	U	U	C	C	C	S	348	1.24
49. <i>Eurema nicippe</i> (Gram.)	—	—	A	C	A	C	C	C	C	C	A	C	U	1516	5.41
50. <i>Eurema mexicanum</i> (Bdv.) R	—	—	S	—	—	—	—	—	—	—	—	S	—	3	0.01

TABLE I. Continued.

Species	1989		1990		1991		1992		1993		1994		1994		1994		1995		1996		All yrs percent composition of total
	Mar.	May	Sep.	Oct.	Jul.	May	Oct.	May	May	Jun.	Sep.	Nov.	Apr.	Apr.	Apr.	Apr.	Apr.	Apr.	Apr.	Apr.	
51. <i>Nathalis iole</i> Bdv.	—	C	A	U	A	C	U	U	A	A	U	C	A	C	C	—	—	—	—	—	27.15
Lycenidae																					
52. <i>Atides halesus</i> (Cram.) B	—	—	—	—	—	S	—	U	U	U	—	—	S	—	—	—	—	—	—	20	0.07
53. <i>Phacostripon alcestis</i> (Edw.) R	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	<0.01
54. <i>Satyrium calanus</i> (Hbn.) R,U	—	—	—	—	—	U	—	C	S	—	—	—	—	—	—	—	—	—	—	25	0.09
55. <i>Calycopis isobeon</i> (Btl. & Drc.)	—	—	—	—	—	C	—	—	—	—	C	U	S	—	—	—	—	—	—	70	0.25
56. <i>Mitoura grynea</i> (Hbn.)	U	U	—	—	U	C	—	—	—	—	U	—	U	S	—	—	—	—	—	86	0.31
57. <i>Fixsenia favonius</i> (Smith) R	—	—	C	—	—	C	—	—	—	—	C	S	U	S	—	—	—	—	—	109	0.39
58. <i>Strymon melinus</i> Hbn.	—	—	C	—	—	U	—	—	—	—	C	S	U	S	—	—	—	—	—	1062	3.79
59. <i>Brephidium exile</i> (Bdv.)	—	—	—	—	—	—	S	—	S	—	—	—	—	—	—	—	—	—	—	3	0.01
60. <i>Leptotes marina</i> (Reak.) B	—	—	—	—	—	—	—	—	—	—	—	S	—	—	—	—	—	—	—	6	0.02
61. <i>Hemiarctus ceraunus</i> (F.) R	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	0.02
62. <i>Hemiarctus isola</i> (Reak.)	—	A	C	C	C	C	U	U	C	C	U	U	C	U	C	U	C	U	U	820	2.92
63. <i>Everes comyntas</i> (Godt.) B,R	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	0.02
Riodimidae																					
64. <i>Calephitis nemesis</i> (Edw.)	—	S	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	0.02
65. <i>Calephitis rausoni</i> McAlp.	—	—	—	—	—	—	S	—	—	—	—	—	—	—	—	—	—	—	—	1	<0.01
Libytheidae																					
66. <i>Libytheana carinenta</i> (Cram.)	—	C	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	39	0.14
Nymphalidae																					
67. <i>Agraulis vanillae</i> (L.).	U	C	C	C	C	C	C	C	U	C	U	C	U	C	U	C	U	U	U	433	1.54
68. <i>Dryas julia</i> (F.) U	—	—	—	—	S	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	0.01
69. <i>Heliconius charitonius</i> (L.).	—	—	—	—	S	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	0.01
70. <i>Polygonia interrogatoris</i> (F.) R	—	S	U	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	0.03
71. <i>Polygonia comma</i> (Harr.) R,U	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	<0.01
72. <i>Nymphalis antiopa</i> (L.) B,R	—	S	—	—	—	S	—	—	S	S	—	—	—	—	—	—	—	—	—	6	0.02
73. <i>Vanessa virginiensis</i> (Dry)	U	C	—	—	—	C	U	U	C	C	U	U	C	U	C	U	C	U	C	368	1.31
74. <i>Vanessa cardui</i> (L.) R	—	U	U	—	—	U	—	—	S	—	—	—	—	—	—	—	—	—	—	65	0.23

TABLE I. Continued.

Years Species	1988		1989		1990		1991		1992		1993		1994		1994		1995		1996		All yrs percent composition of total	
	Mar.	May	May	Sep.	Jul.	May	Oct.	May	May	Sep.	Jun.	Sep.	Nov.	Apr.	Apr.	Apr.	Apr.	Apr.	Apr.	Apr.		
75. <i>Vanessa atalanta</i> (L.)	U	C	C	C	—	C	U	U	U	C	C	U	U	U	U	U	C	U	S	S	324	1.15
76. <i>Junonia coenia</i> (Hbn.) B, R	—	—	C	C	U	C	C	—	—	—	—	—	—	—	—	—	—	—	—	—	193	0.691
77. <i>Junonia nigrossuffusa</i> B. & MD. R	—	—	—	—	—	S	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	0.02
78. <i>Euptoieta claudia</i> (Cram.) R	U	A	C	C	U	A	C	U	C	C	C	U	S	C	S	C	C	S	S	S	705	2.51
79. <i>Anthanasia texana</i> (Edw.) R	S	A	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	143	0.51
80. <i>Phycodes phaon</i> (Edw.)	—	C	U	U	U	A	U	S	C	U	C	U	C	U	U	U	U	U	U	U	321	1.14
81. <i>Phycodes vesta</i> (Edw.)	—	A	C	C	—	C	U	—	—	—	—	—	—	—	—	—	—	—	—	—	213	0.76
82. <i>Charitryas nictes</i> (Dblld.) R	—	—	C	C	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	48	0.17
83. <i>Chlosyne lacinia</i> (Gey.)	—	C	—	—	—	U	C	—	—	—	—	—	—	—	—	—	—	—	—	—	116	0.41
84. <i>Chlosyne janais</i> (Drury) R	—	—	—	—	—	S	S	—	—	—	—	—	—	—	—	—	—	—	—	—	13	0.05
85. <i>Thessalia theona</i> (Mén.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	0.03
86. <i>Texola elada</i> (Hew.) R	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	0.03
87. <i>Basilarchia archippus</i> (Crm.) R	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	0.01
88. <i>Basilarchia astynax</i> (F.)	—	—	—	—	—	—	—	—	—	—	—	S	—	—	—	—	—	—	—	—	2	0.01
89. <i>Adelpha bredowii</i> (Gey.)	—	—	—	—	—	—	—	—	—	—	—	U	U	U	U	U	U	S	S	S	35	0.12
90. <i>Mestra amymone</i> (Mén.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	97	0.35
91. <i>Anaea andria</i> Scd. R	—	—	—	—	—	—	—	—	—	—	—	U	S	U	U	U	U	U	U	U	58	0.21
92. <i>Asterocampa celtis</i> (Bd. & Lt.) R	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	25	0.89
93. <i>Asterocampa leila</i> (Edw.) R	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	0.11
94. <i>Asterocampa clyton</i> (Bd. & Lt.) R	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	0.02
Satyridae																						
95. <i>Megisto cymela</i> (Cram.) R, U	—	—	—	—	—	—	—	—	—	C	U	—	—	—	—	—	—	—	—	—	197	0.70
96. <i>Megisto rubricata</i> (Edw.)	—	C	C	C	U	C	—	—	—	—	—	—	—	—	—	—	—	—	—	—	76	0.27
97. <i>Cercyonis pegala</i> (F.) R	—	C	A	C	C	C	C	S	C	C	C	S	—	—	—	—	—	—	—	—	339	1.21
98. <i>Hermeuptychia hermes</i> (F.) U	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	0.01
Danaidae																						
99. <i>Danaus plexippus</i> (L.)	—	—	U	U	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	327	1.17
100. <i>Danaus gilippus</i> (Cram.)	—	C	C	C	U	C	C	U	C	C	C	U	C	U	U	U	U	U	U	U	201	0.72
																				28035	*100.00	

TABLE 2. Records of butterfly species in the Frio-Sabinal region from sources other than the present survey. Bold initials indicate new county records since 1993, following Table 1. Abbreviations: CB: Charles Bordelon, Jr.; ECK: Ed Knudson; JD: Joseph F. Doyle III; JR: Joann Karges.

Species no.	Family & species	County	Reference
Hesperiidae			
101.	<i>Epargyreus clarus</i> (Cram.) U	Uvalde.	ECK, <i>in litt.</i> 1996.
102.	<i>Chioides albofasciatus</i> (Hew.)	Uvalde.	Stanford & Opler (1993). CB, Lep. Soc. Summ. 1993.
103.	<i>Urbanus proteus</i> (L.) U	Uvalde.	ECK, <i>in litt.</i> 1996.
104.	<i>Urbanus dorantes</i> (Stoll.) U	Uvalde.	ECK, <i>in litt.</i> 1996.
105.	<i>Achalarus jalapus</i> (Plötz) U	Uvalde.	CB, Lep. Soc. Summ. 1994.
106.	<i>Astraptus fulgerator</i> (Walch) U	Uvalde.	CB, Lep. Soc. Summ. 1993.
107.	<i>Cogia hippalus</i> (Edw.)	Uvalde.	ECK, <i>in litt.</i> 1996.
108.	<i>Cogia outis</i> (Skin.)	Uvalde.	Stanford & Opler (1993, p. 21).
109.	<i>Staphylus mazans</i> (Reak.)	Uvalde.	Stanford & Opler (1993, p. 27).
110.	<i>Staphylus hayhurstii</i> (Edw.)	Bandera.	Stanford & Opler (1993, p. 28).
111.	<i>Achlyodes thraso</i> (Hbn.) U	Uvalde.	ECK, <i>in litt.</i> 1996 (<i>milhrdates</i>).
112.	<i>Grais stigmatica</i> (Mab.)	Uvalde.	Stanford & Opler (1993, p. 36).
113.	<i>Chiomara asychis</i> (Stoll.) U	Uvalde.	ECK, <i>in litt.</i> 1996.
114.	<i>Erynnis tristis</i> (Bdv.) U	Uvalde.	CB, Lep. Soc. Summ. 1993. Listed in Stanford & Opler 1994 unpubl. suppl.
115.	<i>Pyrgus oilens</i> (L.)	Uvalde.	ECK, <i>in litt.</i> 1996. Listed in Stanford & Opler (1993).
116.	<i>Helioptes macaira</i> (Reak.) U	Uvalde.	JR, Lep. Soc. Summ. 1995.
117.	<i>Helioptes lavianus</i> (Hewitson) U	Uvalde.	JD, Lep. Soc. Summ. 1995.
118.	<i>Ancylomypha numitor</i> (F.)	Real, Bandera.	Stanford & Opler (1993, p. 65).
119.	<i>Ancylomypha arene</i> (Edw.)	Uvalde Co.	Stanford & Opler (1993, p. 65).
120.	<i>Polites vibex</i> (Gey.)	Bandera, Uvalde.	Stanford & Opler (1993, p. 75).
121.	<i>Amblyscirtes aenus</i> Edw. U	Bandera, Uvalde.	Stanford & Opler (1993, p. 87).
122.	<i>Amblyscirtes oslari</i> (Skin.)	Bandera, Uvalde.	ECK, <i>in litt.</i> 1996. Stanford & Opler 1993, p. 87. ECK, <i>in litt.</i> 1996.

TABLE 2. Continued.

Species no.	Family & species	County	Reference
123.	<i>Amblyscirtes eos</i> (Edw.)	Bandera, Uvalde.	Stanford & Opler (1993, p. 89). ECK, <i>in litt.</i> 1996.
124.	<i>Calpodex ethlius</i> (Stoll.) U	Uvalde Co. Concan.	ECK, <i>in litt.</i> 1996.
125.	<i>Megathymus yuccae</i> (Bdv. & Let.)	Bander, Real, Uvalde.	Stanford & Opler (1993, p. 101). ECK, <i>in litt.</i> 1996.
Pteridae			
126.	<i>Paramidea midea</i> (Hbn.)	Uvalde.	Stanford & Opler (1993, p. 121). ECK, <i>in litt.</i> 1996.
127.	<i>Anteos clorinde</i> (Godt.) U	Uvalde.	ECK, <i>in litt.</i> 1996.
128.	<i>Anteos maerula</i> (F.) U	Uvalde.	ECK, <i>in litt.</i> 1996.
129.	<i>Eurema proterpia</i> (F.) U	Uvalde.	ECK, <i>in litt.</i> 1996.
Lycanidae			
130.	<i>Chlorostrymon simaethis</i> (Drury) U	Uvalde.	ECK, <i>in litt.</i> 1996.
131.	<i>Ministrymon clytie</i> (Edwards) U	Uvalde.	CB, Lep. Soc. Summ. 1994.
132.	<i>Ministrymon azia</i> (Hew.) R, U	Real, Uvalde.	Stanford & Opler 1994, unpubl. supp. Stanford & Opler 1994, unpubl. supp. ECK, <i>in litt.</i> 1996.
133.	<i>Xamia xami</i> (Reak.) U	Uvalde.	ECK, <i>in litt.</i> 1996.
134.	<i>Incisalia henrici</i> (G. & R.)	Bandera, Real, Uvalde.	Stanford & Opler (1993, p. 158). ECK, <i>in litt.</i> 1996.
135.	<i>Parrhasius m-album</i> (Bdv. & Let.) U	Uvalde.	CB, JD, ECK, Lep. Soc. Summ. 1993. Stanford & Opler 1994, unpubl. supp.
136.	<i>Strymon alea</i> (Godm. & Salv.) U	Uvalde.	CB, ECK, Lep. Soc. Summ. 1995.
137.	<i>Strymon columella</i> (F.)	Uvalde.	Stanford & Opler 1993, p. 164. ECK, <i>in litt.</i> 1996.

TABLE 2. Continued.

Species no.	Family & species	County	Reference
138.	<i>Zizula cyna</i> (Edw.)	Uvalde.	Stanford & Opler 1993, p. 170. ECK, <i>in litt.</i> 1996.
Riodinidae			
139.	<i>Calephelis perditalis</i> B & McD. U	Uvalde.	ECK, <i>in litt.</i> 1996.
140.	<i>Caria ino</i> (Godm. & Salv.) U	Uvalde.	ECK, <i>in litt.</i> 1996.
Nymphalidae			
141.	<i>Dione moneta</i> Hbn. U	Uvalde.	ECK, <i>in litt.</i> 1996.
142.	<i>Euptoieta hegesia</i> (Cram.) U	Uvalde.	ECK, <i>in litt.</i> 1996.
143.	<i>Phycoides tharos</i> (Drury) U	Bandera, Real, Uvalde.	Stanford & Opler (1993, p. 211). ECK, <i>in litt.</i> 1996.
144.	<i>Phycodes tulcis</i> (Bates) U	Uvalde Co.	Stanford & Opler (1994 unpubl. supp.).
145.	<i>Anartia jatrophae</i> (Johansn.)	Uvalde Co.	Stanford & Opler (1993, p. 221).
146.	<i>Siprocta stelenes</i> (L.)	Bandera, Uvalde.	Stanford & Opler (1993, p. 222). ECK, <i>in litt.</i> 1996.
147.	<i>Eunica monima</i> (Stoll.) U	Uvalde.	ECK, <i>in litt.</i> 1996.
148.	<i>Dynamine dyomis</i> Gey. U	Uvalde.	NR, JR, CN, ECK, CB, JD, Lep. Soc. Summ. 1995
149.	<i>Biblis hyperia</i> (Cram.) U	Uvalde.	ECK, <i>in litt.</i> 1996.
150.	<i>Anaea aidea</i> (Guer.-Mén.) U	Uvalde.	ECK, <i>in litt.</i> 1996.
Danaidae			
151.	<i>Danaus eresimus</i> (Cram.)	Uvalde.	Stanford & Opler (1993, p. 257). ECK, <i>in litt.</i> 1996.

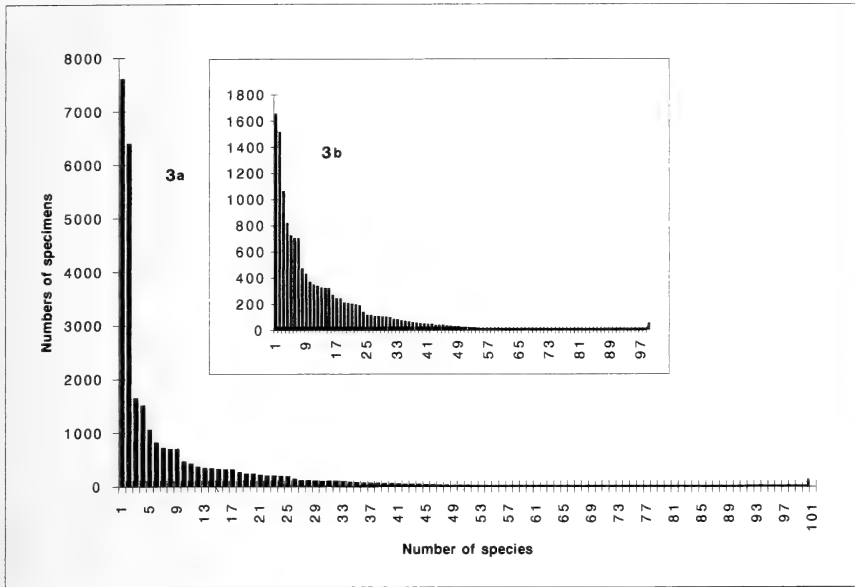


FIG. 3. Abundance versus species of butterflies recorded on transects from the upper Frio-Sabinal region 1988–1996, showing a typical monotonically decreasing profile (3a). 3b (inset) shows the profile with the two commonest species, *N. iole* and *b. philenor* removed.

scrutiny of all white butterflies netted or observed at each locality, even in the cultivated areas around Utopia and Leakey townships.

5. Among the Hesperioidea, specimens of *Erynnis* Shrank and *Pyrgus* Hbn. were netted and examined whenever possible to minimize the chance of overlooking similar species. *P. philetas* Edw. was found to occur in the hotter, later part of the year at some sites, but all *Erynnis* examined proved to be *E. horatius* (Scudd. and Burg.) or *E. funeralis* (Scudd. and Burg.), with the exception of a single *E. juvenalis* (F.) taken at the Blanket Creek in March 1988.

6. The apparent absence of *Polites vibex* (Gey.) was also noteworthy because it has been recorded previously in Bandera and Uvalde counties, as well as Kerr and Medina (Stanford and Opler 1993). Occasionally, males may have been confused with *Hylephila phyleus* (Drury) on transects, or females overlooked among clusters of the more common *Atalopedes campestris* (Bdv.), even though we were actively looking for *P. vibex*.

Assessment of relative completeness of county inventories. Records of butterfly species for counties on the Edwards Plateau range from 170 in Bexar, to only two in Midland (Stanford and Opler 1995 un-

TABLE 3. Counts of butterfly species from well-collected counties of the Edwards Plateau, by geographical range. See text for methods of assigning butterfly species to a particular range. *"Tom Green" is a conglomerate based on records of the moderately worked nearby counties (providing a provisional estimate for the central northern region of the Plateau).

Geogr. element	Brewst.	Pecos	Terrill	V. Verde	Edwards	Kinney	Real	Uvalde	*"Tom Green"	Kerr	Bandera	Medina	Brew	Conal	Travis	MEANS
N/NW	15	3	5	6	8	4	14	15	12	21	14	5	19	14	19	11.4
NE/E	18	7	9	18	7	12	28	36	20	44	28	18	47	40	50	24.8
S	20	4	7	11	5	11	12	43	6	29	8	10	49	29	43	18.3
W/SW	77	13	19	16	10	19	15	20	11	22	7	12	24	16	21	19.5
COSM.	31	25	28	29	17	27	29	31	36	31	29	33	31	30	31	28.8
TOTALS	161	52	68	80	47	73	98	145	85	147	86	78	170	129	164	—

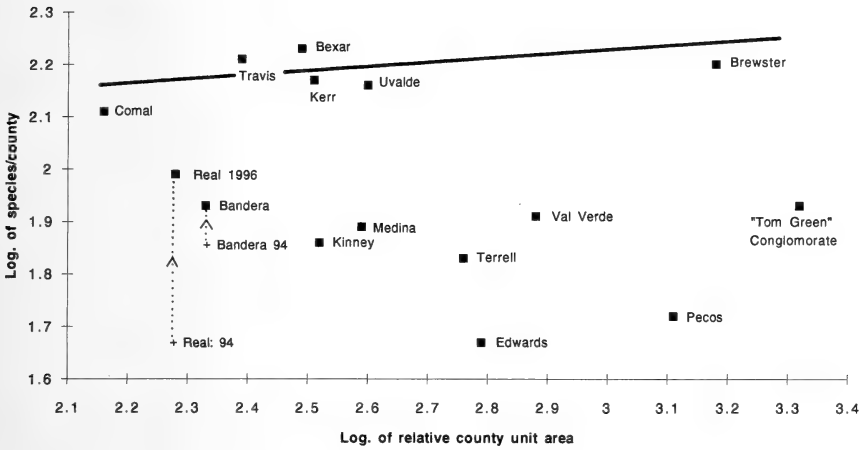


FIG. 4. Log-log relationship between total species recorded in each county versus area in square kilometers, assuming similar ecological parameters (after Preston 1962). Values on or near the line are presumed to be close to the "maximum". Counties falling below the line are probably under-collected, but may have less diverse habitat.

publ. supp.). Of course Midland is an extreme case, but unequal collecting effort may still be an important, but overlooked, factor when relatively high species totals are being compared. The cosmopolitan butterfly species were summed for each of the 16 sampled counties of the Edwards Plateau. Thirteen had records of 27–33 such species and three had 17–25, with a mean of 28.8 (Table 3). In the case of Real Co., 49 species in total had been recorded by 1993, of which 23 were cosmopolitan. These might seem to be appropriate numbers, because Real is one of the smallest counties on the Plateau, but Stanford and Opler's (1993) data base showed *Vanessa cardui*, *V. virginiensis*, *J. coenia*, *A. texana*, *F. favonius* and *E. vestris* still unrecorded, so Real was obviously under-collected. During the present survey, the species total for Real has risen to 98, with a cosmopolitan element of 29.

When the data on number of species per county from the Edwards Plateau counties are log-transformed and plotted against log(county area) (Fig. 4), the well-collected counties such as Bexar, Brewster, Comal, Kerr, Travis and Uvalde fall close to the line, while most of the others counties fall well below it. The recent data from the Frio-Sabinal surveys have shifted the values for Bandera and more markedly, Real Co., closer to the line in Fig. 4. This data indicate that the theoretical "maximum" species total for both these counties could be 160–165 species, if ecological parameters and migratory patterns are approximately comparable across the Plateau (see Discussion).

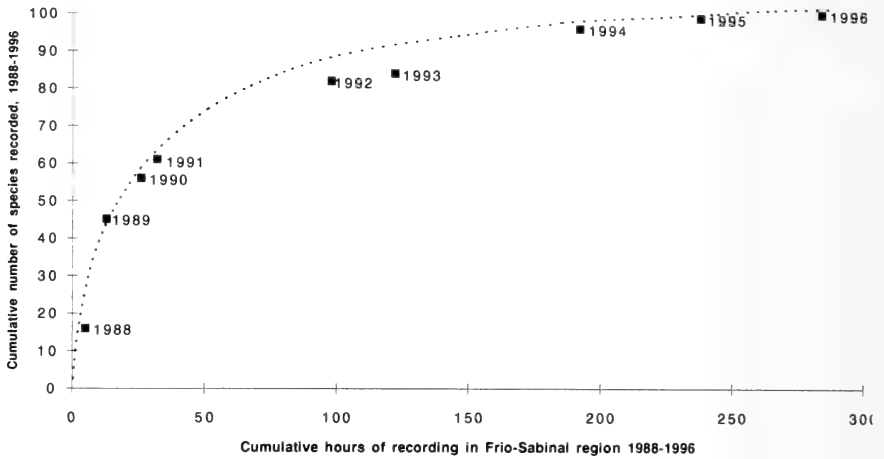


FIG. 5. Clench (1979) estimated "maximum" number of species for a by plotting cumulative number of species against cumulative sampling time. The curve for Frio-Sabinal seems asymptotic after 8–9 years of recording.

When the Edwards Plateau data are plotted following the models of Clench (Fig. 5), and Holloway (Fig. 6) however, the asymptotic curves indicate that the "maximum" number of species in Bandera and Real counties might be only 110–120, not 160–165.

Linkages across the Edwards plateau. Species totals for Edwards (47 species), Pecos (52), Terrell (68), Kinney (73) and Kimble counties

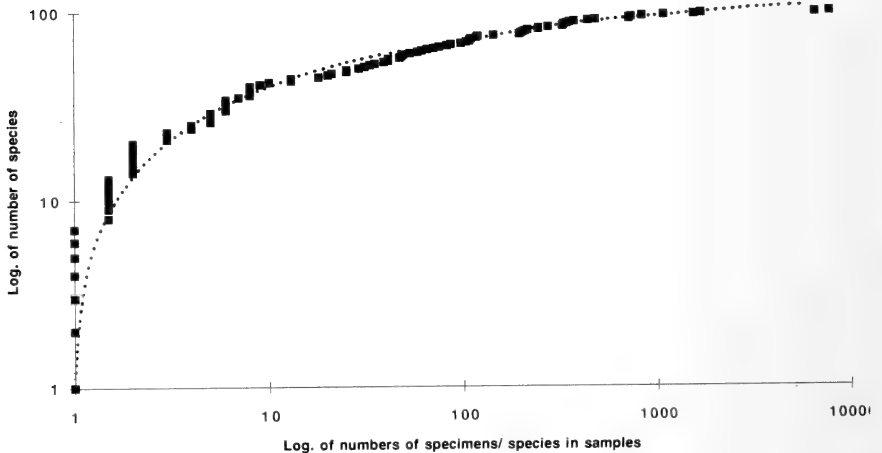


FIG. 6. Holloway (1979) plotted log species number against log number of specimens in large samples. The asymptotic curve produced from the Frio-Sabinal data is similar to Fig. 5.

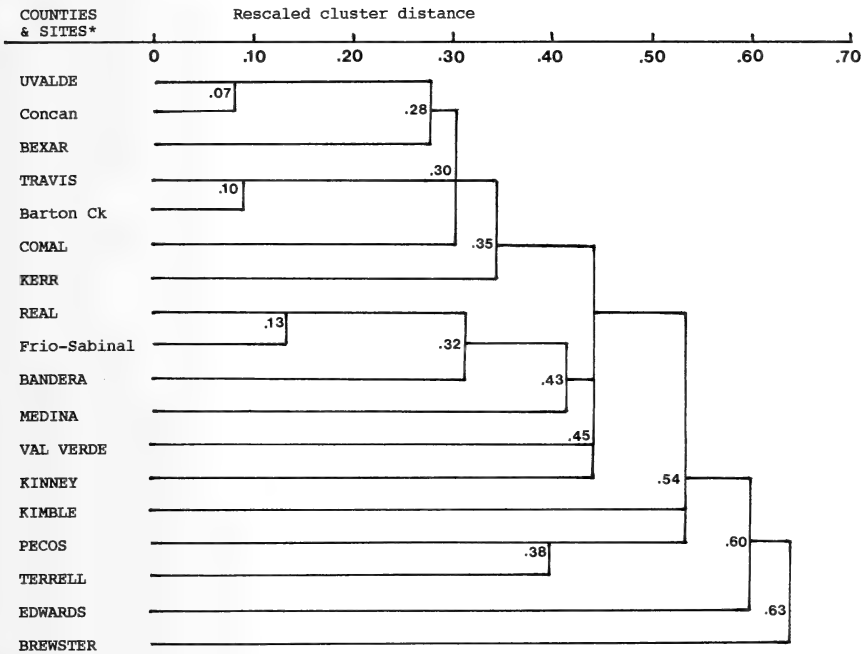


FIG. 7. Dendrogram showing provisional interrelationships of the butterflies of the Edwards Plateau. Dissimilarity coefficients were calculated for each pair of taxa of the total species sample. The butterfly fauna in the southeastern cluster of counties is more cohesive than those in the west. The relative isolation of Brewster County was anticipated, but that of Edwards may be a function of under-collecting.

(62), are likely to be too low, although all but the last range from relatively dry to arid (Riskind and Diamond 1988). The estimate for Tom Green county (85) is a composite (see Table 3 caption) and should be interpreted with special caution. Totals for other counties (78 to 170 species), i.e., Bandera, Bexar, Brewster, Comal, Kerr, Real, Travis, and Uvalde counties are not likely to change by more than 5–20% in the near future. Projecting totals by weighted averages is risky without good information.

The dendrogram (Fig. 7) shows the dissimilarity coefficients for pairs of counties or groups of counties. Lower numbers (a lower dissimilarity coefficient) indicate a greater degree of overlap in the butterfly fauna of those regions. This dendrogram demonstrates the relative distinctiveness of Brewster Co., even from Pecos and Terrell counties, despite their having some faunal components in common. Edwards appears almost as isolated as Brewster. The general faunal cohesion of the southeastern block of counties, Travis, Comal, Bexar, Kerr and Uvalde is confirmed, as is the anticipated similarity of Real and Bandera counties. The

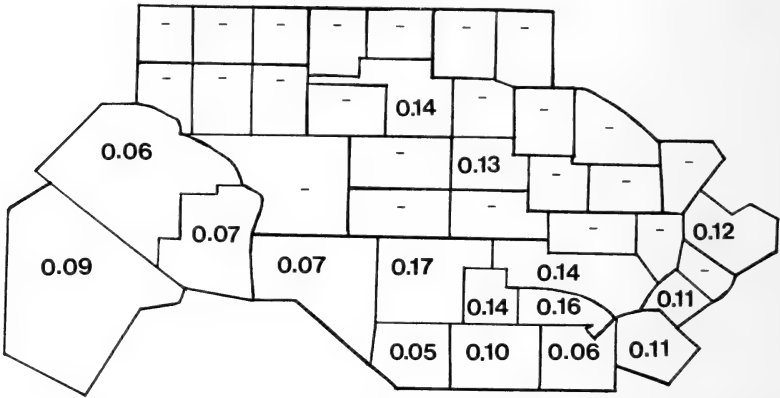


FIG. 8. N-NW species as a proportion of the butterfly fauna of 16 sampled counties on the Edwards Plateau.

Barton Creek site is shown to be usefully representative of the fauna of Travis, as are Concan of Uvalde Co., and Frio-Sabinal of Bandera and Real counties. Remaining counties also appear relatively isolated but interpretation is best reserved until more information is available.

A frequency count revealed that only 37 species were known to occur in all but one to three of the counties, while 114 of the 261 had been recorded in only one to three counties. Among families, restricted distribution was most apparent in the HesperIIDae; 54% and 57% of all Pyrginae and Hesperinae, respectively, were restricted to three or fewer of the sample counties, generally in the western sector of the Plateau.

Comparative distributions of butterfly species on the Edwards plateau. The data matrix was used to show all species classified by: A) Geographical components by counties (Table 3), B) Species in ecological habitats by counties (Table 4) and taxon (subfamilies) (Table 5); C) Relative position by county with respect to overall range (Table 6). All data are given as numbers, not percentages.

Comparison of geographical components. Butterfly species were allocated to one of five groups based on their geographical distribution relative to the Edwards Plateau (Table 3): 1) N/NW-species which have predominantly California-Rockies-Great Plains distributions (Fig. 8); 2) NE/E-prairie-eastern coastal woodlands (Fig. 9); 3) S-tropical coastal forest (Fig. 10); 4) SW/W (Sonoran-Coahuilan) (Fig. 11), and 5) COSM-cosmopolitan species, or ranging at least through Mexico-Texas-central Gulf states (not figured). Most attributions are from Durden (1982); species not recorded by him are by my allocation. Data were extracted from Stanford and Opler (1993), and their unpublished supplements of 1994, 1995. Accounts by Howe (1975), Pyle (1981), Scott (1986), Opler

TABLE 4. Numbers of butterfly species from 16 selected counties across the Edwards Plateau, classified by habitat zones following Durden (1982). Parenthetical values for Brewster County include 37 species not yet recorded east of this county.

Habitat v. county	Brewst.	Pecos	Terrell	V. Verde	Edwards	Kinney	Real	Uvalde	Tom Green	Kimble	Kerr	Bandera	Medina	Bear	Comal	Travis
A. Disturbed sites	9(10)	6	8	8	4	7	9	8	9	6	99	8	8	9	7	11
B. Great Plains flora	10(11)	6	8	8	5	5	12	10	12	7	15	11	6	14	14	16
C. Dry warm temp. —subtropical	24(25)	14	17	15	9	14	14	17	14	13	17	14	13	20	19	21
D. Subtropical thorn forest	8(11)	4	5	6	5	8	5	9	5	3	6	5	4	12	6	7
E. Subtrop. thorn scrub/desert	8(12)	3	5	5	6	6	5	8	5	4	6	1	3	8	4	4
F. Oak/Jun. Sonor. grass/woodland	3(24)	1	1	2	2	1	2	3	1	1	2	1	1	3	1	2
G. Broad temp.— trop. woodland	5(6)	0	1	2	1	2	3	4	1	1	5	2	1	3	3	3
H. Eastern mixed forest	1	0	0	0	0	0	1	1	1	0	1	1	0	1	1	1
I. Gulf Coast trop. woodland	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
J. Subtropical & Gt. Plain brush	3(4)	3	3	4	0	3	5	6	5	2	7	4	5	6	7	5
K. Subtrop. mont. woodland	7(9)	1	3	0	1	2	2	5	2	1	8	3	2	4	2	6
L. Eastern decid. woodland	10	4	6	11	6	5	15	17	11	11	19	17	13	19	18	19
M. Appalach.-Miss. Basin woodland	4	1	1	1	2	2	4	5	3	3	9	3	3	8	6	10
N. Southern coast woodland	2	1	1	1	0	2	2	4	2	0	4	3	3	10	5	6
O. Western decid. woodland	6	1	3	3	2	2	5	6	4	2	6	5	1	7	7	6
P. Endemics of S. Madre/Balcones	0	0	0	2	0	0	0	2	0	0	1	0	1	2	2	3
Q. Endemics of C. Texas/Coahuila	3	2	1	4	2	3	5	5	3	3	5	5	3	5	5	5
R. South tropical woodland	21(23)	5	5	8	2	11	9	35	7	5	26	3	11	37	22	38
TOTALS	124(161)	52	68	80	47	73	98	145	85	62	147	86	78	170	129	164

TABLE 5. Numbers of butterfly subfamilies from 16 selected counties across the Edwards Plateau classified by habitat zones following Durden (1982). The 37 species recorded from Brewster or counties further west are excluded (see Table 4).

Habitat vs. taxon	Pyrg.	Hesp.	Megath.	Papil.	Pierid.	Liphr.	Thescl.	Polyom.	Riod.	Libyth.	Helico.	Arg/ML.	Nymph.	Satyr.	Danaid.	Totals
A. Disturbed sites	0	0	0	0	7	0	0	0	0	0	0	0	3	0	1	11
B. Great Plains flora	1	5	0	1	0	0	1	1	0	0	0	1	2	4	0	16
C. Dry warm temp. —subtropical	10	6	1	1	3	0	2	1	2	0	0	4	0	0	1	32
D. Subtropical thorn forest	2	3	3	0	1	0	2	2	1	0	0	0	1	0	0	15
E. Subtrop. thorn scrub/desert	4	1	0	0	0	0	3	0	0	0	0	4	0	0	0	12
F. Oak/Jun. Sonor. grass/woodland	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	3
G. Broad temp.— trop. woodland	2	1	0	1	1	0	0	0	0	0	0	1	0	0	0	7
H. Eastern forest	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
I. Gulf Coast trop. woodland	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
J. Subtropical & Gt. Plain brush	0	0	1	0	1	0	2	0	0	0	0	4	0	0	0	9
K. Subtrop. mont. woodland	4	5	0	1	0	0	1	0	0	0	0	0	1	0	0	12
L. Eastern decid. woodland	3	9	0	1	0	0	2	0	0	1	0	2	2	0	0	20
M. Appalach.-Miss. Basin woodland	4	0	0	0	1	1	1	1	0	0	0	1	1	0	0	10
N. Southern coast woodland	3	5	0	1	1	0	0	0	0	0	0	0	1	1	0	12
O. Western decid. woodland	2	0	0	1	2	0	0	0	0	0	0	1	2	0	0	8
P. Endemics of S. Madre/Balcones	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	3
Q. Endemics of C. Texas/Coahuila	0	1	1	0	0	0	1	0	2	0	0	0	0	0	0	5
R. South tropical woodland	16	1	0	4	8	0	1	2	0	0	5	1	10	0	1	49
TOTALS	53	38	6	12	25	1	18	8	7	1	5	19	25	5	3	226

TABLE 6. Numbers of butterfly species in 16 selected countries across the Edwards Plateau, classified by ranges and range limits following Durden (1982).

Range vs. county	Pecos	Terrell	V. Verde	Brewstr.	Edwards	Kinney	Real	Uvalde	Tom Gr.	Kimble	Kerr	Bandera	Medina	Bexar	Comal	Travis
A. At eastern limit of range	6	8	8	56	4	7	9	8	9	6	99	8	8	9	7	11
B. In eastern part of range	6	8	8	10	5	5	12	10	12	7	15	11	6	14	14	16
C. In middle part of range	14	17	15	24	9	14	14	17	14	13	17	14	13	20	19	21
D. At northeast limit of range	4	5	6	8	5	8	5	9	5	3	6	5	4	12	6	7
E. At northwest limit of range	3	5	5	8	6	6	5	8	5	4	6	1	3	8	4	4
F. At northern limit of range	1	1	2	3	2	1	2	3	1	1	2	1	1	3	1	2
G. In northern part of range	0	1	2	5	1	2	3	4	1	1	5	2	1	3	3	3
H. At southeast limit of range	0	0	0	1	0	0	1	1	1	0	1	1	0	1	1	1
I. At southwest limit of range	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
J. At southern limit of range	3	3	4	3	0	3	5	6	5	2	7	4	5	6	7	5
K. In southern part of range	1	3	0	7	1	2	2	5	2	1	8	3	2	4	2	6
L. At western limit of range	4	6	11	1	6	5	15	17	11	11	19	17	13	19	18	19
TOTALS	52	68	80	161	47	73	98	145	85	62	147	86	78	170	129	164

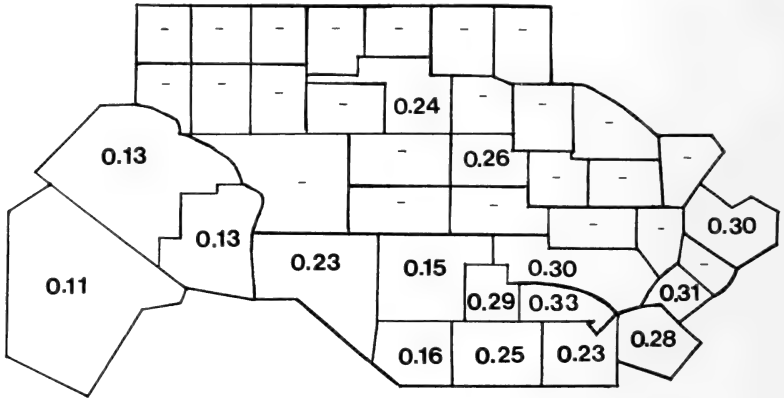


FIG. 9. N-NE species as a proportion of the butterfly fauna of 16 sampled counties on the Edwards Plateau.

and Krizek (1984), Opler and Malikul (1992) and Neck (1996) were consulted for clarification of habitat and eastward range, when necessary.

The distribution of each regional geographical component is presented as the proportion of total species recorded for each county. Paired *t*-tests indicated that the variances of samples were not significantly different from those corrected for relative area ($p = 0.37-0.51$). Significant differences between the geographical groups were confirmed by ANOVA ($p < 0.01$). The N/NW element (0.06–0.17) is uniformly weak across the Plateau (Fig. 8). NE/E species account for 0.25–0.33 of each total in most of the eastern and central region, falling to 0.11–0.13

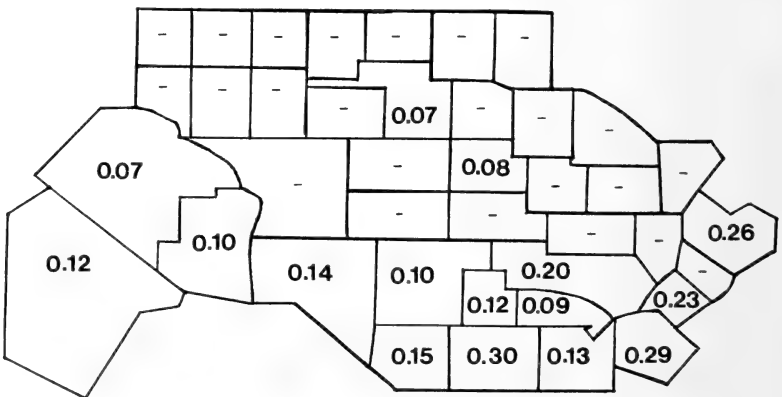


FIG. 10. S species as a proportion of the butterfly fauna of 16 sampled counties on the Edwards Plateau.

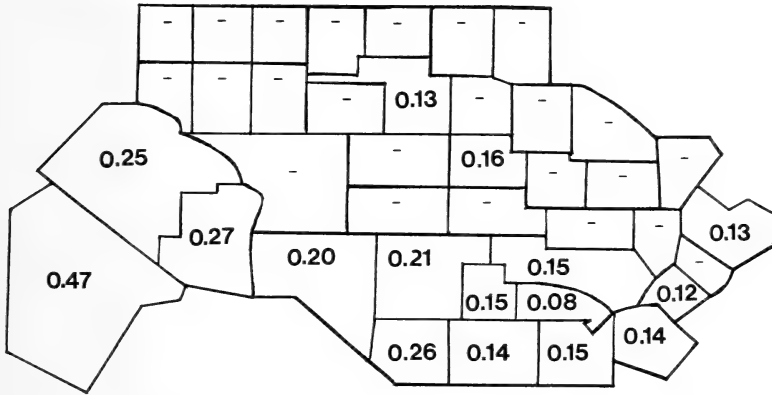


FIG. 11. W-SW species as a proportion of the butterfly fauna of 16 sampled counties on the Edwards Plateau.

in the west (Fig. 9). The S (tropical) element is strongly represented only in the southeast region of the Plateau (Fig. 10), while the W/SW (Sonoran–Coahuilan) element (Fig. 11) is predominant (0.21–0.47) in the western and southwestern counties, but 0.16 or less in the central and eastern regions.

Comparison by habitat zones. Butterfly data from the 16 counties were tabulated by subfamily against 17 habitat types designated by Durdin (1982) by county (Table 4) and by taxon (Table 5). Some interesting patterns were noted, which do not require statistical analysis.

Type A: *Disturbed habitats* were typified by 11 species but dominated by Pieridae (7 species–64%).

Type B: *Great Plains grassland habitat* supported 16 species on the Plateau; Hesperinae (5) and Satyrinae (4), together comprising 56% of the total.

Types C–E: The intergrading dry, warm subtropical habitats, *Arid woodland* (C), *Thorn forest* (D) and *Thorn scrub* (E) together accounted for 58 of the total species, dominated by Hesperidae (29), comprised of Pyrginae (16), Hesperinae (10) and Megathyminae (3). Together with Theclinae (7) and Melitaeinae (8), these taxa accounted for 75% of the total.

Type J: In the subtropical *Great Plains brush habitat* nine species were recorded; four (44%) were Melitaeinae.

Type K: In *Subtropical montane woodlands* 12 species were represented, Hesperidae; (9, 75%), Pyrginae (4) and Hesperinae (5).

Type L: *Eastern deciduous woodland habitat* accommodated 20 species of the total; (9, 45%) were Hesperinae.

Type M: *Basin woodlands* were characterized by 10 species of which four (40%) were Pyrginae.

Type N: *Southern coast woodlands fauna* comprised 12 species, again dominated by HesperIIDae (67%—Pyrginae 3, HesperIIDae 5).

Type R: The largest faunal group of butterflies was that associated with *South tropical woodlands*, 49 species, mostly sporadic in their appearance in any given county, and dominated by Pyrginae (16, 33%), subtropical Pieridae (8, 16%) and subtropical Nymphalinae, Apaturinae and Heliconiinae (10, 20%).

Types F—I and O—Q (see Table 5 and Durden 1982): the remaining seven habitat types were sparsely characterized by 1–8 species (mean 5.7) scattered across the range of families and subfamilies.

Overall, the HesperIIDae was the best represented family in the 16 counties, (97, 43% of the total), while the Pyrginae was the most abundant subfamily (53, 23.5%).

Comparisons of range limits. The diversity of the butterfly fauna of the Edwards Plateau is largely a function of its strategic position (see above); but despite a respectable total of 227 species for the 16 counties, even excluding those found only in Brewster or westward, it is surprisingly difficult to point to any one category, other than the Eastern deciduous woodland group which could truly be said to be characteristic of the geographic unit.

Of the 11 cosmopolitan species associated with disturbed habitats (Durden's Category A), only one (9%), the northern straggler *Colias philodice*, reaches its southern limit of range limit on the Plateau (Table 6). Of the 15 species of the Great Plains fauna (B), five (33.3%) are at their southern or eastern limit, while only five (25%) of the Eastern deciduous woodland species (L) are at their S or SW limit (Table 6).

However, the number of species which reach a range limit on the Plateau comprise more than 50% in all remaining ecological habitat groups (Table 6); C (50%), D and E (73%), F (66.6%), G (86%), H and I (100%), J (55%), K (83%), M (80%), N (91.5%), O (62.5%), P (100%), Q (60%) and R (57%). The implication is that a moderate change in one or more climatic factors could have a significant effect on present species composition. Given the altitude of much of the region (300 m+), an extended period of cooler climate might eliminate many of the southern components, upwards of 60–100 species. Warming trends might seem more likely at present, but the effect would perhaps be more variable, depending whether seasonal and annual rainfall decreased or not.

DISCUSSION

Location and environment. Much of the Edwards Plateau is a southward extension of the Great Plains Physiographic Province (Hunt

1974), and the southern extremities of the Rocky Mountains are only some 200 km from its northwestern margin. Altitudes ranges from about 900 m in northern counties such as Tom Green, to 300 m at Concan in north-central Uvalde Co. on the southern extremity of the Balcones Escarpment. The western section of the Plateau blends into the arid, subtropical Trans-Pecos region. The major rivers and associated riparian systems generally run northwest to southeast; their ecological influence is widespread and particularly significant in the southeast and less so in the southwest. The counties of the Edwards Plateau are on hard, porous limestone (Gould 1969, Ajilvsgi 1984), except where the central, basaltic Llano Uplift breaks through. In contrast, on the eastern margin of the Plateau, counties such as Bastrop, Lee, Fayette and most of Caldwell have sandstone and shale soils, with podsoles, peat bogs, and Neogene sands and clays covered with coastal-type prairie (Durden 1982).

Isohyets over western and central Texas have a consistent general north-south orientation (Rislin & Diamond 1988), with a marked clinal decrease in annual rainfall from east to west. As a consequence, Brewster, Pecos and Terrell counties have annual rainfalls of only 20–35 cm. Eastern and northeastern counties receive more than twice that (ca. 90 cm). Significant differences in rainfall occur even across the south-central region of the Plateau and along the complex southern margin of the exposed limestone scarp of the Balcones Fault. The upper Frio-Sabinal area receives about 30% less rain annually (60 cm) than Austin (85 cm).

Floristic patterns on the plateau. The geography, physical environment and climatic characteristics of the Plateau have all played roles in colonization and establishment of distribution patterns of the historical and extant flora and fauna. Amos and Rowell (1988) applied principal component analysis (PCA) to a large database of woody and endemic vascular plant records, to try to determine the ecological relationships, floristic patterns, and perhaps origins of the regional components. The analysis identified two major floristic zones across the Plateau: a numerous and diverse eastern component and a less rich and less widespread western one. Val Verde County was identified as the major transitional zone. A third, southern element of Neotropical origin was important only in the counties along the southern rim of the Plateau. Simple regional characterizations are complicated by the existence of parallel ecological habitats within each floristic zone (Gehlbach 1988). For example, the woody taxa of the Plateau tend to form tight geographical clusters (Amos and Rowell 1988), while in contrast, the vascular endemics, are clustered in a relatively few eastern counties without any such detectable associations.

Flora in adjacent zones at the same latitude across the Plateau can be surprisingly dissimilar. Using data of Ajilvsgi (1984) and Enquist (1987),

I examined a sample of 313 vascular plants from about 70 families (not just endemics), and compared the composition of the south-central Edwards Plateau (Real, Bandera, Uvalde and Kerr counties) with that of the South Central Vegetation Zone, the westerly section of which takes in parts of Travis, Hayes, Comal and Bexar counties on the curved margin of the Balcones Fault between San Antonio and the Austin region. Although 148 species were common to both regions, 52.7% of the flora was not shared; 73 species in South Central are not known from the Edwards Plateau and 92 found on the Plateau are not recorded from South Central.

North-south differences in flora can be quite marked over relatively small distances as well. The upper Frio-Sabinal vegetation consists predominantly of Juniper-Oak savanna (Amos and Gehlbach 1988). The northern, eastern and western margins do not include any transitional areas, but intergrade with Mesquite Savanna in the north-central parts of Uvalde and Medina counties along the southern margin of the Balcones Fault (Simpson 1994).

The eastern counties have much more complex vegetation patterns. Llano County and the western part of Burent lie in the Central Texas Mesquite-Oak Savanna; Hays, Travis and Williamson straddle the southern tongue of the Blackland Prairie; while the eastern counties of Lee, Bastrop, Caldwell and Fayette are in the Post Oak Savanna zone (Simpson 1994).

The origin of the small but widespread eastern deciduous element on the Plateau remains an enigma. Amos and Rowell (1988) conclude that the following explanation remains the most likely; i.e., that it represents an isolated remnant of an earlier cool climate forest which extended into and through the Gulf states. The distributions of groups of endemic plants, often taxonomically related within each cluster, seems to imply that the Plateau had several long periods of climatic and ecological stability during the Tertiary.

These clusters of floristic endemics are not matched by corresponding distribution patterns among butterfly taxa, which show little endemism in the region (see Durden 1982). As a general rule, winged insects would seem to have greater potential for mobility and rapid colonization than most plants with distributions restricted to certain ecological regimes.

On the other hand, there is marked correspondence between components in the butterfly fauna and large-scale geographical groupings in the regional floras. In the butterflies, a western-southwestern element is strong in Brewster, Pecos and Terrell and Kinney counties, but declines by nearly 50% to the north and east (Fig. 11). This equates with the Far West vegetation zone of Gould (1969) and Ajilvsgi (1984). The subtrop-

ical south-southeastern element makes up 25–30% of the butterfly species in some southeastern counties (Fig. 10), but is almost insignificant in the northern counties of higher altitude and in the western counties, most of which have limited riparian habitat. This component parallels the mixed South Central and Coastal Texas vegetation zones. The north-east-eastern butterfly component contributes about 25–33% to the total species in the eastern and northern counties (Fig. 9), and can be equated to the South Central vegetational zone. Finally, the butterfly element of largely northwestern distribution, relatively weak in all sampled counties (6–17% of total species, Fig. 8), is not just equivalent to the Panhandle vegetation zone of Gould (1969) and Ajilvsgi (1984) but has its origins beyond the Plateau, as part of the large western Woodlands and Chaparral zone. Amos and Rowell (1988) also stressed that the NW region of the Edwards Plateau was floristically allied with the High Plains, not the rest of the Plateau.

For much of the year, central Texas is usually hot and dry, conditions to which many Hesperiiidae are well adapted, but not so many other butterfly taxa. The relative species richness of the south-central and eastern Edwards Plateau is supported by the extensive rivers that flow south and southeast from the high country to South Texas, and the variable riparian habitat associated with them. The importance of healthy riparian systems to butterfly diversity and conservation in two other semi-arid warm temperate regions has been previously noted by Yela (1992: Central Spain) and Gaskin (1996: Greece). This important habitat also facilitates the frequent penetration of southern tropical and subtropical species of Lepidoptera into the relatively northern and eastern counties of the Plateau (Fig. 12), even when wind directions are not particularly favorable.

Geographical range, climatic zone and general adaptation to a particular ecological regime are useful characteristics by which we can classify faunal components such as butterflies. In most cases, however, a significant fraction of any county record consists of a long "tail" of occasional visitors, non-resident species, and the updated Frio-Sabinal list is no exception (Tables 1, 2). There is a natural tendency to focus on the new and unusual, but this can divert attention from the species which are important, consistent components of local ecosystems. Each individual species, sub-species and often, population, needs a suite of natural resources to survive; a favorable temperature range, suitable food plants for oviposition, nutrition for larvae and adults, relatively safe perches for adults at night, and sites for pupation and whichever instar over-winters. Each stage of the life history is vulnerable to a range of density dependent and independent events over which individuals have relatively little control.

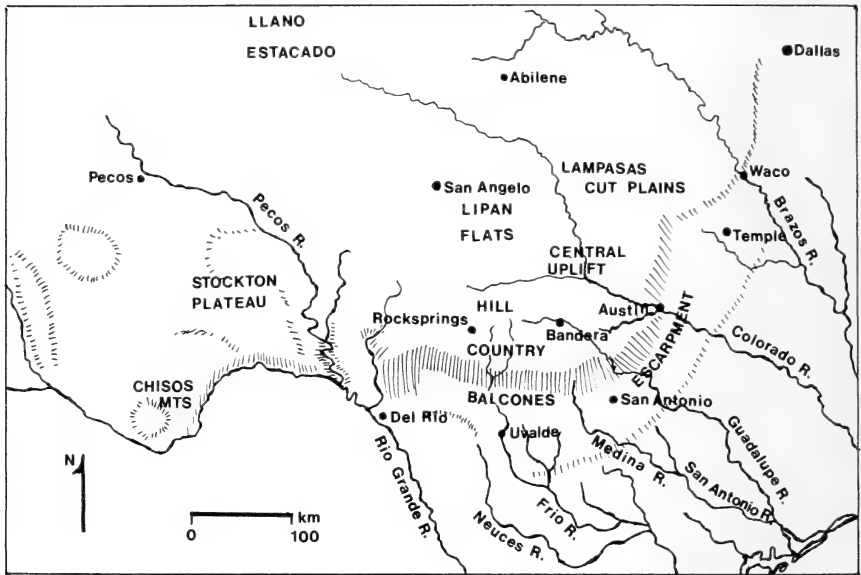


FIG. 12. Major landform features of the greater Edwards Plateau (*sensu* Gould 1969) and associated structures in the trans-Pecos region. Decline in altitude to the S and SE, together with the relative abundance of rivers and riparian habitat in that region probably facilitates butterfly dispersal and seasonal migration northwards.

We need to understand the potential importance of rather subtle factors. Durden (1982) for example, noted that the tropical elements of the butterfly fauna of south Texas and northern Mexico are most commonly encountered in the Austin region when the daily photoperiod is shortest. Not all his rarities found around Austin were dated, but at least 11 unique or scarce records of southern species were reported between late September and November (Durden 1982).

Consistent differences in local climatic conditions can exert effects important over relatively short distances. For example, there is a general similarity between the three intensively worked sites in this article; Barton Creek, Concan and upper Frio-Sabinal. Yet altitude in most of the Frio-Sabinal region exceeds that of the Austin Barton Creek site studied by Durden (1982) by about 100–300 m, providing somewhat cooler, windier weather for part of the year, especially at night. Concan, in north-central Uvalde is right on the southern edge of the escarpment, and about 150 m lower in altitude than my sites, with corresponding higher humidity and somewhat different soils and drainage. The relative frequency of dispersive weather systems over the three sites may also vary because of the different isohyet regimes and topographies.

Such variation can have important effects on microhabitats and conservation of semi-isolated butterfly populations. For example, spacing of trees and amount of understory can differ in subtle ways that do not easily yield to simple measurement. At one site in central Europe, for example, Kudrna (1993) discovered that a population of a *Parnassius* species was in serious decline because the degree of shading of the food plant in the understory had slowly increased to a point where the thermal regime was too cool for the larvae to complete their metamorphosis within the available growing season.

Even when resources for adult and larval butterfly species visibly occur throughout a region, spacing and density of these host plants can differ from one site to another. Such variation may be apparent to searching butterflies, but not necessarily to entomologists. There are many more mysteries on the Edwards Plateau still waiting to be solved.

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RELATIONSHIP OF HOST PLANT DENSITY TO SIZE
AND ABUNDANCE OF THE REGAL FRITILLARY
SPEYERIA IDALIA DRURY (NYMPHALIDAE)

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ABSTRACT. Populations of the Regal Fritillary, *Speyeria idalia* Drury have been declining across prairies in the USA. We hypothesized that larval food limitation may be a factor in this decline, and explored this by studying the following characteristics for *S. idalia* in Iowa, South Dakota, North Dakota, and Kansas: population size (via mark-recapture), adult weight; abdominal, thoracic, and wing lengths; adult head capsule widths. Violet densities and abundance estimates were calculated for all sites. These estimates of the insect's larval hostplant availability were correlated to the size of the butterfly populations and the weights of the insects. Iowa prairies had significantly lower violet densities. Weights of *S. idalia* were significantly lower in Iowa compared to Kansas and S. Dakota.

Additional key words: growth, geographic variation, host plants, violets, *Viola pedatifida*.

The Regal Fritillary, *Speyeria idalia* Drury (Nymphalidae, Argynniinae), is a prairie butterfly that has experienced severe population declines because of habitat destruction. *S. idalia* is one of the "most characteristic" indicators of high quality prairie in North America (Hammond & McCorkle 1983). With the disappearance of prairie habitat, widespread populations of *S. idalia* also have declined in numbers and distribution. *S. idalia* was listed as a Category II species (possible candidate for listing) under the Endangered Species Act until 1996, when this category of protection was deleted by the U.S. federal government (USFWS 1996). *S. idalia* currently has a special "status of concern" in national grasslands in North Dakota and South Dakota, and the Iowa Department of Natural Resources has listed it as a sensitive species (J. Fleckenstein, pers. comm.). Hammond and McCorkle (1983/1984), Johnson (1986) and Swengel (1997) also noted general declines in *S. idalia* populations. Hammond and McCorkle (1983/1984) specifically noted a relationship between habitat loss and population declines in *S. idalia*.

Our documentation of small population sizes of *S. idalia* in Iowa during 1995 (Table 1) suggests that the insect could go extinct locally. *Speyeria idalia* was found at only 11 of 52 prairies, and only five of these 11 prairies had populations of *S. idalia* estimated at over 50 individuals. Because we found a number of intermediate to small populations of *S.*

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TABLE 1. *Speyeria idalia* population size estimates in 1995. ¹P. C. Hammond's estimate. These data taken from Debinski & Kelly (1998).

Prairie name	Population estimate	Method
Page Private Prairie	2	individuals observed
Sheeder Prairie	50	mark-recapture
Reichelt Unit of Stephens State Forest	4	individuals observed
Polk City Prairie	1	individuals observed
Moeckley Prairie	220	mark-recapture
Ringgold Wildlife Area	7	individuals observed
Doolittle Prairie	2	individuals observed
Rolling Thunder Prairie	120	mark-recapture
Kalsow Prairie	500	visual estimate ¹
Loess Hills Wildlife Area sect. 9	160	mark-recapture
Loess Hills Wildlife Area sect. 21	2	individuals observed

idalia in Iowa in 1995, we began to focus on the causes of this species' population decline.

Other research confirms the detrimental effects of food limitation on insects. Larval food limitation in the Painted Lady Butterfly (*Vanessa cardui*) negatively affected growth, survival and body mass in a laboratory setting (Poston et al. 1977, 1978, Kelly 1996). In Diptera, reduction in adult body size and fecundity, as well as increased larval mortality, were demonstrated from larval food limitation in a laboratory setting (Collins 1980). Nymphal food limitation was implicated in reducing the fecundity of female mantids (Dictyoptera) in field populations (Eisenberg et al. 1981). A field study also demonstrated that food-limitation negatively affected bombardier beetle reproduction and suggested that such limitation may explain spatial differences in assemblage composition among age classes of these insects (Juliano 1986). Fecundity in lepidopterans is also affected by limited adult nectar sources (Boggs and Ross 1993), although there is evidence for use of stored nutrients during egg production (Boggs 1997).

Our objectives were to assess whether low host plant availability was correlated to individual body weight and overall population size of *S. idalia*. As a means of comparison, we investigated these traits in *S. idalia* from eight sites in Kansas, South Dakota, and North Dakota, where hostplant abundance is greater than in Iowa. Iowa prairies tend to be isolated plots of natural areas surrounded entirely by agricultural development, and habitat fragmentation has probably had a negative effect on this species. In contrast, *S. idalia* populations surveyed in Kansas, South Dakota, and North Dakota are bordered by habitats that still accommodate *S. idalia* to some extent, albeit in lower densities. We focused our research on the following questions: (1) does the larval host-plant, Blue Prairie Violet (*Viola pedatifida*), serve as a limiting factor for *S. idalia* populations by virtue of its limited abundance in Iowa prairies;

TABLE 2. *Viola pedatifida* population estimates in 1995. Note: Sites listed in Table 2 but not Table 1 had no *S. idalia* seen in 1995.

Prairie name	Violet density estimate plants / m ²	Violet population estimate
Page Private Prairie	1.5	95
Sheeder Prairie	1.1	39,200
Reichelt Unit of Stephens State Forest	2.5	128,000
Polk City Prairie	0.9	310
Hawthorn Wildlife Area	1.9	424,000
Kish-ke-kosh Preserve	9.7	12,900
Raymond-Hilts Private Prairie	4.6	900
Howe Private Prairie	5.2	1,100
Moeckley Prairie	0.7	35,000
Ringgold Wildlife Area	0.45	22,600
Doolittle Prairie	0.62	9,200
Rolling Thunder Prairie	1.9	210,000
Kalsow Prairie	0.48	148,000
Loess Hills Wildlife Area sect. 9	2.7	183,000
Loess Hills Wildlife Area sect. 21	1.5	98,000

and (2) because body weight positively influences fecundity in lepidopterans (Boggs and Ross 1993, data on *Speyeria mormonia* Boisd.), do adult females of *S. idalia* in Iowa prairies, where hostplant density is low, weigh less than *S. idalia* females in areas where hostplant density is greater? That is, can field data demonstrate that smaller adult females emerge on prairies having lower hostplant density?

MATERIALS AND METHODS

Tall-grass prairie is deemed the primary habitat of this species (Hammond & McCorkle 1983/1984, Opler & Krizek 1984, Shull 1987, Panzer et al. 1995), and the butterfly's presence is correlated with the presence of violets (*Violaceae*). *Speyeria idalia*'s larval host plants include *Viola pedata* (Bird's-foot Violet) (Opler & Krizek 1984, Shull 1987), *V. pedatifida* (Blue Prairie Violet), *V. papilionacea* (Common Blue Violet), *V. lanceolata* (Lance-leafed Violet) (Scott 1986), and *V. nuttallii* (Nuttall's Violet) (this study). Regions in Iowa where *S. idalia* is most abundant contain largely Blue Prairie Violet.

We measured wing length (as in Boggs 1988), thoracic and abdominal length and adult head capsule width of individual *S. idalia* adults at eight field sites in Iowa. We compared these measurements with those of adult *S. idalia* adults captured on eight sites in Kansas, South Dakota, and North Dakota. Field sites in Iowa were chosen after the 1995 field season when we surveyed more than 50 prairie areas in Iowa to determine which sites had violets and, of those, which had *S. idalia* (Table 2). We chose to focus on some of the larger *S. idalia* populations in Iowa

during 1996. Then, we examined prairie sites outside Iowa known to have relatively large, consistently observed populations of *S. idalia* as comparison sites for Iowa prairies to test our food-limitation hypothesis.

We estimated hostplant abundance as the number of violet stems/m² during April–June. Violet species found in Iowa and Kansas were *V. pedatifida* and occasional small patches of *V. papilionacea*, whereas the predominant species found in the South Dakota and North Dakota prairies was *V. nuttallii*. Because the total leaf area of plants counted in sites with the Nuttall's and Blue Prairie Violets appeared quite similar, we disregarded the species of violet in the statistical analysis. Stem-per-quadrat measurements of the dominant violet species were recorded in the alternate 1 m² subplots of each of five 10 × 10 m plots (a total of 50, 1 m² subplots per 100 m²). These plots were located in the areas of highest violet density. We also estimated the percentage of total violet coverage by evenly spacing 100 1 m² plots across the surveyed area of each prairie.

From these initial data, we calculated estimated hostplant abundance by multiplying the percent hostplant coverage (average of five 10 × 10 m plots) by the number of acres of habitat present or surveyed. This type of estimate skews the results toward higher values of host plant density, but it is consistently biased across all our sample sites. In each large prairie, we surveyed *S. idalia* populations in an area of 64.8 ha (200 acres) as determined by landmarks and section lines corresponding to detailed maps. In sites of less than 64.8 ha area, we surveyed the entire habitat for *S. idalia*. There were a few cases where habitat constraints prohibited sampling larger prairies at the full 64.8 ha scale. Ultimately, we used the two violet population estimates to examine the correlation between the hostplant abundance at each site with the *S. idalia* population estimate. Table 3, "Violet Estimate (or Extrapolation) for Entire Site" reflects the number of violet plants in the entire area of contiguous undegraded prairie (areas of 6.9 to 25,911 ha), whereas "Violet Estimate for Sampled Area" reflects the violet population in the area we surveyed for insects (areas of 6.9 to 64.8 ha).

Adult *S. idalia* at each site were captured with a field net, placed in a glassine envelope and weighed using a medium resolution electronic scale with a precision of 0.01 g and repeatability to 0.005 g. The weight of the envelope was voided to determine the weight of the insect. Other body measurements of abdominal, thoracic and wing length, as well as head capsule width, were taken to the nearest 0.1 mm with dial calipers. Head capsule widths in both larval and adult Lepidoptera have been noted as measures of development and nutrition (Bastian & Hart 1990, Charlet & Gross 1990, McClellan & Logan 1994). All measurements were performed before the oviposition season (Mattoon et al. 1971).

TABLE 3. 1996 violet density estimates, violet presence over entire area, and violet density estimate. ~ No population estimate possible without recaptures.

Survey Locations	Violet spp.	Five Plot Density stems/sq.m	100 Point Coverage as a percent	Hectares of Habitat	Hectares surveyed	Violet est. (or extrapolation) for entire site.	Violet est. for sampled area.	<i>S. idalia</i> 1996 pop. est.
Iowa	<i>V. peda.</i>	1.04	0.32	101.2	20.2	33,089	67,484	143
	<i>V. peda.</i>	0.52	0.43	10.1	10.1	22,757	22,757	159
	<i>V. peda.</i>	2.38	0.07	404.9	8.1	673,430	12,472	20
	<i>V. peda.</i>	1.02	0.13	485.8	64.8	644,171	85,925	258
	<i>V. peda.</i>	0.44	0.20	64.8	64.8	57,542	57,542	296
	<i>V. peda.</i>	0.49	0.18	64.8	64.8	57,387	57,387	453
	<i>V. peda.</i>	0.55	0.38	64.8	64.8	135,924	135,924	198
	<i>V. peda.</i>	2.36	0.36	49.8	49.8	423,101	423,101	57
	<i>V. nuttallii</i>	2.78	0.13	485.8	64.8	1,755,681	234,187	408
	<i>V. nuttallii</i>	6.26	0.28	486.0	64.8	8,518,608	1,135,814	315
South Dakota	<i>V. nuttallii</i>	5.52	0.33	323.9	64.8	5,900,162	1,180,397	396
	<i>V. nuttallii</i>	5.08	0.24	161.9	64.8	1,973,885	790,042	494
	<i>V. nuttallii</i>	5.86	0.22	81.0	64.8	1,044,252	835,402	200
	<i>V. nuttallii</i>	5.56	0.65	25,910.9	64.8	936,419,926	2,341,872	444
North Dakota	<i>V. peda.</i>	1.60	0.40	6.9	6.9	44,270	44,270	98
Kansas	<i>V. peda.</i>	3.50	0.53	3,481.8	64.8	64,587,390	1,202,040	~

Thus, the abdominal length measurements reflect pre-reproductive body dimensions.

A Lincoln-Peterson estimator with continuity correction was used to estimate population size (Brower et al. 1990). On the first day of a mark-recapture exercise, each insect was marked with a Sanford® Sharpie® ultra fine permanent marker and released for potential recapture. These marks may remain on a living insect indefinitely and were not observed to induce mortality or to limit flight mobility (pers. obs., see Nagel et al. 1991). Our sequence of site surveys generally went from south to north, so that we could obtain population size estimates that included both males and females after initial emergence. Each site was surveyed for a total of six person-hours per day, usually two consecutive days during the mark-recapture effort. We limited sampling at each site to two days to allow surveying at 16 sites. *Speyeria idalia* has a long flight period, especially in Kansas (relative to other butterflies that are univoltine). Maximum adult survival time has been estimated at 57 and 69 days for males and females respectively (B. Barton, pers. comm.).

Statistical analyses were conducted using Excel for Microsoft Windows, and included *t*-tests and multiple regression analysis. For each of the comparisons, Iowa insects or violets were grouped in comparison to insects or violets from the other states. In comparing weights, males and females were analyzed separately because of their difference in size.

RESULTS

Violet density. Iowa violet densities were significantly lower than those in other states, based upon our five plot density estimates ($t = -5.17$, $df = 10$, $p < 0.001$) and our estimates for the sampled areas ($t = -3.41$, $df = 7$, $p < 0.01$). Our extrapolations of total violets on entire sites did not show significant differences between Iowa and other states; there was considerable variance among the estimates. We found a positive, but non-significant correlation between the violet estimate for sampled areas and butterfly population estimates across all states ($r^2 = 0.25$, $df = 1, 13$, $p < 0.06$), and no significant relationship between estimated *S. idalia* populations and violet density for entire sites.

***S. idalia* population sizes vs. habitat area.** We found large populations of *S. idalia* across tall and mixed prairies of larger areas (Table 4) ($r^2 = 0.52$ for *S. idalia* population estimate versus hectares surveyed, $df = 1, 13$, $p < 0.01$). The greatest correlation observed was between the size of *S. idalia* male population estimates and hectares surveyed ($r^2 = 0.75$, $df = 1, 11$, $p = 0.17$). All analyses of correlation between recapture rates and habitat area or area surveyed yielded only slightly positive values and none was statistically significant ($r^2 \leq 0.49$, $df = 1, 11$, $p = 0.22$). There was the paucity of female *S. idalia* in Iowa prairies. In two days

TABLE 4. 1996 Mark-recapture raw data and Lincoln-Petersen estimators of 16 *S. idalia* populations. ~No population estimate possible without recaptures.

Survey locations	Mark-recapture dates	Male- first day m_1	Female	Male- second day n_2	Female	Male- recapture m_2	Female	Lincoln- Petersen pop. est	Hectares surveyed	Insect density est. (insects/ha)
Iowa	Loess Hills, Section 21	17	4	18	4	3	0	143	20.2	7.1
	Sheeder Prairie	52	0	32	0	15	0	159	10.1	15.7
	Stephens State Forest	7	0	6	0	3	0	20	8.1	2.5
	Ringgold Wildlife Area	59	1	42	0	12	0	258	64.8	4.0
	Caylor State Preserve	36	1	60	1	8	0	296	64.8	4.6
	Anderson State Pres.	65	2	50	1	8	0	453	64.8	7.0
	Kalsow State Pres.	31	1	30	0	5	0	198	64.8	3.1
	Rolling Thunder	16	2	11	3	5	1	57	49.8	1.1
	Murdo	32	36	24	30	7	3	408	64.8	6.3
	Wall	27	34	22	27	7	4	315	64.8	4.9
South Dakota	Harp Dam	17	28	14	24	1	3	396	64.8	6.1
	Richland Dam	6	45	10	41	1	4	494	64.8	7.6
	Antelope Creek	15	29	12	26	3	7	200	64.8	3.1
	Shenoyenne Nat'l Grass.	14	22	10	34	1	2	444	64.8	6.9
Kansas	Dorothy Akins	49	13	11	7	31	0	98	6.9	14.3
	Konza Prairie	40	24	38	32	0	0	~	64.8	~

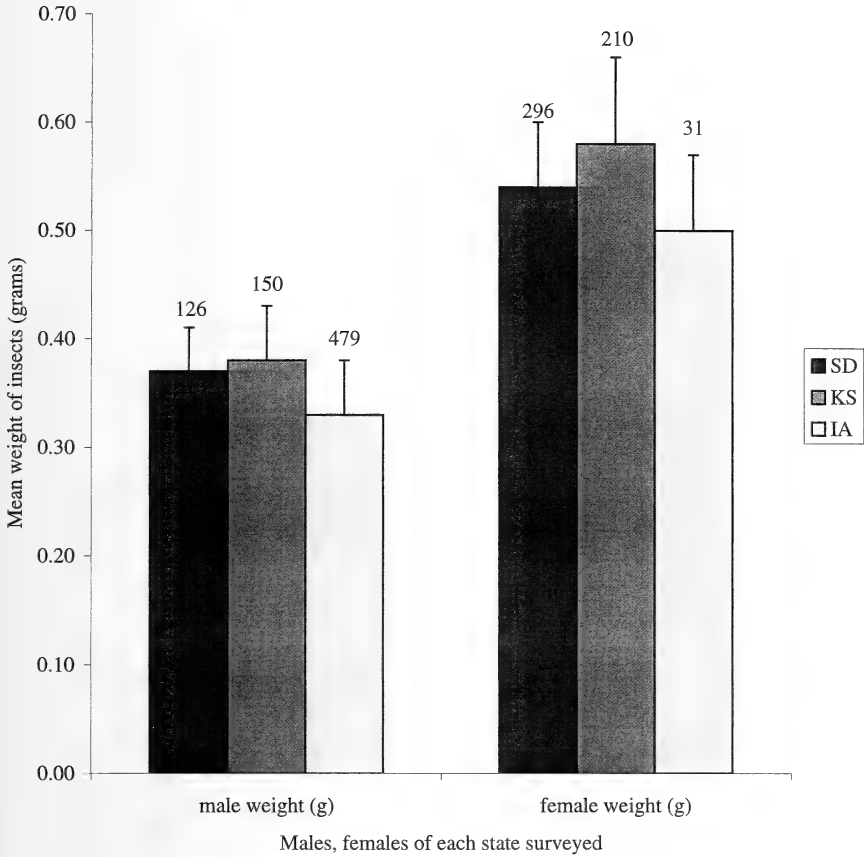


FIG. 1. Male and female mean weights (g) of Regal Fritillary (*Speyeria idalia*) adults from Iowa, South Dakota and Kansas in 1996. Bars indicate standard error and numbers indicate total insects weighed at all sites in that state.

during the peak flight period at Sheeder Prairie, we were able to catch 84 males and not a single female. Overall in Iowa, after spending nearly a month surveying areas in the state, we caught 479 males and only 31 females. Note that this number is somewhat larger than the values shown in Table 3 because there was a second site in the Loess Hills where the population was too small to conduct a mark-recapture estimate.

Insect body measurements. *S. idalia* weights were significantly lower in Iowa compared to other states (Fig. 1). Iowa male weights averaged lower than North Dakota, South Dakota, and Kansas weights for a difference significant at the $p < 0.001$ level (same results with separate t -tests: $H_A \text{ weight}_{IA} < \text{weight}_{SD \& ND}$, $df = 125$ and $H_A \text{ weight}_{IA} < \text{weight}_{KS}$,

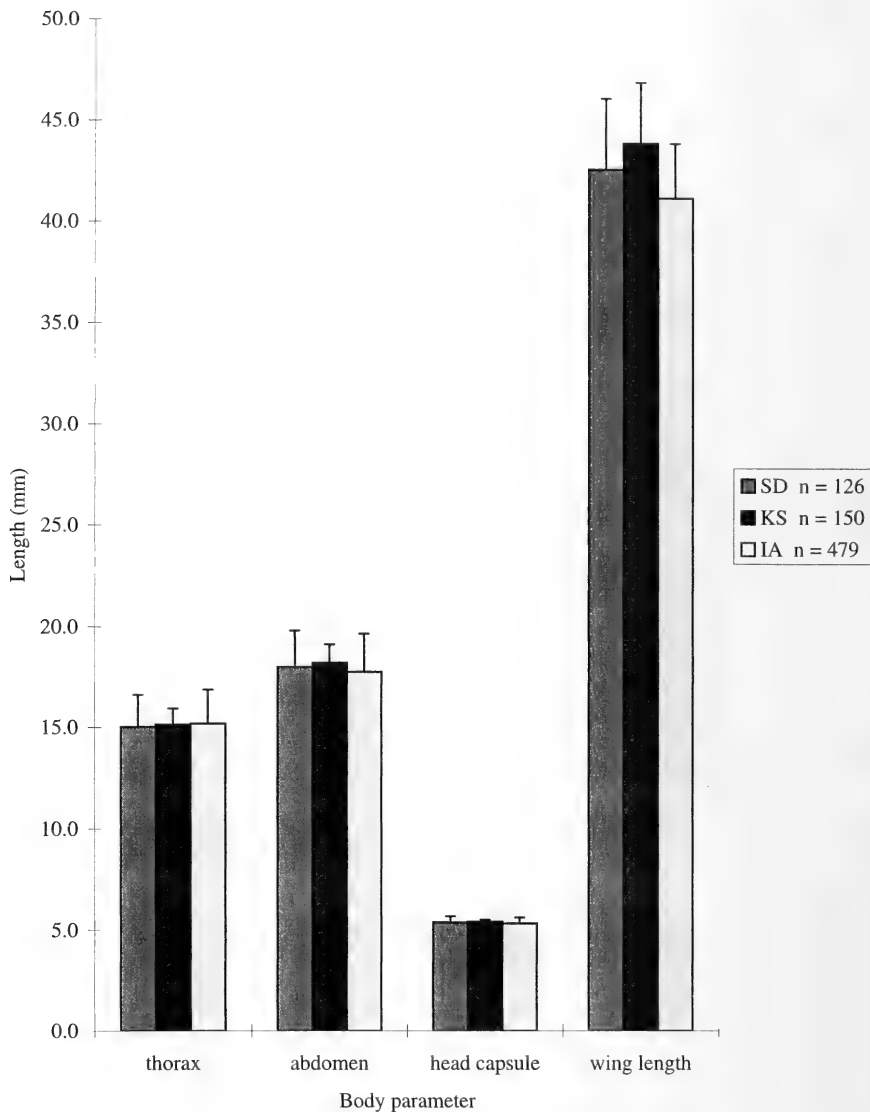


FIG. 2. Male Regal Fritillary (*Speyeria idalia*) adult body measurements from Iowa, South Dakota, and Kansas in 1996. Bars indicate standard error. Note sample size in legend.

df = 149). Iowa female weights averaged less than North Dakota and South Dakota female weights for a difference significant at the $p < 0.01$ level, df = 30 and less than Kansas weights for a difference significant at the $p < 0.001$ level, df = 30. Of the other body measurements, only male wing length seemed to vary geographically (Figs. 2, 3). Iowa male wing

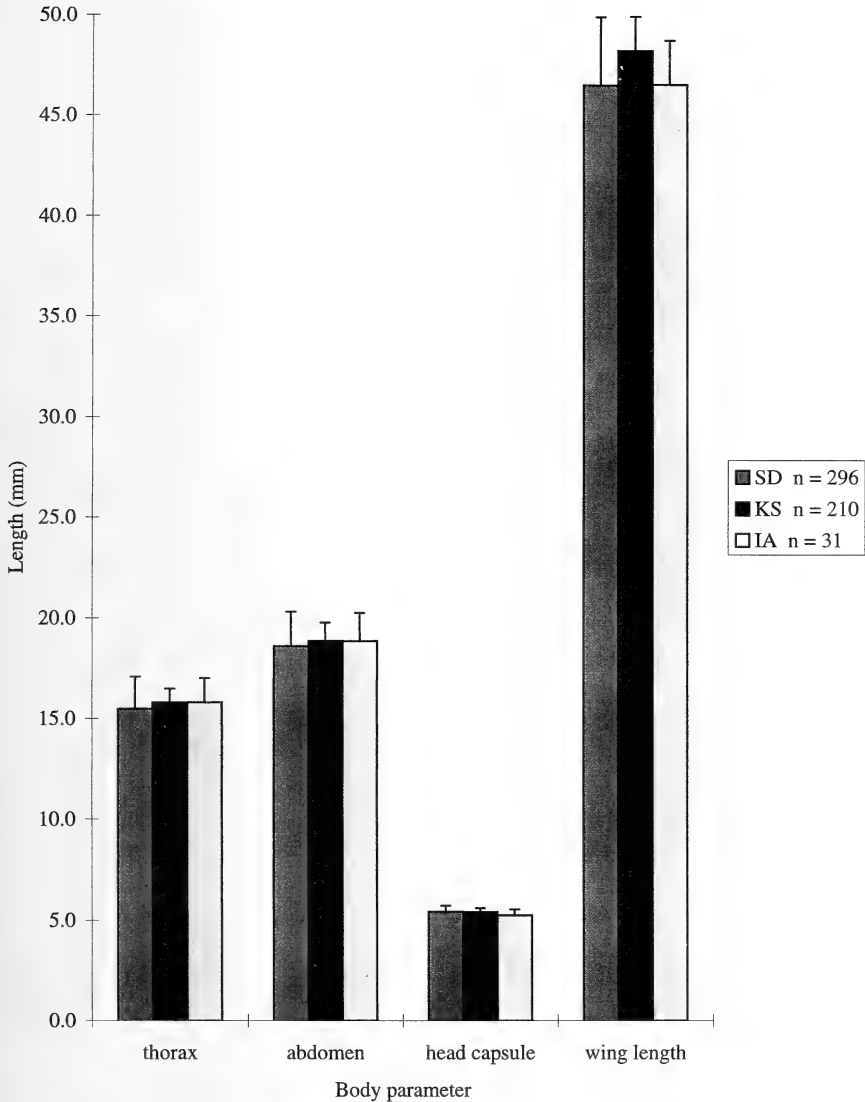


FIG. 3. Female Regal Fritillary (*Speyeria idalia*) adult body measurements from Iowa, South Dakota, and Kansas in 1996. Bars indicate standard error. Note sample size in legend.

lengths were less than North Dakota, South Dakota, and Kansas male wing lengths for a difference significant at the $p < 0.001$ level in both comparisons: H_A wing length_{IA} < wing length_{SD & ND}, $df = 125$ and H_A wing length_{IA} < wing length_{KS}, $df = 149$. None of the other insect body measurements varied significantly with geography. The correlation be-

tween insect body mass and all other parameters was between $r^2 = 0.60$ and $r^2 = 0.70$ (and not significant) at all sites surveyed for *S. idalia*.

DISCUSSION

Our data suggest that Iowa prairies produce comparable densities of *S. idalia* to the Dakotas and Kansas, but the total population size is smaller because the prairies (and thus total number of host plants available) are smaller (Table 4). These differences could have important conservation implications for the long term viability of *S. idalia* in Iowa. The correlation between *S. idalia* population sizes and violet density, however, was not as high as we had expected. Other factors obviously enter into the process of predicting an expected population size of this insect. For instance, one site in the Loess Hills Wildlife Area (section 9) in Monona County, Iowa had been burned in early 1996, and the fire may have killed most of the *S. idalia* larvae. This site was omitted from our food limitation study due to its low population size. A similar explanation may apply for the Hawthorn Wildlife Area in Mahaska County, Iowa, where a large *V. pedatifida* population consistently has been burned. Fire management may explain the low *S. idalia* populations at these sites as well, as Swengel (1996) specifically noted *S. idalia* as one of several prairie specialist butterflies that was most negatively affected by fire.

Another factor that complicates our correlations between *S. idalia* abundance and habitat parameters is the degree of isolation of some habitat areas where *S. idalia* is absent or found in small numbers. The extent of *S. idalia*'s decline and population isolation in Iowa has reached a point where distance from existing populations could be excluding the insect from otherwise suitable habitat. Sites that may have served as stepping stones (e.g., Smith & Gilpin 1997) in the past may be less effective now because of marginal hostplant and adult nectar resources. Thomas (1983) hypothesized that the butterfly *L. bellargus* may spread out in good years, but have a much more limited distribution in poor years. Similarly, Thomas and Harrison (1992) found that *Plebejus argus* populations in North Wales had high turnover of small populations and that the persistence of this spatially dynamic species depends on some suitable habitat being continuously available within relatively large areas. As each prairie site in Iowa becomes more marginal (through habitat destruction or lack of management), isolation from sites with stable *S. idalia* populations increases.

There may be a threshold value of hostplant abundance necessary to support a *S. idalia* population, and knowledge of this value would provide useful information in conservation decisions. Three other areas (not included in the 1996 mark-recapture comparisons or insect measurements) in Iowa with violets had only a few *S. idalia* individuals present.

Hostplant abundance at these sites was approximately 125,000 plants. Two other sites with an estimated violet population of around 13,000 had no *S. idalia*. We note that the violet estimates varied somewhat between 1995 and 1996, but this can probably be explained by a higher intensity of sampling during 1996.

The relationship between prairie area and male population size was not surprising given the fact that males patrol territories across the prairie. Thus, the more area we surveyed, the greater our success in marking male individuals. The females exhibited almost no territorial behavior, and to complicate our efforts at population estimates, females did not appear in sufficient numbers to provide reliable population data in Iowa prairies.

We arrived at the peak of female populations in South Dakota and North Dakota in mid-August of 1996. Here, females outnumbered males in all sites we visited. None of the grasslands in either state were as isolated as most of the prairies in Iowa, with the exception of the Wall, South Dakota site. This area had many *S. idalia* in a brushy drainage, but not nearly as many were found in the surrounding grazed area that isolated the drainage. This latter site yielded the highest male recapture rate (24%) of all North Dakota and South Dakota sites. The contrast in quality of surrounding habitat seemed to influence recapture rates and thus population estimates. That is, if less acceptable habitat surrounded the patch we surveyed, we were more successful with recaptures. Perhaps this result was an effect not only of the total area of habitat used, but also of the isolation of that habitat.

One of the more interesting results of our study was that adult *S. idalia* from Iowa were significantly smaller than the *S. idalia* from other states. This difference could potentially be the product of genetic drift working on small populations. *S. idalia* is a very strong flier, and in highly fragmented habitats there could be strong selection pressure against individuals that disperse (one could view this as dispersal suicide in highly agricultural landscapes). Those that remain may be the individuals that are less likely to disperse (i.e., smaller individuals). Hence there could be an opportunity for rapid genetic evolution. This same phenomenon has been observed in *Papilio machaon* in the UK (Dempster 1995).

Nearly all body measurements were predictable from the weight of the insect, although no substantial variation existed in thoracic length, abdominal length, or adult head capsule width. With the exception of wing length and overall insect weight, we found no difference in the means of other body parameters according to location or sex. We attributed the variation in weight between sexes to the greater abdominal mass (not necessarily length of body segments) of a female developing

eggs. However, it is interesting to note that female wing length did not vary significantly between Iowa and other states even though weight did differ significantly.

Hammond and McCorkle (1983/1984) attribute the decline of a number of *Speyeria* populations to the extent of detrimental environmental disturbances caused by humans. In Iowa prairies, the almost complete elimination of tallgrass prairie, erratic distribution of the remaining remnants, as well as low abundance of violets may be responsible for the small *S. idalia* populations. We focused our research on prairies that were relatively pristine, but even some of these prairies have had disturbances that affected all or part of the landscape. Many of the sites we surveyed in Iowa have extensive areas of invasive Brome Grass (*Bromus* spp.) that contain few if any violets, but *S. idalia* adults often patrol these areas and feed at the nectar sources present in them. Such areas with no violets may be detrimental to female fecundity (i.e., sinks (Pulliam 1988)) if adult females spend significant time searching there in vain for areas with hostplants where they could oviposit.

Two unanswered questions remain. First, are hostplants limiting to *S. idalia*? Second, if so, how does the limitation of larval hostplants affect this insect? Quantifying not only the total biomass required to support one insect through its life, but also an entire population, would lend helpful evidence to conservation efforts. Females probably scatter eggs in the vicinity of violets, but do not oviposit directly on the violets (D. Wagner, pers. comm., Barb Barton pers. comm.). Thus mortality is probably highest in the first larval instar. An average *S. idalia* larva consumes 3–4 *viola* plants during the course of its growth (D. Wagner, pers. comm.). Estimating the total number of individuals necessary to maintain a viable population would be another important clue in conserving the species. In addition, knowing specifically how the effects of food limitation are manifested in an individual insect (number of eggs laid, total lifespan, delayed emergence, etc.) versus a population (adverse fluctuation in population size from year to year, or perhaps unequal sex ratios) would aid in gathering more meaningful field data and interpreting results. For example, male adults emerge earlier (at least two weeks) than females. If male larvae consume host plant resources faster than females, females may lack sufficient resources to finish their larval stage.

Ideally, we would use examples of stable *S. idalia* populations in native prairies to guide decisions regarding burning, grazing, or planting restored prairies in Iowa. Laboratory data would be helpful in assessing how much violet biomass is required to support each insect. Field work suggests that hostplant density and nectar availability could be just as important to the persistence of *S. idalia* populations as the amount of habitat available. Ultimately, we are interested in a threshold value of vi-

olet biomass necessary for preserving or restoring prairie areas with *S. idalia* populations. The quality of surrounding habitat available to the insects, as well as the isolation from other *S. idalia* populations, will also undoubtedly be important factors in the long-term persistence of *S. idalia* populations.

ACKNOWLEDGMENTS

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STUDIES IN THE GENUS *HYLEPHILA* BILLBERG, I.
INTRODUCTION AND THE *IGNORANS* AND *VENUSTA*
SPECIES GROUPS (HESPERIIDAE: HESPERIINAE)

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ABSTRACT. This paper, the first of three, introduces the primarily South American genus *Hylephila* Billberg (1820) and notes the great similarity of both the male and the female genitalia. Four species groups are recognized, and a key to these based on superficial characters is provided. These assemblages—the *boulleti* group (nine or ten species), the *ignorans* group (two species), the *venusta* group (three species), and the *phyleus* group (ten species)—are diagnosed and their distributions are mapped and/or discussed. The first three groups are almost entirely Andean (or are from nearby ranges at high elevations) and are nearly or quite allopatric, and additionally, are scarce in collections. The *phyleus* group expresses the geographic range of the genus (from the length and breadth of South America, plus the Antilles, north to the United States, coast to coast), largely owing to one familiar, weedy species, *H. phyleus* (Drury 1773).

Two species groups are treated in this paper. The *ignorans* group with *H. ignorans* (Plötz) and *H. adriennae*, **new species** and the *venusta* group, with *H. lamasi*, **new species**, *H. venusta* (Hayward) and *H. kenhaywardi* MacNeill, **new name** [new name for *H. venusta haywardi* (Ureta 1956), not Bryk (1944)] are described and figured comparatively including their male and female genitalia (those of the female for the first time). Ova of three of the species were obtained by dissection, and these are briefly described for the first time. Because of some confusion about the relationship of *Hylephila* with *Linka lina* (Plötz), this is discussed and the male and its genitalia are figured comparatively.

Additional key words: South America, biogeography, altiplano, oreol biomes (high mountain), *Linka lina*, páramos, genitalia (male and female).

INTRODUCTION

The principally Andean and Patagonian genus *Hylephila* Billberg (1820) is a tightly knit unit of about twenty-five species based mainly upon features of the male and female genitalia and of the short antennae, each with a (usually) minute apiculus, superficial appearance notwithstanding. The species are medium-sized (forewing length to 17 mm) to small (forewing length at least 8 mm), generally orangish, hesperiine skippers belonging to the "M" group of Evans (1955) along with the close relatives *Polites* Scudder (1872) and *Wallengrenia* Berg (1897) (MacNeill 1975, 1993). Males may or may not have a stigma.

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The genus occurs through the Austral regions of the Western Hemisphere and the oreale (high mountain) biomes of South America as well. It spans the North American continent from New York to northern California (plus very recently nearly all of the Hawaiian Islands [Tashiro & Mitchell 1985]). It is present in almost all of the Antilles, Central America, and all of South America from northern Colombia to Pcia. Magallanes in southern Chile. Most of that distribution can be attributed to just one weedy species, *H. phyleus* (Drury 1773), the type of the genus and the only one that occurs on the mainland north of Colombia.

In the most recent review of the genus Evans (1955) named several taxa and ended up with eleven species. One of these, *H. fassli* Draudt (1923), has been shown by Mielke (1993) and Mielke and Schroeder (1994) to belong to the genus *Thespieus* Godman (1900). All ten of the remaining species recognized by Evans we will retain in our treatments. Several of the subspecies recognized by Evans and by Ureta (1956) will be elevated to species rank, and about ten species will be described as new in this and subsequent papers.

These studies were initiated by one of us (J.H.) in Chile so that he could complete his ongoing work on the butterflies of Chile. We agreed to collaborate on the *Hylephila* study in the middle 1960's but with neither of us able to devote much time to it. Until recently our collaboration consisted of one of us (J.H.) preparing and studying hundreds of genitalic dissections, and both of us periodically exchanging information, accumulating material, and interpreting what we were seeing in the laboratory and in the field. The present paper is based upon our notes and further intensive study by C.D.M.

These studies, which are continuing, will be presented in three papers. This, the first, comprises the introductory matter and the treatment of the two smallest species groups. The second (by C.D.M.) will treat the *boulleti* group, restricted to the Andes of central and southern Peru, eastern Bolivia, northern Chile and Argentina. The third paper (also by C.D.M.) will treat the remainder of the genus, the *phyleus* group from North and South America.

TECHNIQUES, METHODS, AND MATERIALS

Since the synonymies of all the taxa treated by Evans (1955) were listed in that work, they will not be repeated in these papers unless there are concept changes. Generally only citations of illustrations or post-Evans references will be listed in our synonymies. For species previously described, redescrptions will treat only characters not previously described or emphasized.

Terminology for stigmal characters is a modification of that used by

MacNeill (1964, 1993); for venation, MacNeill (1964); for the intervein spaces, Miller (1970); for genitalia, Klots (1970), Burns (1987), and MacNeill (1993).

The genitalia were dissected after soaking the abdomen in a 10% KOH solution overnight at room temperature (C.D.M.) or right after gently heating for short periods prior to dissection (by J.H.). Dissected genitalia were compared, illustrated, and stored in, a glycerin medium. Dissections by J. Herrera are cited as JH, by C. D. MacNeill as CDM, and by J. M. Burns as JMB.

A number of female abdomens were, in addition, and prior to KOH treatment, soaked overnight in a 10% "901" solution (active ingredient trisodium phosphate) (by C.D.M.) using the technique discussed by VanCleve and Ross (1947) and by Thompson (1954). This technique was used to recover hesperiid eggs from dried museum specimens as reported by MacNeill (1964) and Herrera et al. (1991). It was possible to estimate the general size of ova, the nature of the reticulation, the number of ova per female, and, on one occasion, the first instar chaetotaxy of a *Hylephila* larva by this method. Ova were measured using an ocular micrometer. Reticulation was observed by letting the alcohol storage medium dry briefly from the egg surface. Successful recovery of ova was well under fifty percent per dissection.

THE GENITALIA

The male genitalia of the single North American species have been illustrated adequately since Scudder (1889). The Skinner and Williams (1924) figures, reproduced in Lindsey et al. (1931), clearly define the genus by showing well the very distinctive triangular-shaped valva and the enormous juxta. Eaton (1932) was the first to illustrate comparatively both a South American species and *H. phyleus*, and he captured a few of the important differences as well as some of the similarities. Hayward (1934b) figured the male genitalia of *H. phyleus*; but his illustration is remarkably similar to Godman's (1900) inadequate figure, showing identical distortions and misinterpretations. Although he treated two additional species in the text of a previous paper (Hayward 1934a), he offered no genitalic comparisons; so his figure is of little use beyond generic discrimination. Again, Hayward (1937) figured (badly) the genitalia of *H. phyleus* and *H. fasciolata* (Blanchard), exaggerating the differences and obscuring the similarities; and he (Hayward 1940) compared the male genitalia of two additional species showing features that he misinterpreted or features that did not exist. The figures by Hayward (1950), by Evans (1955), and by Ureta (1956) are not useful. The genitalic figures of Draudt's (1923) types by Mielke (1993) and by Mielke

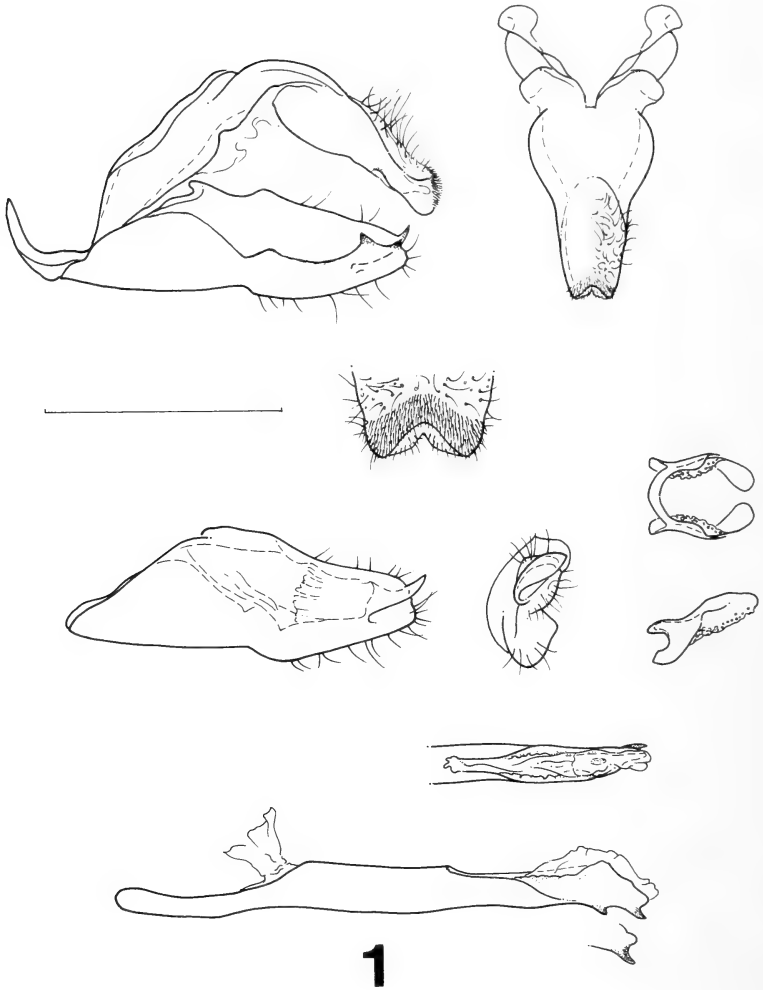


FIG. 1. Male genitalia of *Linka lina*. Uncus (lateral and dorsal aspects, tip enlarged), valvae (right outer and caudal aspects), juxta (left lateral and ventral aspects), penis (left lateral aspect and caudal one-half dorsal aspect). Páramo E. Usaquen, IX-3-70, Cundinamarca, COLOMBIA, R. E. Dietz (genitalic dissection # ♂5028-JH) (USNM). Scale = 1 mm.

and Schroeder (1994), however, are sufficiently accurate for us to recognize the taxon *H. peruana* Draudt.

The male genitalia are extremely important tools useful in the recognition of the genus, in the clustering of taxa into species groups, and in the discrimination of species. The female genitalia are more conservative but are very useful at the genus and species group levels and are only slightly less so at the species level. The discriminatory differences at the



FIG. 2. Male stigma pockets of *Hylephila adriennae*, paratype. N. of Duriamena Valley, II-16-75, Sierra Nevada de Santa Marta, COLOMBIA, G. I. Bernard (genitalic dissection # 53997-JH) (CDM). Left forewing underside (partial aspect).

species level often are in minute features of the pectines, titillators, and cornuti in males and in proportions of the ductus bursae in females.

The male genitalia of *Hylephila* (Figs. 9–13) always have the vinculum conspicuously inclined caudad (from ventral to dorsal), hence the basal margin of the valva (that margin against the vinculum from near the saccus to the appendix angularis) is usually much longer than the dorsal margin. The ventral margin of the valva is a shallow, convex curve to the, often beaked, caudal horizontal cleft, which in caudal view is somewhat diagonally inclined mesad and slightly expanded laterally as opposing flanges ornamented with knuckle-like dentitions.

The uncus is moderately sclerotized and bears dorsally a pair of darkened pectines (MacNeill 1993) and ventrally, the paired, more or less sclerotized, terminally minutely hirsute, gnathos. The transtilla is small, vague, and not to scarcely sclerotized. The juxta is massive, very elongate, anteriorly with a midventral projection and short, stout, paired lateral prongs projecting forward, and caudally bearing paired dorsal humps and a pair of ventrolateral, ragged clefts separating an irregularly defined midventral “floor.” The penis is slender and at its caudal end bears, dorsolaterally, two thorn-like, unidentate titillators (Burns 1987, see comment below) usually basally attached to the penis by slender sclerotic straps (more or less inconspicuous) folded inward until the vesica is everted. The term “titillators” seems more applicable than the MacNeill (1993) use of “rostella” since these are “hinged” and eversible

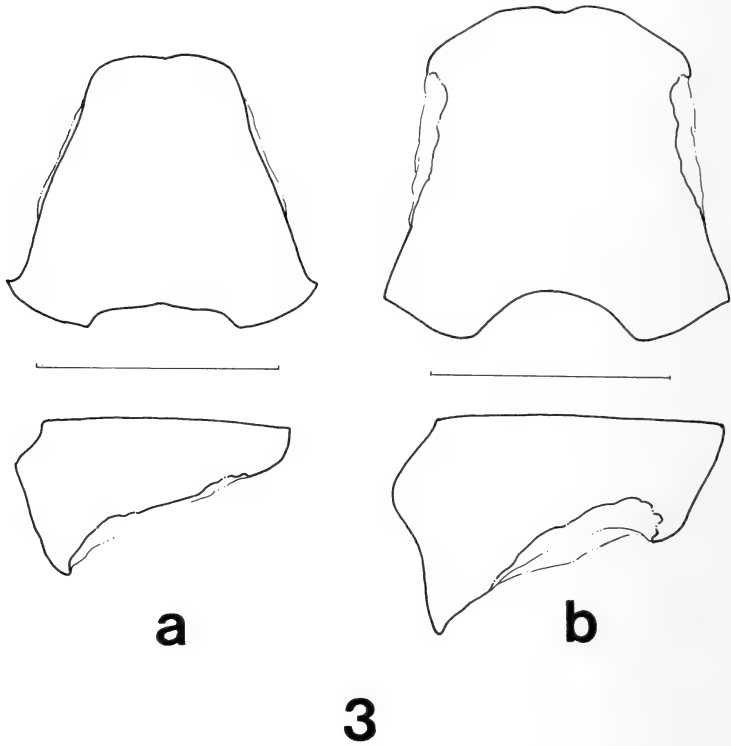


FIG. 3. Male eighth tergites (dorsal and left lateral aspects) of two species of *Hylephila*. **a.** *H. ignorans*, upper Albarregas Valley, 3250–3500 m, VI-20-75, Cordillera de Mérida, Mérida, VENEZUELA, M. J. Adams (genitalic dissection # ♂6107-CDM) (CDM). **b.** *H. adriennae*, paratype, Headwaters of Rio Cambirumeina, S. slope Cerro Icachui, 4000–4400 m, COLOMBIA, A. M. Shapiro & A. R. Shapiro (genitalic dissection # ♂3918-JH) (UCD).

and, in one species, the connection to the penis is completely absent so that they appear as free vesical structures. Also present is a pair of vesical cornuti, usually bidentate, best seen when the vesica is everted.

The eighth tergite is caudally narrowed and bears, near the caudal margin, a vestiture of long, stiff, bristle-like scales arising from enlarged, posteriorly directed, tuberculate sockets (Figs. 4–8). These scales are brittle and easily break. Several apparently penetrate and occasionally lodge in the ventrolateral pleural membranes caudad of the eighth segment of some females during copulation (Fig. 20). The function, if any, of this phenomenon is unknown.

The female genitalia (Figs. 14–20) usually have the eighth sternite at least weakly sclerotized and the eighth tergite with the apophyses anteriores sclerotically conjoined with the, usually medially undivided,

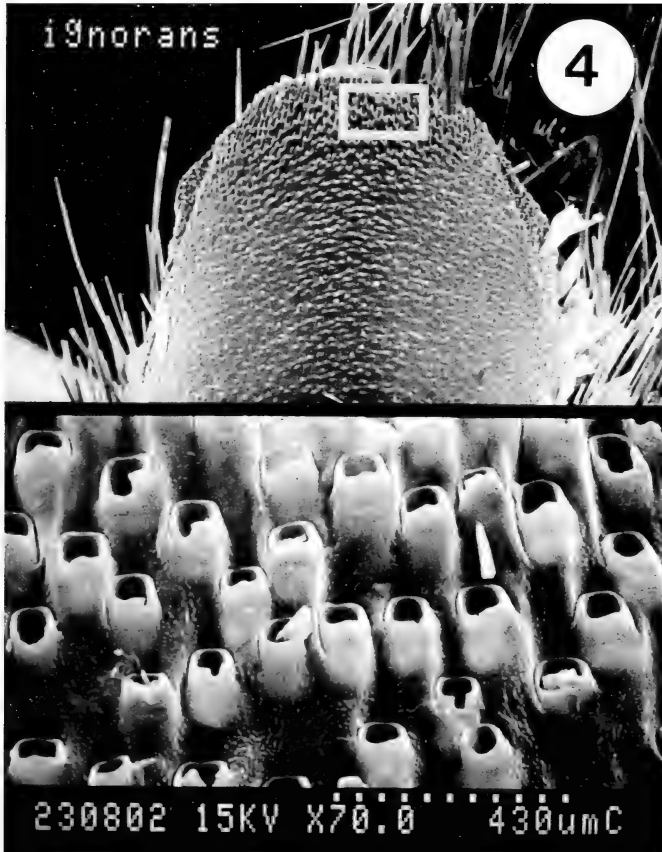


FIG. 4. Male eighth tergite (dorsal aspect) of *H. ignorans* (descaled to show caudal array of tuberculate bristle-sockets at 70 \times with inset enlarged below to 143 microns/cm), Cabana de los Curas, Páramo Los Conejos—Páramo La Culata, 3500 m, II-12-83, B. Rodrigues & J. DeMarmels (# σ SEM-2-CDM) (MIZA).

lamella postvaginalis. The ostium bursae is very broad. The ductus bursae has the antrum dorsally usually well sclerotized (but not in the species groups treated here) at least proximally (but not usually conjoined caudad with the lamella postvaginalis) and often dorsally with an irregular longitudinal inward fold at least caudally, and ventrally the lamella antevaginalis is plicate membranous and caudally very broad. The ductus bursae cephalad of the antrum is abruptly constricted, then asymmetrically and tortuously wrinkled (usually with a left-lateral pouch) and bent dorsad to the dorso-left-lateral ductus seminalis but ventrally expanded cephalad under the dorsocephalad positioned corpus bursae.

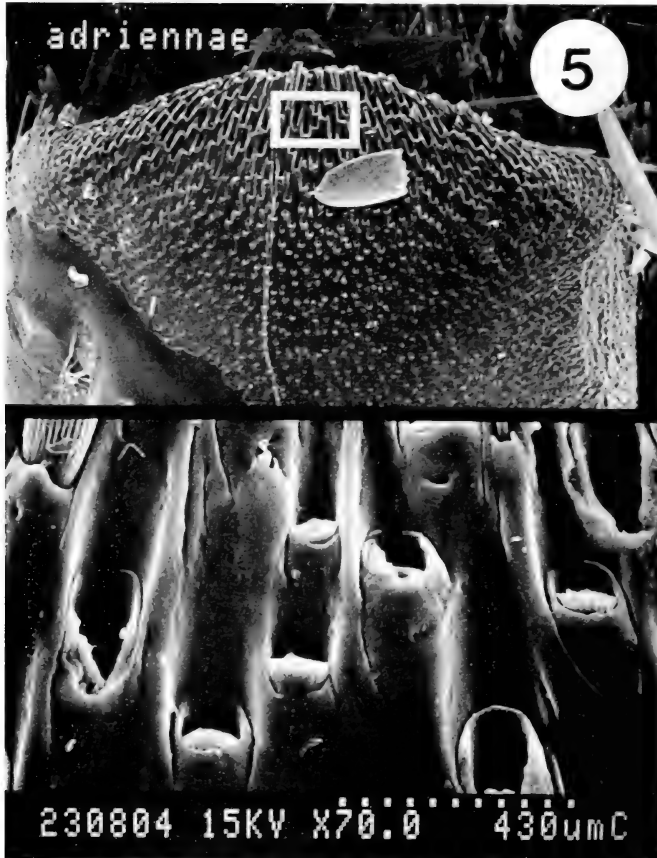


FIG. 5. Male eighth tergite (dorsal aspect) of *H. adriennae*, paratype (descaled to show caudal array of tuberculate bristle-sockets at 70× with inset enlarged below to 143 microns/cm), same data as Fig. 3b (# ♂SEM-3-CDM) (CDM).

THE SPECIES GROUPS

Considerations of male and female genitalia together with general appearance and geographic distribution suggest that the genus *Hylephila* sorts rather easily into four distinct species groups, each of which has significant Andean or Patagonian representation.

Artificial Key to Species Groups

- 1- Tegulae usually black with contrasting, broadly pale yellow edges when fresh or worn; from high ranges in central Peru south to northern Argentina and Chile *boulleti* Group
- Tegulae usually pale golden to orange-brown owing to an even vestiture of long, golden hairs; or if worn and with contrasting, broad, pale edging, from the Andes of central Chile south to Peia. Coihaique and adjacent Argentina 2

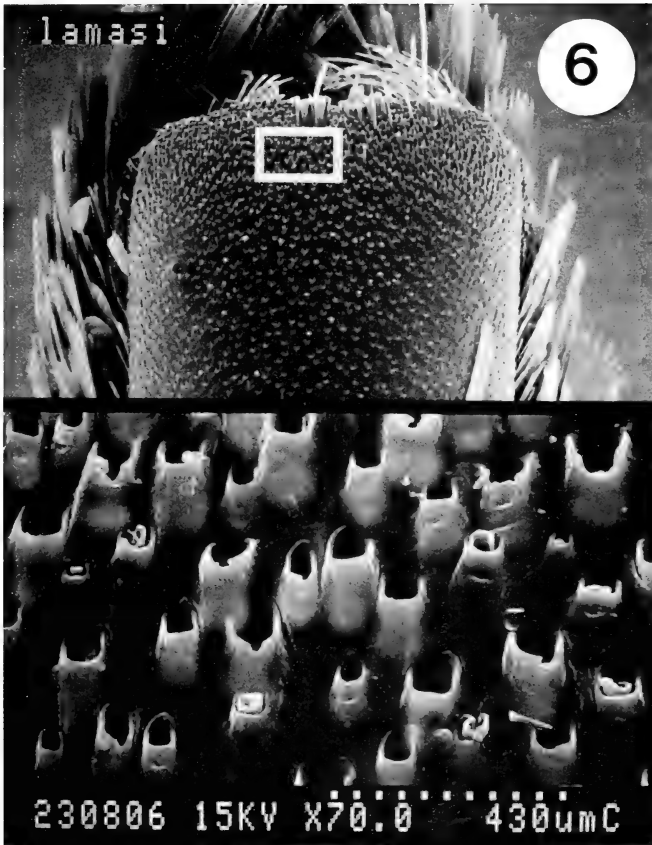


FIG. 6. Male eighth tergite (dorsal aspect) of *H. lamasi*, paratype (descaled to show caudal array of tuberculate bristle-sockets at 70× with inset enlarged below to 143 microns/cm), Salinas de Chilca, Lima, PERU, IV-14-74, G. Lamas, (# ♂SEM-5-CDM) (CAS).

- 2- Palpal vestiture of second segment anteriorly shaggy with long, black hairs mixed with pale, hair-like scales; restricted to páramos of high northern ranges in Colombia and Venezuela *ignorans* Group
- Palpal vestiture of second segment anteriorly of imbricate, broad, whitish scales, or if shaggy, few or no black hairs anteriorly, the black hairs restricted to the ventral face and anterolateral angles; not in high, northern páramos of Colombia and Venezuela 3
- 3- Males without a stigma; hindwing below with dark streaks and pale veins and/or with a pale ray from cell nearly to margin; in Andes of Chile and Argentina; or if no pale ray from hindwing cell to margin, from central coastal Peru *venusta* Group
- Males with a stigma; hindwing below without such markings; or if with a pale ray, from high Andes of Ecuador; range of genus *phyleus* Group

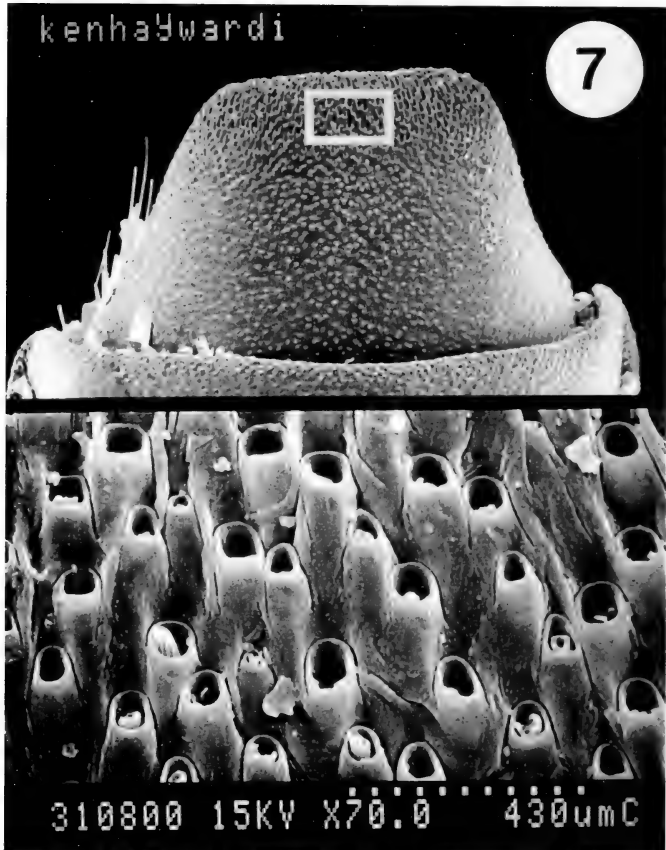


FIG. 7. Male eighth tergite (dorsal aspect) of *H. kenhaywardi* (descaled to show caudal array of tuberculate bristle-sockets at 70 \times with inset enlarged below to 143 micron/cm), Caballo Muerto, 4000 m, Salar de Maricunga, Copiapó, CHILE, J. Herrera (# δ SEM-6-CDM) (CDM).

THE *PHYLEUS* GROUP

Only one of these groups, the *phyleus* group, represents the geographic range of the genus. The oreal portion of this group's range is in the páramos of the Ecuadoran (and north Peruvian?) Andes (Fig. 32). Farther south, in Peru, Bolivia, Chile and Argentina it overlaps, but generally subtends, the high Andean ranges of two other species groups, the *boulleti* and *venusta* groups. This group comprises about ten species of medium-sized, tawny to bright orange skippers having prominent stigmata in males and having females often conspicuously darker in wing pattern. The markings vary; but on the hindwings below they usually lack a well defined, contrasting pale ray in space M1–M3, and the veins

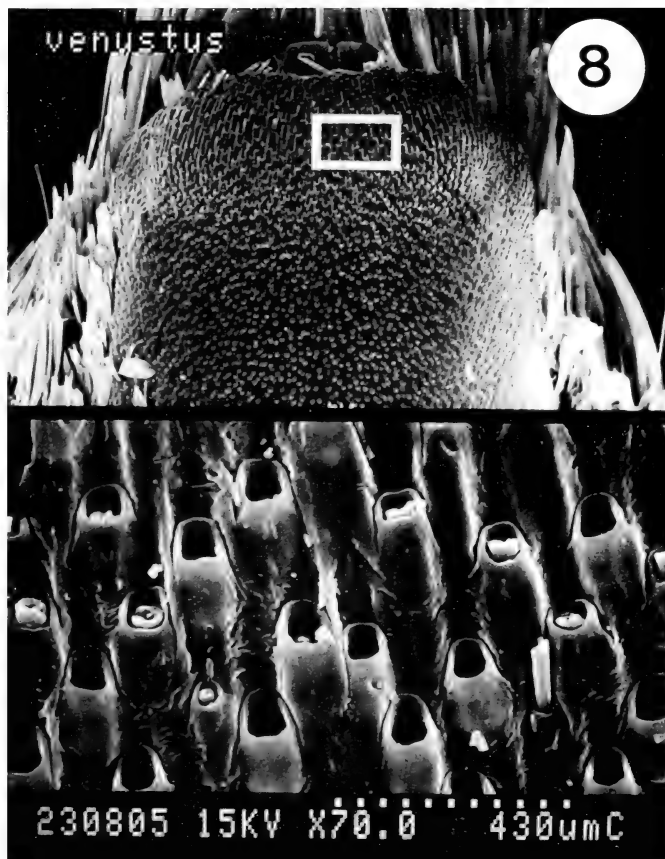
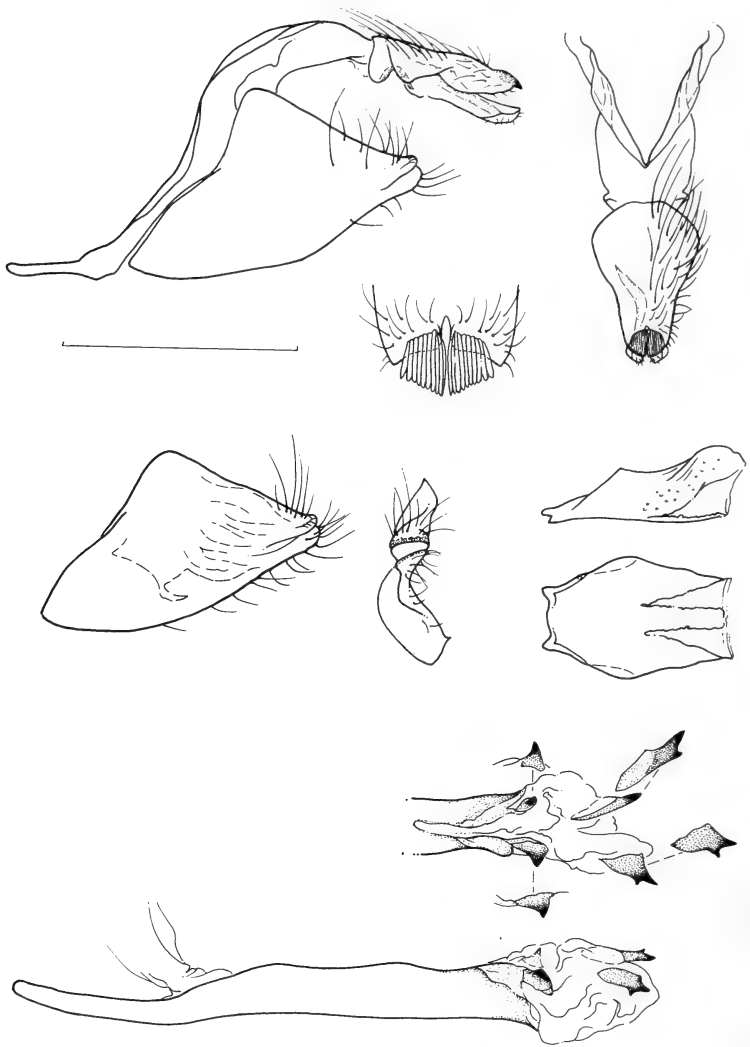


FIG. 8. Male eighth tergite (dorsal aspect) of *H. venusta* (descaled to show caudal array of tuberculate bristle-sockets at 70 \times with inset enlarged below to 143 microns/cm), Termas Chillán, Ñuble, CHILE, II-21-65, J. Herrera (# ♂SEM-4-CDM) (CDM).

do not appear to be conspicuously pale. The male forewings tend to be quite pointed apically, and the hindwings usually have a prominent tornus. The tegulae appear to be golden because they are uniformly clothed with long, golden, hair-like scales. The hind tibiae bear the usual two pairs of spurs. The dorsal part of the antrum in females is well sclerotized, and in males the gnathos is usually scarcely sclerotized and is not massive nor divergent ventrad from the uncus (but the uncus may be bent dorsad from the gnathos). The uncus often has a pair of dorsolateral, anterior horns.

The remaining three groups of *Hylephila* fairly well partition the Andes biogeographically (see Figs. 32, 33), evidently with little or no over-



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FIG. 9. Male genitalia of *H. ignorans*. Uncus (lateral and dorsal aspects, dorsal of pectines enlarged), valvae (right inner, left outer, and caudal aspects), juxta (left lateral and ventral aspects), penis (vesica everted, left lateral aspect, and caudal one-half dorsal aspect). Data as Fig. 3a. Scale = 1.0 mm.

lap between them. Each group of high Andean *Hylephila* remains scarce in collections, however, represented by poor series and few localities so that a satisfactory knowledge of their relationships and distributions is presently not possible. Nevertheless, of the considerable literature that has been consulted during the course of this study, papers by Adams (1973), Cabrera and Willink (1980), Clapperton (1993), Descimon (1986), Heppner (1991), Irwin and Schlinger (1986), Lamas (1982), Peña (1966), and Shapiro (1991, 1992) have significantly contributed to our present understanding of the distribution of the genus in the high Andes.

THE *IGNORANS* GROUP (FIG. 32)

In the páramos of the Venezuelan Andes, in the disjunct Colombian Sierra de Santa Marta, and, we expect, in the páramos of the several Colombian Andean ranges as well, occurs the *ignorans* group, a group of smallish, dark skippers marked much like certain *Polites* of western North America. This group is not well understood at present, and our knowledge of *Hylephila* of the high Andes of Colombia and northern Ecuador is nil. The two species here recognized in this group do not seem to be very closely related. Males of one species have a dark, tripartite stigma (Fig. 2) and the usual two pairs of spurs on the hind tibiae; the other species does not. Males are not conspicuously lighter than females in wing color. The hindwings above have a broad, inwardly uncut dark margin, and below are without a well defined pale ray in spaces M1–M3 or with a ray only in the lower half of that space (M1–M2), and the veins are somewhat pale. The wings are rather rounded and stubby. The tegulae are black with very narrow pale edges in worn specimens where the dark, golden, hair-like scales are largely missing; but when fresh, the tegulae appear dark, orange-brown as does the rest of the body dorsally. The antrum in females is not, or scarcely sclerotized dorsally; and the gnathos of males is slightly sclerotized, massive, and slightly to somewhat divergent ventrad. The uncus is without horns.

North Andean affinities in birds are reported for high tepuis in the south Venezuelan-Guyanese Pantepui region (Mayr & Phelps 1967). Dr. Jürg DeMarmels (1995, *in litt.*) has suggested that northern Andean representatives of this genus could be present in the Pantepui at lower elevations than in the Andes. Bell (1932) reported on a very small number of hesperiids collected by G.H.H. Tate during two American Museum of Natural History expeditions in the Pantepui, and no *Hylephila* were collected. A recent preliminary report by Fratello (1996) on a trip to a Guyanese tepui indicated that no hesperiids were collected above about 1500 m, and no specimens of *Hylephila* were mentioned. *Hylephila* may well occur in open areas on the high tepuis, but we suspect

that such species would belong to the *phyleus* group rather than to any other species group.

THE *BOULLETI* GROUP (FIGS. 32, 33)

The *boulleti* group is characteristic of the oreal bogs and grassy flats of high central Peru and south throughout the altiplano of southern Peru, Bolivia, northern Argentina and northeastern Chile, and the pre-Andean ranges (the Sierras Pampeanas) bordering the Argentine Provinces of Catamarca and Tucumán. This is a group of nine or ten small to medium-sized, usually tawny skippers, with or without a male stigma. This structure, if present, may be tiny and obscure, large and obscure, or large and conspicuous. The hind tibiae usually have two pairs of spurs. The wing patterns are remarkably alike. It frequently is necessary to dissect the male genitalia to identify a specimen. On both surfaces of the hindwing, there is a well-defined pale ray in the cell and through spaces M1–M3. Bold black spots are characteristic below basally, discally, and at the margin, where they appear to be defined or cut by white or pale veins (like Fig. 31). The forewings of the male usually are more or less pointed, and the hindwings are apically produced and with or without a prominent tornus. The tegulae are black with a contrasting broad, pale yellow to white, edging. The dorsal part of the antrum in females is well sclerotized to unsclerotized; and in males, the gnathos is sclerotized, massive, and ventrally divergent to scarcely sclerotized, not massive, and not divergent ventrad. The uncus is without horns. Female genitalia in some species are very similar and identification is often difficult except through association with males.

This group is generally very poorly collected and at most localities more than two or three specimens are rarely taken. We have been able to assemble adequate series of only two of the species. Most of the rest are known from one or two specimens and we have seen no females of more than half of the species belonging to this group.

THE *VENUSTA* GROUP (FIGS. 32, 33)

From the Andes in northern Santa Cruz Province in Argentina and the Chilean Province of Coihaique northward through the western slopes of the Chilean Andes to the province of Parinacota occur the two allopatric Andean species of the *venusta* group. Another, probably very primitive, species from the coastal lowlands of central Peru seems to belong here as well. The species of this group are small to medium-sized, orange to tawny skippers lacking stigmata in males. The hind tibiae have two pairs of spurs. The females are no darker or are only slightly so in wing markings than are males. On the hindwing below, the two Andean

species have a well defined pale ray from the cell through spaces M1–M3, and one of the species has conspicuous pale veins. The coastal Peruvian species has, on the hindwings below, all of the cell and the basal half of space M1–M2 dusky, with all of the veins pale fulvous. The forewings of both sexes are broadly rounded in the Andean species and pointed in the coastal Peruvian species, which also has a slightly more prominent tornus on the hindwing. The tegulae are golden in fresh specimens. The entire antrum in females is more or less membranous and very broad caudad, and in males the gnathos is well sclerotized, massive, and ventrally divergent. The uncus in males lacks horns.

The three species in this group are not common in collections. As in the *boulleti* group, they rarely have been collected more than two or three at a time and only in a few widely separated localities. The species seem to be totally allopatric, and they do not look superficially very much alike.

THE *LINA* LINK

Plötz (1883) addressed many species of "*Hesperia*," among which were a number of *Hylephila*. Several were described as new, and two of these will be considered in this paper. *Hesperia lina* Plötz was described from Bogotá on page 209. This animal is not a *Hylephila*; but it has the pale fulvous of the hindwing below restricted by conspicuous marginal, discal, and basal black blotches cut by white or pale veins suggestive of some of the high Andean *Hylephila*. Draudt (1923:pl.181d) figured it reasonably well as *Polites lina* except that on the hindwing below the posterior arm of the pale fulvous macular band is more regular and intact on the specimens we have seen ($n = 5$) (Fig. 31). Dyar (1913) listed four specimens (of *Hylephila peruana* Draudt, which we have examined) as *Hylephila lima* (sic) (Plötz), and we have seen Chilean specimens of *Hylephila boulleti* (Mabille) identified as *Hylephila lima* (sic) (Plötz). Hayward (1947) listed *Polites lina* (Plötz) in his catalogue of Colombian hesperiids and called attention to Dyar's misspelling of the Plötz name. Evans (1955) gave it his generic name *Linka*, placing it next to *Polites* Scudder, with the comment "Near *Hylephila* but the antennae and genitalia differ." He cartooned the male genitalia so that about all that is revealed is that the valva is not shaped like that in *Hylephila*.

As there has been some confusion regarding the relationship of this species and *Hylephila*, we figure here the male genitalia of *Linka lina* (Plötz) for comparative purposes (Fig. 1). Note the slender penis with a pair of ventral, in line, rostellae and no vesical cornuti; the smaller, more erect, ventrally less sclerotized juxta; the relatively erect vinculum and corresponding shorter basal margin of the valva; the membranous central area of the uncus dorsad; the coarsely pubescent, dorsocaudal uncal

tip instead of pectines; the membranous, minute hidden gnathos; and the eighth tergite near the caudal margin lacking greatly enlarged, posteriorly directed, tuberculate sockets bearing long, stiff, bristle-like scales. These are all features not shared with *Hylephila*.

THE *IGNORANS* GROUP

Superficial Key to the Species

Hind tibia with a single pair of spurs; male without stigma; small, forewing length 9.5–11.5 mm	<i>H. ignorans</i> (Plötz)
Hind tibia with two pairs of spurs; male with a prominent stigma; larger, forewing length 11.5–16.0 mm	<i>H. adriennae</i> , new species

Hylephila ignorans (Plötz)

(Figs. 3a, 4, 9, 14, 21, 22, 31)

Hesperia ignorans Plötz, 1883. Stett. Entomol. Zeit. 44:207, (pl. 647).

Polites ignorans, Godman, 1907. Ann. Mag. Nat. Hist. ser. 7, 22 (116):144; Draudt, 1923: In Seitz, Gross-Schmett. Erd. 5:929, pl. 181e.

Hylephila ignorans, Evans, 1955: Cat. Amer. Hesp. part IV, pp. 315, pl. 75; Lewis, 1973: Butterflies of the world, p. 246, pl. 83, fig. 18.

Plötz (1883) listed the single specimen he had as being from "Vaterland?" suggesting doubt about the locality. The color figure he made of the type, a female, was never published. That drawing, indicated as t.647 in the original description, was examined by Godman who stated (1907:144) that "there is a ♀ very like it, from Mérida, Venezuela, in the G. & S. coll." We take that statement to effectively fix the type locality to the vicinity of Mérida, Venezuela.

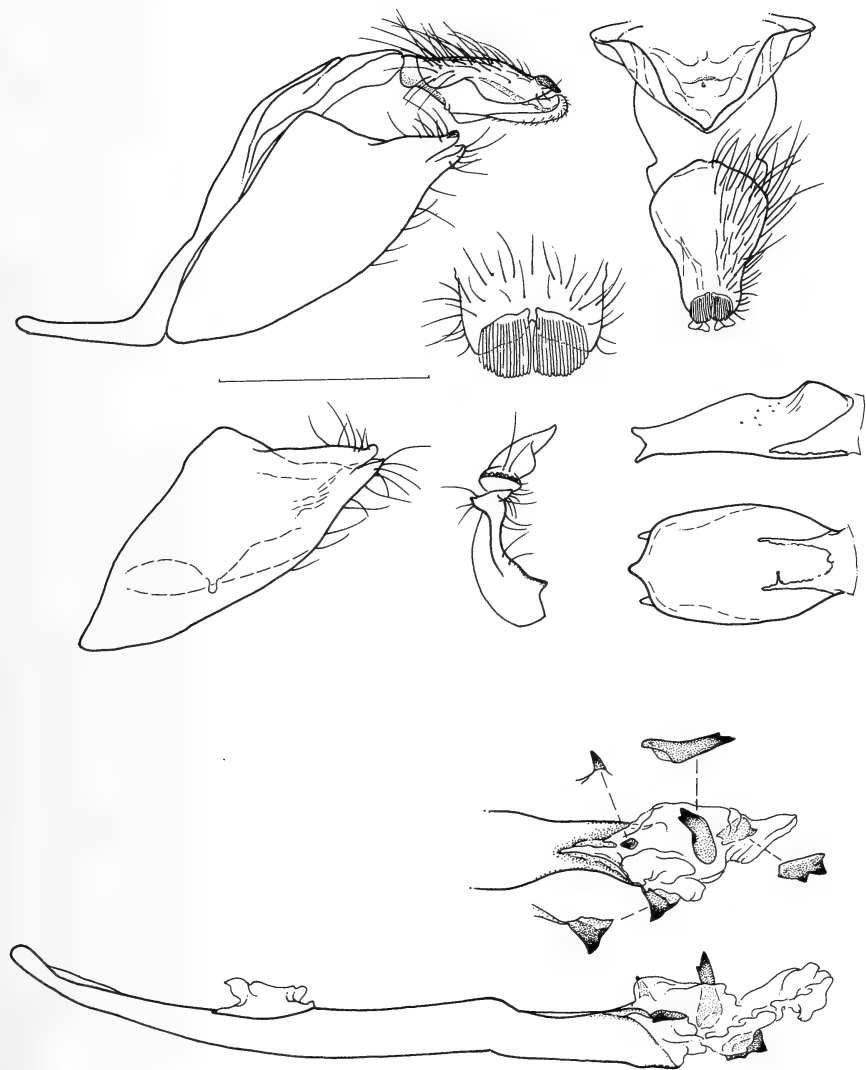
Description. *Male. Head.* Palpi shaggy, third segment scarcely or not protruding beyond hair-like, golden vestiture of front of second segment. Eyelash long, greater than two-thirds eye diameter. Antennae dorsally black, anteriorly golden on club, ventrally white; club about one-half length of shaft, nudum light brown; shaft about equal to dorsal width of head.

Body and tegulae. Dorsally black with dense, long, golden vestiture. Legs slender, hind tibiae with a single pair of spurs.

Wings. Stubby, rounded. Forewing length 9.0–10.5 mm (n = 10). Above stigma absent, yellow-fulvous broadly in cell and nearly to costal margin, fringes orange, basal half with mixed black scales. Below, forewing as above but costa dark to subapical spots with white overscaling at anterior edge, fringes terminally orange, then finely black, and basally white. Hindwing below brown with a discal, narrow, fulvous macular band in spaces Cu2–2A through Sc+R–Rs, which is bordered proximally and distally by black spots except proximal to space M1–M3. A subdiscal black spot in cell as well as a basal one, and a basal dark, subcostal streak below a basal, whitish costal streak. Overscaling golden with a vague lilac tint, whitish along veins.

Genitalia. Eighth tergite (Figs. 3a, 4) evenly tapered to caudal margin, not deeply emarginate laterally just before caudal margin; terminal bristle sockets minute, not conspicuously enlarged caudad, squarish in cross section. Valva (Fig. 9) in lateral view short, with length of basal margin less than one and one-half times depth of valva. Penis short, scarcely exceeding length of entire genitalic capsule (saccus, vinculum, tegumen, and uncus) and less than twice length of valva; titillators sclerotically strapped to penis, similar, subequal in size and shape; cornuti asymmetric, bidentate. Juxta with ventro-caudal clefts one-half length of juxta, and separated median floor nearly or quite reaching caudal margin of juxta. Uncus with caudal cleft distinctly exceeding the pectines cephalad in dorsal view.

Female. Head and body. Similar to male except antennae with golden on club extending down shaft.



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FIG. 10. Male genitalia of *H. adriennae*, paratype. Uncus (lateral and dorsal aspects, dorsal of pectines enlarged), valvae (right inner, left outer, and caudal aspects), juxta (left lateral and ventral aspects), penis (vesica everted, left lateral aspect and caudal one-half dorsal aspect). Data as fig. 3b. Scale = 1.0 mm.

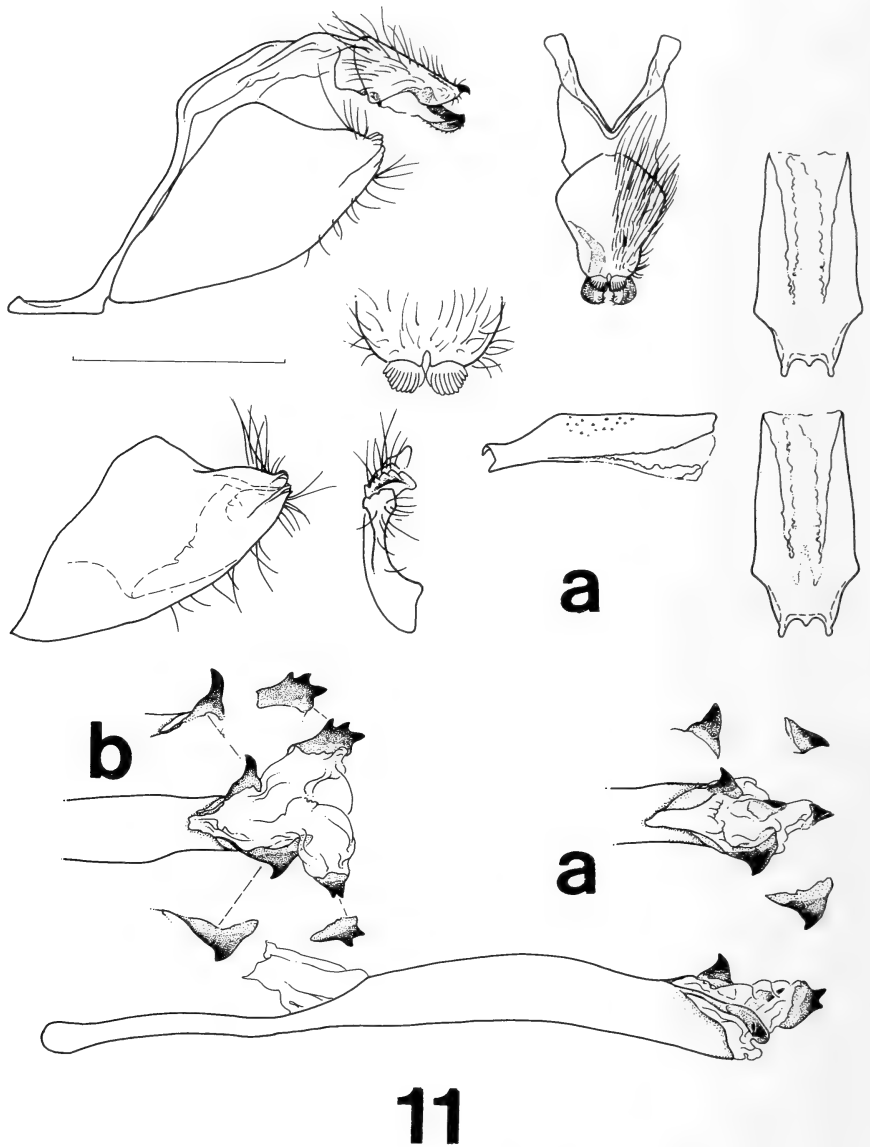


FIG. 11. Male genitalia of *H. lamasi*, holotype. **a.** Uncus lateral and dorsal aspects, dorsal of pectines (enlarged) valvae (right inner, left outer, and caudal aspects), juxta (left lateral and two interpretations of ventral aspects), penis (vesica somewhat everted, left lateral and caudal one-half dorsal aspects). Paracas, sea level, IV-5-75, Ica, PERU, G. Lamas M. (genitalic dissection # ♂3740-JH) (MUSM). **b.** Paratype. Penis (vesica everted, caudal one-half dorsal aspect). Salinas de Chilca, sea level, IV-14-74, Lima, PERU, G. Lamas, (genitalic dissection # ♂6267-CDM) (MUSM). Scale = 1.0 mm.

Wings. Forewing length 10.5–11.5 mm ($n = 6$), above with dark discal spots in spaces Cu2–2A and Cu1–Cu2 larger and usually with a dark dash in cell.

Genitalia (Fig. 14). Eighth sternite often nearly or quite conjoined anterolaterally with lamella postvaginalis which is medially connected, each half conspicuously produced cephalad by a ventrally folded flap forming a nipple-like pocket and more medially, by a sclerotized, bifurcate intrusion into the dorso-caudal portion of the otherwise membranous antrum. Ductus bursae sclerotized just caudad of the ductal constriction, the left-lateral pocket more or less conspicuous.

Distribution. We have seen only 16 males and 6 females (4 ♂, 2 ♀ dissected), all from above 3000 m in the páramos of the Cordillera de Mérida, Venezuela, most collected during the month of February but also some in April and June.

Discussion. This small species suggests a small *Polites* in wing pattern, especially on the underside. The only *Hylephila* with which it can be confused is the next species from which it is easily separated by its smaller size and the more yellowish fulvous upper side of the forewings (compare Figs. 21, 22 and Figs. 23, 24). The single pair of hind tibial spurs, the lack of a male stigma, and the apparent restricted distribution also distinguish this species from the next.

Hylephila adriennae MacNeill & Herrera, new species

(Figs. 2, 3b, 5, 10, 15, 23, 24)

Description. *Male. Head.* Palpi shaggy, third segment barely protruding anteriorly in dorsal view; in lateral and ventral views more or less distinctly protruding from mixed black and pale golden-fulvous, hair-like vestiture of front of second segment. Eyelash long, about two-thirds eye diameter. Antennae dorsally black, anteriorly golden on club and shaft, ventrally checkered to white; club less than one-half length of shaft, nudum brown; shaft length greater than dorsal width of head. Vestiture of golden hairs over black scales dorsally; tip of collar fringe, eye ring (briefly interrupted dorsally), and vertex medially behind antennae whitish or pale buffy.

Body dorsally black with golden hair-like vestiture, tegulae similar but with a thin edging of buffy scales. Ventrally shaggy and paler. Legs with hind tibiae bearing two pairs of spurs.

Wings. Stubby, rounded. Forewing length, holotype 12.5 mm, paratypes 11.5–13.5 mm ($n = 39$). Above, stigma present (Fig. 2), somewhat conspicuous, microandroconial mass gray, upper and lower brush patches weakly present, post-stigmal patch broad, dark brown, iridescent greenish in side illumination. Fulvous dark orange, restricted by broad, dark border to apical and subterminal spots, upper and lower cell streaks and often vaguely to costa above end cell, discal in spaces M3–Cu1, Cu1–Cu2, and wedge-shaped in lower half of Cu2–2A, and these three spots outwardly prolonged along the veins. Brown markings more or less heavily overscaled with fulvous except for a fine, darker marginal line. Fringes brown. Below, rich fulvous in distal two-thirds of cell, a costal streak in basal half, discal spots paler fulvous, in Cu2–2A, half as broad in Cu1–Cu2, and as a small spot in M3–Cu1, apical and subterminal spots white. Distinct black streak costally on basal one-third and black spots basal in cell and end cell as well defining basally and (except in Cu2–2A) marginally the apical, subterminal, and discal whitish or fulvous spots, but separated from marginal black line by a thin band of lilac overscaling which is broadened along veins apically and costally to base. Hindwings above dark brown, heavily overscaled with fulvous; five fulvous discal spots forming a macular band from space Cu1–Cu2 to Rs–M1, the spot in M2–M3 extended basad toward discal cell; margin with fine, dark line. Fringes with basal half brown, terminal half pale fulvous. Below brown with a thin, irregular, whitish macular band from space Cu1–Cu2 (or offset basad in upper half of Cu2–2A) to space Sc–Rs. Lilac overscaling over all but black spots, macular band, and vannal area; costa lilac, veins Cu2 to Sc whitish, basal black streaks in Sc–R1 and Cu2–2A, black spots basal and end cell, and wedge-shaped discal and submarginal black spots defining the macular band, distally bordered by a lilac overscaled band broadening vannally, and a thin black marginal line. Fringes basally white, medially black, and terminally pale fulvous.

Genitalia. Eighth tergite (Figs. 3b, 5) laterally conspicuously emarginate immediately

before caudal margin, terminal bristle sockets conspicuously enlarged caudad, rounded in cross section. Valvae (Fig. 10) in lateral view, slender, elongate, the length of the basal margin more than one and one-half times valva depth. Penis slender, greatly exceeding length of whole genitalic capsule (saccus, vinculum, tegumen, and uncus) and subequal to twice length of valva; titillators asymmetric, the right reduced, slender, without broad base of left and scarcely sclerotically strapped to penis; cornuti asymmetric, bidentate. Juxta with ventral caudal clefts less than one-half length of juxta, and separated midventral floor nearly or quite reaching caudal margin of juxta. Uncus with caudal cleft not exceeding the pectines cephalad in dorsal view.

Female. Head. Antennae dorsally black, anteriorly checkered black and buff, ventrally white, club about one-half length of shaft which is subequal to dorsal width of head.

Wings. Forewing length, allotype 14.5 mm, paratypes 12.5–16.0 (n = 13). Above and below as male but generally darker, elongate spot of hindwing macular band in space M2–M3 tends to be extended basally to end of cell where it is interrupted, then continued vaguely to base; macular band may have spots at each end.

Genitalia (Fig. 15). Eighth sternite not conjoined with lamella postvaginalis. Lamella postvaginalis medially united, each half shallowly produced cephalad forming an anterior bulge not nipple-like, medially produced ventrad into a double-folded flap just caudad of the membranous antrum. Ductus bursae sclerotized just caudad of ductal constriction, the left-lateral pocket conspicuously produced.

Types. Holotype ♂, COLOMBIA, Dept. Cesar. Headwaters of Río Cambirumeina, S. slope Cerro Icachui, 4000–4400 m, Sierra Nevada de Santa Marta, 10°45'N, 73°34'W, I-(18–22)-77. A.M. & A.R. Shapiro (genitalic dissection # ♂3668-JH), in CAS. Allotype ♀, COLOMBIA, Sierra Nevada de Santa Marta, E. above San Pedro de la Sierra, 2900–3900 m, III-9-75, M.J.Adams, in BMNH.

Paratypes. 37 ♂ and 14 ♀ (7 ♂, 6 ♀ dissected) as follows: 4 ♂, 1 ♀, same data as holotype (genitalic dissections #s ♂3917-JH, ♂3918-JH, ♀3880-JH, ♂SEM #3-CDM); 1 ♂, same data as allotype; 2 ♂, same data but G. I. Bernard; 1 ♂, same locality but III-4-75, G. I. Bernard; 4 ♂, 1 ♀ same locality but III-5-75, M. J. Adams (genitalic dissection # ♀6191-CDM); 1 ♂, 3 ♀, same data but G. I. Bernard (genitalic dissections #s ♂6190-CDM, ♀6151-CDM); 1 ♂, same locality but III-7-75, G. I. Bernard; 2 ♂, 1 ♀, same locality but III-8-75, G. I. Bernard; 1 ♂, same data but M. J. Adams; 1 ♂, 1 ♀, same locality but III-10-75, G. I. Bernard (genitalic dissection # ♀3998-JH); 1 ♂, same data but M. J. Adams; 2 ♀, same locality but III-11-75, M. J. Adams (genitalic dissection # ♀6108-CDM); 2 ♂, 1 ♀, COLOMBIA, Sierra Nevada de Santa Marta, N. of San Sebastián, 2800–3400 m, II-15-75, M. J. Adams (genitalic dissection # ♂6150-CDM); 2 ♂, COLOMBIA, Sierra Nevada de Santa Marta, N. of Durameína Valley, 3500 m, II-16-75, M. J. Adams; 2 ♂, same data but G. I. Bernard (genitalic dissection # ♂3997-JH); 3 ♂, 1 ♀, COLOMBIA, Sierra Nevada de Santa Marta, Mamanacana Valley, 3600–4000 m, II-17-75, M. J. Adams (genitalic dissections #s ♂6216-CDM, ♀6217-CDM); 2 ♂, 1 ♀, same data but G. I. Bernard; 5 ♂, 1 ♀, COLOMBIA, Sierra Nevada de Santa Marta, Upper Cambirumeina Valley, 4000–4100 m, II-19-75, M. J. Adams (genitalic dissection # ♂6215-CDM), 2 ♂, 1 ♀, same data but G. I. Bernard. Paratypes will be placed in the following collections: BMNH, USNM, AMNH, CMNH, AME, CAS, UCD, MUSM, MIZA, MBUZ.

Etymology. We are pleased to name this pretty species for Adrienne R. Shapiro, wife and co-collector of the short series brought to our attention by Arthur M. Shapiro, who also alerted us to the long series of this insect in papers at the BMNH collected by Michael Adams and George Bernard.

Diagnosis and discussion. This dark species looks even more like a *Polites* than does *H. ignorans* owing to the irregular, distinct, pale macular band contrasting with the dark, lilac-tinted underside of the hindwings. The short, stubby wings add to the *Polites* likeness (Figs. 23, 24). This very distinctive-looking *Hylephila* is apparently endemic to high elevations in the isolated, non-Andean, Sierra Nevada de Santa Marta of extreme northern Colombia where it flies from mid-January through at least mid-March. Ova recovered from one female (# ♀6217-CDM) were surprisingly large for a species of *Hylephila*. Measurements averaged 0.97 mm × 0.68 mm (range 0.92 mm × 0.60 mm to 1.0 mm × 0.72 mm [n = 7]). The reticulation was scarcely discernible at 50× magnification, the surface ap-

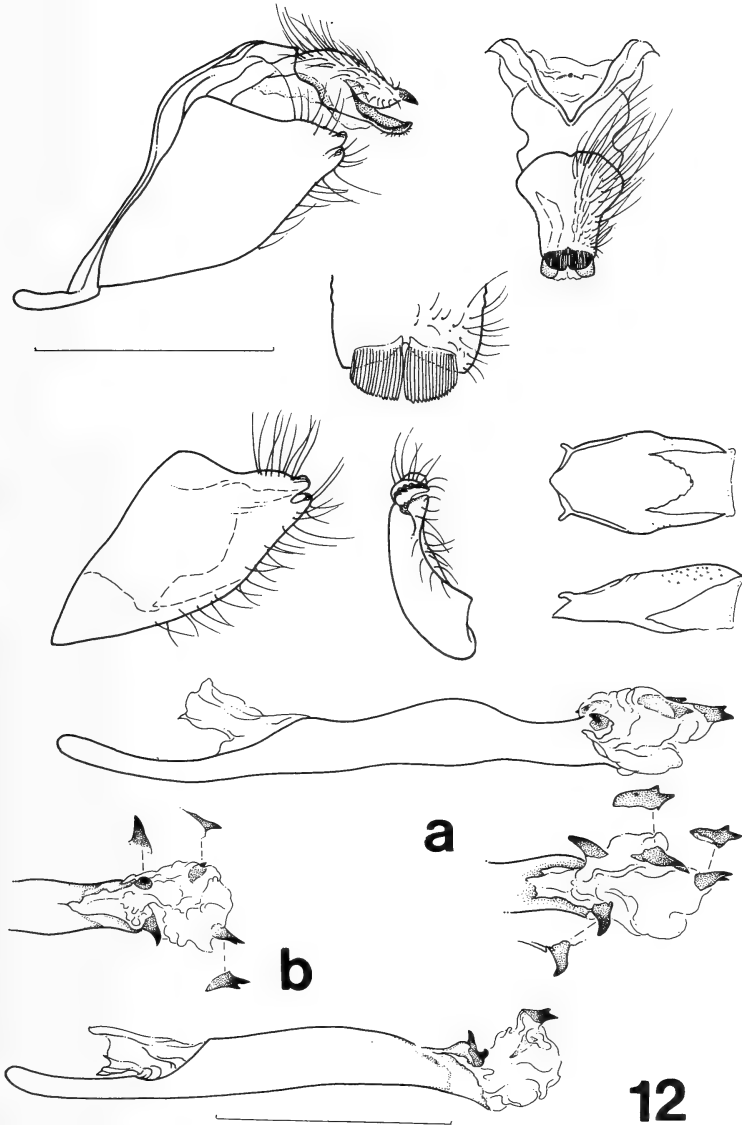
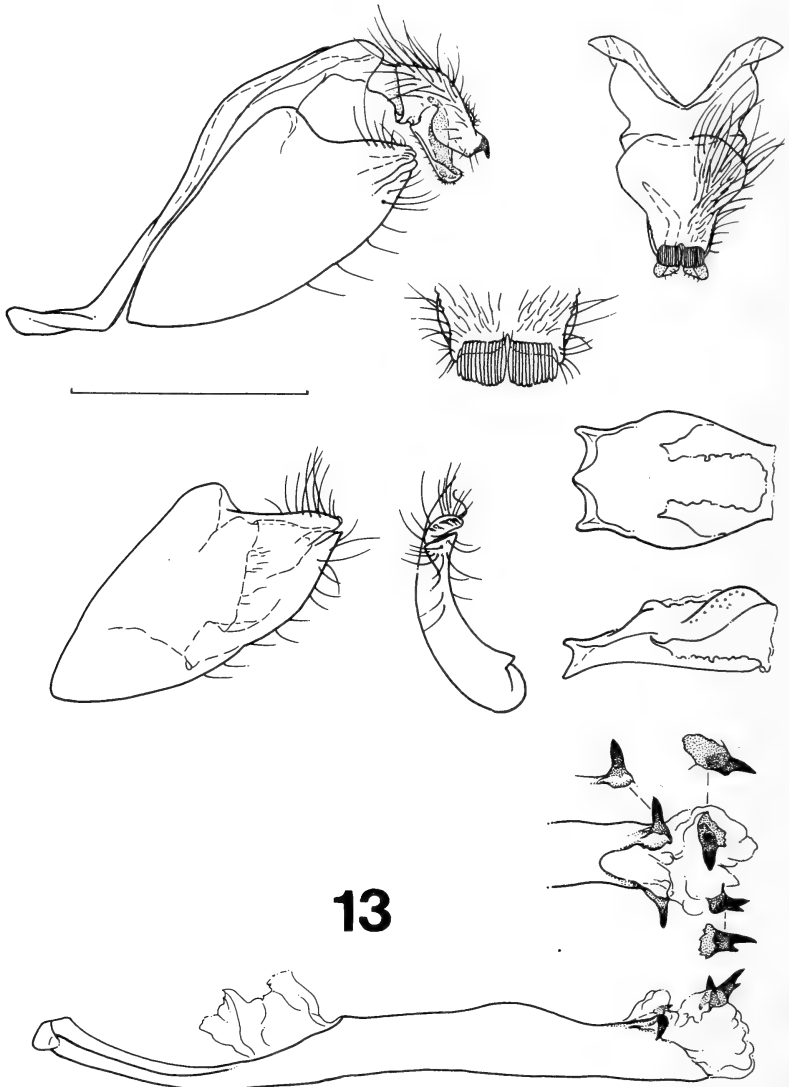


FIG. 12. Male genitalia of *H. kenhaywardi*. **a.** Uncus (lateral and dorsal aspects, dorsal of pectines enlarged), valvae (right inner, left outer and caudal aspects), juxta (left lateral and ventral aspects), penis (vesica everted, left lateral and caudal one-half dorsal aspects). Caballo Muerto, Atacama, CHILE, J. Herrera (genitalic dissection # ♂3707-JH) (CDM). **b.** Penis (vesica everted, left lateral and caudal one-half dorsal aspects). Caballo Muerto, Salar Maricunga, 4000 m, Atacama, CHILE, J. Herrera (genitalic dissection # ♂3910-JH) (CDM). Scale = 1.0 mm.



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FIG. 13 Male genitalia of *H. venusta* showing uncus (lateral and dorsal aspects, dorsal pectines enlarged), valvae (right inner, left outer and caudal aspects), penis (vesica everted, left lateral, and caudal one-half dorsal aspects). La Parva, 2800 m, III-31-83, Santiago, CHILE, J. Herrera (genitalic dissection # ♂6152-CDM) (IEUM). Scale = 1.0 mm.

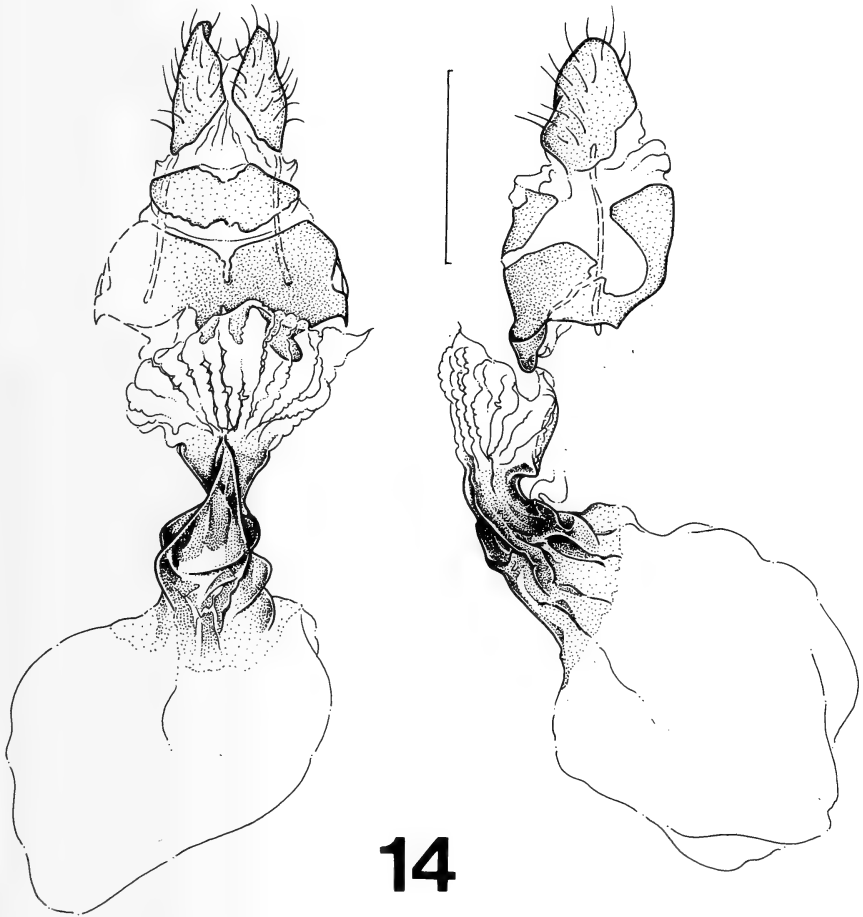


FIG. 14. Female genitalia of *H. ignorans* showing ventral and right lateral aspects. Mucubaji, 3350–3700 m, VI-3-75, Cordillera de Mérida, Mérida, VENEZUELA, M. J. Adams (genitalic dissection # ♀6001-CDM) (CDM). Scale = 1.0 mm.

pearing minutely granular. The ova were relatively few in number; only about a dozen were recoverable.

THE VENUSTA GROUP (FIGS. 32, 33)

Superficial Key to the Species

- 1- Hindwing below within space M1–M3 a pale fulvous ray from end cell to near margin and no dark ray from base to near margin in space Cu2–2A. Fringes broad, nearly or quite exceeding marginal width of space Cu1–Cu2 2
- 1- Hindwing below with at least basal half of space M1–M3 black, no fulvous ray from end cell to dark marginal border, and a dark ray from base nearly or quite to margin in space Cu2–2A. Fringes not as broad as marginal width of space Cu1–Cu2 *H. lamasi*, new species



FIG. 15. Female genitalia of *H. adriennae* showing ventral and right lateral aspects, paratype. E. above San Pedro de la Sierra, 2900–3900 m, III-11-75, Sierra Nevada de Santa Marta, COLOMBIA, M. J. Adams (genitalic dissection # 96108-CDM) (UCD). Scale = 1.0 mm.



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FIG. 16. Female genitalia of *H. lamasi* showing ventral and right lateral aspects, paratype. Same data as Fig. 6 (genitalic dissection #6269-CDM) (MUSM). Scale = 1.0 mm.



FIG. 17. Female genitalia of *H. kenhaywardi* showing ventral and right lateral aspects. Geisers del Tatio, 4590 m, 1-7-72, Cord. Antofagasta, CHILE, J. Herrera (genitalic dissection # ♀3865-JH) (CDM). Scale = 1.0 mm.

- 2- Hindwing below with veins whitish, contrasting with macular band, pale ray in space M1-M3 full width of space from end cell to near margin *H. venusta* (Hayward)
- 2- Hindwing below with veins pale fulvous as in macular band, pale ray in space M1-M3 narrow from end cell to macular band then broad to near margin *H. kenhaywardi*, new name

***Hylephila lamasi* MacNeill & Herrera, new species**

(Figs. 6, 11, 16, 25, 26, 32)

Description. *Male.* **Head.** Palpi not shaggy, third segment clearly protruding from whitish scales of front of second segment. Eyelash short, less than one-half eye diameter.

Antennae dorsally black, ventrally checkered black and buff, club about one-third length of shaft, nudum brown, shaft length subequal to dorsal width of head. Vestiture of long, golden hairs.

Body. Dorsal vestiture of long, golden hairs, tegulae similar, outwardly edged with buffy, golden scales. Ventrally pectus buff, remainder similar with hairs laterally golden.

Wings. Forewing pointed, length holotype 13.5 mm, paratypes 12.5–14.0 mm (n = 6). Above, fulvous extensive from base to deeply indented fuscous border (obscuring apical spots), except a dark dash from end cell nearly to border in space M1–M2 and the upper half of space M2–M3; a small brown discal spot mid-space Cu1–Cu2 almost centered over a dark brown, discal dash in upper half of space Cu2–2A where wedge-shaped border spot is elongate inwardly to partially lap under the discal brown dash, this space shaded dusky to base, more or less completing a dark discal ray from base to margin. Below as above but fuscous markings much reduced; no (or faint) discal brown spot in space Cu1–Cu2; basally except costad, fuscous projecting discally as two prongs, anteriorly under vein Cu2 and posteriorly under 2A. Hindwing above fulvous extensive from base in lower half of cell nearly to margin above Cu2 through wedge-shaped dark border spots; dusky ray below cell and Cu2, then a fulvous ray above 2A, and vannal area dusky fulvous above and below vein 3A. Fulvous extension anteriorly in submarginal spaces M1–M3, Rs–M1, and distally along vein Rs. Conspicuous fuscous basal half space M1–M3, space Rs–M1, and anterior to vein Rs. Below as above, veins fulvous, basal half space M1–M3 fuscous and fuscous ray from base to near margin in anterior half space Cu2–2A. Fringes above and below fulvous anteriorly, orange vannally.

Genitalia. Eighth tergite (Fig. 6) with terminal bristle sockets scarcely conspicuously enlarged caudad, squarish in cross section. Valva (Fig. 11) in lateral view, length of basal margin slightly more than one and one-half times valva depth. Penis slender, very long, more than twice length of valva; titillators sclerotically strapped to penis, similar, the right slightly to conspicuously (compare Figs. 11a and 11b) more slender than the left (and longer); cornuti asymmetric, one simple, unidentate (usually broadly bidentate to tridentate), the other narrowly bidentate. Juxta with ventral clefts difficult to see, apparently one-half or more length of juxta; separated mid-ventral floor scarcely sclerotized and evidently not nearly or quite reaching caudal margin of juxta. Uncus with caudal cleft greatly exceeding pectines cephalad in dorsal view; pectines minute, dorsally arched. Gnathos well sclerotized dorsally but ventrally only caudad, projecting caudad well beyond pectines in dorsal view, and diverging well ventrad from uncus.

Female. As male. Forewing pointed, length 13.5 mm–15.0 mm (n = 4). Markings as male but fuscous more extensive above and below.

Genitalia (Fig. 16). Eighth sternite a slender band, its width less than one-fourth its length. Lamella postvaginalis medially united. Antrum entirely membranous. Ductus bursae sclerotized just caudad of the ductal constriction (which is immediately ventrad of the ductus seminalis junction) as well as cephalad and ventral to the corpus bursae, left-lateral pocket scarcely produced.

Types. Holotype ♂, PERU, Ica, Paracas, sea level, 5-IV-75, G. Lamas M. (genitalia dissection # ♂3740-JH) in MUSM.

Paratypes. 5 ♂ and 4 ♀ as follows (5 ♂, 4 ♀ dissected): 2 ♂, same data as holotype (genital dissections #s ♂3739-JH, ♂6192-CDM); 3 ♂, 3 ♀, PERU, Lima, Salinas de Chilca, 14-IV-74, G. Lamas (genital dissections #s ♂6267-CDM, ♂6268-CDM, ♀3741-JH, ♀6193-CDM, ♀6269-CDM, ♂SEM #5-CDM); 1 ♀, PERU, Ancash, Gramadal, 10 m, 9-II-76, G. Lamas (genital dissection # ♀6266-CDM). Paratypes will be deposited in MUSM, USNM, and CAS.

Etymology. We are delighted to name this distinctive species for Gerardo Lamas, who collected all known specimens as well as a number of high Andean *Hylephila* in Peru, and who has contributed enormously to our knowledge of the Lepidoptera of Peru.

Diagnosis and discussion. This species is distinguished from all other *Hylephila* by the extensive fulvous above cutting deeply into the fuscous margins and interrupted on the forewings by a prominent, elongate, fuscous spot beyond the end of the cell and by the more or less conspicuous elongate, dark, spot in the upper half of space Cu2–2A connecting, ray-like, the base to the margin. The hindwing has these two markings as fuscous rays

more prominent from base to margin. On the underside these markings are repeated, particularly on the hindwing where the fulvous is extensive along the veins (Figs. 25, 26). The males lack a stigma, and the genitalia of both sexes differ from those of others in the genus as shown in Figs. 11 and 16.

This species is known only from three widely separated, maritime localities in south-central Peru, where it has been taken from February to April. Ova were recovered from one dissection (# ♀6266-CDM), and they were large for the genus. Measurements averaged 0.85 mm in diameter and 0.59 mm in height; range 0.83 mm × 0.56 mm to 0.86 mm × 0.63 mm (n = 7). The shape was evenly hemispherical without a basal flange; and the reticulation was minute, appearing smooth except under 50× magnification, when it became evident and seemed to be evenly expressed from near the base to the micropyle. The female carried relatively few eggs, and only nine were recoverable.

Hylephila kenhaywardi MacNeill, new name

(Figs. 7, 12, 17, 27, 28, 32, 33)

Hylephila bouletti, (sic) Ureta, 1938c (nec Mabille, 1906). Rev. Chile Hist. Nat. (Pura Apl.) 42:298.

Andinus venustus haywardi Ureta, 1956. Bol. Mus. Nac. Hist. Nat. 26:174, 175, pl. II, figs. 6a, 6b, 7; Ureta, 1963. Bol. Mus. Nac. Hist. Nat. 28:78; Camousseight, 1980. Mus. Nac. Hist. Nat., Publ. Ocas. no. 32:32.

Hylephila venusta haywardi, Peña & Ugarte, 1997. Las mariposas de Chile, the butterflies of Chile, p. 133, fig. (photo only).

Holotype. When Ureta (1956) described *A. venustus haywardi*, Evans (1955) had already placed *Andinus Hayward* as a junior synonym of *Hylephila* Billberg. *Hylephila venusta haywardi* thus became a junior secondary homonym of *Hylephila fulva* ssp. *haywardi* Bryk (1944) when it was described.

The male holotype of *A. venustus haywardi* Ureta is in the collection of MHNS (No. 790) (Camousseight 1980). One of us (C.D.M.) has examined this specimen and designated it the holotype of *Hylephila kenhaywardi* MacNeill, new name for *Andinus venustus haywardi* Ureta. It bears the following labels:

Red, black bordered, type set: "HOLOTIPO"

White, black-bordered, hand printed: "Río Toro/3400 mts/19-1-37"

White, unbordered: "♂"

White, unbordered but vertically divided by black line:

to left, type set: "CHILE/M.N./H.N."

to right, type set: "Tipo/No"

below, hand printed: "790"

Large, white, black-bordered, hand-printed: / "Andinus/venustus/haywardi/Ureta '56"

lower left, type set: "Det."

Red bordered, type set: "HOLOTYPE"

hand-printed: "*Hylephila kenhaywardi*/MacNeill '95"

Etymology. The name is a familiar, abbreviated combination of Kenneth Hayward, whom Ureta (1956) originally honored in naming this skipper.

Description. Male. Head. Palpi shaggy, third segment scarcely protruding from long, hair-like, buffy-white vestiture of second segment where black hairs are conspicuous laterally. Eyelash about one-half diameter of eye. Antennae dorsally black flecked with golden scales, ventrally buff-white; club nearly or quite one-half length of shaft, nudum one-half length of club; shaft length slightly greater than dorsal width of head.

Body. Dorsally and tegulae black under vestiture of dense, long, golden hairs, ventrally buff-white; legs golden buff.

Wings. Forewing stubby, rounded, average length 10.0 mm, range 9.0–11.0 mm (n = 42). Markings of both wings above with fulvous a cold tawny, fuscous marginal spots sagittate, partially obscured by tawny overscaling except for a fine, dark brown, marginal line. Forewing fringes orange to pale, grayish brown; hindwing mostly pale orange. Below, fuscous markings variable, light to dark but usually appearing vaguely defined owing to ex-



FIG. 18. Female genitalia of *H. venusta* showing ventral and right lateral aspects. Río Guenquel, III-4-69, ARGENTINA, J. Herrera (genitalic dissection # ♀3865-JH) (CDM). Scale = 1.0 mm.

tensive pale, tawny overscaling; costal area above forewing cell grayish. Hindwing with veins tawny, not contrasting with pale, tawny macular band, fulvous ray in space M1-M3 usually with that portion proximal to macular band irregularly reduced, not equal to full width of space M1-M3 from macular band to cell; fine, brown, marginal line on both wings. Fringes both wings basal half gray, distal half brown to tawny, that of the hindwing tornus usually all tawny.

Genitalia. Eighth tergite (Fig. 7) with terminal bristle sockets scarcely enlarged, squarish in cross section. Valva (Fig. 12) in lateral view, basal margin more than one and one-half times valva depth, dorsal margin more or less evenly tapered caudad, caudal half

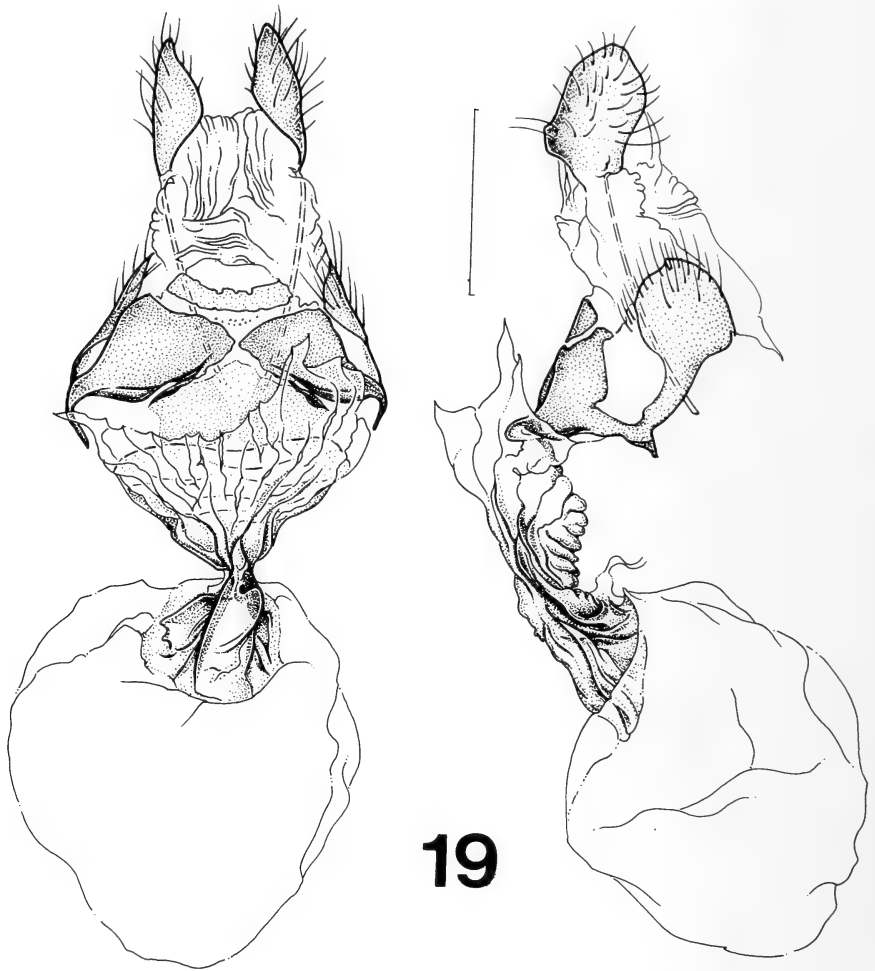


FIG. 19. Female genitalia *H. venusta* showing ventral and right lateral aspects, same data as Fig. 13 (genitalic dissection # ♀6153-CDM) (IEUM). Scale = 1.0 mm.

of ventral margin nearly straight to narrow "beak." Penis less than twice length of valva; titillators sclerotically strapped to penis, similar, slender, and evenly tapered from broad base to curved, thorn-like point; cornuti nearly similar, bidentate. Juxta with ventral clefts one-half or more length of juxta; separated midventral floor not nearly reaching caudal margin of juxta. Uncus in dorsal view with anterior half bulbous, laterally emarginate to the parallel-sided caudal half; caudal cleft scarcely to distinctly exceeding the pectines cephalad; pectines not minute, arched dorsad.

Female. Entirely as male except genitalia (only distinguishable by examination of abdominal tip), except subtly, and separable from the next species as follows:

Wings. Forewing length average 11.0 mm, range 10.0 mm–12.0 mm (n = 6). Hindwing apex only slightly produced, vein Rs not or scarcely longer than 2A of forewing.



FIG. 20. Female genitalia of *H. ancora* (Plötz), not treated in this paper, but showing presumed brittle, dorsocaudal bristles of male lodged in caudopleural membrane of female. Rio Lavatudo, estr. Lages—S. Joaq, S. Joaquim, 1000 m, II-24-73, S.C., BRASIL, O. Mielke (genitalic dissection # 93746-JH) (UFPC). Scale = 1.0 mm



FIGS. 21–26. Adults of three species of *Hylephila* with males (odd numbers) and females (even numbers) in dorsal views (above) and ventral views (below) (all $\times 1$). **21, 22**, *H. ignorans* male, Mucubaji Research Sta., II-6-7-78, Mérida, VENEZUELA, J. Heppner (genitalic dissection # X-1678-JMB) (USNM). Female, same data as Fig. 14. **23, 24**, *H. adriemae* male holotype, other data as Fig. 3b (genitalic dissection # ♂3668-JH) (CAS). Female paratype, other data same as Fig. 15 except III-5-75, G. E. Bernard (genitalic dissection # ♀6151-CDM) (CDM). **25, 26**, *H. lamasi* male holotype, data same as Fig. 11a (MUSM). Female paratype, other data same as Fig. 11b (genitalic dissection # ♀3741-JH) (MUSM).



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FIGS. 27-31. Adults of two species of *Hylephila* and one species of *Linka* with males (odd numbers) and females (even numbers) in dorsal views (above) and ventral views (below) (all $\times 1$). 27, 28, *H. kenhaywardi* male, Baños El Toro, I-7-72, CHILE, J. Herrera (genitalic dissection # 3704-JH) (CDM). Female, Ojos de Hecar, Nov. 1965, Cord. Antofagasta, CHILE, L. Peña (genitalic dissection # 96206-CDM) (AME). 29, 30, *H. venusta* male, Pradera del Sol, II-21-65, Chillán, CHILE, J. Herrera (genitalic dissection # 3915-JH) (CDM). Female, Termas Chillán, II-20-65, Nuble, CHILE, J. Herrera (genitalic dissection # 3702-JH) (CDM). 31, *Linka lina* male, Mts. at Bogotá, COLOMBIA, Carnegie Mus. acc. # 5537 (CMNH).

Genitalia (Fig. 17). Eighth sternite a slender band broadest medially and tapered laterad, its width about one-fourth its length. Lamella postvaginalis broadly united medially and not abruptly bent cephalad. Antrum membranous, dorsally not transversely plicate and slightly sclerotized caudad, immediately in contact with lamella postvaginalis, appearing as a small, median, rectangular, or at least parallel-sided, extension of the lamella, and sclerotized dorsally cephalad and laterally caudad of ductus seminalis, then anteriorly only dorsolaterally around conspicuous left-lateral pocket, and weakly right-laterally cephalad a distance a little greater than length of antrum.

Distribution. We have seen 51 ♂ and 6 ♀ (14 ♂, 6 ♀ dissected) from the high desert valleys and plateaus west of the crest of the Chilean Andes, most from elevations of 3000–4600 m, representing a few, widely separated, localities. The type locality is Río Toro in the Province of Elqui. We have examined additional specimens from Provincia Elqui (Baños del Toro, Río Seco, and Río La Laguna [near Paso Agua Negra]). From Provincia Copiapó we have seen material labelled Caballo Muerto, Salar Maricunga, and Hacienda Castilla. For El Loa Province we have seen material from Ojos de Hecar and Geisers del Tatio, and from the Province of Parinacota we have specimens from Murmuntani. The species flies from January to March.

The record from Hacienda Castilla is puzzling. The locality is far from the Andes. It is only 800 m in elevation in the Llanos Hornillos in western Copiapó Province, and represents a region quite different geographically, altitudinally, and ecologically from the (apparent) usual habitat of *H. kenhaywardi*. The record requires confirmation and, for now, must be considered doubtful.

Discussion. This is one of the smallest species of the genus. It is easily recognizable by reference to Ureta's (1956) figures (and by our Figs. 27, 28) of the adults. The pale fulvous with soft fuscous markings above and below, and the lack of contrasting white veins on the hindwing below, together with its small size, will separate this round-winged species from *H. venusta* and all other species of the genus.

Thirty-two ova were dissected from one female (# 96206-CDM) and were small. Eight were sufficiently mature to measure and were surprisingly variable. Average diameter was 0.62 mm by 0.50 mm height. They ranged from 0.58 mm × 0.40 mm to 0.66 mm × 0.50 mm. The reticulation was minute but shallowly discernable at 50× magnification.

Hylephila venusta (Hayward)

(Figs. 8, 13, 18, 19, 29, 30, 33)

Pamphila sp., Ureta, 1935. Bol. Mus. Nac. 14:94.

Hylephila bouletti, Ureta, 1938a, (nec. Mabille, 1906). Bol. Mus. Nac. Hist. Nat. 16:115–116; Ureta, 1938b. loc. cit. p. 129.

Andinus venustus Hayward, 1940. Rev. Soc. Entomol. Argent. 10:285, 286, figs. 8, 9; Hayward, 1950. Genera et species anim. Argent. II, pp. 39, 40, Tabs. IV, fig. 15, XII, figs. 17, 18.

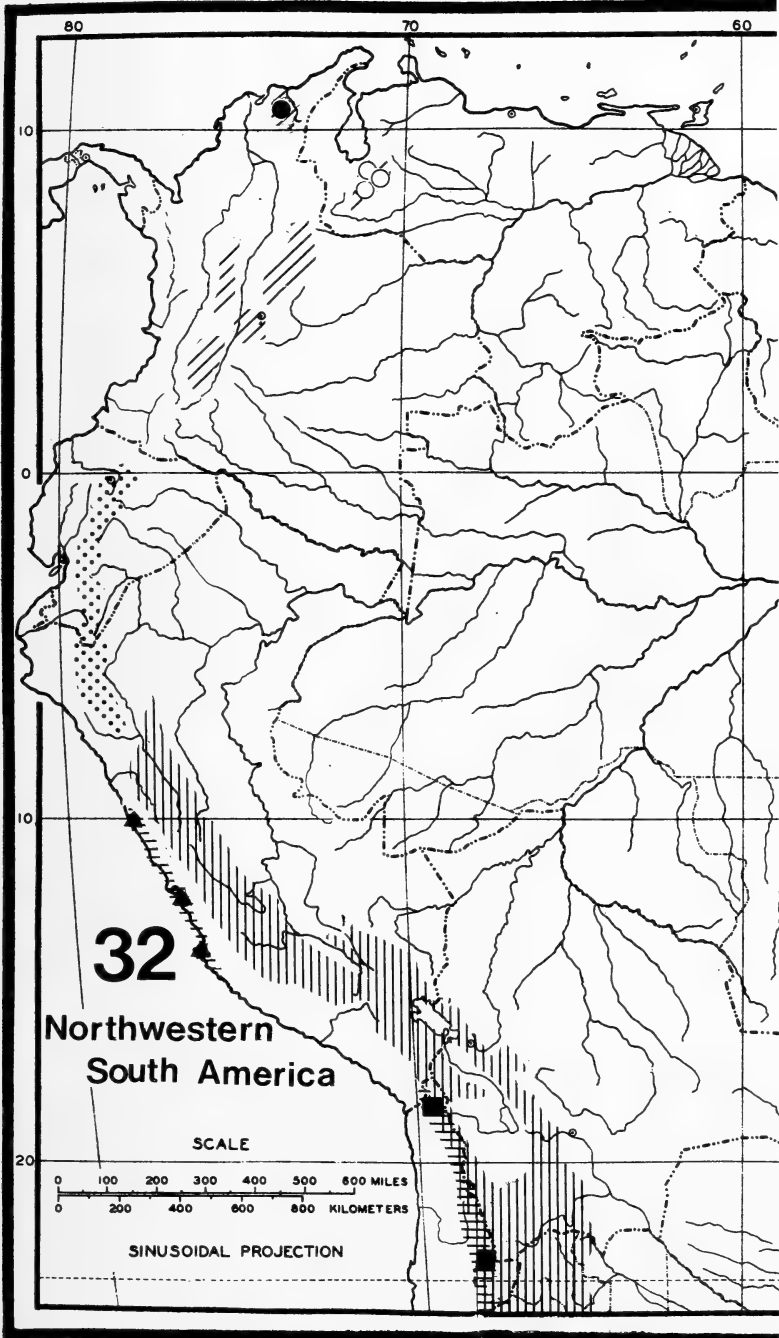
Hylephila venustus, Evans, 1955. Cat. Amer. Hesp. part IV, pp. 314, 315, pl. 75.

Hylephila venusta, Peña & Ugarte, 1997. Las mariposas de Chile, the butterflies of Chile, p. 133, figs. (not photo).

The holotype is from (the Andes east of) Chillán, Chile, and is in the collection of IML, Tucumán, Argentina.

Description. *Male.* **Head.** Palpi somewhat shaggy, third segment scarcely to slightly protruding from white, hair-like vestiture of front of second segment. Eyelash short, not

FIG. 32. Postulated distribution of high Andean *Hylephila* species groups: *ignorans* group, diagonal line overlay; *phyleus* group (in part), stipple overlay; *bouletti* group, vertical line overlay; *venusta* group (including coastal Peruvian species), horizontal line overlay. In *ignorans* grp., solid circle = *H. adriennae*, open circles = *H. ignorans*; in *venusta* grp., solid triangles = *H. lamasi*, solid squares = *H. kenhaywardi*.



or scarcely exceeding one-half eye diameter. Antennae dorsally black, anteriorly weakly checkered black and white on shaft, golden on and near club, ventrally white on shaft, buff to golden on club; club about one-third length of shaft, nudum slightly less than one-half length of club, pale brown; shaft length about equal to or slightly greater than dorsal width of head.

Body. Dorsally and tegulae clothed with fine, long, golden hairs; ventrally and legs shaggy with white to buff-white vestiture.

Wings. Forewings stubby, rounded, length 12.0–14.5 mm ($n = 17$). Above reddish fulvous with fuscous discal bar in spaces M1–M3, Cu2–2A, and centered over the latter, a smaller fuscous spot; border broad and deeply cut by fulvous extensions along veins. Fringes basally dark, terminally orange. Below as above but fuscous reduced, base of costal cell whitish, and narrowly on costa to apex and basal one-half of fringes gray. Hindwing above reddish fulvous as on forewing, fuscous border broad, usually much less deeply indented along veins than forewing, continuing broadly around costa to base, fringes basally brown, terminally orange but vannally entirely orange. Below fulvous paler than on forewing, space M1–M3 clear, pale fulvous from cell nearly to margin, veins usually white, separating discal, wedge-shaped black spots in spaces M3–Cu1, Cu1–Cu2, and Cu2–2A, and with marginal black spots more or less continuously from at least Cu1–Cu2 to Rs–M1, basal spot in cell scarcely or not separated from black dot end cell. Costal cell and space 2A–3A dusky from base to termen. Fringes from apex to vein 2A basal one-half whitish, terminally dusky.

Genitalia. Eighth tergite (Fig. 8) with terminal bristle sockets scarcely enlarged caudad, somewhat squarish in cross section. Valva (Fig. 13) in lateral view, basal margin slightly more than one and one-half times valva depth, broadly beaked owing to strongly emarginate dorsal margin and greatly and continuously curved ventral margin. Penis long, nearly or quite twice length of valva; titillators sclerotically strapped to penis, similar, very slender, and nearly straight with parallel sides; cornuti asymmetric, one narrowly bidentate, the other weakly bidentate or tridentate with one tooth long and one much shorter. Juxta with ventral clefts about one-half length of juxta, separated midfloor nearly or quite reaching caudal margin of juxta. Uncus in dorsal view anterior half bulbous, laterally emarginate to parallel sided or tapered caudal half; caudal cleft not to somewhat exceeding pectines cephalad; pectines normal, not minute.

Female. Head and body very like male. Antennal club longer, nearly one-half length of shaft.

Wings. Forewing length 13.5–15.5 mm ($n = 5$). Markings slightly stronger. Hindwing apex more produced, vein Rs clearly longer than vein 2A of forewing, below veins whitish to pale fulvous.

Genitalia (Figs. 18, 19). Eighth sternite a slender band, its width one-fourth or less its length. Lamella postvaginalis nearly or just medially united, the anterior border medially V-shaped with the ends anterolaterally bent ventrad. Antrum membranous, dorsally usually transversely plicate and scarcely sclerotized except for a weakly sclerotized triangular caudal area fitting into the anterior V of lamella postvaginalis and posterolaterally abruptly sclerotized and flanged ventrad, more or less sclerotically connected ventrally to bend of lamella postvaginalis. Ductus bursae gradually sclerotized anteriorly just caudad of ductal constriction, then cephalad sclerotized mainly laterally, leaving mid-ventral and mid-dorsal areas membranous, expanded ventrocephalad a distance about equal to or less than length of antrum, left-lateral pocket scarcely produced.

Distribution. *Hylephila venusta* flies from January through March at high elevations where it ranges from the southern Andes at Río Guenquel in northeastern Santa Cruz Province, Argentina (opposite Puerto Ibáñez, Chile), north to La Parva in Santiago Province, Chile. The type locality is (east of) Chillán in Ñuble Province, Chile, and Hayward (1940) listed it from nearby Neuquén Province, Argentina. We have seen only 19 ♂ and 5 ♀ (15 ♂, 5 ♀ dissected) from the above localities as well as from Laguna de la Laja, Bio Bio Province and Volcan San José, Cordillera Province, all in Chile.

Discussion. The population samples we have seen are small, and some of the specimens are well worn, but they suggest perhaps three differing, widely separated, populations based upon differences in markings and slight differences in male and female geni-

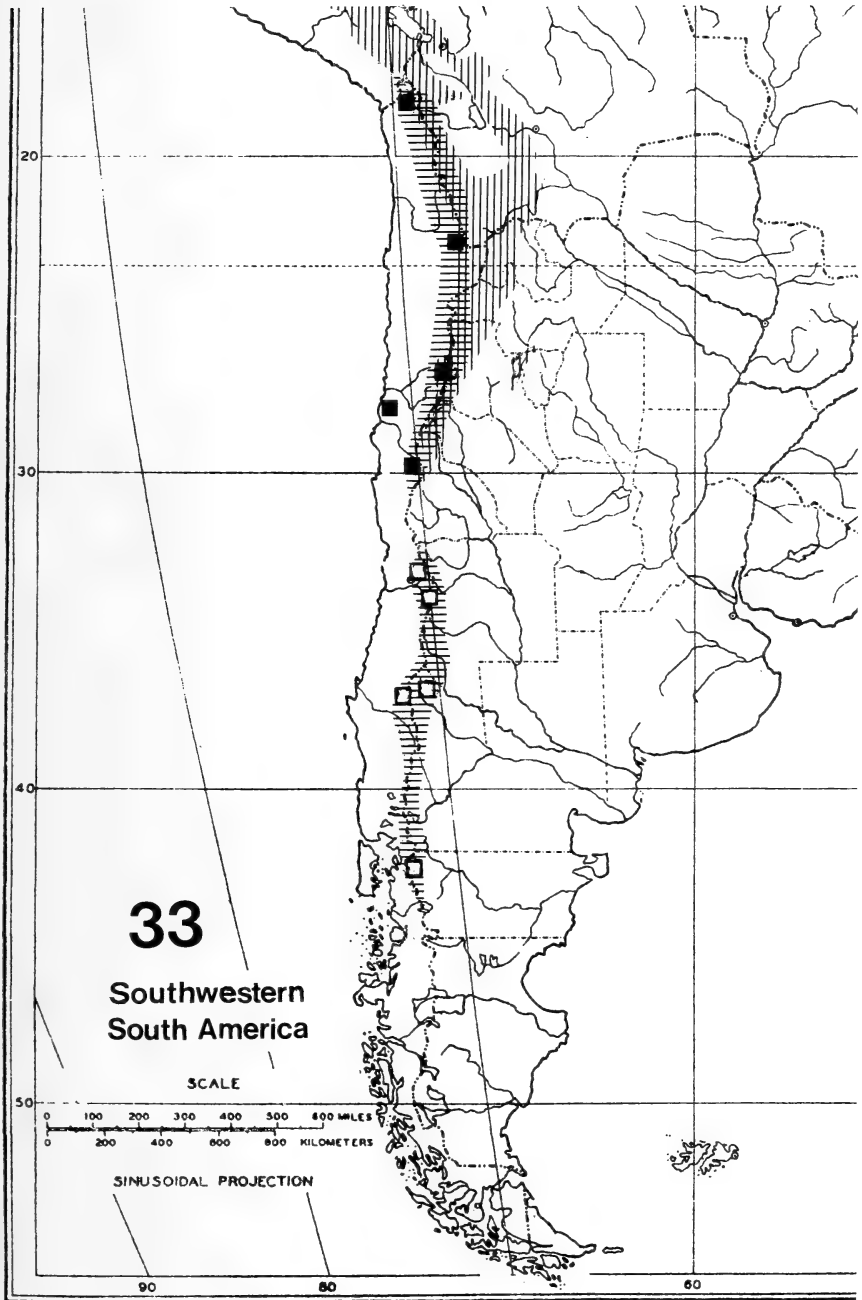


FIG. 33. Postulated distribution of high Andean *Hylephila* species groups: *boulleti* and *venusta* grps. overlay as in Fig. 32. In *venusta* grp., solid squares = *H. kenhaywardi*, open squares = *H. venusta*.

talia. These three occur in the Andes east of Santiago, Chile; in Chile and Argentina east of Chillán, Chile; and in Chile and Argentina southeast of Puerto Aisén, Chile.

The northernmost material examined, from east of Santiago (4 ♂, 3 ♀), is somewhat worn but appears paler than does that from the vicinity of the type locality. The veins of the underside of the hindwings are less whitened, especially on females, and the discal fuscous markings on the forewings are heavier. The male valva is broader and caudally more blunt, the uncus in dorsal view is more bulbous cephalad, and the lateral margins of the caudal half are more tapered, (i.e., not parallel) than in more southern material. In the female (Fig. 19) the lamella postvaginalis is vaguely or distinctly separated midventrally, but the antrum is distinctly transversely plicate, and the left-lateral pocket of the ductus bursae is small but evident.

Specimens from the vicinity of the type locality we have seen (13 ♂, 1 ♀) tend to have a deeper, more reddish fulvous and broader fuscous borders above, with less bold discal fuscous markings; the veins of the hindwings below are white even in the female. The male valva is more slender and caudally more pointed than in either more northern or more southern material; and the female has the two halves of the lamella postvaginalis conjoined midventrally, the antrum is transversely plicate dorsally, and the ductus bursae has the left-lateral pocket obscure.

In the southernmost specimens examined (2 ♂, 1 ♀) the fulvous is paler than that of the Chillán material, but the female is not as pale nor as boldly marked with fuscous as are the La Parva specimens. The males have white veins on the hindwings below, but the female does not. In the males the valva is broader and caudally more blunt than in males from Chillán, but not as blunt as in males from east of Santiago. The female (Fig. 18) has the two halves of the lamella postvaginalis narrowly joined, the antrum is not clearly transversely plicate, and the left-lateral pocket of the ductus bursae is not evident.

Ureta (1938a) reported this species (as *H. bouletti*) visiting flowers of white clover, *trifolium repens* (L.), and *Medicago sativa* (L.) (both Fabaceae).

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TAXONOMY AND NOMENCLATURE OF
STRYMON ISTAPA AND *S. COLUMELLA* (LYCAENIDAE:
THECLINAE: EUMAEINI)

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ABSTRACT. *Strymon istapa* has been considered a junior synonym of *S. columella*, but its female genitalia distinguish it from all other *Strymon*, including *S. columella*, and it is uncertain which *Strymon* species is most closely related to *S. istapa*. *Strymon istapa* ranges from the southern United States to Perú and Brazil, but is allopatric with *S. columella*, which is restricted to the Antillean islands from Vieques and Palominos to Antigua. The poorly-known South American range of *S. istapa* is documented, and geographical variation of its genitalia is illustrated. The nomenclature is summarized in a synonymic list, including the recognition of *S. columella* and *S. istapa* as distinct species, a **NEW STATUS**.

Additional key words: Antilles, genitalia, brush organs.

Even though the species widely called *Strymon columella* F. (Clench 1961, 1964, Howe 1975, Opler & Krizek 1984, Scott 1986) is a well-known, oftentimes common species that occurs from California, Arizona, Texas, and Florida south into Latin America, its identity has been unsettled for two centuries. Fabricius (1793) named *Hesperia columella* (this genus now belongs to the Hesperiiidae) from “Americae meridionalis Insulis” with a verbal description that did not adequately distinguish the species. Few authors over the next 150 years agreed on the identity of this species and its relatives. Comstock and Huntington (1943) summarized this discordant history and attempted to correct the taxonomy of the *Thecla columella* group (*Thecla* F. was the genus then in use for most Neotropical Theclinae).

Because Comstock and Huntington apparently did not know that a type of *T. columella* was extant in Copenhagen’s Zoological Museum (Aurivillius 1898), they mistakenly recognized *T. columella* as the widespread species mentioned above and named a related new species (*T. antigua*) from Antigua and nearby islands. After Ziegler (1960) and Clench (1961) transferred *T. columella* and related species to *Strymon*, Riley (1975) and Smith et al. (1994) synonymized *S. columella* and *S. antigua* and noted that they refer to the same subspecies. As Comstock and Huntington remarked, the taxonomic history of *S. columella* is “slightly confusing.”

As part of a study of the genus *Strymon*, we have examined the morphology of species in the *Strymon columella* group from the Antilles (Comstock & Huntington 1943, Smith et al. 1994), specifically *S. columella*, *S. toussainti* Comstock & Huntington (a senior synonym of *S. andrewi* Johnson & Matusik and *S. amonensis* Smith et al., Robbins & Nicolay 1999), *S. limenia* Hew., *S. bubastus* Stoll, *S. istapa* Reakirt, and *S. christophei* Comstock & Huntington. This paper (1) shows that *S. columella* (= *S. antiqua*) is not conspecific with *S. istapa* (the widespread "*S. columella*" that occurs from Florida to California and to South America); (2) illustrates the wing pattern and genitalia of *S. columella* and *S. istapa*; (3) documents geographical variation in the genitalia of *S. istapa*; (4) illustrates the poorly-known South American distribution of *S. istapa*; and (5) summarizes the nomenclature of these two species.

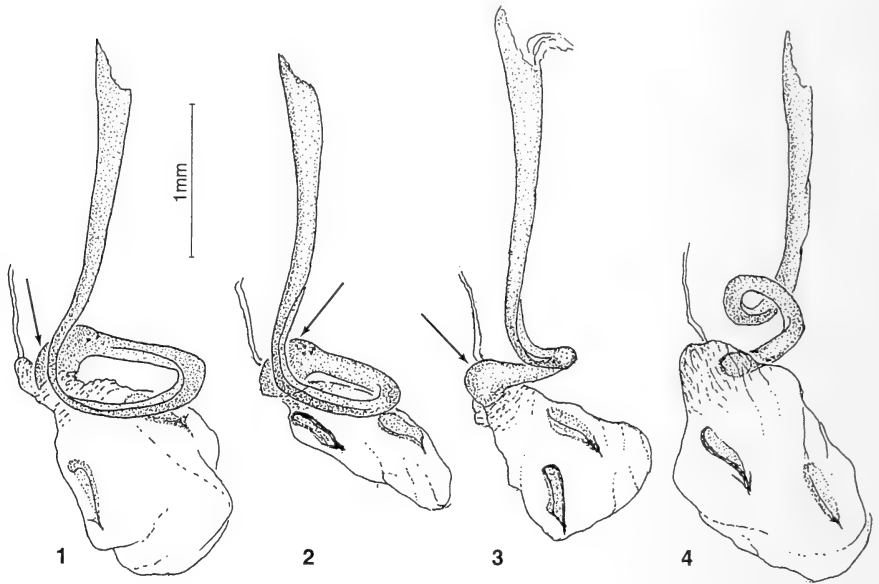
MATERIAL EXAMINED

Museum collections that contained specimens used in this study are: AMNH, American Museum of Natural History, New York, USA; AME, Allyn Museum of Entomology, Florida Museum of Natural History, Sarasota, Florida, USA; BMNH, The Natural History Museum, London, UK; CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; INPA, Coleção Entomológica do Instituto Nacional de Pesquisas da Amazônia, Amazonas, Brazil; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts, USA; UFPR, Universidade Federal do Paraná, Curitiba, Paraná, Brazil; UNAM-IB, Instituto de Biología, UNAM, Mexico City, Mexico; USNM, National Museum of Natural History, Washington, DC, USA.

RESULTS

Female genitalia. Female genitalia distinguish *S. istapa* from all other eumaeines. The anterior ductus bursae forms an enlarged bell-like chamber (arrows in Figs. 1–3), which appears to be unique within the Eumaeini. *Strymon columella* (Fig. 4) and the other members of the Antillean *S. columella* group lack the enlarged chamber (see also illustrations in Robbins & Nicolay 1998).

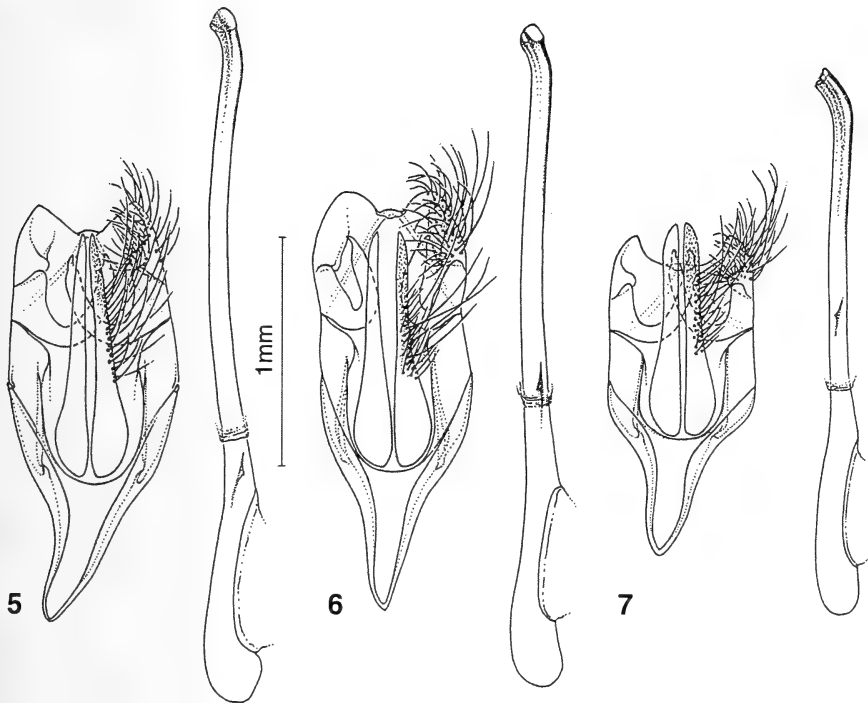
The female genitalia of *S. istapa* vary geographically. The length of the ductus bursae, including extent of the "loop," is greatest in the Antilles and southern United States and is progressively smaller to the south on the mainland (Figs. 1–3). Additionally, the exact shape of the loop in the ductus bursae varies, sometimes greatly, among individuals from any one locality, but the anterior ductus bursae with an enlarged bell-like chamber is consistent throughout its extensive range.



FIGS. 1–3. Bursa copulatrix of *S. istapa* in lateral left aspect showing geographical variation in size. 1. Mexico; 2. Panamá; and 3. Maranhão, Brazil. Arrows point to enlarged chamber at anterior end of the ductus bursae. FIG. 4. Bursa copulatrix of *S. columella* (from Vieques) in lateral aspect, with anterior ductus bursae lacking an enlarged bell-like chamber.

Two other female genitalic structures in the Antillean *S. columella* complex provide evidence on the relationship between *S. istapa* and *S. columella*. In *S. columella*, *S. limenia*, and *S. christophei* the “loop” of the ductus bursae is dorsal of the ductus bursae (Fig. 4) while it is ventral (Figs. 1–3) in *S. istapa*, *S. toussainti*, and *S. bubastus*. In *S. limenia*, *S. bubastus*, and *S. toussainti* the posterior tip of the corpus bursae is sclerotized and the ductus seminalis arises anterior of this sclerotized tip (illustrated in Smith et al. 1991, Robbins & Nicolay 1999). In *S. istapa* (Figs. 1–3), *S. columella* (Fig. 4), and *S. christophei*, the posterior tip of the corpus bursae is not sclerotized.

Male genitalia. Geographical variation of the male genitalia in *S. istapa* (Figs. 5–7) is analogous to that of the female genitalia. The male genitalia are largest in the Antilles and southern United States and are progressively smaller to the south on the mainland. Otherwise, the male genitalia of *S. istapa*, *S. toussainti*, *S. limenia*, and *S. columella* are barely distinguishable. Those of *S. toussainti* and *S. limenia* are similar in size to those of *S. istapa* at the southern end of its range while those of *S. columella* are similar in size to those at the northern end (Fig. 8).



FIGS. 5-7. Male genitalia of *S. istapa* in ventral aspect and its aedeagus in lateral aspect showing geographical variation in size. **5**, Mexico; **6**, Panamá; and **7**, Meta, Colombia.

The male genitalia of *S. bubastus* and *S. christophei* differ from those in the remainder of the *S. columella* group. The dorsal part of the labides of *S. bubastus* are more rounded and posteriorly produced than those of the other species. The holotype male of *S. christophei*, which is the only male of this species that was available for study, has a wider cornutus than *S. istapa*.

Male *Strymon* have brush organs (*sensu* Eliot 1973) above the vinculum and attached to the intersegmental membrane between the 8th abdominal segment and the vinculum. However, the brush organs may be very small in some individuals of *S. bubastus*. Of 18 male *S. istapa* from Florida and the Antilles, 5 had small brush organs and 13 had none. Individuals with and without brush organs occur in Florida, the Cayman Islands, Cuba, and Puerto Rico, and we believe that this is the first report of an eumaeine dimorphic for the presence of brush organs. All individuals of *S. istapa* from other areas had brush organs.

Wing pattern. The ventral forewing postmedian line, which consists of a series of spots from veins R2 to Cu2, is a good character for distin-

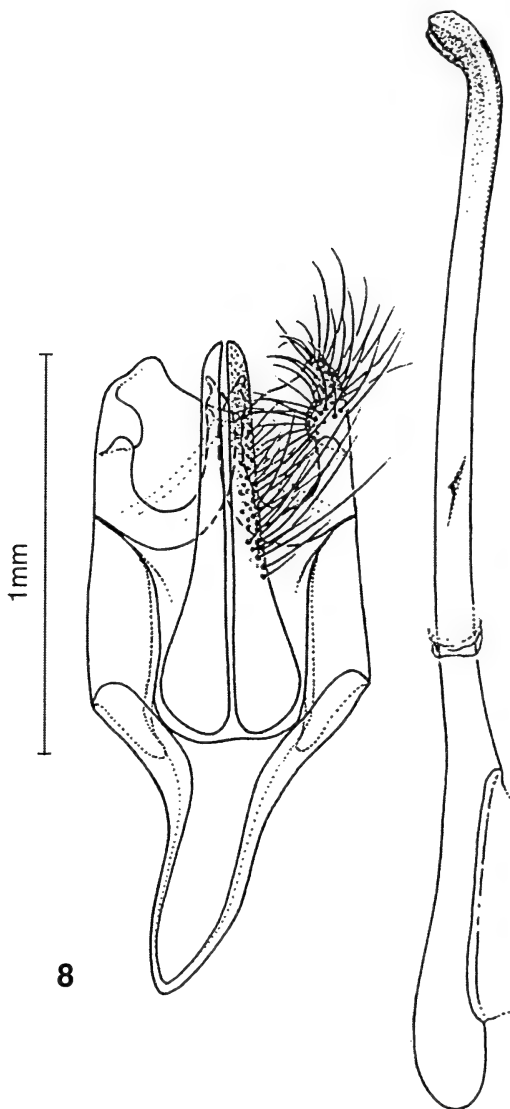


FIG. 8. Male genitalia of *S. columella* (from Vieques) in ventral aspect and its aedeagus in lateral aspect.

guishing taxa in the Antillean *S. columella* group (Comstock & Huntington 1943). In *S. toussainti*, the spot in cell M1–M2, and to a lesser extent in cell M2–M3, is displaced basally more than 0.35 mm (arrow in Fig. 14) while the spots from veins R2 to M3 are essentially co-linear in others of the *S. columella* complex, with occasional minor variation in *S.*

limenia. In *S. bubastus*, the spot in cell M3-Cu1 is displaced distally (arrow in Fig. 12) while the spots from veins M3 to Cu2 are co-linear, or nearly so, in the other species of the *S. columella* complex. Finally, the spot in cell M2-M3 is displaced distally more than 0.5 mm in *S. christophei* (arrow in Fig. 15). These characters are well-illustrated in Smith et al. (1994).

The ventral hindwing pattern also has useful distinguishing characters in the *S. columella* complex (Figs. 9-15). The postmedian line of *S. columella* is co-linear from the costa to vein Cu2 (arrow and circle in Fig. 11), unlike the others in which the spots in cells M1-M2 and M2-M3 are displaced distally. *Strymon christophei* is unique in lacking basal spots. Finally, the ventral hindwing patterns of *S. istapa* and *S. bubastus* are exceedingly similar (Figs. 9, 12).

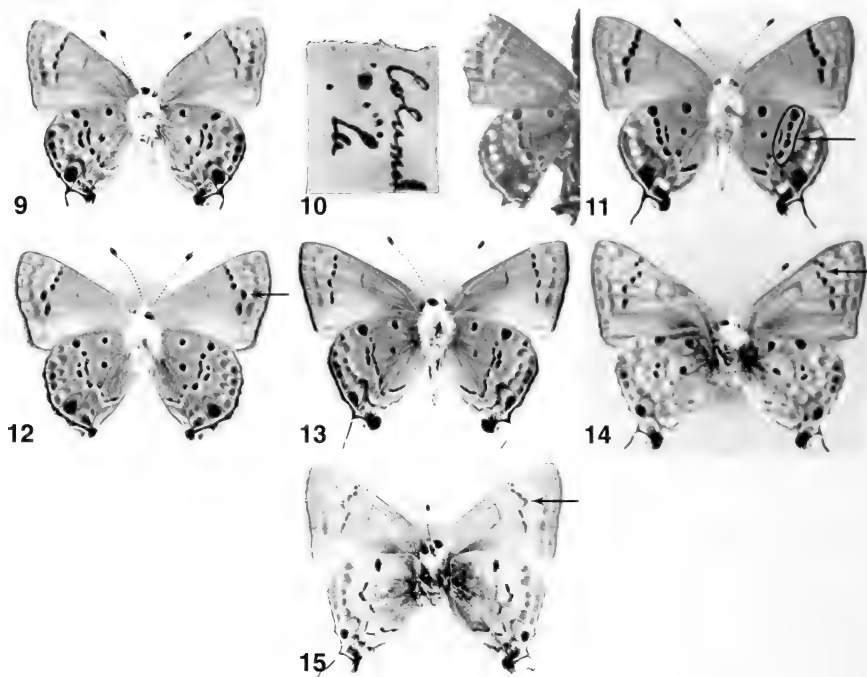
While *S. columella*, *S. istapa*, *S. toussainti*, *S. limenia*, and *S. christophei* have a hindwing tail, *S. bubastus* lacks one throughout its extensive range except for a small tail on one Bolivian male, whose wing pattern and genitalia identify it as *S. bubastus* (Figs. 9-15).

DISCUSSION

Taxonomy. *Strymon istapa* and *S. columella* are distinct species, as noted originally by Comstock and Huntington (1943), on the basis of their female genitalia and wing pattern. The female genitalia of *S. istapa*, with the enlarged chamber at the anterior end of the ductus bursae, differ from those of all other members of the *S. columella* complex. The straight ventral hindwing postmedian line of *S. columella* differs from that of all other species in the *S. columella* complex.

It is unclear whether *S. istapa* and *S. columella* are closest relatives. The "ventral loop" of the ductus bursae in *S. istapa* is shared with *S. bubastus* and *S. toussainti*, but not with *S. columella*. The lack of a sclerotized posterior tip of the corpus bursae in *S. istapa* is shared with *S. columella* and *S. christophei*. The ventral hindwing pattern of *S. istapa* is most similar to that of *S. bubastus*. The male genitalia of *S. istapa* are quite similar to those of *S. limenia*, *S. toussainti*, and *S. columella*. Although phylogenetic analysis might resolve relationships, we are as yet unsure whether the Antillean *S. columella* complex is monophyletic.

We found no convincing evidence in the variation of the genitalia or wing pattern that more than one species is represented within the wide distribution of *S. istapa*. Geographical variation in size of the male and female genitalia appears to be clinal. Differences in wing pattern on islands are slight. Although the male genitalic brush organs are small or absent in specimens from Florida and the Antilles, similar variation (but of smaller magnitude) also occurs in *S. bubastus*.



FIGS. 9–15. Ventral wings of the Antillean *S. columella* complex. 9, *S. istapa*; 10, Syntype of *S. columella* (courtesy of F. M. Brown); 11, *S. columella*; 12, *S. bubastus*; 13, *S. liemenia*; 14, holotype of *S. toussainti*; and 15, holotype of *S. christophe*. Arrows point to characters discussed in the text.

Habitat and range. As characterized, *S. istapa* is a denizen of disturbed, usually xeric, habitats in Florida, the Antilles, and the United States (California) south to Brazil (Maranhão) and Perú (San Martín) on the mainland. *Strymon columella*, on the other hand, is restricted to the Antilles from Vieques and Palominos to Antigua (Smith et al. 1994). The Antillean distributions of these species are well documented (Comstock & Huntington 1943, Riley 1975, Smith et al. 1994). They are allopatric; *S. istapa* occurs in the Greater Antilles east to Puerto Rico while *S. columella* occurs only on the islands east of Puerto Rico.

Although *S. istapa* is often a very common species in the Antilles and Central America, it is rare and poorly documented in South America. For example, Clench (1961) did not record it from South America, and the recent Bolivian record (Smith et al. 1994) is probably based on the one tailed individual of *S. bubastus*. The confirmed South American distribution of *S. istapa* (Fig. 16) includes the provinces of Meta (Colombia, specimens in USNM), Nueva Esparta (Venezuela, specimen in

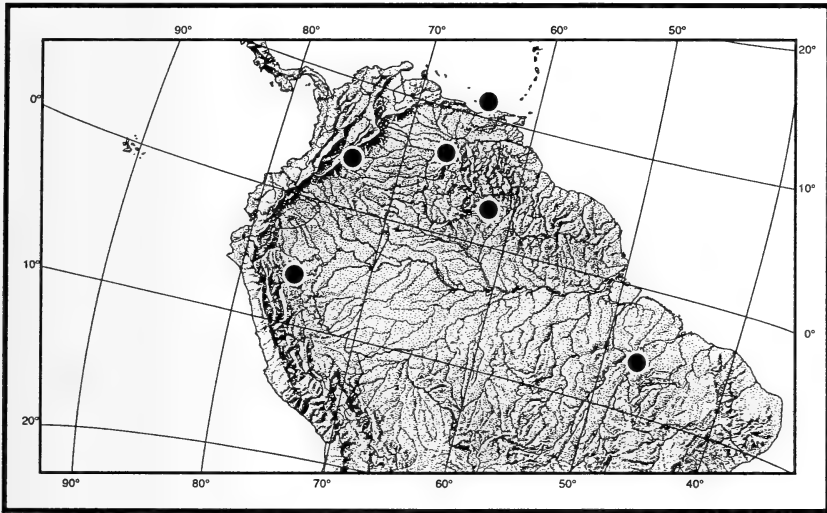


FIG. 16. South American distribution of *S. istapa*.

USNM), Bolivar (Venezuela, specimen in MCZ), San Martín (Perú, specimen in USNM), Roraima (Brazil, specimen in INPA), and Maranhão (Brazil, specimens in UFPR).

Nomenclature. The nomenclature of *S. columella* is straightforward. The type of *S. columella* (F.) in Copenhagen (Fig. 10) is the same species as *S. antiqua* (type in AMNH), as previously noted (Smith et al. 1994). The name *S. erytalus* Butler originally appeared as a synonym of *S. columella*, and was a reference to a manuscript name (Barnes & Benjamin 1926). Comstock and Huntington (1943) synonymized it with *S. columella*.

The nomenclature of *S. istapa* is also uncomplicated. No type of *S. istapa* (Reakirt) is known (Miller & Brown 1981), but the original description of a female from Mexico, with two dark brown basal spots on the ventral hindwings, could refer to no other Mexican species. The identity of this name has been consistent for over a century (Scudder 1889), even if the taxonomy has been confused. Similarly, types of *S. modesta* (Maynard) and *S. ocellifera* (Grote) are unknown (Miller & Brown 1981), but their identities have been consistent since Scudder (1889). We have seen types of *S. cybira* (Hewitson) (in BMNH), *S. arecibo* (C. & H.) (in AMNH), and *S. clarionica* (Vázquez) and *S. socorroica* (Vázquez) (in UNAM-IB), and all represent the same biological species that we recognize as *S. istapa*.

The following synonymic list summarizes these results.

- Strymon columella* (Fabricius, 1793)
 = *Tmolus erytalus* Butler, [1870]
 = *Thecla antiqua* Comstock & Huntington, 1943
Strymon istapa (Reakirt, [1867]) **REINSTATED STATUS**
 = *Lycaena modesta* Maynard, 1873
 = *Callicista ocellifera* Grote, 1873
 = *Thecla cybira* Hewitson, 1874
 = *Thecla arecibo* Comstock & Huntington, 1943
 = *Thecla clarionica* Vázquez, 1958
 = *Thecla socorroica* Vázquez, 1958

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TAXONOMY OF *STRYMON TOUSSAINTI*,
S. ANDREWII, *S. AMONENSIS*, AND *S. RHAPTOS*
(LYCAENIDAE: THECLINAE)

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ABSTRACT. *Strymon toussainti*, *S. andrewii*, and *S. amonensis* have been considered closely related Antillean species, but their genitalia and wing pattern vary continuously without clearly distinct states. The genitalia of the holotype and allotype of *S. andrewii* do not match those of its paratypes collected in the same series, but are quite similar to those of *S. eurytulus*. Since the male holotype of *S. andrewii* is actually a female, it appears that the genitalia and adults of the holotype and allotype were improperly associated. The Argentine *S. rhapsos* is known from one male and one female whose genitalia and wing pattern are indistinguishable from those of *S. toussainti*. It appears that they were mislabeled. The following names are junior synonyms of *S. toussainti* (Comstock & Huntington 1943): *Strymon andrewii* Johnson & Matusik, 1988; *S. rhapsos* Johnson, Eisele & MacPherson, 1990; and *S. amonensis* Smith, Johnson, Miller & McKenzie, 1991.

Additional key words: Eumaeini, Antilles, genitalia, brush organs.

The Antillean species *Strymon toussainti* (Comstock & Huntington), *S. andrewii* Johnson & Matusik, and *S. amonensis* Smith et al. differ from other members of the *S. columella* complex. The ventral forewing spot in cell M1–M2, and to a lesser extent in cell M2–M3, is displaced basally more than 0.35 mm (Figs. 1–3). This shared trait suggests a close, perhaps monophyletic, relationship among these three species. However, Johnson and Matusik (1988) mentioned that *S. andrewii* may be as closely related to *S. istapa* (Reakirt) (*S. columella cybira* [Hew.] in their paper) as to *S. toussainti*, and Smith et al. (1994) raised the possibility that *S. andrewii* might be most closely related to *S. christopheii* (Comstock & Huntington). To complicate matters, *S. rhapsos* Johnson, Eisele & MacPherson from the mountains of Patagonia in Argentina also shares this forewing trait (Fig. 4), making for a confused taxonomic and biogeographical situation. The purpose of this paper is to 1) determine if *S. toussainti*, *S. andrewii*, *S. amonensis*, and *S. rhapsos*—the four species with the basally displaced forewing spot—are closely related to each other; 2) examine the evidence for the distinctness of these taxa; and 3) discuss possible explanations for the unusual Antillean-Patagonian distribution of these butterflies.

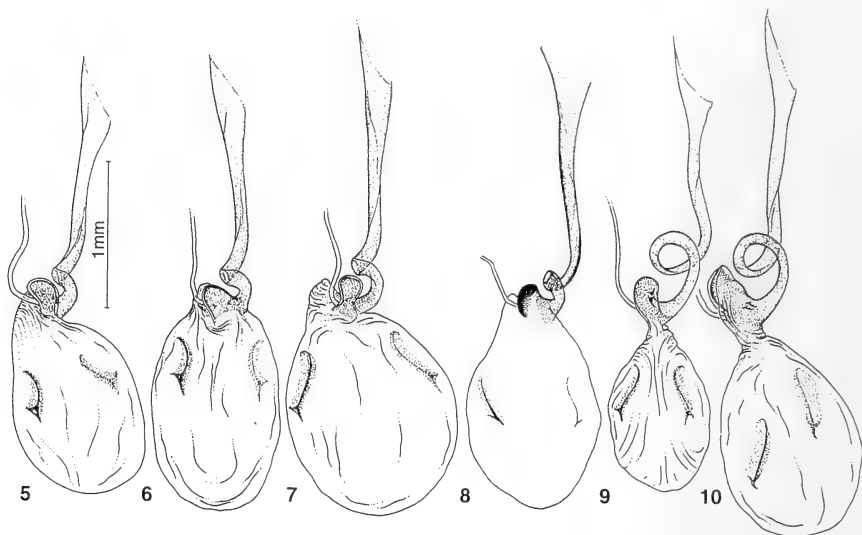


FIGS. 1–4. Ventral wings. 1, male holotype of *S. toussainti*; 2, “male” (=female) holotype of *S. andrewi*; 3, male paratype of *S. amonensis*; and 4, male holotype of *S. rhapsos*. Arrows refer to characters discussed in the text.

MATERIAL EXAMINED

This study was based on 11 males and 12 females of *S. toussainti*, *S. andrewi*, *S. amonensis*, and *S. rhapsos*. Included were the holotype and 10 paratypes of *S. toussainti*, the holotype and 5 paratypes of *S. andrewi*, 4 paratypes of *S. amonensis*, and the holotype and allotype of *S. rhapsos*. Although 24 paratypes of *S. amonensis* were reported to be deposited in the museums above (Smith et al. 1991), only four were found, and none had abdomens or associated genitalia. Thus, we reproduced the genitalic figures in the original description of *S. amonensis*.

Although most specimens used in this study belong to the National Museum of Natural History, Washington, DC, USA (USNM), specimens were also borrowed from the following museums (with their abbreviation and the curator who made the loan): American Museum of Natural History, New York, USA (AMNH, J. S. Miller); Allyn Museum



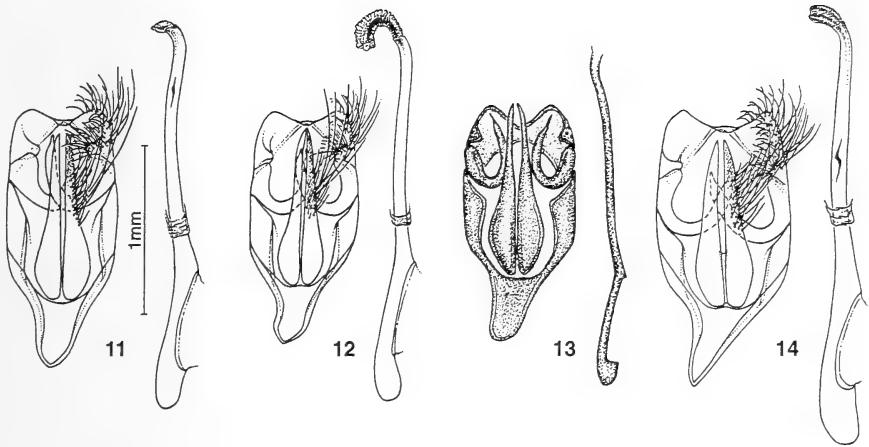
FIGS. 5–10. Bursa copulatrix in lateral aspect. **5**, allotype of *S. toussainti*; **6**, allotype of *S. rhapsos*; **7**, paratype of *S. andrewi*; **8**, reproduction of allotype of *S. amonensis* (scale approximated); **9**, allotype of *S. andrewi*; and **10**, *S. eurytulus* from Argentina.

of Entomology, Florida Museum of Natural History, Sarasota, Florida, USA (AME, J. Y. Miller and L. D. Miller); and Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA (CMNH, J. E. Rawlins).

RESULTS

Female genitalia. The female genitalia of *S. toussainti*, *S. andrewi*, *S. amonensis*, and *S. rhapsos* do not differ from each other in any substantive way. We illustrate the female genitalia of paratypes for all four (Figs. 5–8). Smith et al. (1991) noted that the posterior tip of the corpus bursae of *S. amonensis* is heavily sclerotized and that this structure is unique among Antillean *Strymon*. However, *S. toussainti*, *S. andrewi*, and *S. rhapsos* share this structure, as do *S. limenia* and *S. bubastus*. Johnson et al. (1990) described the “u” shaped anterior ductus bursae of *S. rhapsos* (Fig. 6) as unique in *Strymon*, but it also occurs in *S. toussainti* (Fig. 5), *S. andrewi* (Fig. 7), *S. amonensis* (Fig. 8), and *S. bubastus*.

The female genitalia of three paratypes of *S. andrewi* that we dissected (Fig. 7) differ from those of the allotype of *S. andrewi* (Fig. 9, also illustrated in Johnson & Matusik 1988), even though two of the paratypes and the allotype were collected at the same locality one day apart. The genitalia of the allotype are similar to those of *S. eurytulus* (Fig. 10), a common species from the southern part of South America.



FIGS. 11–14. Male genitalia in ventral aspect with aedeagus in lateral aspect. **11**, holotype of *S. toussainti*; **12**, holotype of *S. rhapsos*; **13**, reproduction of holotype of *S. amonensis* (scale approximated); and **14**, “holotype” of *S. andrewi*.

Either the genitalia of the allotype were incorrectly associated or its female genitalia are highly aberrant. In either case, female genitalia do not provide definitive evidence for the specific distinctness of *S. andrewi*.

Male genitalia. The male genitalia of *S. toussainti*, *S. amonensis*, and *S. rhapsos* do not differ in any substantive way. We illustrate the genitalia of the holotype for each species (Figs. 11–13). We could not confirm the differences noted by Smith et al. (1991). These reported differences, particularly in the shape of the valves, are small compared with the intraspecific genitalic variation reported in other eumaeines (e.g., Brown 1983, Robbins 1990, 1991), and we doubt that they are likely to be a reliable distinction between species. In fact, we find few, if any, structural differences between the male genitalia of these species and those of *S. limenia* and *S. istapa* from the southern part of its range (Robbins & Nicolay 1999).

Johnson and Matusik (1988) illustrated the male holotype of *S. andrewi* and its genitalia, but these genitalia present two problems. First, the illustrated adult (Fig. 2), which we have examined, is a female. It lacks dorsal forewing androconia and its right foretarsus (the left one is broken) is five segmented with a clawed pretarsus, and its forewings have the rounded female *Strymon* shape (Fig. 2) in contrast to the more angular male forewing shape (Figs. 1, 3, 4). Thus, the holotype “male genitalia” belong to some other specimen. The second problem with the “male genitalia” of the holotype is analogous to the situation described for the female genitalia of the allotype. The male genitalia associated with the holotype (Fig. 14) are the same as those of *S. eurytulus* except for the cornutus, which is larger than

those in other males belonging to the Antillean members of the *S. columella* complex. The genitalia of the one male paratype of *S. andrewi* that were available to us were missing the distal parts of one valve and the aedeagus, but were otherwise not different from the male genitalia of *S. toussainti*. And again, the "male holotype" and paratype were part of the same collecting series. Since the "male genitalia" of the holotype that Johnson and Matusik (1988) illustrated do not belong to the holotype, they do not provide evidence for the specific distinctness of *S. andrewi*.

Wing pattern. The *S. toussainti* species complex is distinguished by a ventral forewing spot in cell M1–M2 (arrows in Figs. 1–4), and to a lesser extent in cell M2–M3, displaced basally more than 0.35 mm. All specimens of *S. toussainti*, *S. andrewi*, *S. amonensis*, and *S. rhapsos* that we have examined possess this trait, but the three smallest females had this segment displaced the least. Two paratypes of *S. toussainti* (AMNH) lack this trait, but they are actually *S. istapa*. Since Comstock and Huntington (1943) distinguished *S. toussainti* from *S. istapa* by the basally displaced forewing spot, we doubt that these specimens are original paratypes.

Other wing pattern characters suggested to distinguish species in the *S. toussainti* species complex are the amount of blue on the dorsal wings (Johnson & Matusik 1988), the amount of red comprising the anterior four spots of the ventral hindwing line (Smith et al. 1991), and the "boldness" of the ventral hindwing spots, particularly the one near the hindwing anal margin (Smith et al. 1994).

The extent of dorsal blue coloration is similar in all males that we examined. Viewed under a dissecting microscope, the dorsal wings of males tend to have a few light blue scales, which are relatively inconspicuous to the naked eye, scattered among a majority of brown scales. The extensive area of dorsal blue scales illustrated for the "male" holotype of *S. andrewi* (Johnson & Matusik 1988) describes the female dorsal pattern, which is logical because the holotype is a female.

The extent of dorsal blue coloration varies considerably among females. They may have blue scales on the forewing base posterior of the cubital vein, on the hindwing base posterior of the radial vein, and on the distal hindwing posterior of the cubital vein (illustrated in Johnson & Matusik 1988). In these areas, the blue scales vary from scattered to extensive. Indeed, the entire range of variation occurs in females of the type series of *S. andrewi* that we examined. Virtually identical variation also occurs in Antillean females of *S. istapa* and some other *Strymon* species. In sum, extent of dorsal blue coloration does not seem to be a reliable distinguishing trait for Antillean *Strymon*.

As a measure of the red in the postmedian line spots, we counted the number of orange and red scales in the spot in hindwing cell SC+R1–RS for types of all the species. Among types of *S. toussainti*, it ranged from

3 to 30 scales in 6 males, and from 2 to 14 scales in 4 females. Among types of *S. andrewi*, the number of orange and red scales was 34 in the one male without rubbed wings, and ranged from 0 to 25 scales in 4 females. Among types of *S. amonensis*, it ranged from 2 to 9 in 2 males, and from 1 to 18 in 2 females. The amount of red in this spot appears to be too variable to be a distinguishing trait for these species.

The ventral hindwing postmedian spot at the anal margin is well-developed in the four paratypes of *S. amonensis* that we examined, but was also well-developed in four of six types of *S. andrewi* and in 2 of 11 types of *S. toussainti*. Since "boldness" is a subjective and variable criterion, it does not seem to distinguish these species.

DISCUSSION

Taxonomy. There is no definitive evidence supporting the hypothesis that *S. andrewi*, *S. amonensis*, and *S. rhaptos* are distinct from *S. toussainti*. Variation of male genitalia, female genitalia, and wing pattern appears to be continuous without distinct states. The troubling complication is that the genitalia of the type series of *S. andrewi* represent two phenotypes. The genitalia of the two types previously dissected, presumably by Johnson and Matusik, resemble those of *S. eurytulus*, whereas the genitalia of the four types that we dissected resemble *S. toussainti*. Further, we know that the "male" holotype genitalia were incorrectly associated because the holotype is a female. For these reasons, the hypothesis that Johnson and Matusik improperly associated the genitalia of the holotype and allotype with those of another *Strymon* species, probably *S. eurytulus*, is better supported than the idea that two species are represented in the type series of *S. andrewi*.

Biogeography and *S. rhaptos*. *Strymon toussainti* and its synonyms *S. andrewi* and *S. amonensis* refer to butterflies on the neighboring Antillean islands of Mona and Hispaniola, but the male and female types of *S. rhaptos* are from the mountains of Patagonia, Argentina. There appear to be two possible explanations for this unusual situation. First, *S. toussainti* has a widely disjunct distribution in the Antilles and in the mountains of Patagonia. Second, the types of *S. rhaptos* were of Antillean origin, but were mislabeled.

There is evidence for both these explanations. In support of the first explanation (a widely disjunct distribution), according to the data labels on the types of *S. rhaptos*, Herrera collected the male type, and Shapiro caught the female. Both Herrera and Shapiro are well-known collectors of Argentine Lepidoptera, and Shapiro has not been to Hispaniola (Shapiro, pers. comm). (No other specimens of *S. rhaptos* are known.) However, the male holotype was not labeled by Herrera, who is now deceased, but rather has a label printed by Johnson when he spread the

specimen (Johnson, pers. comm.). Similarly, the female type was spread and labeled by Johnson (Shapiro, pers. comm.). Further, Johnson has collected in Hispaniola (Johnson & Matusik 1988), increasing the likelihood that the types were mislabeled. Lastly, we know of no other butterfly with a disjunct distribution in the Antilles and the mountains of Patagonia. Although we cannot resolve this situation definitively at present, the second explanation seems more likely.

Nomenclature. The following synonymic list summarizes our taxonomic results. All citations are listed in the Literature Cited.

Strymon toussainti (Comstock & Huntington, 1943)

= *Strymon andrewi* Johnson & Matusik, 1988 **NEW SYNONYM**

= *Strymon rhapsos* Johnson, Eisele & MacPherson, 1990 **NEW SYNONYM**

= *Strymon amonensis* Smith, Johnson, Miller & McKenzie, 1991 **NEW SYNONYM**

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We thank J. S. Miller, J. Y. Miller, L. D. Miller, and J. E. Rawlins for loaning specimens from collections under their supervision. We are grateful to John Burns and Douglas Ferguson for confirming that the "male holotype" of *S. andrewi*, which was illustrated in the original description, has a five-segmented foretarsus with pretarsal claws. For reading and commenting on the manuscript, we thank A. Brower, C. Covell, D. Ferguson, J. Glassberg, D. Harvey, G. Lamas, L. Miller, J. Y. Miller, A. Shapiro, F. Sperling, J. B. Sullivan, and B. Ziegler. We are grateful to V. Malikul for the genitalia drawings and to G. Venable for digitizing the figures and composing the plates.

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Note Added In Proof: The USNM received the four paratypes of *S. amonensis* mentioned in Smith et al. (1991) too late (October 1998) to be incorporated into the study, but the morphology of these specimens is consistent with our results.

A NEW SPECIES OF *HULSTINA* FROM CALIFORNIA
(GEOMETRIDAE: ENNOMINAE)

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ABSTRACT. A new geometrid species, *Hulstina nevadaria* (TL, Tom's Place, Mono County) is described, illustrated and compared to other members of the genus.

Additional key words: Mono County, Sierra Nevada, Ennominae.

In Rindge's (1970) revision of *Hulstina*, the species *Hulstina grossbecki* Rindge (Geometridae) was described from specimens from coastal southern California and northern Baja California, Mexico. The validity of one specimen from Tom's Place, Mono County, California, on the lower eastern slope of the Sierra Nevada was questioned. Additional specimens from this locality were found, and, after further study, it was determined that these moths represent an undescribed species which is described below.

Hulstina nevadaria R. M. Brown, new species

Description. *Male* (Fig. 1): head with tan and dark brown scales; front flat with tufts of horizontal scales ventrally; palpi porrect from middle of eye, extending beyond front by width of eye; tongue well developed; antennae pectinations from anterior half of segment, longest pectinations 1.1 mm long, covered ventrally by fine setae, terminal few segments without pectinations. Thorax dorsally tan with scattered dark brown scales, ventrally with less dark brown scaling; collar with dark brown band; legs with scattered dark brown scales, metathoracic legs with tibia slightly swollen; abdomen concolorous with thorax, dorsally with paired brown connected spots at the posterior margin of segment. Forewing length 13-15 mm ($n = 4$); upper surface with ground color whitish, dusted with dark brown scales; transverse lines dark brown; basal area white; antemedial line tending to be geminate, prominent posterior of median vein; postmedial prominent posterior of vein cu_2 , remainder of postmedial line represented by spots on veins; median area varies in width and color intensity, darkest posterior of median vein; medial line weakly represented; postmedial with tan shadow line followed by white line; subterminal line scalloped with inward pointing streaks; white streak on cu_2 loosely united with white postmedial

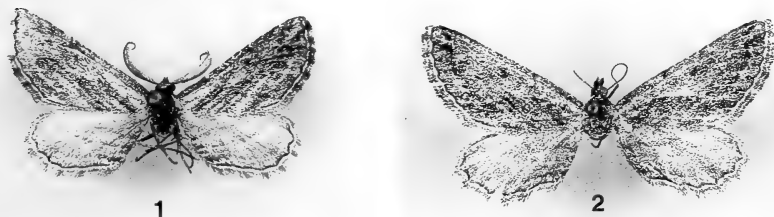


FIG. 1. Male of *Hulstina nevadaria*, upper surface. FIG. 2. Female of *Hulstina nevadaria*, upper surface.

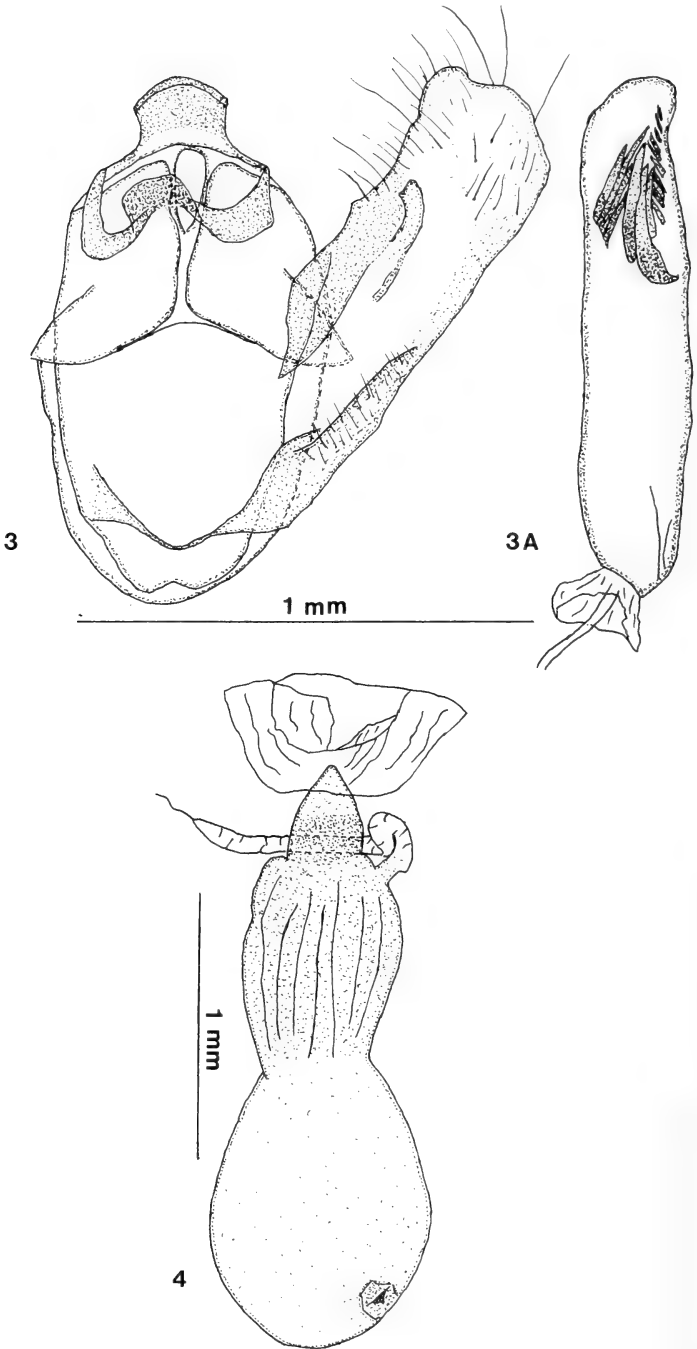


FIG. 3 and 3A. Male genitalia of *Hulstina nevadaria* FIG. 4. Female genitalia of *Hulstina nevadaria*.

shadow line forming an irregular loop; discal area, a smooth blend of light and dark scales, discal spot brown; subterminal area tending to be darker than remainder of wing; veins lined by light tan; terminal line dark brown; fringe white at base, double rowed, dark brown checked at veins. Hindwing color lighter than forewing; lines weakly represented except at anal margin; terminal line and fringe as on forewing. Under surface of forewing brownish; costa speckled; postmedial line originating as a large brown spot on costa, then represented by spots on veins; discal spot brown. Hindwing whitish brown with postmedial line as on forewing; terminal line and fringe as on upper surface. *Female* (Fig. 2): similar to male, maculation less distinct; forewing length 13–14 mm ($n = 2$). *Male genitalia* (Fig. 3): uncus wide, posterior margin rounded; gnathos without median enlargement, median area finely spiculate; valve with costa well sclerotized to one-half of costal margin, with raised truncated process curved toward costa, arising from inner margin, sacculus swollen, lightly sclerotized, valve with distal margin broadly truncated; aedeagus 1.2 mm long, 0.3 mm at widest point, bluntly rounded at posterior end; vesica with two adjacent groups of cornuti in posterior half, cornuti on right side are fewer in number and tend to be longer than those on left. *Female genitalia* (Fig. 4): ductus bursae small, wider than long, anterior margin well defined, with a slight convex bend, posterior margin ill defined by scattered sclerotized spots, with lightly sclerotized triangular piece projecting posteriorly; ductus seminalis arising on right side of corpus bursae near ductus bursae, twisting and wrapping ventrally around ductus bursae; corpus bursae constructed roughly in middle, posterior half lightly sclerotized, somewhat rugose longitudinally, wider than ductus bursae; anterior half subglobular, membranous and wider than posterior portion; signum small, variable in shape and number of marginal points.

Types. Holotype (Fig. 1) ♂: California, Mono Co., 1 mile west Tom's Place, 13-VIII-57 (J. Powell), genitalia slide R. M. Brown no. 745. Allotype (Fig. 2) ♀: same data as holotype, genitalia slide R. M. Brown no. 746. Paratypes: 2 ♂, 1 ♀ same data as holotype, 1 ♂ same locality, 6-VIII-59 (C. D. MacNeill). The holotype, allotype and three paratypes will be in the Essig Museum of Entomology, University of California, Berkeley, California. One paratype is retained in my collection.

Diagnosis. *Hulstina nevadaria* belongs to Group II as defined by Rindge (1970). The lack of a spine extending across the face of the valve, the truncated distal margin of the valve and locality will separate *H. nevadaria* from the other species in Group II. *Hulstina aridata* Barnes & Benjamin of Group I flies with *H. nevadaria*, the two species can be confused based on maculation. However, *H. aridata* lacks a tongue and the upper forewing generally has a white area at the base of the subterminal line; in *H. nevadaria* this white area is greatly reduced or lacking. Generally *H. nevadaria* is more brownish than *H. aridata*, which tends to be gray.

Etymology. This species is named for the Sierra Nevada mountain range.

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GENERAL NOTES

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EARLY STAGES OF *MYSCELIA CYANIRIS CYANIRIS* (DOUBLEDAY) FROM PANAMA (NYMPHALIDAE, NYMPHALINAE)

Additional key words: Natural History, *Adelia triloba*, Euphorbiaceae, Central America.

The genus *Myscelia* Doubleday comprises ten species that are distributed from the Southern United States to Northern Argentina (Jenkins 1984, D'Abrera 1987). In a recent systematic revision, Jenkins (1984) considered *Myscelia* closely related to the genus *Catonephele* Hübner, and he suggested that *Myscelia* butterflies oviposit on the Euphorbiaceae, thus sharing this host plant family with members of the genera *Biblis* F., *Mestra* Hübner, *Hamadryas* Hübner, *Dynamine* Hübner, *Eunica* Hübner, *Catonephele* Hübner and *Nessaea* Hübner. The three species of *Myscelia* found in Panama and Costa Rica show a color pattern common to many species in the genus: upperside iridescent blue over white bands on a brown ground color and a cryptic brown underside, with females being less brightly colored than males (see DeVries 1987).

Myscelia cyaniris cyaniris (Doubleday), has been observed to oviposit on *Dalechampia triphylla* and an unidentified canopy vine (both Euphorbiaceae) in Costa Rica (DeVries 1987). Records from Panama include *Adelia triloba* (Euphorbiaceae), from populations at Cana, Darién (field notes of the late G. Small) and Barro Colorado Island, Panama (A. Aiello, pers. com.). A pupa was found on *Croton bilbergianus* (Euphorbiaceae) at Barro Colorado Island (A. Aiello, pers. com.). As the life history, early stages and oviposition behavior of *Myscelia* butterflies are poorly known (DeVries 1987), I here describe the life cycle of *M. cyaniris cyaniris*, and provide line drawings of the head for each larval instar and photographs of the mature larva and pupa. Material described here originated from the edge of second growth forest in Soberania National Park, Panama Province, Panama, and all early stages were raised in plastic containers at ambient temperature. Although the descriptions reported here are more detailed, my observations show broad similarity to the unpublished notes on material field-reared by G. Small (lot number GS-83-51).

Oviposition behavior and host plant. On 4 November, 1994, I observed a female lay eggs on a small isolated individual of *Adelia triloba* (ca. 40 cm; Euphorbiaceae) at the edge of the forest under full sun, therefore confirming G. B. Small's host plant record. The butterfly examined the young tips of several branches before laying an egg, often leaving the plant to perch in the high branches of neighboring trees, and later returning to it. Several eggs were laid on the plant during each oviposition event, and each egg was deposited singly on the underside of young leaves and buds. Eggs also were found on a larger specimen of *A. triloba* (ca. 70 cm), located near the forest edge and surrounded by shrubby vegetation. Eggs were collected on the same two plants on 4–7 November, and 8 December, 1994.

Egg (n = 9). White; cylindrical, 0.6 mm wide and 0.6 mm tall; 11 vertical ribs; micropyle surrounded by a marked depression adorned with conspicuous vertical ribs that form a serrated "crown" approximately 0.2 mm tall.

Larva (Figures 1 and 2). *First instar* (n = 4, 2–3 days). Head beige with short, brownish primary setae; body pale green with very short, dark primary setae; larva rests on a "frass chain" at the tip of the leaf midvein with epicranium appressed to substrate. *Second instar* (n = 3, 2–3 days). Head mottled in brown and creamy white, adorned with ubiquitous small creamy-white tubercles which are slightly more prominent in the genal region of the epicranium; pair of thick, blunt scoli adorned with small tubercles, and approximately two thirds of the head height; frons with a dark medial line. Body green with short, white, tubercle-like, sub-dorsal, lateral and sub-lateral scoli; body color darker green anteriorly, fading toward posterior section of the body; ventral side yellow-green; thoracic legs brownish, abdominal prolegs yellow-green; larvae rest on a "frass chain" with epicranium appressed to substrate. *Third instar* (n = 3, 2–3 days). Head dark brown with ubiquitous small creamy-white tubercles which are slightly more prominent in the genal region of the epicranium; frons black; head scoli approximately 3.5 times longer than head height, proportionately more slender than the scoli of the second instar, the shaft of each scoli is adorned with three whorls of black spines:

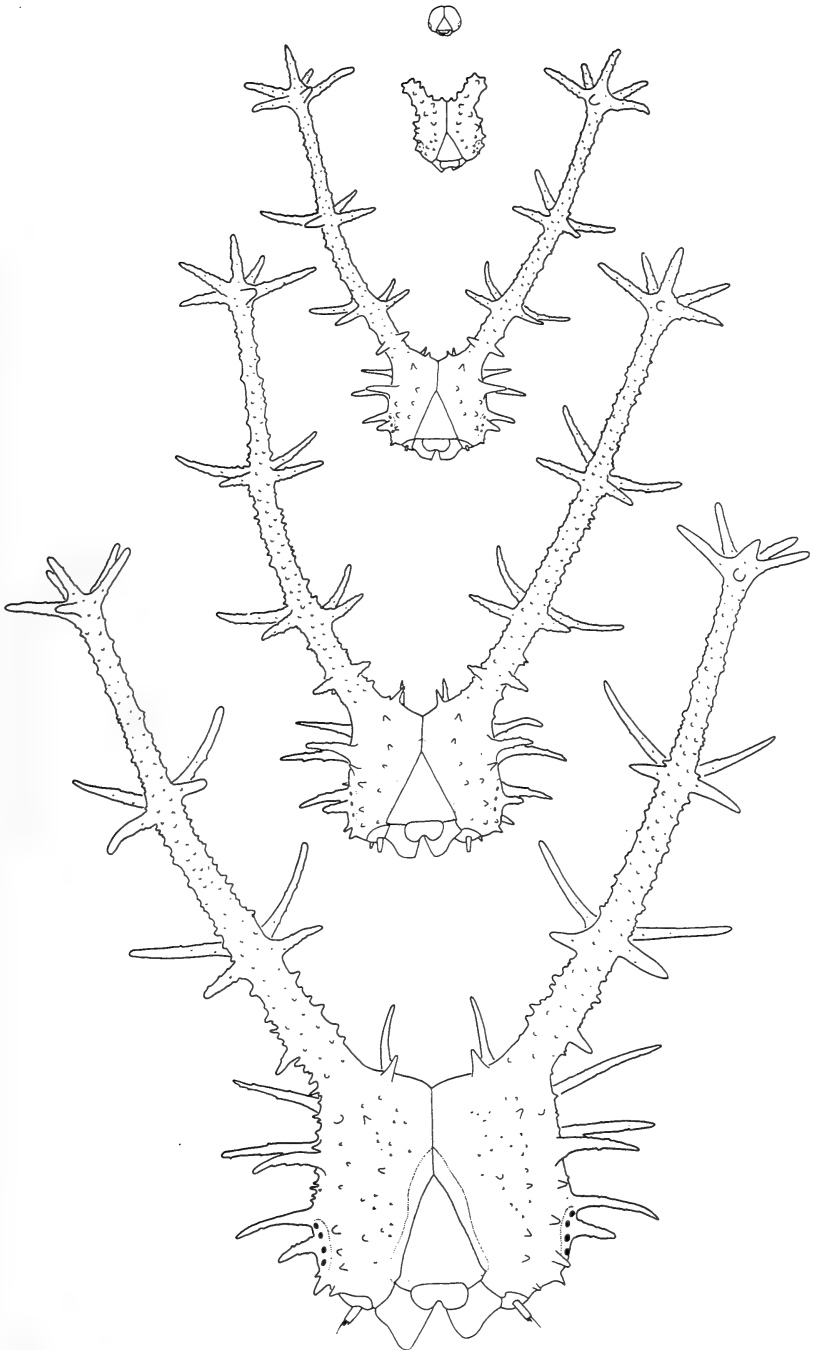


FIG. 1. Frontal view of the head capsules of *Myscelia cyaniris cyaniris* from Soberania National Park, Panama; top to bottom: first to fifth instar.

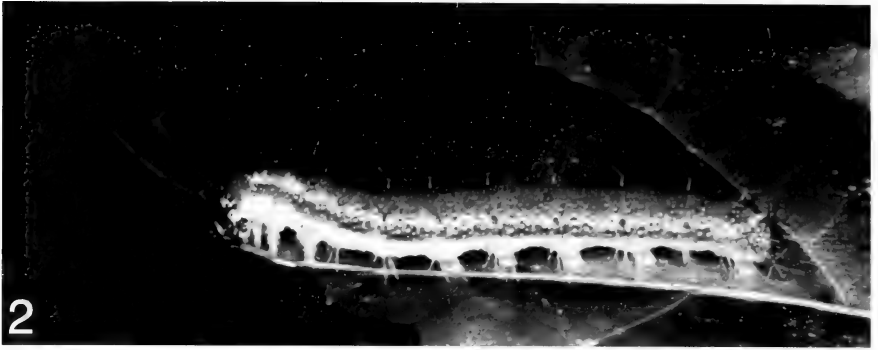


FIG. 2. Mature larva of *Myscelia cyaniris cyaniris* from Soberania National Park, Panama. FIG. 3. Pupa of *Myscelia cyaniris cyaniris* from Soberania National Park, Panama.

a six-branched whorl located at the distal tip of the scolus, a four-branched whorl located at two thirds of the length of the scolus, and a four-branched whorl located at one third of the length of the scolus, the latter is followed by a pair of smaller spines located on the anterior side near the base of the scolus; the shafts of the scoli are dark proximal to first whorl of spines and creamy-white between whorls; four pairs of post-genal whitish spines distributed from the top of the head to stemmatal region; single whitish spine below each scolus located at mid distance between base of scolus and stemmatal region. Body green with short, white, sub-dorsal, lateral and sub-lateral scoli; sub-dorsal scoli adorned with three terminal spinules in a whorl; sub-dorsal scoli on thoracic segment T3 and abdominal segments A7 and A8 arise from orange tubercles; A7 with two mid-dorsal scoli, posterior scolus larger than anterior; A8 with one mid-dorsal scolus; ventral side translucent green; legs same as in second instar; larvae no longer rest on "frass chains", resting on the leaf surface with epicranium appressed to substrate. *Fourth instar* ($n = 3$, 2–3 days). Head same as in third instar, except for the frons, which is white. Body similar to third instar; green spotted with white; color light green on the dorsal section of the body, becoming darker on the dorso-lateral and lateral sections; sub-dorsal longitudinal row of white spots giving the appearance of a white stripe to the naked eye;

thin whitish supra-spiracular stripe; ventral side translucent green; thoracic legs and abdominal pro-legs green; larvae rest on leaf surface with epicranium appressed to substrate. *Fifth instar* (n = 3, 4–7 days, Figs. 1–2). Head anteriorly black with ubiquitous small creamy-white tubercles; frons creamy-white; post-gena creamy white; red marks between occiput and base of the head scoli; head scoli approximately 2.5 times the head height; the shaft of each scolus is adorned with three whorls of black spines: a six-branched whorl located at the distal tip of the scolus, a four-branched whorl located at two thirds of the length of the scolus, and a four-branched whorl located at one third of the length of the scolus, the latter is followed by a pair of smaller spines located on the anterior side near the base of the scolus; the shafts of the scoli are dark proximal to first whorl of spines and creamy-white between whorls; spines of the proximal and medial whorls with a creamy-white transverse stripe at midlength; single lateral spine located near the base of the scoli; four pairs of large post-genal whitish spines distributed from the top of the head to stemmatal region; single whitish spine below each scolus located at mid distance between base of scolus and stemmatal region; one small whitish spine in the stemmatal region, and another immediately posterior to it. Body green spotted with white; dorsally green, dorso-laterally yellowish green; sub-dorsal longitudinal row of white spots giving the appearance of a white stripe to the naked eye; dark green stripe immediately below row of white spots; yellowish longitudinal spiracular stripe; T2–A8 with sub-dorsal scoli which are yellow at base and green distally, terminating in a whorl of three (T2, A1–7), six (T3), or four (A8) long spinules striped in black and white; T2–3 with green lateral scoli terminating in a whorl of three spinules; A2–8 with green lateral scoli adorned with two terminal spinules; A1–8 with green sub-lateral scoli with three terminal spinules; A1–6 with green mid-dorsal scoli adorned with two terminal spinules; A7 with two green mid-dorsal scoli, anterior adorned with two terminal spinules, and posterior terminating in a whorl of four spinules; A8 with thick green mid-dorsal scoli terminating in a whorl of five spinules; A10 with thick green scoli terminating in a whorl of five spinules and located laterally to the anal plate; ventral side green to blue-green; thoracic and abdominal legs green to blue-green; larvae rest on leaf surface with epicranium appressed to substrate.

Pupa (n = 2, 7–8 days, Fig. 3). Body projecting forward to attain a horizontal position. Color predominantly green with white and brown markings. Head adorned with pair of short white conical ornaments; antennae whitish; legs pale green; thoracic segments T1 and T2 predominantly dark green dorsally; T2 with a pointed keel; T3 and abdominal segment A1 pale green dorsally and dark green laterally; A4 with lateral dark green rounded markings terminating on a yellowish lateral stripe that runs at the edge of wing pad; wing pad pale green, raised posteriorly to form a ridge, which is marbled in white and brown; faint dark green dorsal midline; dorso-lateral and ventral regions of the abdomen with a whitish shade posterior to wing pad; cremaster brown.

I thank A. Aiello for providing unpublished records (Aiello Lots 83–21 and 78–106); D. Harvey for facilitating access to Gordon Small's unpublished notes housed at the Smithsonian Institution (lot numbers GS-83-51 [n = 6; 13 May, 1983], GS-83-55 [n = 2; 16 May, 1983], GS-83-56 [n = 1; 18 May, 1983], GS-83-58 [n = 2; 20 May, 1983], and GS-83-81 [n = 1; 9 June, 1983]); R. Srygley for photographing the larva and pupa; A. Aiello, P. DeVries, R. Hanner and D. Jenkins for comments on the manuscript; and P. DeVries for logistical support. Permits for collecting and exporting specimens were issued by InReNaRe through the Smithsonian Tropical Research Institute, Panama. Support for this research was provided in part by the National Science Foundation (DEB98-06779 to P. DeVries and C. Penz).

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BOOK REVIEWS

PAPILIONIDAE Y PIERIDAE DE MÉXICO: DISTRIBUCIÓN GEOGRÁFICA E ILUSTRACIÓN, by Jorge E. Llorente-Bousquets, Leonor Oñate-Ocaña, Armando Luis-Martínez, and Isabel Vargas-Fernández. Illustrations by Pál János. 1997. Published by Comisión Nacional Para el Conocimiento y Uso de la Biodiversidad (CONABIO) and Facultad de Ciencias, Universidad Nacional Autónoma de México. 227 + 8 pages, 28 color plates, 116 distribution maps. Softcover, glossy paper, 21.5 × 28.0 cm, ISBN 968-36-6456-3. Available from the Museo de Zoología, Facultad de Ciencias, UNAM, Apdo. Postal 70-399, Ciudad Universitaria, 04510, México D.F., e-mail: ivf@hp.fcencias.unam.mx, for about U.S. \$35.00.

Since its formation in 1978, the “Alfonso L. Herrera” Zoology Museum (MZFC) in the Sciences Department at Mexico's National Autonomous University has been one of the leading Mexican natural history research institutions, with collections and specialists in groups such as ectoparasites, fish, reptiles, amphibians, birds, mammals, and Lepidoptera, especially butterflies. In the last 20 years, this institution has amassed and assembled one of the largest and most complete collections of Mexican butterflies. Published results of fieldwork by museum faculty in the Mexican states of Veracruz, Oaxaca, Guerrero, Colima, and Jalisco have revealed a much more diverse butterfly fauna in those states than was previously believed, and have made available a tremendous amount of new information on the temporal and geographical distribution of the butterfly fauna in western Mexico.

For a nation with approximately 2000 species of butterflies (including skippers), surprisingly few regional lists of species and no comprehensive field guides to any group of butterflies are available. This new book, treating all the species of Papilionidae and Pieridae of Mexico, is the field guide that naturalists interested in the larger butterflies of Mexico have been long awaiting. Complete data from over 50,000 specimens in these families, from the MZFC collection, most major butterfly collections in the United States, and from previous literature sources, are presented in telegraphic form (arranged by species and state). Distribution maps are provided for each species that show specific records plotted on small maps of Mexico, with state boundaries indicated. All species of Papilionidae and Pieridae are illustrated in 28 color plates, showing subspecific and other variation among certain species in many cases. Other useful features of the book include a complete listing of type localities of all subspecies treated, a gazetteer of localities listed in the book, arranged by state, giving the latitude and longitude of each locality (Appendix II), a tabular representation of much of the data presented in the book, and an extensive bibliography of Mexican Papilionidae and Pieridae (Appendix III).

Only a small amount of text is present in the book, which is entirely in Spanish. The majority of the volume of the book is taken up by appendices listing data from all specimens examined, and data from literature sources. The listing of locality data for each species is split into two sections. The first section (Appendix I), preceding the distribution maps, lists data for all localities plotted on the distribution maps (Appendix IV). The second part (Appendix V), following the maps, lists data for each species that could not be plotted on the maps, such as general state or regional records, and records of localities that are too vague to be plotted. Most of the records in this section are from literature sources, all of which are cited in Appendix III.

The subspecific status of *Euchloe hyantis* (W. H. Edwards, [1871]) in Mexico is confused in the book. While *E. hyantis lotta* (Beutenmüller, 1898) is listed as being described from Arizona, all Chihuahua records are considered to be *hyantis hyantis*, and Baja California records to be *hyantis lotta* in Appendix I and on the distribution maps. In Appendix V, Baja California, Chihuahua, and Sonora records are all correctly listed together as *E. hyantis lotta*, as *E. hyantis hyantis* does not occur in Mexico (many authors now treat *E. lotta* and *hyantis* as separate species—an issue that will not be dealt with here). No other major errors or inconsistencies were noticed in the book.

This book is an extremely useful, lightweight, portable field guide that will be of great use to all naturalists and entomologists interested in the Mexican butterflies and Mexican biogeography in general. It does not contain the basic introductory information on butterflies that clutters the beginning of so many field guides or discussions for each species

based on speculation or personal observations. The book includes the raw data for 180 butterfly subspecies collected over a period of almost 20 years and leaves the interpretation of the data to the reader. Although the book is written in Spanish, readers without any knowledge of the language will be able to easily extract almost all of the information in the book, due to its lack of an extensive text, its clear, logical organization, and its excellent distribution maps and color plates. The only shortcoming of the color plates is the failure to illustrate the ventral surfaces of many of the species illustrated. For collection-based research, however, the plates are more than adequate.

This book is a must for all lepidopterists interested in Neotropical or southern Nearctic butterfly fauna (including southwestern United States), as well as entomologists and naturalists with a general interest in Lepidoptera. Specific locality and literature information on extremely rare endemic species, including *Pterourus esperanza* (Beutelspacher, 1975), and *Protographium thyastes occidentalis* (R. G. Maza, 1982), among others, will be of great value to conservationists. We can only hope that this team of researchers will produce similar field guides on other families of Mexican butterflies!

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HISTÒRIA NATURAL DEL LEPIDÒPTER *GRAELLSIA ISABELAE* (GRAELLS, 1849), by Josep Ylla i Ullastre. 1997. Published by Institut d'Estudis Catalans, Carrer del Carme 47, E-08001 Barcelona, Spain (mpascual@iec.es). 232 pages, 27 color photographs, 68 tables, 60 figures (mostly graphs). Soft cover, dust jacket, 18 × 24.5 cm, ISBN 84-7283-375-5. Available from the publisher for 2000 Spanish pesetas plus 500 pesetas postage (about U.S. \$16.25). Printing limited to 600 copies.

This book stands alone as the single most detailed and intensive piece of work on the biology of any species of Saturniidae. The subject of the study, which was Dr. Ylla's dissertation (1992, Autonomous University of Barcelona), is the beautiful Spanish moon moth (*Graellsia isabelae* (Graells)), a close relative of our luna moth (*Actias luna* (L.)). Virtually every aspect of the biology, distribution, species-level taxonomy, and summary of the existing literature about the moth has been covered. The text is written in Catalan, the regional language of Catalonia, but if one can read other Romance languages, much valuable information can be extracted from the book. The tables and graphs are quite clear in their presentation, so that language is a minimal barrier. Incidentally, the magnificent dust jacket has a large color photograph of a male moth in profile, enlarged to the point that individual scales can be seen. The moth is revered by the Spaniards, with the species named for their beloved Queen Isabel II, and the genus named for their famed entomologist Dr. Mariano de la Paz Graells.

The author meticulously made observations and recorded data for a decade (1981-1991) on this insect. This was possible because he lives in the pine forests where the moth is common. (I had the good fortune in 1995 to visit the author at his home to see for myself the habitat of this famous moth and to experience Catalonian hospitality.) The moth is strictly univoltine, overwintering in the pupal stage. The primary hostplant is Scots pine (*Pinus sylvestris* L.). Although "protected" from collecting by Spanish law, the moth is not at all endangered. In recent years one threat to its populations in Catalonia has been the aerial spraying of diflubenzuron to kill caterpillars of the pine processionary moth (*Thaumetopoea pityocampa* (D. & S.)). This situation is parallel to the flawed policy in the United States where *Bacillus thuringiensis* is used to kill caterpillars of the gypsy moth (*Lymantria dispar* (L.)), but which also kills many other non-target Lepidoptera in our forests.

There is a section showing range maps as depicted by several earlier authors, as well as sections on parasitoids, diseases, and hostplant trials. Data were recorded on flight times, diapause, emergences (circadian and seasonal), larval development, phototaxis, muscular

tremors, pheromone response, mating behavior, adult longevity, embryonic development (incubation periods), wingspan, oviposition, sex ratio, and biometrics of pupae. In many cases, temperature and relative humidity were faithfully recorded and correlated with moth responses, and males and females were graphed separately in those studies where such data can vary according to sex. The author offers hypotheses for the patchy and limited distribution of the moth in the mountains of Spain and France based on its ecological profile. The bibliography is, of course, exhaustive for what has been published on *G. isabelae*, but also cites many other works because Ylla has compared his observations on *G. isabelae* to those in published works concerning other insects.

For those wishing to have an ideal model of how to carry out and to present detailed observations and conclusions on the ecology of a moth, this work will serve them well. Where similar studies (although of much lesser scope) have been or will be published by workers on Saturniidae in other regions, it will be both interesting and useful to compare and contrast those results with what is found in this book. Studies on our own large and common saturniids like *Antheraea polyphemus* (Cram.), *Callosamia promethea* (Dru.), or *Hyalophora euryalus* (Bdv.) should be made and compared to this one. With the exception of the important studies on *Hyalophora* Duncan by Michael Collins, current work on Saturniidae largely remains on a non-quantitative level. This book by Ylla thus grabs our attention as being a highly impressive and excellent study that stands alone in the field of literature on Saturniidae and is perhaps even rare for any species in the entire order Lepidoptera. The published study is much to the credit of the author, his university, and his advising professor Dr. Víctor Sarto i Monteys. I highly recommend the book to insect ecologists and saturniid enthusiasts alike, and I urge those who obtain it to make use of it in their own studies.

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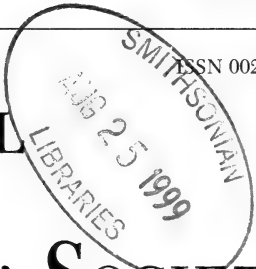
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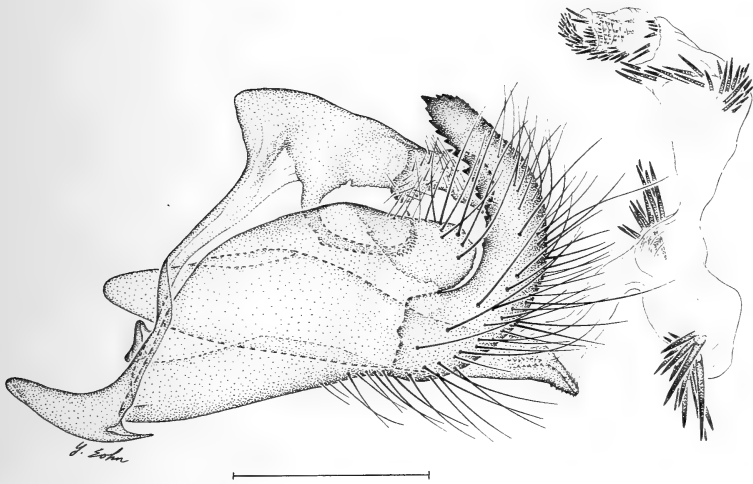
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THE LIFE HISTORY OF THE MARITIME RINGLET, *COENONYMPHA TULLIA NIPISQUIT* (SATYRIDAE)

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ABSTRACT. The immature stages of *Coenonympha tullia nipisquit* McDunnough are described and illustrated and an account of their biology and behavior under field conditions is given. The caterpillar host plant is *Spartina patens* (Ait.) Mühlenberg, a common grass in the salt marshes where this butterfly occurs. Although the immature stages are subject to inundation by salt water during the tide cycle, the life history appears to be similar to other members of the *C. tullia* complex. Comments on the taxonomic status of *C. t. nipisquit* are also given.

Additional key words: Salt marsh, host plant, endangered, *Coenonympha tullia inornata*.

The Maritime ringlet, *Coenonympha tullia nipisquit* McDunnough is the only member of the *C. tullia* (Müller) species complex in North America that is restricted to a salt marsh habitat. This subspecies has an extremely restricted distribution and is known from only a few localities, all near the Chaleur Bay in northeastern New Brunswick and Quebec on the east coast of Canada (Thomas 1980, Dion 1995, Handfield, pers. comm.). The largest colonies occur in three salt marshes within or near the city limits of Bathurst, N.B., increasing the risk that these habitats will be disturbed by urban and industrial sprawl and pollution. This could result in a reduction in the population numbers and possible extinction of this butterfly. For this reason, *C. t. nipisquit* has been recently listed as endangered in Canada by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and by the Province of New Brunswick.

Coenonympha tullia nipisquit was described by McDunnough, in 1939, from specimens collected in salt marshes near Bathurst, N.B. Although the butterfly can be relatively numerous within the limited salt marsh habitats, little was known about the life history, biology and eco-

logical requirements of this insect. In this paper the immature stages of *C. t. nipisiquit* are described and an account of their biology and behavior under field conditions is given.

MATERIALS AND METHODS

Study sites. *Coenonympha tullia nipisiquit* was studied in salt marshes in the estuary of the Peters River in Beresford, N.B. (near the Bathurst city limit), and at the Daly Point Reserve in Bathurst, N.B. The most common plants where *C. t. nipisiquit* occurs are *Spartina patens* (Ait.) Mühlenberg (salt meadow grass), *S. alterniflora* Loiseleur-Deslongchamps (Graminaceae), *Glaux maritima* L. (Primulaceae), *Limonium nashii* Small (sea lavender) (Plumbaginaceae), *Plantago maritima* L. (Plantaginaceae) and *Solidago sempervirens* L. (seaside goldenrod) (Asteraceae). The density of each species varies throughout the two sites forming a series of distinctive plant assemblages that occur in a mosaic or in zones within the marshes. *Spartina patens* is the most abundant species of plant at these two sites and forms dense stands covering as much as 75% of the marshes. *Coenonympha tullia nipisiquit* densities are usually highest in these sections of the marsh. All the marsh habitats are periodically flooded during high tides, sometimes to a depth of 0.5 to 1.0 meters. Wetter and more frequently flooded sections of the marsh, characterized by varying densities of *S. alterniflora*, occur near tidal ponds and creeks. Drier, infrequently flooded areas occur adjacent to forests or sand dunes bordering the salt marshes. These latter sites are often invaded by plant species associated with upland habitats.

Insect rearing. The life history and description of the immature stages were determined from insects reared from ova to adults on potted *S. patens* (45 cm diam. pots) collected from the Peters River estuary and maintained outdoors under natural photoperiod and temperature conditions in Fredericton, N.B. Ova were obtained from 4 fresh female *C. t. nipisiquit* collected on August 8, 1992. Females were put into 2 liter plastic ice cream containers with a screened cover with *S. patens* as an oviposition substrate. The container was placed in a location under partial shade and the ova were removed on a daily basis and placed among the stems of the potted *S. patens*. The behavior of the immatures and measurements of each life stage were recorded periodically (day and night) throughout their development, until adult emergence. Additional data were obtained from field observations and collections of the larvae and pupae at the Peters River and Daly Point salt marshes.

All descriptions and measurements are of living larvae and pupae. Morphological observations and measurements were made with aid of a stereomicroscope equipped with an ocular micrometer.

TABLE 1. Width of the head capsule and range of body lengths (resting larva) from post-molt to pre-molt of the five instars of *Coenonympha tullia nipisiquit* McDunnough.

Instar	Sample size	Mean width of head capsule (mm)	Mean body length (mm)	
			Post-molt	Pre-molt
First	11	0.64	2.6	4.7
Second (pre-diapause)	10	0.89	4.8	5.4
Second (post-diapause)	8	0.89	5.6	7.6
Third	6	1.07	8.2	10.0
Fourth	6	1.61	10.3	15.5
Fifth	6	2.40	13.3	23.4

Oviposition behavior. The sequence of behaviors culminating in oviposition and the host plant used for oviposition were determined from following females in flight and searching for ova from regions where females had been flushed.

RESULTS

Description of the immature stages. Egg. Eggs are subconical in shape (widest at the base), 1.0 mm in diameter and 1.1 mm in height (N = 10) (Fig. 1). Each egg has 40 to 48 shallow vertical ribs with a few transverse ridges. The micropyle lies on a slightly mounded prominence. Eggs are pale green when first laid and after 3 to 4 days they become light tan and mottled with irregular light brown patches. The duration of the egg stage is between 10 and 15 days under natural temperature conditions (N = 20).

Larvae. *Coenonympha tullia nipisiquit* has 5 larval instars. The size (head capsule width and body length) of each stage is shown in Table 1. Second through the fifth instar larvae exhibit a similar color pattern and differ only in size. These are shown in Figs. 2-5. Only the first and last instar larvae will be described.

First instar larva. Newly eclosed larvae are between 2.6 and 2.7 mm in length (N = 10), taper slightly and end in two short conical tails. The ends of the tails are reddish brown. The head is sub-globose and broader than the second segment. After eclosion the larvae are light tan with a mid-dorsal and 3 longitudinal light brown stripes, and a cream colored longitudinal stripe just below the spiracles. The brown spiracles are contained in the most ventral brown stripe. The head capsule and underside of the body are tan. Numerous small whitish tubercles each with a short, bent, light brownish process or seta cover the body and head. As the larvae feed they gradually become green and begin to exhibit a color pattern similar to the next four larval instars.

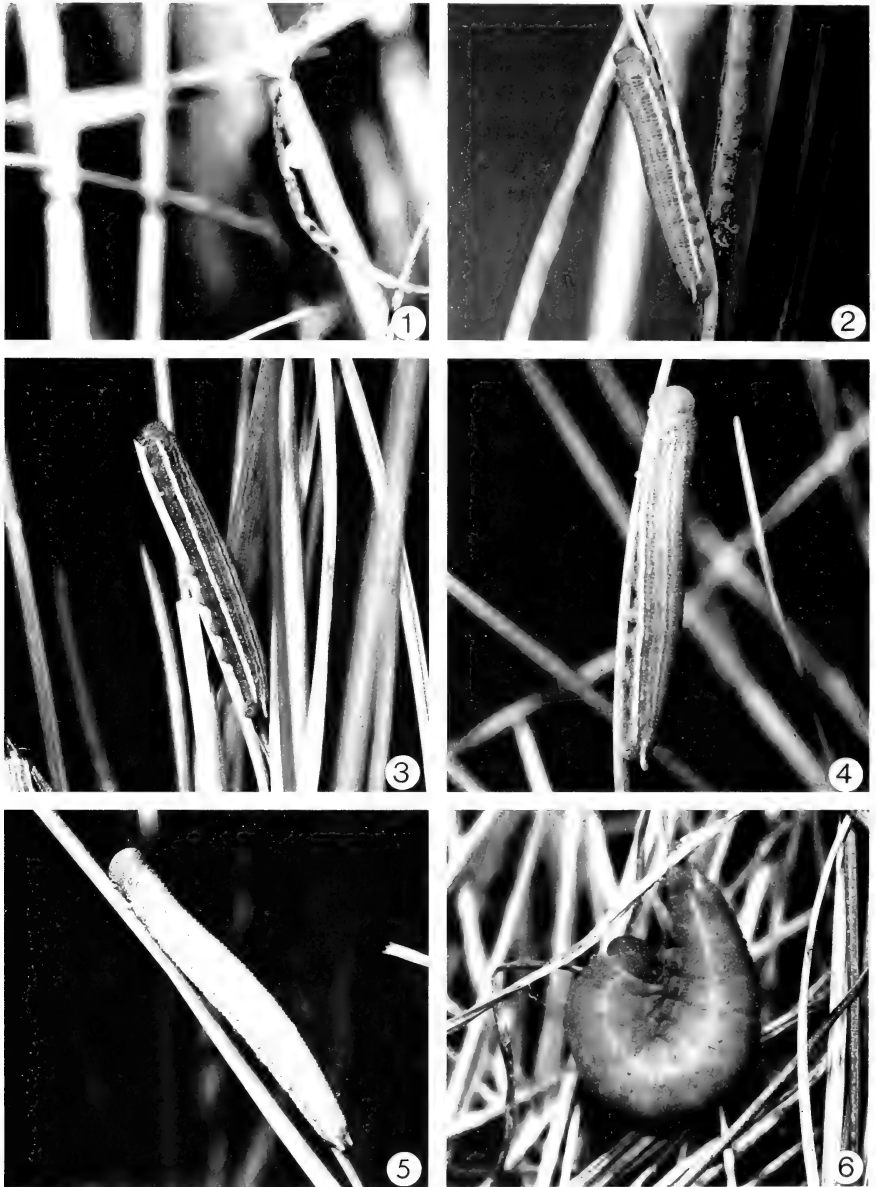


FIG. 1. Field collected egg of *C. t. nipisiquit* on dead blade of *S. patens*. FIG. 2. Post diapause second instar larva of *C. t. nipisiquit* resting on blade of *S. patens*. Length of larva was 7.0 mm. FIG. 3. Third instar larva of *C. t. nipisiquit* feeding on blade of *S. patens*. Length of larva was 9.2 mm. FIG. 4. Fourth instar larva of *C. t. nipisiquit* resting on blade of host plant. Length of larva was 12 mm. FIG. 5. Fifth (last) instar of *C. t. nipisiquit* resting on blade of host plant. Length of larva was 25 mm. FIG. 6. Prepupa of *C. t. nipisiquit* attached to stem of host plant.

Fifth instar larva. The mature last instar larvae are between 20.0 and 31.0 mm in length (mean = 23.4 mm) ($N = 6$), broadest (3.5 to 4.0 mm in width) and slightly arched dorsally between segments 3 and 7, and then taper gradually and end in two short conical tails or bifurcations (Fig. 5). The head is sub-globose, narrowing toward top and broader than first and second segments behind head. Small whitish tubercles, each with a short, bent (usually directed downward or posteriorly), light brownish semitransparent seta cover the head and body, giving the larvae a granular appearance. The overall color of the larvae is green to yellow green with a series of longitudinal stripes. Going dorsally to ventrally, there is a dark green mid-dorsal stripe edged on either side by pale yellowish green and a broad pale to yellowish green lateral stripe. These are followed by a narrow dark green lateral stripe edged on either side with pale yellow green, a broad green lateral band that gradually becomes dark green, and a yellow lateral stripe. The brown spiracles are in contact with the upper margin of this yellow band. The head is dark green and the ocelli, mandibles, and labrum are brown or light brown. The underside of the body and thoracic legs are dark green, tarsi brownish, prolegs are dark green with brown crochets. The two conical tails are yellowish green becoming reddish brown distally.

Pupa. The pupae are 11.0 mm to 13.0 mm (mean = 11.9 mm) in length and 4.0 mm to 5.0 mm (mean = 4.4 mm) in width ($N = 12$). They are cylindrical, stout, with the anterior end truncated and the abdomen swollen and conical distally. Pupae are suspended by a cremaster attached to a silk pad, usually on a grass stem. The pupae are usually bluish green with a series of black stripes. In the most common pattern (Figs. 7 & 8) there is one black stripe on the dorsal edge of each wing case from the base to inner angle. The inner margin of this stripe is whitish becoming bluish green. There is usually a curved stripe on central portion of wing case reaching the hind margin and a short stripe on hind margin of wing case. On the ventral side of the pupa there are two parallel stripes on the antennal cases and a larger stripe between the wings. There also may be a short lateral black stripe on each side of the last one or two segments of the abdomen. However, there is much variability in the extent of the pattern of stripes among individuals. The extremes of patterns among the individual pupae examined in this study (25) range from uniform bluish green with the black stripes nearly completely absent (Fig. 9) to individuals in which the black stripes have greatly expanded, obliterating all but a few green patches on the wing cases and between the abdominal segments (Fig. 10).

Oviposition behavior. The adults fly during a four to five week period from mid to late July to the third week in August. Females mate shortly after emergence near the pupation site and begin to oviposit

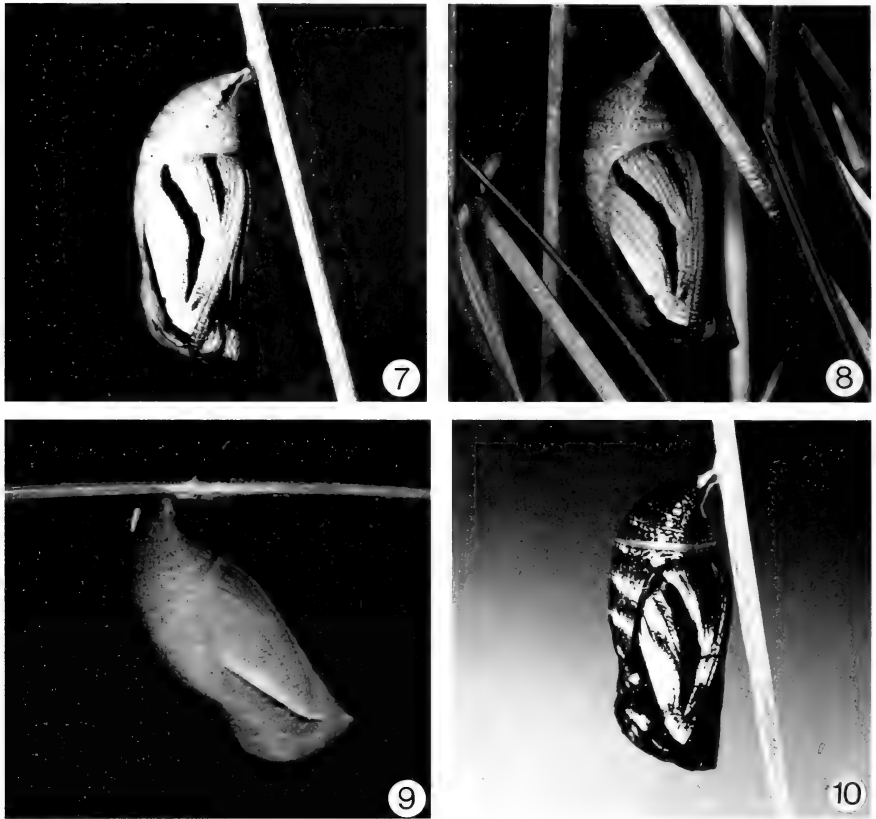


FIG. 7. Pupa of *C. t. nipisiquit* exhibiting typical pattern of dark lines. Pupal length was 12.5 mm. FIG. 8. Pupa of *C. t. nipisiquit* in typical pupation site near the base of *S. patens* canopy. Note how the color pattern confers crypsis to the pupa within the grass stems. FIG. 9. Pupa of *C. t. nipisiquit* in which dark lines are greatly reduced. Pupal length was 12.0 mm. FIG. 10. Pupa of *C. t. nipisiquit* with a greatly expanded pattern of dark stripes. Pupal length was 12.1 mm.

shortly after uncoupling. The primary larval host plant of *C. t. nipisiquit* is salt meadow grass, *S. patens*. Females were observed ovipositing on this grass and all larvae ($N = 35$) located in the marshes were either feeding or resting on this grass which is often the most abundant species of plant in the areas where *C. t. nipisiquit* is common. Larvae will complete development under laboratory conditions on *Festuca rubra* L. (Graminaceae), which also occurs in the salt marshes. However, this species of grass was generally not common where *C. t. nipisiquit* is most abundant, larvae have not been found on it, and females have not been

observed ovipositing on this plant. It therefore, remains to be determined if *F. rubra* is used by *C. t. nipisiquit* in nature.

The description of oviposition behavior was based on observations of 10 females at the Daly Point and Peters River salt marshes. Females begin to oviposit shortly after mating. Oviposition usually begins after a short flight (10 to 20 m) a short distance above the plant canopy. Most females abruptly drop into the canopy, move to the litter layer (area of dense dead grass stems) near the base of the grass, and begin to walk on the litter. Eggs are laid singly near the tips of thin (0.2 to 0.5 mm diam.) dead blades of *S. patens* near the base of the stems of the living plant between 1 and 7.5 cm (mean = 1.6 cm, N = 23) above the surface of the litter layer (Fig. 1). Each female lays 2–5 eggs (one per grass blade) before moving to another location. Eggs are scattered, but usually 3.0 to 15.0 cm from each other.

Females oviposit in a variety of microhabitats within the salt marsh, including regions dominated by *S. patens* (90 to 100% of stem density), wetter areas (more frequently flooded during high tides) where *S. alterniflora*, *G. maritima*, and *P. maritima* were dominant and *S. patens* comprised only about 10% of the stem density, and in areas with intermediate plant compositions. In all these areas eggs were laid at the base of living *S. patens* plants. Eggs are laid during the third or fourth week of July to the third week in August and hatch in 10–14 days.

Behavior of immature stages. Pre-diapause larvae. The neonate larvae initially feed on the egg shell and on the end of the dead grass blade to which the eggs were attached before moving to young shoots of *S. patens*. Most larvae feed head end up on the tips of young shoots of *S. patens* that were within or just protruding from the litter region at the base of the mature grass stems, although a few larvae also feed on the tips of mature leaves. The caterpillars consume only the distal 1/2 to 3/4 cm of the shoot before moving to another stem. When larvae are not feeding they usually rest on a grass stem with the head facing down.

The first instar larvae molt to the second instar after 15 to 17 days (early to mid Sept.). The second stage larvae continue to feed on the developing shoots within the litter zone. During mid to late October the second instar larvae stop feeding and enter diapause.

Diapause. Except for becoming slightly deeper green, the color pattern of the second instar larvae changes little after onset of diapause. Diapausing larvae range in length from 4.9 to 6.2 mm (mean = 5.4; N = 10). On potted plants most diapausing caterpillars rest along the undersides of dead grass stems between 2 and 4 cm below the surface of the previous year's litter (top layer) and 3 to 5 cm above the soil surface (N = 20). Larvae were not found near the saturated soil surface. In the salt

marsh at Daly Point one diapausing second instar larva was located a few days after the snow melt in late April. The larva was on the underside of a dead grass stem 5 cm above the soil surface within the litter zone.

Post-diapause larvae. The second instar larvae resume feeding on the developing shoots of *S. patens* from early to late May. Early in the season most of the larvae feed on the new shoots that were still within the litter layer. Later in the spring as the shoots begin to protrude above the litter zone the larvae begin feeding on shoots above this layer. During much of May and early June the larvae only feed during the day and stop feeding prior to 17:00 h and crawl into the litter, even on warm nights ($>10^{\circ}\text{C}$).

The second instar larvae molt to the third instar from mid May to early June and continue to feed on the new shoots of *S. patens*. The duration of the third instar larvae is 13 to 16 days. Most larvae molt to the fourth instar by late June.

Most fourth instar larvae feed near the top of the grass canopy and consume between 2 to 3 cm of the new growth (shoot) before moving to another stem. The larvae rest head down at the base of the grass stems at night as in the previous instars or higher up on the stems when not feeding during the day. The fourth instar lasts between 12 and 14 days.

Between mid June and early July most caterpillars molt to the last (fifth) instar. This stage lasts about 15 days and unlike the previous instars, caterpillars of this stage also feed nocturnally. The full grown caterpillars begin pupating in late June and continue to pupate until early August depending on the microclimatic conditions near the feeding site. Prior to pupation, the larvae attach themselves via a silk pad to stems of the host plant and the larval stripes become obscure or vanish entirely (Fig. 6).

Pupae. Most *C. t. nipisiquit* pupate near the base of grass stems within the grass canopy. On potted *S. patens*, pupae were attached via a silk pad to either living (86%) or dead grass stems between 2.5 cm below and 22.5 cm above the litter zone (mean = 5.2 cm; $N = 37$; canopy height was about 40 cm). In the field the cryptically colored pupae were very difficult to locate among the dense grass stems (Fig. 8). However, pupal exuvia could often be located near freshly emerged adults or mating pairs. Most pupal exuvia in the salt marsh were 2.5 cm below to 12.5 cm above the litter zone (Mean = 7.4 cm; $N = 18$) and all but two were attached to living stems of *S. patens*. Most were in areas of dense *S. patens* between 20 and 30 cm in height. However some exuvia were found in areas where *S. alterniflora*, *G. maritima*, and *P. maritima* dominated the plant community.

The pupal stage lasts 9 to 11 days. Most adult emergence occurs between 10:00 and 16:00 h ($N = 25$), however, there were insufficient ob-

servations to determine a specific emergence pattern. After eclosion, adults climb to a position near the top of the canopy, expand the wings and are ready for flight in about one hour.

DISCUSSION

The immature stages of *C. t. nipisiquit* are similar to those of the other members of the *C. tullia* complex in North America (Edwards 1887, 1897, Davenport 1941, Brown 1955, 1958, 1964, Brown & Heineman 1961). The ova of *C. t. nipisiquit* are slightly larger (1.1 mm high, 1.0 mm diam.) than the ova from females of *C. t. "inornata."* from Grindstone and Picton Islands in the St Lawrence River (0.9 mm high, 0.7 mm diam., May–June flight; 0.71 high, 0.75 diam., late August flight) (Brown 1958, Brown & Heineman 1961), but similar in size to ova of *C. t. inornata* from Lake Nominique, Quebec (about 1.0 mm) (Davenport 1941). Egg size was not given in the descriptions of the other North American populations. The only significant difference among the larvae of the subspecies, where descriptions are available, is that the larvae and chrysalids of some western populations, such as *C. t. californica* Westwood and *C. t. ampelos* Edwards exhibit a brownish color form (Edwards 1897, Brown 1964) not observed in *C. t. nipisiquit* or *C. t. inornata* (Davenport 1941, Webster in litt.).

Coenonympha tullia nipisiquit is unusual among the North American *Coenonympha* in that the entire life cycle of the butterfly occurs in a salt marsh habitat. During parts of the monthly tide cycle the entire marsh may be covered to a depth of 0.5 to 1.0 meters and thus all life stages of this butterfly are subject to the effects of flooding by salt water. Because of this, Brown (1955) suggested that the life history would differ from other *tullia* in North America. However, the life cycle of *C. t. nipisiquit* appears to be similar to other members of the *C. tullia* complex (Davenport 1941, Brown 1955, 1964). How the various life stages of *C. t. nipisiquit* withstand the effects of the salt water during high tides remains to be determined.

Coenonympha tullia nipisiquit is distinctive in the late summer flight season of the single generation of adults that is 3 to 5 weeks later than *C. t. inornata* in Bathurst, N.B. (Webster, in litt.). The difference in timing is probably in part, related to differences in the diapause characteristics of the two subspecies. *Coenonympha tullia inornata* diapauses as a third or fourth instar larvae in N. B. (Webster, in litt.), while *C. t. nipisiquit* diapauses in the second instar. Microclimatic differences between the preferred habitats of these two subspecies may accentuate the differences in emergence patterns created by diapausing in different instars. In the Bathurst area, *C. t. inornata* occurs in fields adjacent to the salt marshes. These upland habitats are slightly warmer because they are

less directly affected by the cooling effects of the sea breezes and they are not subject to the effects of inundation by cold water during the tide cycle. This would accelerate development of the larvae in the upland habitats compared to those in the salt marshes.

The late flight season of *C. t. nipisiquit* may also be linked to the availability of nectar which is generally unavailable prior to late July in the salt marsh habitat. Emergence of *C. t. nipisiquit* generally coincides with the flowering of a number of species of plants in the salt marshes including *L. nashii*, the principal nectar source of *C. t. nipisiquit* (Webster, in litt.).

A few comments are required regarding the taxonomic status of *C. t. nipisiquit*. *Coenonympha tullia nipisiquit* was arbitrarily classified as a subspecies of *C. inornata* (Edwards) in Brown (1955), Miller and Brown (1981), and Hodges (1983) and a subspecies of *C. tullia* in Scott (1986). However, Davenport (1941) has provided the only complete taxonomic revision of *Coenonympha* to date and showed that both *inornata* and *nipisiquit* should be classified as subspecies of *C. tullia*. This classification scheme may need to be revised in view of the recent range expansion of *C. t. inornata* in New Brunswick.

Prior to the 1970's, *C. t. nipisiquit* was the only *Coenonympha* in New Brunswick. During the 1970's *C. tullia inornata* moved into New Brunswick from the west and can now be found in almost any open grassy area throughout the province (Christie 1983, Thomas 1996) including the edges of the salt marshes occupied by *C. t. nipisiquit*. The two subspecies are now sympatric and they appear to be reproductively isolated due to differences in flight season and habitat preference and behave as separate species. Although the two subspecies appear to be reproductively isolated, little evidence is available on the genetic relatedness of the two subspecies in the area of sympatry. In a study by Wier-naz (1989), in which genetic changes associated with the recent range expansion of *C. tullia inornata* were examined, it was shown that the allele frequencies of *C. t. nipisiquit* were significantly different from all populations of *C. tullia inornata* examined. However the author did not comment on the taxonomic significance of these results and was apparently unaware that these two subspecies were sympatric in Bathurst, N.B. Studies are currently underway to re-examine the taxonomic relationship between these two subspecies.

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IDENTIFICATION OF MAJOR COMPONENTS OF THE FEMALE PHEROMONE GLANDS OF *EUCHAETES EGLE* DRURY (ARCTIIDAE)

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ABSTRACT. Extracts of the female pheromone glands of *Euchaetes egle* were analyzed using gas chromatography, infrared spectroscopy and mass spectroscopy. Identified compounds of the pheromone gland extract include a simple alkane (2-methyloctadecane), one diene (*Z,Z*-6,9-heneicosadiene), two trienes (*Z,Z,Z*-3,6,9-eicosatriene, *Z,Z,Z*-3,6,9-heneicosatriene), and one tetraene (*Z,Z,Z*-1,3,6,9-heneicosatetraene). The primary compound was found to be *Z,Z,Z*-3,6,9-heneicosatriene. Male sensitivity to these compounds was determined using an electroantennogram assay, and *Z,Z,Z*-1,3,6,9-heneicosatetraene elicited the greatest male response. Trienes are found in pheromone glands of the Arctiidae, Geometridae, Lymantriidae, and Noctuidae, suggesting that the use of these in compounds in pheromone glands is a plesiomorphic character for Arctiidae.

Additional key words: pheromones, mating behavior, Arctiidae.

In Lepidoptera, reproductive isolation among species can be achieved via temporal, chemical, or behavioral mechanisms. In moth systems, temporal and chemical isolation mechanisms are particularly important (Roelofs & Cardé 1974, Meyer 1984). Temporal isolation is achieved by variations in flight times. Chemical isolation is achieved by variations in the female pheromone blend, which is emitted from glands located in terminal abdominal segments (Baker 1985, Linn & Roelofs 1989).

Lepidopteran female pheromone glands vary in structure, ranging from a simple band of glandular tissue to eversible sacs or folds (Jefferson et al. 1971, Percy & Weatherston 1974, Percy-Cunningham & MacDonald 1987). Female pheromone glands in arctiids usually are paired, air-filled tubular invaginations that open dorsally between the eighth and ninth abdominal segments (Meyer 1984, Conner et al. 1980). The glands have two layers: an outer cellular layer and an inner cuticular layer (Fig. 1). The cuticular layer is then elaborated into internal cuticular spines (Fig. 2) (Conner et al. 1980, Yinn et al. 1991). To release the pheromone, arctiid females rhythmically protrude the eighth and ninth segments (Conner et al. 1985).

Female pheromone blends are typically composed of straight-chained hydrocarbons, 16 to 22 carbons in length. These compounds can contain

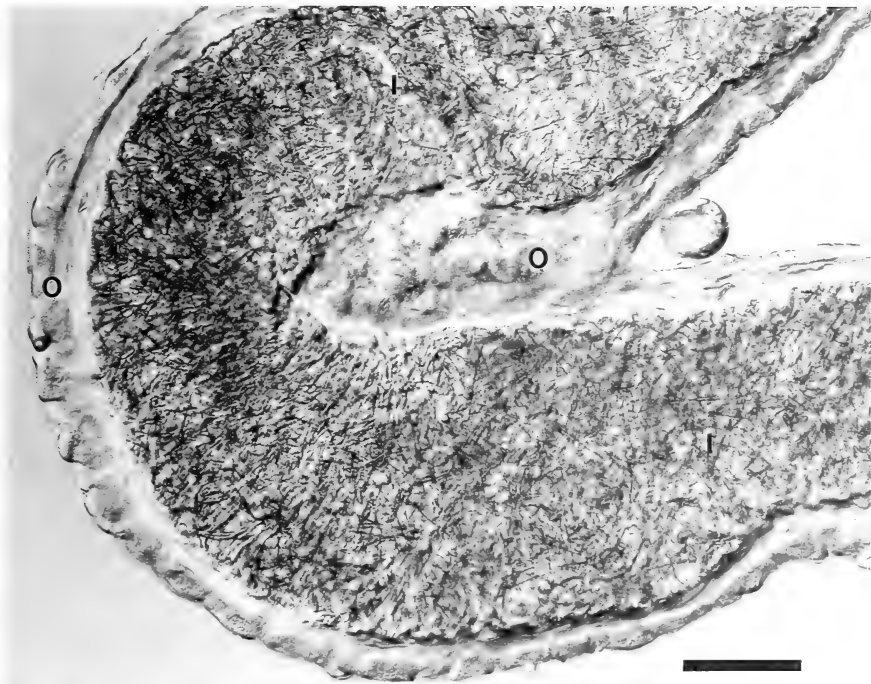


FIG. 1. Portion of the *E. egle* female pheromone gland, viewed using differential interference contrast (DIC) microscopy (O = outer cellular layer, I = inner cuticular layer, scale bar = 100 μ m).

a variety of functional groups, such as alcohols, aldehydes, acetate esters, epoxides and ketones (Leonhardt 1985, Mayer & McLaughlin 1991). In members of the Arctiidae, the major female pheromone components are trienes, triene derivatives, or 2-methylalkanes (Mayer & McLaughlin 1991). In this study, we examined the pheromone blend of *Euchaetes egle* Drury, the milkweed tussock moth, and determined male electroantennogram response to identified major components of the female's pheromone blend.

MATERIALS AND METHODS

Insects. Adult female *E. egle* were collected by James Adams in Dalton, Georgia. These gravid females were shipped to Wake Forest University, Winston-Salem, North Carolina. Eggs from these females and subsequent generations were also reared on *Asclepias syriaca*.

Female pheromone identification. Pheromone glands were extracted from nine adult females before the calling cycle, and placed in

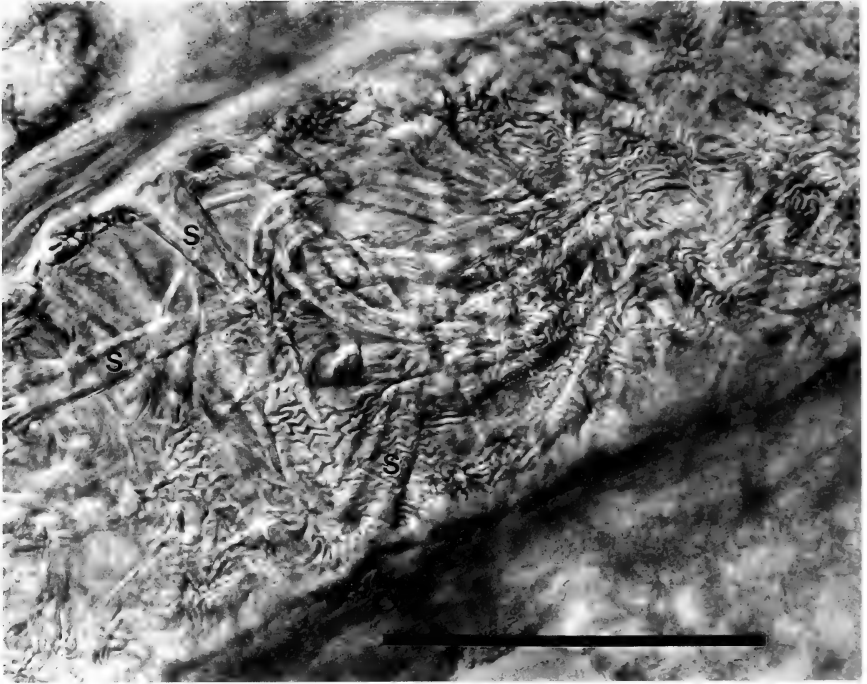


FIG. 2. Lumen of the *E. egle* female pheromone gland, viewed using DIC microscopy (S = cuticular spines, scale bar = 100 μ m).

100 μ l of methylene chloride. No internal standard was used. Glands were extracted overnight. This extract was subjected in 1 μ l aliquots to gas chromatography/infrared spectroscopy/mass spectrometry on a Hewlett Packard (HP) 5890 GLC coupled with both an HP 5965A infrared detector and an HP 5970 mass selective detector. Components of the pheromone blend were separated on a DB1 fused silica capillary column, measuring 60 m \times 0.32 mm \times 0.5 mm thickness. The initial temperature was held at 100° C for 2 min and then increased to 240° C at 2.5°C/min.

The *E. egle* pheromone blend was compared to a set of nine standards, that were subjected to the conditions given above. These standards were: (1) Z,Z-6,9-heneicosadiene (> 99% pure); (2) Z,Z,Z-1,3,6,9-heneicosatetraene (> 95% pure); (3) Z,Z,Z-3,6,9-octadecatriene (> 99% pure); (4) Z,Z,Z-3,6,9-icosatriene (92% pure); (5) Z,Z,Z-3,6,9-heneicosatriene (99% pure); (6) Z,Z,Z-3,6,9-docosatriene (94% pure); (7) 2-methyloctadecane (99% pure); (8) 2-methylheneicosane (75% pure);

and (9) 2-methyldocosane (82% pure). Standards were analyzed as a 1:1:1:1:1:1:1:1:1 blend. Standards were run in concentrations that bracketed all extract concentrations.

Z,Z,Z-1,3,6,9-heneicosatetraene was undetectable using the methods described above due to its instability at high temperatures (Jain et al. 1983). Because of this instability, the pheromone and standard blends were also analyzed using an HP 5790A gas chromatograph with an on-column injection port and a flame ionization detector. An Ultra II (5% phenyl methyl silicone) column was used for this analysis (25 m, 0.32 ID, 0.52 mm film thickness). Carrier flow was set at 5.0 ml/min. The initial temperature was 50°C, which was held for 5 min. and then increased 5°/min until it reached 280°C. Extracts of pheromone glands and the nine-component standard blend were injected as 1 µl aliquots and compared. The percentage of each sample in the extract was also calculated by dividing the abundance of the individual compound by the total abundance of all compounds.

Electroantennograms. Electroantennograms (EAG's), as described in Rodgers (1991), were used to determine male responsiveness to possible components of the female pheromone blend of *E. egle*. Antennae were removed from 1 to 2 day old males (n = 7). The proximal end of the antenna was placed in a Petri dish containing EAG saline (NaCl 7.5 g/l, CaCl₂ 0.21 g/l, KCl 0.35 g/l, NaHCO₃ 0.2 g/l) (Rodgers 1991). Several segments were removed from the distal end of the antenna. The remaining distal end was placed in contact with a input electrode. The input electrode, via a high impedance electrode (Tektronix model 013-0071-00), was connected to a Tektronix 5115 storage oscilloscope. A continuous charcoal filtered airstream (1800 ml/min) was passed over the antenna. Two ml puffs of air were passed through Pasteur pipettes containing filter paper impregnated with one of nine pheromone standards (10 µg dissolved in 100 µl of methylene chloride) and a negative control (methylene chloride). These puffs were injected into the air stream, through an opening in the air supply tube.

Responses to the following nine standards were measured: (1) Z,Z-6,9-heneicosadiene; (2) Z,Z,Z-3,6,9-octadecatriene; (3) Z,Z,Z-3,6,9-eicosatriene; (4) Z,Z,Z-3,6,9-heneicosatriene; (5) Z,Z,Z-3,6,9-docosatriene; (6) Z,Z,Z-1,3,6,9-heneicosatetraene; (7) 2-methyloctadecane; (8) 2-methylheneicosane; (9) 2-methyldocosane. Standards were presented in random order. Antennal responses were measured twice per antenna for all standards and the control (the order of presentation of the stimuli being reversed for the second set of measurements). These responses were then averaged, and compared across all males using one way analysis of variance (ANOVA) and a Scheffe F-test.

TABLE 1. Summary of compounds found in the female pheromone blend of *Euchaetes egle*. Letters refer to compounds in total ion chromatogram, compound X to subsequent analysis, — = trace amount.

Compound	GC retention time	Identification/Comments	Amount in Blend (%)
A	81.5 min	Mass spectrum indicates an alkane	—
B	96.6 min	Parent ion, mass spectrum indicates a branched alkane	—
C	98.0 min	Infrared and mass spectra match 2-methyloctadecane ; presence also confirmed by subsequent gas chromatography.	23.4
D	108.0 min	Infrared and mass spectra indicates an alkane	—
E	109.8 min	Mass spectrum is similar to that of Z,Z,Z-3,6,9- eicosatriene ; presence confirmed by subsequent gas chromatography	2.7
F	128.5 min	Mass spectrum matches Z,Z-6,9-heneicosadiene ; presence confirmed by subsequent gas chromatography	4.3
G	130.0 min	Infrared and mass spectra match Z,Z,Z-3,6,9-heneicosatriene ; presence confirmed by subsequent gas chromatography	37.5
H	157.4 min	Mass spectrum indicates an alkane	—
I	163.1 min	Mass spectrum corresponds to spectrum of Z,Z,Z-1,3,6,9-heneicosatetraene , may be a 22-or 23-carbon tetraene	—
X	—	Retention time in subsequent gas chromatography matches Z,Z,Z-1,3,6,9-heneicosatetraene	14.8

RESULTS

Female pheromone identification. A total ion chromatogram of the *E. egle* pheromone blend extract revealed nine compounds. Of these, three (C, F, G) could be matched to standards (Table 1). The retention time for compound E was close to that of **Z,Z,Z-3,6,9-eicosatriene**, and the compound had a fragmentation pattern indicative of trienes (Descoins et al. 1986). However, the parent ion of compound E had a mass/charge ratio of 281, while the parent ion of **Z,Z,Z-3,6,9-eicosatriene** had a mass/charge ratio of 275. Because compound E was found in trace amounts in the total sample, an infrared spectrum could not be obtained. Compound I did not match any standards tested, but showed a mass spectrum similar to that of **Z,Z,Z-1,3,6,9-heneicosatetraene** (Jain et al. 1983). The other four unidentified components (A, B, D, H) correspond to alkanes of varying chain lengths (McLafferty 1973).

A subsequent analysis using on-column injection, Ultra II 5% phenyl methyl silicone column revealed compounds that had matching retention times to the following standards (relative percentage of compound in the total sample): **2-methyloctadecane** (23.4%), **Z,Z-6,9-heneicosadiene** (4.3%), **Z,Z,Z-3,6,9-eicosatriene** (2.7%), and **Z,Z,Z-3,6,9-heneicosatriene** (37.5%). Additionally, **2-methyldocosane** (1.7%) and **Z,Z,Z-**

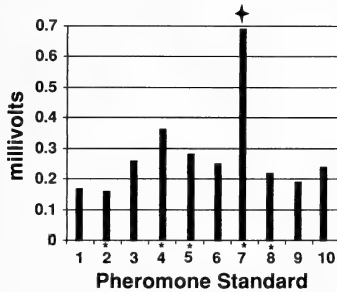


FIG. 3. Mean electrical response of male antennae to female pheromone standards and a control (1–10) ($n = 7$). * = compound found in pheromone blend extract, ◆ = significantly different from control, 1 = Control, 2 = *Z,Z*-6,9-heneicosadiene, 3 = *Z,Z,Z*-3,6,9-octadecatriene, 4 = *Z,Z,Z*-3,6,9-eicosatriene, 5 = *Z,Z,Z*-3,6,9-heneicosatriene, 6 = *Z,Z,Z*-3,6,9-docosatriene, 7 = *Z,Z,Z*-1,3,6,9-heneicosatetraene, 8 = 2-methyloctadecane, 9 = 2-methylheneicosane, 10 = 2-methyldocosane.

3,6,9-docosatriene (1.8%) were also found. This analysis also revealed an additional peak (Compound X; Table 1) at 30.61 minutes, which matches the retention time of *Z,Z,Z*-1,3,6,9-heneicosatetraene (14.8%).

Electroantennograms. Electrical responses of male antennae were significantly higher to *Z,Z,Z*-1,3,6,9-heneicosatetraene (7) than to the control (1) ($P < 0.05$). Responses to other standards, including those compounds found in the *E. egle* pheromone gland extract, were not significantly different than responses to the control (Fig. 3).

DISCUSSION

It should be noted that the compounds identified are components of the extract of a pheromone gland and that this extract may include pheromonal precursors as well as true pheromone components. Compounds found in the pheromone gland extracts of *E. egle* are similar to pheromonal compounds of other arctiids. *Z,Z,Z*-3,6,9-heneicosatriene, is found in *Arctia villica* L. (Einhorn et al. 1984), two species of *Creatonotos* (Bell & Meinwald 1986, Wunderer et al. 1986), *Halysidota leda* Druce (C. Descions pers. comm.), *Paraeuchaetes pseudoinsulata* (Walker) (Schneider et al. 1992), *Phragmatobia fuliginosa* L. (C. Descions pers. comm.), *Syntomeida epilais* Walker (C. Descions pers. comm.), and *Utetheisa ornatrix* L. (Conner et al. 1980, Jain et al. 1983). The triene, *Z,Z,Z*-3,6,9-eicosatriene, is a component of the pheromone blend of *Paraeuchaetes pseudoinsulata* (Walker) (Schneider et al. 1992). Trienes are found in the pheromone glands of Geometridae, Lymantriidae, and Noctuidae (Mayer & McLaughlin 1991). This distribution suggests that triene use is the ancestral condition for Arctiidae, and perhaps much of Noctuoidea.

The other components found in the *E. egle* gland extract are also found in other arctiid pheromone blends. A secondary diene component, Z,Z-6,9-heneicosadiene, is present in pheromone blends of members of *Cretonotos* (Bell & Meinwald 1986, Wunderer et al. 1986), *Paraeuchaetes pseudoinsulata* (Walker) (Schneider et al. 1992), and *Utetheisa ornatix* L. (Jain et al. 1983). Alkanes, such as 2-methylalkanes, are found in the female pheromones of many species of *Holomelina* and in *Pyrrharctia isabella* (J.E. Sm.) (Roelofs & Cardé 1977).

EAG's performed on *E. egle* males (Fig. 3) show that the compound (7), Z,Z,Z-1,3,6,9-heneicosatetraene, elicits the greatest response. It is also found as a secondary component in the pheromone blends of *Arctia villica* L. (Einhorn et al. 1984), and two species of *Utetheisa* (C. Descoins pers. comm., Jain et al. 1983). The tetraene may act as the species specific cue, guiding *E. egle* males to appropriate mates.

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**PSEUDODREPHALYS: A NEW GENUS COMPRISING THREE
SHOWY, NEOTROPICAL SPECIES (ONE NEW) REMOVED
FROM—AND QUITE REMOTE FROM—DREPHALYS
(HESPERIIDAE: PYRGINAE)**

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ABSTRACT. *Drephalys* is polyphyletic: it includes morphologic misfits (closely related to each other) that share nothing but showy color patterns with some real *Drephalys* species. The convergence may involve mimicry. Removed from *Drephalys*, the **new genus *Pseudodrephalys*** has highly distinctive genitalia, marked most of all by an enormous, dentate hook on the valva of the male and by deep notches (perhaps unique among hesperiids) in the ovipositor lobes of the female. Palpi, antennae, and male secondary sex characters of *Pseudodrephalys* differ greatly from those of *Drephalys*. The metatibial tufts of *Pseudodrephalys* males (lacking in males of *Drephalys* and its relatives) are extraordinary because the scales start out hairlike (and pale) but then broaden (and darken) instead of coming to a point. While *Drephalys* rightfully goes in the middle of Evans's B Group of pyrgine hesperiids, *Pseudodrephalys* belongs in Evans's E Group. The three species of *Pseudodrephalys* are *P. atinas* (Mabille), **new combination** (type species), *P. hypargus* (Mabille), **new combination**, and *P. sohni*, **new species** (known from one male that Evans treated as the male of *Drephalys hypargus*). *Pseudodrephalys* is recorded from southern Venezuela, Guyana, French Guiana, Brazil (Amazonas, Pará, Mato Grosso, Rondônia), and eastern Peru.

Additional key words: genitalia (male and female), ovipositor lobes (with deep notches), metatibial tufts (whose hairs widen), palpi, mimicry.

Things are seldom what they seem. That may be more true in skipper systematics than it is in Gilbert and Sullivan's *H.M.S. Pinafore*. Consider, for example, my reassessment of several nonadjacent genera in Evans's 36-genus sequence of **M** or **Hesperia Group** hesperiines:

Evans 1955	Burns 1994a, 1994b
M.7 <i>Yvretta</i>	<i>Polites</i>
	syn. <i>Yvretta</i>
M.13 <i>Polites</i>	syn. <i>Poanopsis</i>
M.17 <i>Atrytone</i>	<i>Atrytone</i>
	<i>Anatrytone</i>
	syn. <i>Mellana</i>
M.21 <i>Poanopsis</i>	
M.25 <i>Mellana</i>	<i>Quasimellana</i> n. gen.

Here are various kinds of major changes, all of them justified primarily on genitalic grounds.

Now consider *Drephalys*. When an *Epargyreus*-like skipper that was reared in Guanacaste, Costa Rica, struck me as an odd species of *Drephalys*, I looked into this genus of large, showy, neotropical pyrgines so as to describe the new Costa Rican species comparatively, in an evo-

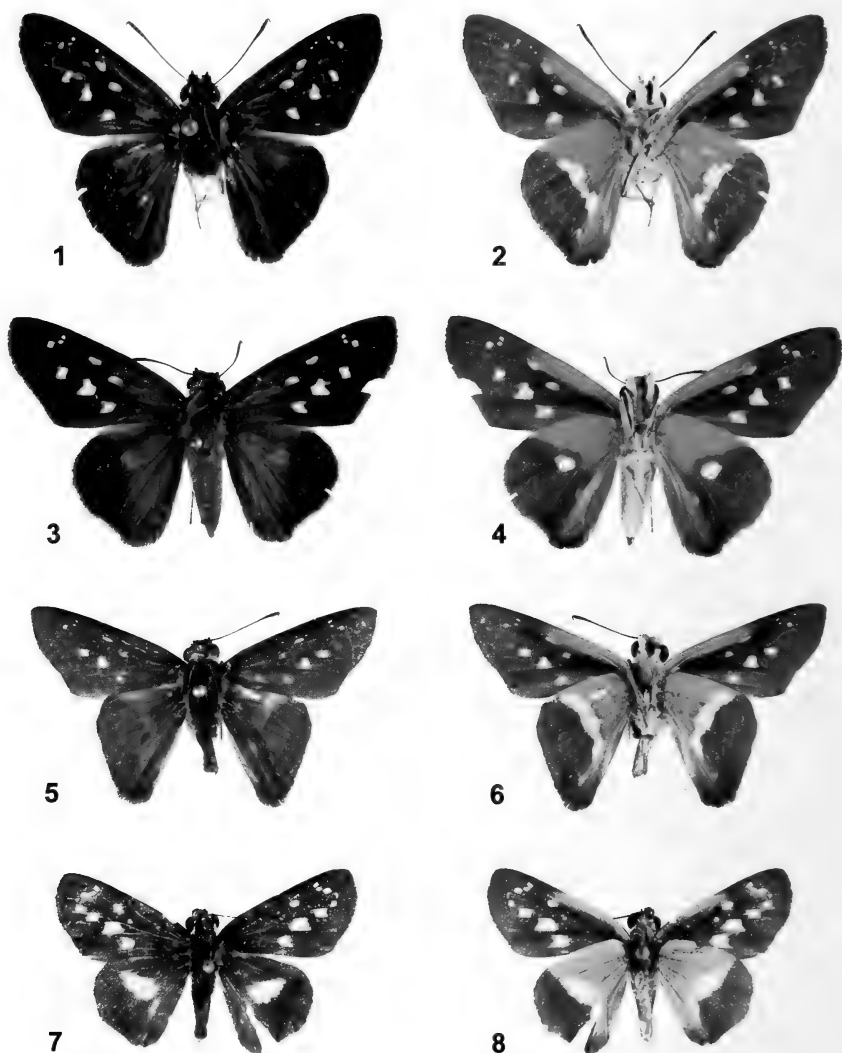
lutionary context, rather than in splendid isolation (Burns & Janzen in press). Because Janzen had had no difficulty in finding wild larvae from which to rear a long series of the new species, I was initially surprised at the rarity of *Drephalys* adults in collections. Then, after gradually pulling together a modest cross section of this genus, I was surprised at its diversity (several more undescribed species), its internal complexity (two widely divergent clusters of species), and, above all, its polyphyly—which this paper will rectify.

A capsule taxonomic history is in order. *Drephalys* was proposed just over a century ago by Watson (1893) who, eleven genera later in the same paper, also proposed *Paradros*, which Godman and Salvin (1894) immediately placed next to *Drephalys*, at the same time even admitting some doubt about the need for any separation. Although Mabile and Boulet (1919) still regarded these genera as close but distinct, Evans (1952:23) merged them—which is right—and commented that “Typically these 2 genera appear very different, but they are connected by intermediate species *and the genitalia conform to a general pattern*” [*italics added*]—which, in light of the various species he included, is wrong. Evans keyed and numbered 13 species in *Drephalys*; but, because 2 of them each comprised a pair of subspecies that are actually separate species, he dealt with 15. Of these, 13 species—as well as 5 species subsequently described by Mielke (1968), Austin (1995), and me (Burns & Janzen in press)—form two well-differentiated groups which I am treating as subgenera, with *Paradros* Watson a synonym of *Drephalys* (*Drephalys*) Watson (Burns & Janzen in press).

However, Evans's (1952) seventh species (Figs. 1–4) and thirteenth species (Figs. 7–12) of *Drephalys* have nothing at all to do with this genus; indeed, they do not even belong in his **B** or **Augiades Group** (of 11 pyrgine genera) which contains it. Not just their genitalia (in both sexes) but other, more readily visible, morphologic features such as their palpi (Figs. 17, 18) and their odor-releasing, male secondary sex characters (Figs. 21–23) are clearly wrong (Figs. 19, 20, 24). Only in superficial color pattern do these misfits suggest certain species of *Drephalys* (e.g., Figs. 13–16).

Though intrasubfamilial in this case, such resemblances between showy, unrelated skippers are reminiscent of intersubfamilial resemblances involving, for instance, various pyrrhopygine genera and the pyrgine genus *Phocides* or the pyrrhopygine genus *Sarbia* and the hesperiine genus *Pseudosarbia*. Especially in light of the sympatry of *Drephalys*/non-*Drephalys* look-alikes, their convergence may involve mimicry.

Evans's (1952) treatment of his thirteenth species of *Drephalys* is longer than any other because he itemizes a number of differences in color pattern between the 1 male and 3 females in the BMNH collec-



Figs. 1–8. The species (and type specimens) of *Pseudodrephalys* in dorsal (odd-numbered) and ventral (even-numbered) views ($\times 1\frac{1}{4}$). **1, 2**, *Pseudodrephalys atinas* ♂, PERU, Madre de Dios, Parque Manu, Pakitza, $11^{\circ}55'48''\text{S}$, $71^{\circ}15'18''\text{W}$, 340 m, 10 October 1991, M. Casagrande (unnumbered genitalic dissection by Mielke in 1992) (MUSM). **3, 4**, *Pseudodrephalys atinas* ♀, holotype, PERU, Pebas, Hahnel (later, J. M. Burns genitalic dissection no. X-4409) (ZMHB). **5, 6**, *Pseudodrephalys sohni* ♂, holotype, BRAZIL, Amazonas, Manaus (J. M. Burns genitalic dissection no. X-4331 of material previously dissected dry by Evans) (BMNH). **7, 8**, *Pseudodrephalys hypargus* ♀, holotype, BRAZIL, Manaus, 1886, Hahnel (later, J. M. Burns genitalic dissection no. X-4408) (ZMHB).



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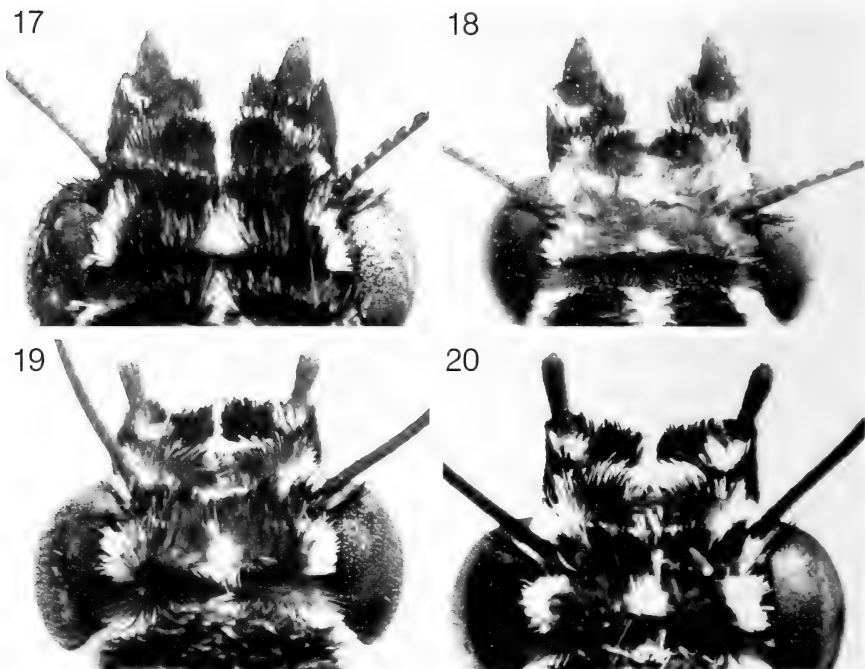


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16

Figs. 9–16. The superficially similar but unrelated species *Pseudodrephalys hypargus* and *Drephalys alcmon* in dorsal (odd-numbered) and ventral (even-numbered) views ($\times 1.3$). **9, 10**, *Pseudodrephalys hypargus* ♂, BRAZIL, Mato Grosso, Diamantino, Alto Rio Arinos, 14°13'S, 56°12'W, 350–400 m, 17 March 1991, E. Furtado (later, J. M. Burns genitalic dissection no. X-4406) (USNM). **11, 12**, *Pseudodrephalys hypargus* ♀, PERU, Madre de Dios, Parque Manu, Pakitza, 11°53'S, 70°58'W, 400 m, 21 October 1990, G. Lamas (later, J. M. Burns genitalic dissection no. X-4407) (MUSM). **13, 14**, *Drephalys alcmon* ♂, BRAZIL, Mato Grosso, Diamantino, Alto Rio Arinos, 14°13'S, 56°12'W, 350–400 m, 6 April 1991, E. Furtado (USNM). **15, 16**, *Drephalys alcmon* ♀, PANAMA, Canal Zone, La Pita, 15 June 1963, G. B. Small (USNM).

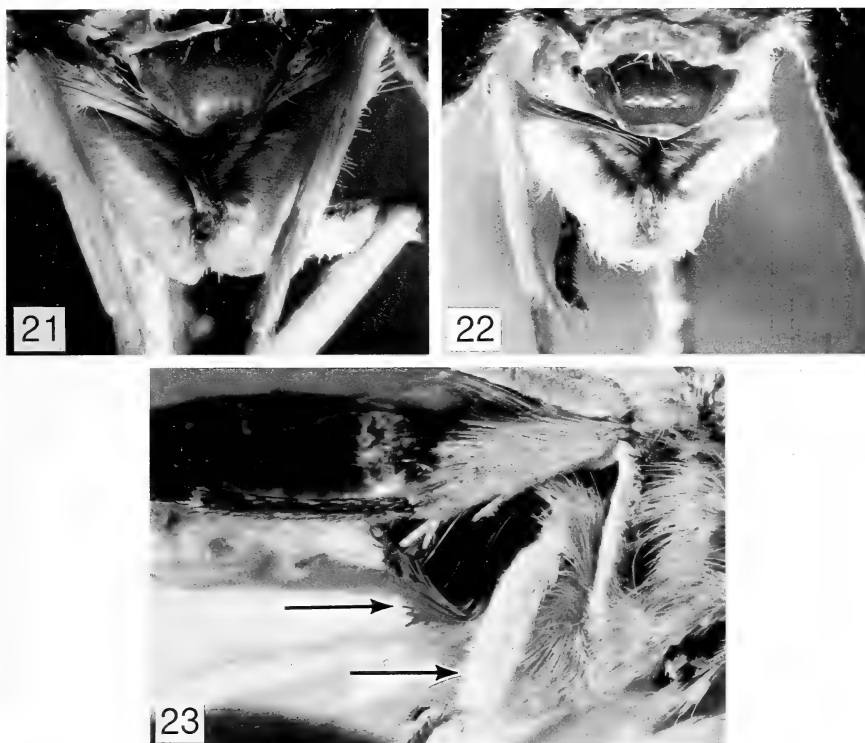


Figs. 17–20. Major differences between palpi of *Pseudodrephalys* and *Drephalys* in dorsal view: third segment centered on second segment and tapered to a fat point versus third segment shifted laterad and slightly swollen to a rounded end. **17**, *Pseudodrephalys atinas* ♂, PERU (same specimen as in Figs. 1, 2). **18**, *Pseudodrephalys hypargus* ♂, PERU, 30 km SW Puerto Maldonado, 300 m, 24 October 1983, S. S. Nicolay (S. S. Nicolay genitalic dissection no. H816) (USNM). **19**, *Drephalys alcmon* ♂, PANAMA, Canal Zone, Cocoli, 2 December 1962 (J. M. Burns genitalic dissection no. X-3446) (USNM). **20**, *Drephalys alcmon* ♀, COSTA RICA, Area de Conservación Guanacaste, Puesto de Almendros, 10 July 1997, D. & J. Lindsley (USNM).

tion. But no such sexual dimorphism exists in this species: the male (Figs. 9, 10) resembles the female (Figs. 7, 8, 11, 12). Evans's male (Figs. 5, 6) is mismatched; it represents an undescribed species that goes with his two misfit species of *Drephalys* in a new and unrelated genus which, with a nod to the *Sarbia/Pseudosarbia* duo, I am calling *Pseudodrephalys*. Evans's caricature of the genitalia of this male (Evans 1952: pl. 12, fig. B.6.13) differs strikingly from those of true *Drephalys* males (Evans 1952: pls. 11, 12, figs. B.6.1–B.6.6, B.6.8, B.6.10–B.6.12).

***Pseudodrephalys*, new genus**
(Figs. 1–12, 17, 18, 21–23, 25–37)

Description. Size. Smallish to medium-sized skippers, with (as usual) females averaging larger than conspecific males. Male (and female) forewing lengths in the three known species: 15.2 (15.9), 17.5 (?), and 19.0 (20.2) mm.



Figs. 21–23. Male secondary sex characters in *Pseudodrephalys*: metathoracic pouch and metatibial tufts. **21**, *Pseudodrephalys atinas*, abdomen removed, posterior view; hairlike scales of both tibial tufts enter anterior end of pouch, curve sharply caudad, and reemerge from posterior end of pouch with their widened ends projecting dorsad; PERU (same specimen as in Figs. 1, 2). **22**, *Pseudodrephalys hypargus*, abdomen removed, posterior view; hairlike scales of left tibial tuft enter anterior end of pouch, curve sharply caudad, and reemerge from posterior end of pouch with their widened ends projecting dorsad (right metathoracic leg missing); PERU, Madre de Dios, Parque Manu, Pakitza, 11°55'48"S, 71°15'18"W, 340 m, 5 October 1991, M. Casagrande (J. M. Burns genitalic dissection no. X-4332) (MUSM). **23**, *Pseudodrephalys hypargus*, abdomen in place, right lateral view; upper arrow points to dark tibial tuft of hairlike scales that are distally widened and sharply curved dorsad but completely free of pouch; lower arrow points to pale outer edge of pouch; BRAZIL (same specimen as in Figs. 9, 10) (USNM).

Facies. Wings of females appreciably broader and rounder than those of conspecific males (commonly true in skippers): cf. Figs. 3, 4 with 1, 2; and Figs. 7, 8, 11, 12 with 9, 10. Color pattern of wings distinctive ventrally: proximal half of costal margin of forewing and proximal half of hindwing rich (orangy) yellow to pale yellow, with hindwing yellow area bordered distally by white band or spot; otherwise brown (Figs. 2, 4, 6, 8, 10, 12). Forewing with hyaline spots in spaces 1b, 2, 3 (in one species, also 4 [Figs. 7–12] and rarely 5 [Figs. 7, 8]), 6, 7, and 8, plus one or two hyaline spots in cell; forewing spots not in contact (except sometimes at apex). Position of cell spot(s) peculiar: one in anterior part of cell, under origin of vein 10 (always present, Figs. 1–12); and one in posterior part of cell, over spot in space 1b (sometimes absent, Figs. 9–12). Apical spots in spaces 7 and 8 in



Fig. 24. Male secondary sex characters in *Drephalys*: costal fold. Dorsal view of right forewing of *Drephalys alcmon*; BRAZIL (same specimen as in Figs. 13, 14).

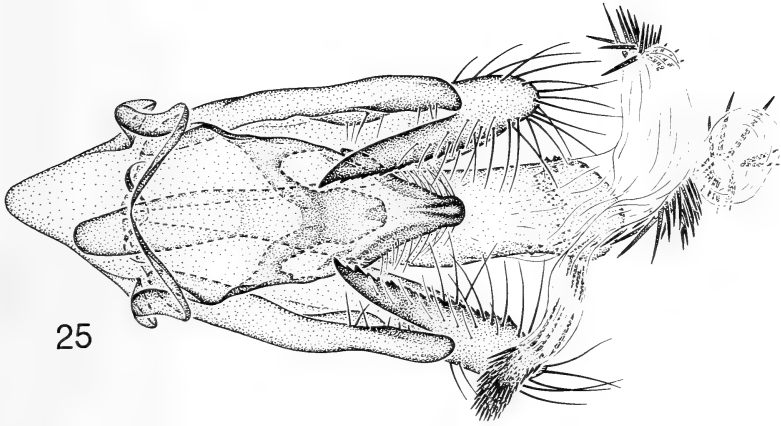
line, but that in space 6 shifted distad, toward apex (Figs. 1–12). Hindwing dorsally with space 8 light yellow or white (in spread specimens, this pale costal area usually tucked beneath forewing and hence hidden; but easily seen on both hindwings in Fig. 1 and barely seen, chiefly on left hindwing, in Fig. 3).

Antenna. Antenna about half as long as forewing costa; club modestly swollen, about one-quarter length of antenna from its base to start of apiculus; apiculus delicate, sharply reflexed, short, about one-third as long as club. Shaft dark brown to black, finely checkered anterodorsally with cream-colored scales. Number of nudum segments 18 to 29, apparently reflecting not only size of a species but also sex of an individual: starting with smallest species, numbers of nudum segments in males (and females) 18–19 (19–22), 22 (?), and 24 (29). In smaller species, nudum segments evenly divided between body of club and apiculus; but in largest species, only 10 segments on apiculus (in female as well as male).

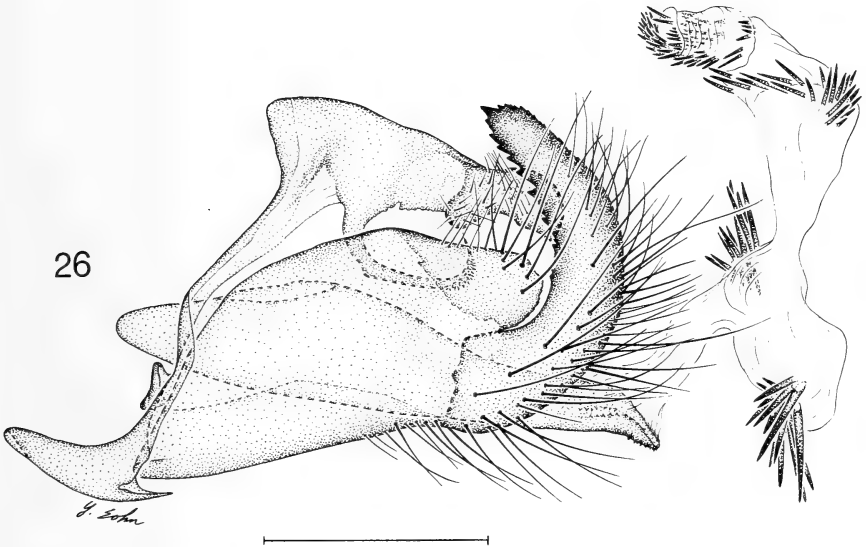
Palpus. Palpus short, pointing forward, its extension anterior to eye about equal to diameter of eye; mostly dark above and light below; third segment bullet-shaped, slightly drooping, and centered on second segment (Figs. 17, 18).

Male secondary sex characters. Metathoracic pouch and metatibial tufts (Figs. 21–23). Pouch tightly clothed with short, whitish scales; these scales finer, hairlike, and sharp over rim of pouch and part way inside; but coarser, slightly spatulate, and blunt deep inside pouch. Tufts comprising extremely long scales, perhaps unique because hairlike and tan to light brown proximally, but broadened and flattened (with their wide ends sometimes notched) and much darker brown distally. No costal fold.

Male genitalia. *Uncus* undivided. In dorsal view (Figs. 25, 27, 32), triangular: apex distal and blunt, and with a prominent middorsal ridge; base proximal, with slight lateral lobes. In lateral view (Figs. 26, 28, 33), the ridged, distal portion resembling a helmet; lobes of proximal portion projecting anteroventrally toward gnathos. *Gnathos*—after medial union of its paired lateral arms—also undivided and more or less triangular in dorsal view, but originating much farther anterior and not extending nearly as far posterior as uncus; roughened with many fine conical teeth distally on ventral surface (Figs. 25–28, 32, 33). *Valva* with huge dentate process arising from ventrodorsal end, curving sharply dorsad (also anteriorly), and extending far above body of valva; otherwise simple (Figs. 25, 26, 29, 31–33). *Aedeagus* simple, though with many spiny cornuti (Figs. 25, 26, 28, 30, 32, 33). Everted vesica more or less narrow (but with one or more blind sacs), with larger spines in

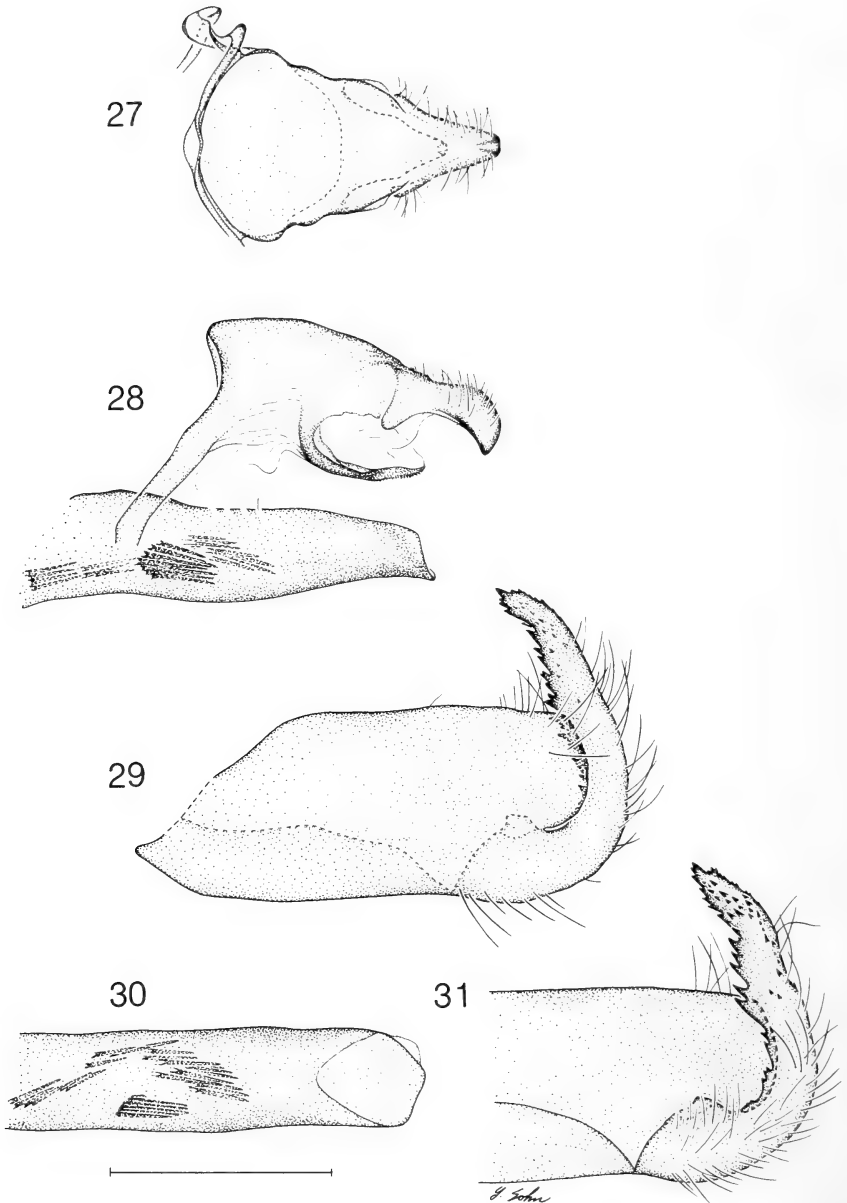


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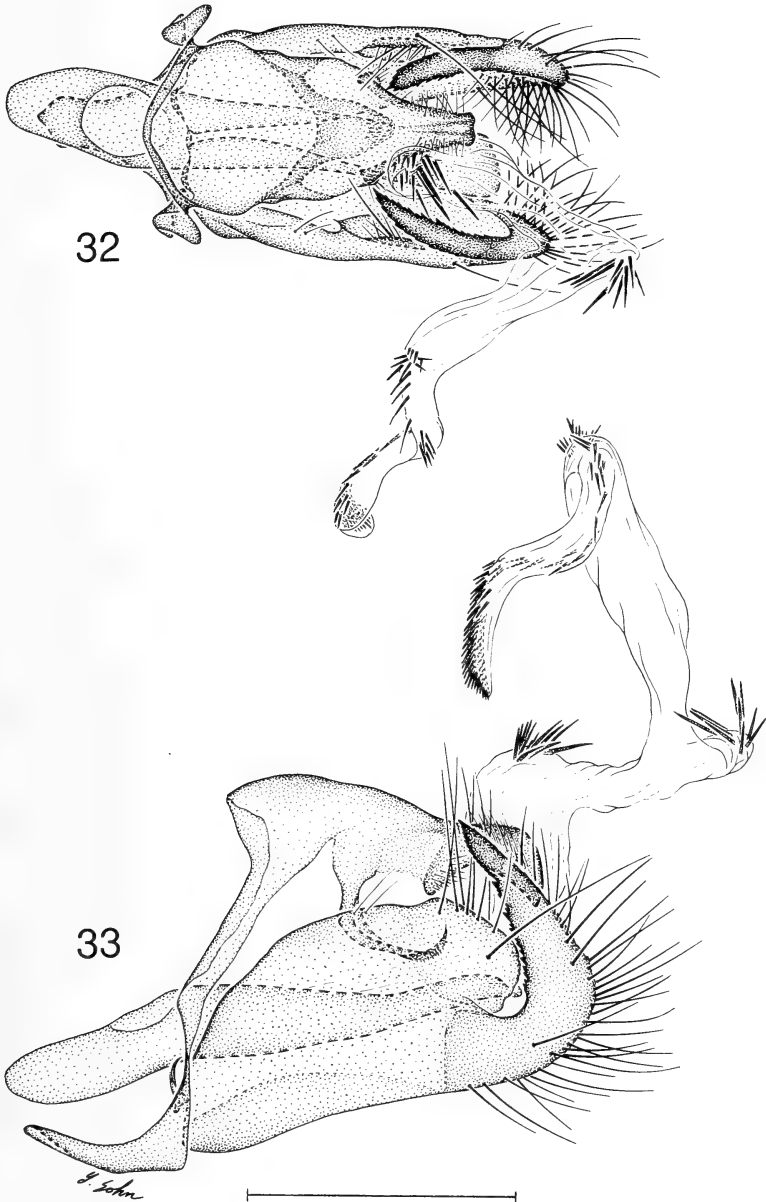


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Figs. 25, 26. Male genitalia of *Pseudodrephalys atinas* from PERU, Madre de Dios, Parque Manu, Pakitza, 11°55'48"S, 71°15'18"W, 340 m, 10 October 1991, M. Casagrande (unnumbered genitalic dissection by Mielke in 1992) (MUSM). Scale = 1.0 mm. **25**, Complete genitalia, with vesica everted, in dorsal view. Rotating the genitalia until the top of the tegumen/uncus is about flat makes some structures appear appreciably shorter than they do in the lower figure (but the scale is the same in both figures). **26**, Complete genitalia (minus right valva), with vesica everted, in left lateral view.



Figs. 27–31. Male genitalia of *Pseudodrephalys sohni*, holotype, from BRAZIL, Amazonas, Manaus (J. M. Burns genitalic dissection no. X-4331 of material previously dissected dry by Evans, who deliberately separated—and unavoidably broke—various parts) (BMNH). Scale = 1.0 mm. **27**, Tegumen, uncus, gnathos, and part of vinculum on right side in dorsal view. **28**, Tegumen, uncus, gnathos, and part of vinculum on left side, plus distal part of aedeagus (with bundled cornutal spines within), all in lateral view. **29**, Left valva in lateral view. **30**, Distal part of aedeagus (with bundled cornutal spines within) in dorsal view. **31**, Distal part of right valva in medial view.



Figs. 32, 33. Male genitalia of *Pseudodrephalys hypargus* from BRAZIL, Mato Grosso, Diamantino, Alto Rio Arinos, 14°13'S, 56°12'W, 350–400 m, 17 March 1991, E. Furtado (J. M. Burns genitalic dissection no. X-4406) (USNM). Scale = 1.0 mm. **32**, Complete genitalia, with vesica everted, in dorsal view. Rotating the genitalia until the top of the tegumen/uncus is about flat makes some underlying structures appear appreciably shorter than they do in the lower figure (but the scale is the same in both figures). **33**, Complete genitalia (minus right valva), with vesica everted, in left lateral view.

two, distinct, tight clusters proximally and with smaller spines in long, loose, linear series distally (Figs. 25, 26, 32, 33). *Juxta* notably small (Figs. 25, 26, 32, 33); **U**-shaped to shallowly **V**-shaped in anterior view.

Female genitalia. *Ovipositor lobes* strongly notched and hence conspicuously bilobed (Figs. 34–37). Three longitudinal, sclerotized bands immediately anterior to ovipositor lobes and dorsal to lamella postvaginalis, the middle band midventrally grooved (these are the only traits treated in this paragraph that are not shown in Figs. 34–37). *Lamella postvaginalis* fully sclerotized, long but especially broad, simple in outline (though with at least a suggestion of laterodistal shoulders), and with a low, midventral ridge posterior to ostium bursae. *Lamella antevaginalis* fully sclerotized, much smaller than lamella postvaginalis, well ventrad of it, and more or less triangular, with apex midventral and posteriorly directed. *Ductus bursae* long, strongly wrinkled in part of its posterior length; *corpus bursae* far anterior and spheroid. Paired, long, posterior (but not anterior) apophyses. Unpaired, somewhat crinkled sac, extending slightly anterior and dorsad of sterigma.

Distribution. Southern Venezuela, Guyana, French Guiana, Brazil (Amazonas, Pará, Mato Grosso, Rondônia), and eastern Peru.

Type species. *Augiades atinas* Mabille (1888:146, fig. 2). Figs. 1, 2 (adult male); 3, 4 (adult female, holotype); 17 (palpi); 21 (male metathoracic pouch and metatibial tufts); 25, 26 (male genitalia); and 34, 35 (female genitalia).

The features that most distinguish *Pseudodrephalys* are genitalic: in males (Figs. 25–29, 31–33), especially the oversized dentate process that curves abruptly up from the ventrodistal end of the valva, as well as the undivided, middorsally ridged uncus, which, in profile, suggests a helmet; and in females (Figs. 34–37), especially the deeply notched ovipositor lobes, plus the wide, simply shaped, and fully sclerotized lamella postvaginalis, situated well dorsad of the lamella antevaginalis. Also highly distinctive are the very long scales of the metatibial tuft of males (Figs. 21–23) which start out hairlike and light but then widen and darken.

Where does *Pseudodrephalys* go? Classification of skippers below the subfamily level is still primitive: what we have are Evans's generic groups. I think that, in general, Evans's (1952, 1953) pyrgine generic groups (**B** to **G**) are much more valid than his (Evans 1955) hesperiine generic groups (**H** to **O**), which are deeply flawed (Burns 1990, unpubl.). *Drephalys* (from which I just extracted *Pseudodrephalys*) is in the middle of Evans's **B** or **Augiades Group**. Evans (1952:5) used palpi of the peculiar form seen in *Drephalys* (Figs. 19, 20) as the primary character state defining this group, and most included genera express it well. Moreover, as in *Drephalys* (Fig. 24), the main secondary sex character of **B Group** males is a costal fold. No **B** (or, for that matter, **C**) **Group** males have a metathoracic pouch with metatibial tufts. This feature and the form of the antenna and palpus put *Pseudodrephalys* in **Group E**. The placement is not too meaningful because **E** is the largest of the pyrgine generic groups (with three times as many genera [ca. 60] as the next largest) and is by far the most heterogeneous and artificial.

In defining **Group B**, Evans (1952:5) used one element of facies: "a very general feature, peculiar to the group, is the presence of 2 hyaline

spots in the cell" of the forewing. Although this peculiarity can also be expressed by *Pseudodrephalys* (Figs. 1–8), convergence is not complete: in **B Group** skippers with two cell spots, the one nearer the body spans the width of the cell (Figs. 13–16), while in *Pseudodrephalys* this spot stays in the posterior part of the cell (Figs. 1–8).

Two species of *Pseudodrephalys* are extremely rare in collections, and the third is scarce.

Pseudodrephalys atinas (Mabille), new combination

(Figs. 1–4, 17, 21, 25, 26, 34, 35)

Augiades atinas Mabille 1888:146, fig. 2.

Paradros atinas: Mabille & Boulet 1919:241; Williams & Bell 1934:269, pl. XIX, fig. 2.

Drephalys atinas: Evans 1952:25; Robbins et al. 1996:244.

Description. Size and nudum. Largest species of *Pseudodrephalys*: male forewing length 19.0 mm; female, 20.2 mm. Nudum segments 24 in male but 29 in female, with only 10 segments on apiculus in each sex.

Facies. Hyaline spots of forewing yellow; none in spaces 4 and 5; two in forewing cell (Figs. 1–4). Space 8 of dorsal hindwing yellow (Figs. 1, 3). Yellow of ventral color pattern rich (orangy). Distal to yellow area on ventral hindwing, in male (Fig. 2), a well-defined white band in spaces 1a (vague), 1c, 2, distal end of cell, and 6; in female (Fig. 4), a well-defined large white spot at distal end of cell (plus very small white spot in space 1c). Large hindwing spot of female showing dorsally as pale yellowish spot (Fig. 3). (Description by Williams and Bell [1934] of individual variation in what they specified as "two male specimens" of this species closely matches the sex differences noted above.) Distal to white band or spot, ground color of ventral hindwing warm, rusty brown, traversed from space 1c to 6 by delicate, irregular band of pale bluish scales (Figs. 2, 4). Similar pale bluish scales on ventral forewing in spaces 4 and 5 between hyaline spots in spaces 3 and 6 (in female, scales in space 5 only).

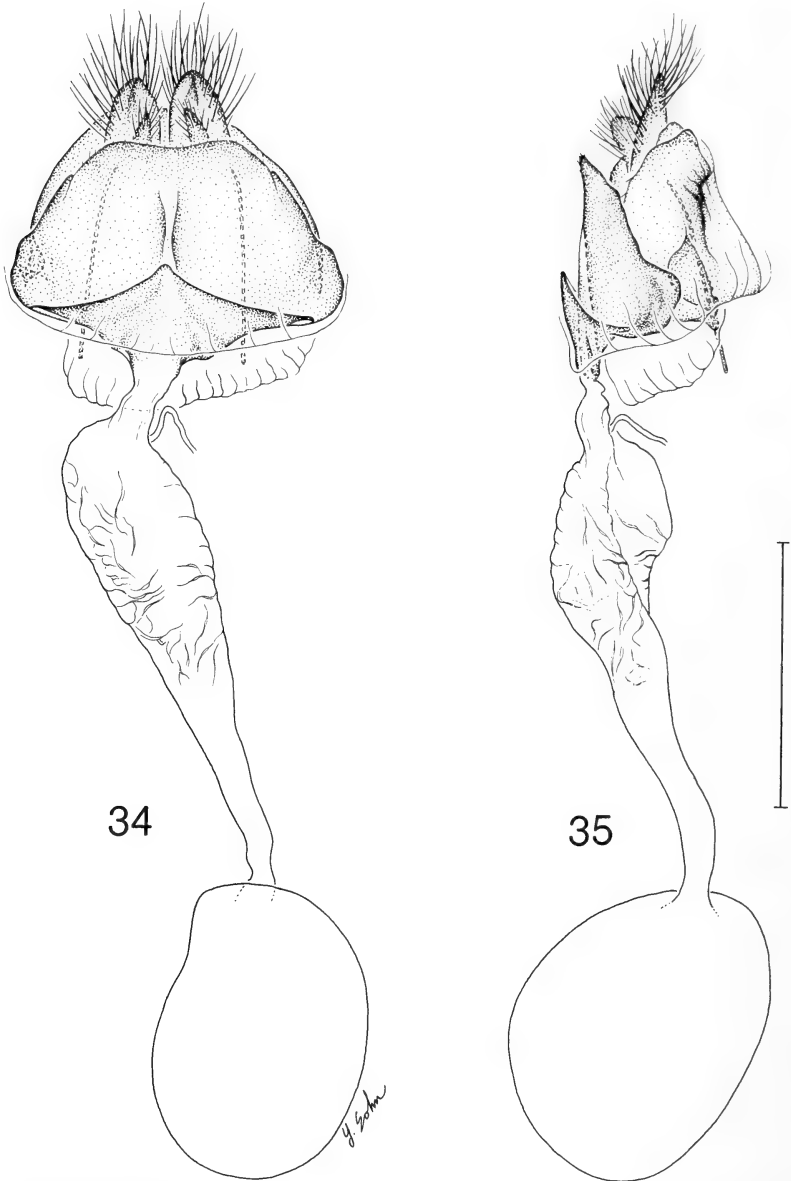
Superficially, *Pseudodrephalys atinas* most resembles such species of *Drephalys* as *D. phoenice* (Hewitson), *D. phoenicoides* (Mabille & Boulet), two undescribed species very similar to these, and an undescribed species related to *D. eous* (Hewitson). Though I have already pointed out various differences between these two genera, I should add that the above-cited species of *Drephalys* have conspicuous pale spots on their brown hindwings dorsally, which are lacking in *P. atinas*, and a much longer antennal apiculus.

Male genitalia. In lateral view (Fig. 26), huge dentate process of valva long, wide, and fairly uniform in width; gap evident between this process and dorsodistal end of valva; body of valva humped in middle of dorsal margin. Fine teeth laterally and ventrally at distal end of aedeagus (Figs. 25, 26). (The only genitalia figure previously published [Williams & Bell 1934] gives the essence of the valva and indicates bundles of spines in the aedeagus, but conveys nothing about the tegumen, uncus, and gnathos.)

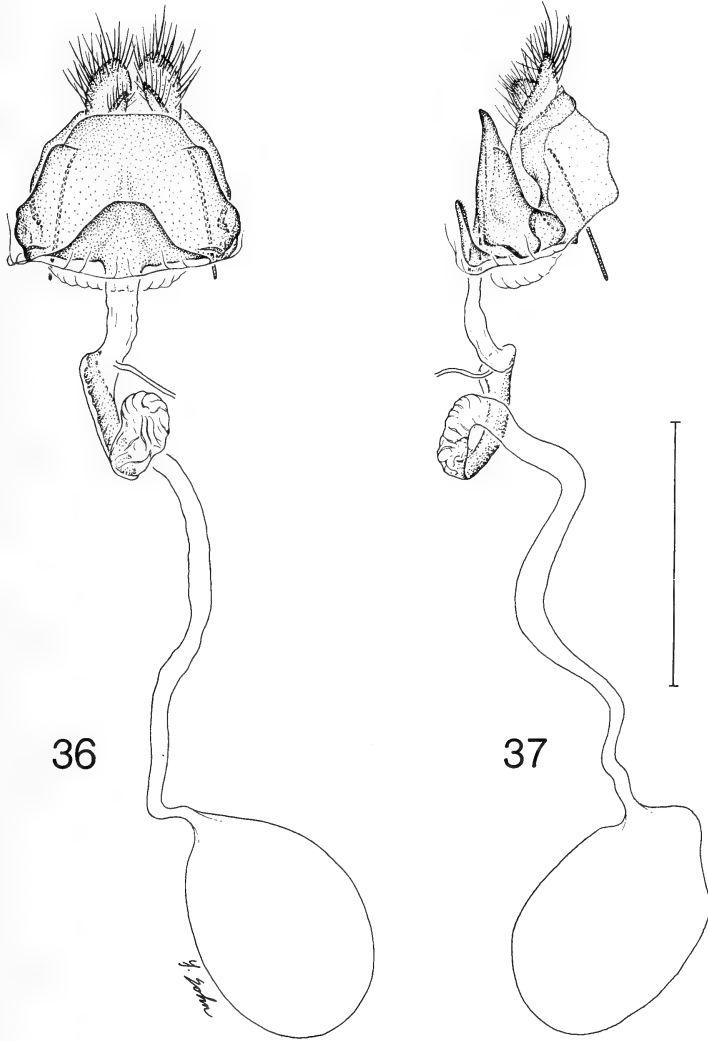
Female genitalia. In ventral view (Fig. 34), lamella antevaginalis a low, broad-based triangle with sharp apex. Ductus bursae fairly straight, swelling abruptly, then diminishing gradually in diameter toward corpus bursae (Figs. 34, 35).

Distribution. Amazonian region of Peru. This is the phrase used by Williams and Bell (1934) for the source of their two specimens, and it is still apt. The two specimens I have seen come from northeastern and southeastern Peru: the latter was recently listed for Pakitzta by Robbins et al. (1996); the former, Mabille's type, is from Pebas.

Material examined. In his brief original description of this species, which dealt only with superficial appearance, Mabille (1888) specified that the sex of his material was female, implied that he had only one specimen, and provided a black and white drawing of it. Though he failed to give its geographic origin or to formally designate a type, his spec-



Figs. 34, 35. Female genitalia of *Pseudodrephalys atinas*, holotype, from PERU, Pebas, Hahnel (J. M. Burns genitalic dissection no. X-4409) (ZMHB). Scale = 2.0 mm. **34**, From posterior to anterior (top to bottom), paired, notched ovipositor lobes; dorsal sclerotization associated with lamella postvaginalis; paired, long posterior apophyses; lamella postvaginalis; lamella antevaginalis; unpaired, somewhat crinkled sac, extending slightly anterior of the lamellae; bursa copulatrix; and part of unpaired ductus seminalis—all in ventral view. **35**, The same in right lateral view (only right notched ovipositor lobe and right posterior apophysis shown; and sac extends dorsad, as well as slightly anterior, of the lamellae).



Figs. 36, 37. Female genitalia of *Pseudodrephalys hypargus*, holotype, from BRAZIL, Manaus, 1886, Hahnel (J. M. Burns genitalic dissection no. X-4408) (ZMHB). Scale = 2.0 mm. **36**, From posterior to anterior (top to bottom), paired, notched ovipositor lobes; dorsal sclerotization associated with lamella postvaginalis; paired, long posterior apophyses; lamella postvaginalis; lamella antevaginalis; unpaired, somewhat crinkled sac, extending slightly anteriorly of the lamellae; bursa copulatrix; and part of unpaired ductus seminalis—all in ventral view. **37**, The same in right lateral view (only right notched ovipositor lobe and right posterior apophysis shown; and sac extends dorsad, as well as slightly anteriorly, of the lamellae).

imen is unmistakable; and its three handwritten determination labels include one in Mabille's own shaky hand.

Holotype. ♀. [PERU: Loreto:] Pebas, [collector:] H[a]h[ne]l (J. M. Burns genitalic dissection no. X-4409) (ZMHB).

Other. PERU: Madre de Dios: Parque Manu, Pakitza, 11°55'48"S, 71°15'18"W, 340 m, 10 October 1991, 1 ♂, M. Casagrande (unnumbered genitalic dissection by Mielke in 1992) (MUSM).

Pseudodrephalys sohni, new species

(Figs. 5, 6, 27–31)

Drephalys hypargus (male only): Evans 1952:27.

Description. Size and nudum. Intermediate species of *Pseudodrephalys*: male forewing length 17.5 mm. Nudum segments 22, evenly split between body of club and apiculus.

Facies. Similar to *atinas*, but forewings and hindwings perceptibly narrower (cf. Figs. 5, 6 with 1, 2). Hyaline spots of forewing white; none in spaces 4 and 5; two in forewing cell, smaller than in *atinas* (Figs. 5, 6). Space 8 of dorsal hindwing pale yellow. Yellow of ventral color pattern lighter than in *atinas* but darker than in *hypargus*. Distal to yellow area on ventral hindwing (Fig. 6), a well-defined white band in spaces 1a, 1c, 2, distal end of cell, 6, and 7. Distal to white band, ground color of ventral hindwing warm, rusty brown, traversed from space 1c to 6 by delicate, irregular band of pale bluish scales (Fig. 6). Similar pale bluish scales on ventral forewing in spaces 4 and 5 between hyaline spots in spaces 3 and 6.

Since *Pseudodrephalys sohni* looks so much like *P. atinas*, it superficially resembles the same set of *Drephalys* species as *P. atinas* (q.v.). However, *P. sohni* is appreciably smaller than any of those species; and, of course, the intergeneric differences noted under *P. atinas* likewise apply.

Male genitalia. In lateral and medial views (Figs. 29, 31), huge dentate process of valva about as long as in *atinas*, but relatively narrow and irregular in width, and more conspicuously dentate; overlap evident between this process and dorsodistal end of valva, with latter much larger than in *atinas*; body of valva with straight dorsal margin. Uncus, in lateral view (Fig. 28), less massive than in *atinas*.

Distribution. BRAZIL: Amazonas: Manaus.

Material examined. Only the specimen that Evans (1952) treated as the male of *hypargus*.

Holotype. ♂. [BRAZIL:] Amazon[a]: Manaus (J. M. Burns genitalic dissection no. X-4331 of material previously dissected dry by Evans) (BMNH).

Etymology. I delight in naming this species for Young T. Sohn, a scientific illustrator in entomology at the Smithsonian Institution, with whom I have worked for fifteen years. His superb and varied renderings of diverse skipper genitalia reflect extraordinary artistic skill, judgment, and patience. He will, when asked, draw genitalia at difficult, unconventional angles so as to convey maximum amounts of crucial information in a minimum number of figures.

Pseudodrephalys hypargus (Mabille), new combination

(Figs. 7–12, 18, 22, 23, 32, 33, 36, 37)

Carystus hypargus Mabille 1891:CXX.

Drephalys hypargus (females only): Evans 1952:27.

Description. Size and nudum. Smallest species of *Pseudodrephalys*: male forewing lengths 15.0, 15.2, and 15.4 mm; female, 15.0, 15.5, 16.0, 16.4, and 16.5 mm. Nudum segments 18, 19, and 19 in males; 19, 21, and 22 in females, about evenly split between body of club and apiculus.

Facies. Hyaline spots of forewing white; present in space 4 and rarely also in 5; one (usually) or two in forewing cell (Figs. 7–12). Space 8 of dorsal hindwing white. Large white area in middle of dorsal hindwing from space 1c, through distal cell, to space 6 (Figs. 7, 9, 11); somewhat variable in size and expression, with portion in posterior part of space 1c partially (Figs. 9, 11) to completely (Fig. 7) isolated; in unworn specimens, also a long line of white hairs in space 1b (Figs. 9, 11). Yellow of ventral color pattern pale. Distal to yellow area on ventral hindwing, a proximally ill-defined white band, extending from space 1c to 7 when complete, but variable in expression (Figs. 8, 10, 12). Distal to white band, ground color of ventral hindwing warm, rusty brown, with or without traces of delicate band of pale bluish scales from space 1c to 6. Similar pale bluish scales sometimes on ventral forewing in space 5 between hyaline spots in spaces 4 and 6.

Superficially, owing to the large white central area of its dorsal hindwing, *Pseudodrephalys hypargus* (Figs. 7–12) departs from its congeners (Figs. 1–6) and resembles *Drephalys alcmon* (Cramer) (Figs. 13–16). But *D. alcmon*, on its dorsal hindwing, has a larger white central area that extends to the inner margin; on its forewing, lacks the hyaline spot in space 4 that *P. hypargus* has, and has a large, cell-spanning hyaline spot (in contact with the spot in space 2) that *P. hypargus* lacks (there is a vestige of such a spot in one female of *P. hypargus* [Figs. 7, 8]). Ventrally, the yellow of the forewing costa is much richer in *D. alcmon*, while the light proximal part of the hindwing is white in *D. alcmon* instead of pale yellow. Differences between these skippers in their antennal clubs (cf. Figs. 9–12 with 13–16), in their palpi (cf. Fig. 18 with 19, 20), and in their male secondary sex characters (cf. Figs. 22, 23 with 24) are glaring.

Male genitalia. In lateral view (Fig. 33), huge dentate process of valva less long, less conspicuously dentate, and more gradually and evenly tapered to distal point than in *atinas* and *sohni*; gap evident between this process and dorsodistal end of valva, much as in *atinas*, but with dorsodistal end of valva larger than in *atinas*, although not as large as in *sohni*. Uncus, in lateral view, less massive than in *atinas*, hence more as in *sohni*.

Female genitalia. In ventral view (Fig. 36), lamella antevaginalis a blunt triangle recalling a normal curve. Ductus bursae narrow, rather uniform in diameter, and looped (or at least sharply curved), with some longitudinal sclerotization in beginning of loop (Figs. 36, 37).

Distribution. Venezuela (Amazonas), Guyana, French Guiana, Brazil (Amazonas, Pará, Mato Grosso, Rondônia), and Peru (Madre de Dios).

Material examined. In his short, superficial original description, Mabilbe (1891) did not formally designate a type but did specify the size, sex, and geographic source of his specimen, as well as indiosyncrasies in its maculation. His calling *hypargus* a species of *Carystus* put *hypargus* in the wrong subfamily.

Holotype. ♀. [BRAZIL: Amazonas:] Manaus, [18]86, [collector:] H[a]h[ne] (J. M. Burns genitalic dissection no. X-4408) (ZMHB). The venation of the left forewing of the holotype is highly abnormal distal to the cell: extra veins appear in spaces 2 and particularly 3, while veins 5 and 6 come together, fuse, and then once more go their separate ways to the outer margin.

Other. BRITISH GUIANA, 1 ♀, Parish (J. M. Burns genitalic dissection no. X-4333) (BMNH). FRENCH GUIANA, 1 ♀ (BMNH). BRAZIL: Pará: Obydos, 1907, 1 ♀, M. de Mathan (BMNH); Mato Grosso: Diamantino, Alto Rio Arinos, 14°13'S, 56°12'W, 350–400 m, 17 March 1991, 1 ♂, E. Furtado (J. M. Burns genitalic dissection no. X-4406) (USNM). PERU: Madre de Dios: 30 km SW Puerto Maldonado, 300 m, 24 October 1983, 1 ♂, S. S. Nicolay (S. S. Nicolay genitalic dissection no. H816) (USNM); Parque Manu, Pakitza, 11°53'S, 70°58'W, 400 m, 21 October 1990, 1 ♀, G. Lamas (J. M. Burns genitalic dissection no. X-4407) (MUSM); Parque Manu, Pakitza, 11°55'48"S, 71°15'18"W, 340 m, 5 October 1991, 1 ♂, M. Casagrande (J. M. Burns genitalic dissection no. X-4332) (MUSM).

Other material. Mielke (pers. comm.) provided the following records from specimens in his own collection and in that of the Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil. VENEZUELA: T. F. Amazonas: Yavita, 120 m, 20 November 1947, 1 ♀, Lichy. BRAZIL: Amazonas: Barcellos, Rio Negro, 29 July 1929, 1 ♀, Zikan; Mato Grosso: Sinop, October 1974, 1 ♂, Alvarenga; Rondônia: Vilhena, 20 November 1986, 1 ♂, Elias.

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THE LIFE HISTORY OF *SCHINIA SANGUINEA* (GEYER)
(NOCTUIDAE:HELIOTHENTINAE) WITH A REPORT ON A
SURVEY FOR HETEROCERA IN SOUTHWESTERN ONTARIO

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ABSTRACT. A survey of the Lepidoptera of the sand dunes and wetlands in an area southeast of Lake Huron in the province of Ontario has yielded adults of *Schinia sanguinea* for life history studies. Data on the species were not available for inclusion in the senior author's monograph on the Heliothentinae.

Additional key words: Lepidoptera survey, immature stages, *Liatris cylindracea*, *Liatris spicata*, *Schinia carmosina*.

During the last several years, the junior author together with K. Zufelt have been conducting a survey of the moths in an area of Ontario southeast of Lake Huron. The study area is a 10,000 acre Great Lakes wetland and dunes complex that includes both Pinery and Ipperwash Provincial parks. The region consists of a series of sand ridges, interspersed with streams, lakes and wetlands, forested areas, oak savannah and prairie remnants. The purpose of the project is to obtain flight data for resident moth species over many years. The records will establish a faunal list as well as provide data on flight periods, number of generations per year, annual fluctuations in population size and species composition. The ultimate objective of the undertaking is to generate interest in conservation of habitats within the region.

To date, the survey has recovered 46 species of Arctiidae and 526 species of Noctuidae. Among the interesting captures during the survey have been *Trichoclea artesta* (Smith) and *Agrotis stigmata* (Morrison) from the beach barrier habitat, and *Oncocnemis riparia* Morrison and *Iodopepla u-album* (Guenee) from the first interdunal swale. The dry ridges yielded *Chaetagnathia tremula* Franclemont and a single specimen of *Cobubatha dividua* (Grote). *Trichosilia manifesta* (Morrison) and *Acrionicta albarufa* Grote were taken in the oak savannah, and *Lemmaria digitalis* (Grote) and *Spartiniphaga inops* (Grote) characterized wetland and stream habitats. *Papaipema aweme* (Lyman) had been collected in the Grand Bend area in 1936 but was not seen during the present survey.

One of the most noteworthy recoveries from this survey has been adults of *Schinia sanguinea* (Geyer, 1832) which were collected by K. Stead at black light. He obtained the specimens in an open dunes area

near Port Franks, Ontario in which *Liatris cylindracea* Michaud was abundant. In his monograph to the North American Heliothentinae, Hardwick (1996) indicated that he considered *sanguinea* to be a separate taxon from the floridian *Schinia carmosina* Neumogen (1883). At the time, few data were available to substantiate this separation. When the immature stages of *sanguinea* were studied recently, it became evident that differences between these and those of *carmosina* warranted recognition of the two as distinct species.

Both species are present in central Florida. The larva of *Schinia sanguinea* is reddish brown with multiple fine broken longitudinal lines and feeds on species of *Liatris*. The larva of *Schinia carmosina* is grey with broad longitudinal bands and feeds on *Carphephorus corymbosus* (Nuttall) Torrey & A. Gray and *Garberia fruticosa*. (Nuttall) A. Gray. Although the adult of *carmosina* is usually smaller and darker than that of *sanguinea*, I cannot, at present, reliably distinguish the two adult moths.

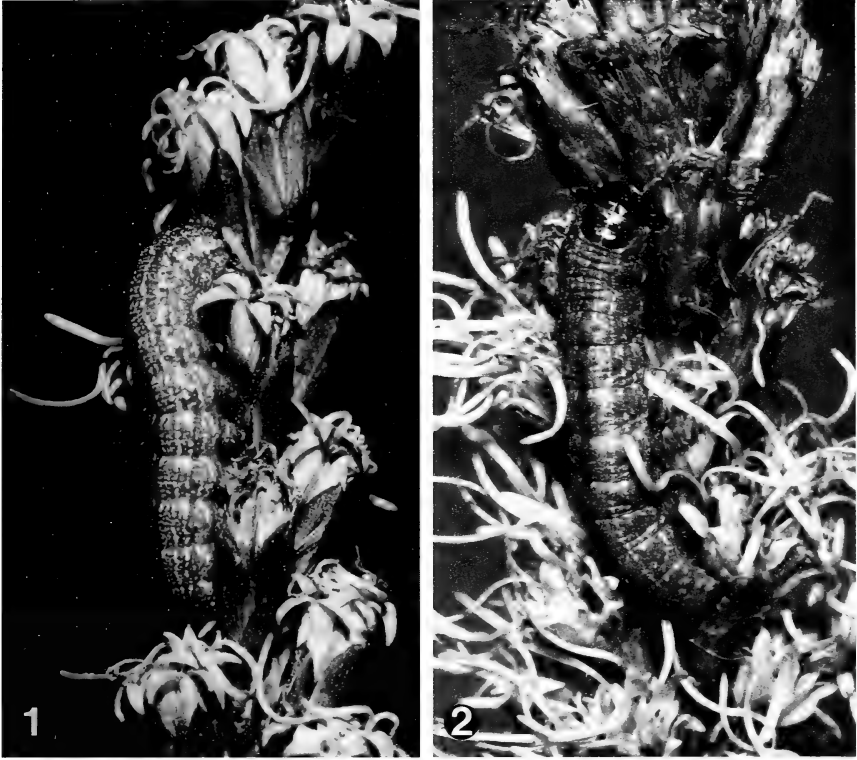
LIFE HISTORY DATA

For practical reasons, the larvae of *S. sanguinea* had to be reared at a site in Quebec remote from the native habitat of the species. Here larvae were fed on *Liatris spicata* (Linnaeus) Willdenow, a commonly cultivated species that is usually available in nurseries. Quantities of this species had been grown for a number of years in the hope that gravid females of *Schinia sanguinea* might eventually be obtained for life history studies.

The following information is based on the progeny of three females taken at Port Franks. These females laid a total of 237 eggs. Females are quite capable of penetrating the tightly closed heads of *Liatris cylindracea* and depositing eggs on the inner surface of the sepals, but they much more commonly oviposit in heads that have opened sufficiently for a number of florets to protrude slightly beyond the apices of the sepals. Eggs are deposited downward from one-quarter to three-quarters the length of the floret and usually between the corolla tube and the pappus. Eggs hatch in four and one-half to five days.

The first instar chews into an adjacent floret and feeds on the contents. The second instar feeds within or between florets and makes its way downward toward the seed layer. During one of the median stadia, the larva leaves the head and either enters a new head or feeds on the seeds from a position on the stem. The larva usually enters a new head from the top, but it may also chew through the sepals at the side of the head to reach the developing seeds.

When the supply of cut *Liatris cylindracea* became exhausted, the young larvae were fed on *Liatris spicata*. Unfortunately, the larvae were



FIGS. 1, 2. Ultimate stadium larvae of *Schinia sanguinea* (Geyer). 1. Lake Placid, Florida. 2. Port Franks, Ontario.

reluctant to accept this different species of *Liatris* as food and fed preponderantly on the green bean that was introduced into the rearing vials as a humectant. Apparently the Port Franks population of *sanguinea* is adapted to *Liatris cylindracea* and intolerant of *Liatris spicata*, despite the fact that *Schinia sanguinea* feeds on a number of species of the genus in eastern North America.

The development of *Schinia sanguinea* larvae appears to be naturally slow. Larvae rest for protracted periods both prior to and subsequent to moulting, but the greatly attenuated development among larvae in the rearings suggests that the unsuitability of diet had interfered with normal development. Some larvae were still feeding two months after hatching. For this reason, no durations of stadia have been cited. The unsuitability of food may also have contributed to possible supernumerary stadia. Reared larvae matured in six or seven stadia.

IMMATURE STAGES

The terminology used in the following larval and pupal descriptions follows Hardwick (1996).

Egg. Large, moderately stout, translucent pallid ivory, almost white, without ribbing or micropylar reticulations. Contents of egg becoming cloudy over period of incubation and with ocellar and mandibular spots becoming evident on day prior to hatching. Larva jack-knifed within chorion becoming evident a few hours before hatching.

First instar. Dirty white with gut contents showing through translucent tissue. Head blackish brown; trunk shields somewhat paler. Larva occasionally becoming suffused with pink as it increases in size.

Second instar. Light to medium grey with gut contents showing through translucent tissue. Prothoracic and suranal shield light to medium brown. Two evanescent white lines becoming evident on trunk as larva increases in size. Larva becoming flushed or mottled with pink, mauve or dull red toward end of stadium.

Median instars. Dark purplish red, occasionally a paler pinkish purple. Head dark orange with dark brown ocelli. Prothoracic and suranal shields concolorous with head or somewhat paler, variably suffused with brown. Trunk with three badly broken, white dorsal lines. Middorsal band somewhat darker than remainder of trunk. A rather diffuse white lateral band with pink median shade. Spiracles brown, located in dorsal margin of lateral band.

Penultimate instar. Medium to dark purplish red. Head dark orange. Prothoracic and suranal shields darker, orange-brown. Middorsal band reddish brown. Subdorsal area purplish red, variably and irregularly marked medially with dull white spots and with badly broken, dull white marginal lines. Supraspiracular area concolorous with subdorsal area and with a badly broken marginal lines and a purple median shade. Spiracles light fawn with brown rims.

Ultimate instar (Figs. 1, 2). Purple, finely and irregularly marked with white spots. Head dark orange with brown ocelli. Prothoracic shield brown, with darker margins and paler patches centrally. Suranal shield orange-brown. Middorsal band brownish purple, the darkest area of trunk. Subdorsal area paler, with evanescent and discontinuous dull white marginal lines, and with fine white markings medially. Supraspiracular area concolorous with subdorsal area and also finely marked with small white spots. Spiracles pallid fawn with dark brown rims.

Macrospinules slender, moderately long, widely and uniformly distributed on trunk. Microspinules absent or so minute that they cannot be detected at a magnification of 50 times. Setae comparatively short and slender. Pinnacula small, light brown. Bases of prespiracular setae on

prothorax in an almost horizontal line, and at most, diverging no more than 15 degrees from the horizontal.

Pupa. Orange-brown, well sclerotized, rather slender, without rounded ridge on dorsum of prothorax. Distiproboscis about three-quarters as long as width of fifth abdominal segment. Anterior band of fifth abdominal very narrow, occupying only about one-quarter total width of segment and well raised above remainder of segment; anterior band smooth except for a single, occasionally double, row of pitting along its posterior margin. Spiracles small but projecting well above general surface of cuticle. Cremaster cone well developed and bearing apically four setae, the median pair longer than lateral pair.

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BOOK REVIEW

OECOPHORINE GENERA OF AUSTRALIA, PART II. THE *CHEZALA*, *PHILOBOTA* AND *EULECHRIA* GROUPS (LEPIDOPTERA: OECOPHORIDAE), MONOGRAPHS ON AUSTRALIAN LEPIDOPTERA, VOLUME 5, by Ian F. B. Common. 1997. CSIRO Publishing, P.O. Box 1139, Collingwood, Victoria, 3066, Australia. xv + 407 pp., 775 photographs and line drawings. Hardcover. ISBN: 0-643-059342. \$130.00 [Australian].

At the age of 81, Ian Common is more prolific now than most of us ever hope to be at the peak of our careers. He is one of a handful of living lepidopterists whose vast accomplishments and contributions will serve many generations of lepidopterists to come. Although the majority of his research has focused on the fauna of the Australian region, various aspects of this work permeate the world literature in a wide variety of lepidopterous families, from microlepidoptera to butterflies.

This book represents Volume 5 of "Monographs on Australian Lepidoptera" and the second part of an ambitious undertaking to revise the genera of the Australian members of the subfamily Oecophorinae (Oecophoridae). In Part I of the revision, published in 1994 as Volume 3 in the monographic series, Common states that the Oecophorinae represent at least 20% of the Australian Lepidoptera fauna, with an estimated 5,000 species, nearly all of which are endemic to Australia. Part II treats 84 genera, 39 proposed as new, and 842 species. Common estimates there are an additional 800 or so undescribed species in the group represented in collections (primarily CSIRO)—a glimpse into the staggering diversity of many of the lesser known microlepidoptera groups around the globe. The revision proposes 160 new combinations (primarily the result of the new genera) and only 5 new synonyms.

Chapter 1 presents a rigorous cladistic analysis of the included genera based on 65 morphological characters (about 50% of which are multi-state). Common employs Hennig86 to derive parsimony trees and PAUP to generate lists of apomorphies for each tree. While the consistency index (CI) for the cladogram of the *Chezala* group is woefully low (i.e., 0.14), CIs for the *Philobota* and *Eulechria* groups are more compelling at 0.56 and 0.53, respectively. The chapter also includes full data matrices for the phylogenetic analyses and lists of synapomorphies for each genus.

Chapter 2 (3 pages) presents brief discussions on morphological features of the head, thoracic appendages, and genitalia (primarily in support of more detailed discussions presented in Part I of the revision); Chapter 3 (1.5 pages) provides general comments on the biology (also much abbreviated compared to Part I); and Chapter 4 (3 pages) addresses generic and species diversity (i.e., richness) by Australian state. The remaining 3 chapters, representing the lion's share of the text, are comprised of detailed descriptions, diagnoses, distributions, and biologies of the genera included in each of the three major lineages (i.e., the *Chezala* group, *Philobota* group, and *Eulechria* group). Each chapter begins with a dichotomous key to the genera, which I did not attempt to use, followed by the generic descriptions or redescrptions. Each generic account concludes with a list of the included ("constituent") species, along with full synonymies. This portion of the text (i.e., chapters 5, 6, and 7) includes 775 photographs and line drawings that illustrate adults, wing venation, genitalia (photographs rather than drawings), and SEMs of the head. For many species there are photographs of live adults in typical resting posture—something rarely seen in publications on microlepidoptera. The illustrations are good to superb in quality. The references section appears complete, and there are indices to both Lepidoptera and plant names, providing easy access to text location.

While the primary focus of the revision is on the systematics of the group, the interesting biology of these moths is noteworthy—the larvae of most species feed in leaf litter of *Eucalyptus* forests on dead leaves of Myrtaceae. Common has reared representatives of 38 of the included genera, and a majority of the biological information presented is based on his personal observations.

Consistent with other volumes of this series, the overall production and presentation are exceptional. Also consistent with the series is the price tag, which may be a little high for most of us. While this volume has no trouble standing on its own merit, in the com-

pany of Parts I (1994) and III (to be published in the future) of the revision of Australian Oecophorinae, it will be stellar—a model of current systematic accomplishment and taxonomic scholarship. Unfortunately, the book may not have a particularly wide appeal to lepidopterists in general, because most seem to have little interest in microlepidoptera. Nonetheless, the information regarding oecophorine biology and diversity will touch a broader audience than lepidopterists alone. CSIRO and Ian Common are to be congratulated on another outstanding contribution to the knowledge of the Lepidoptera of Australia.

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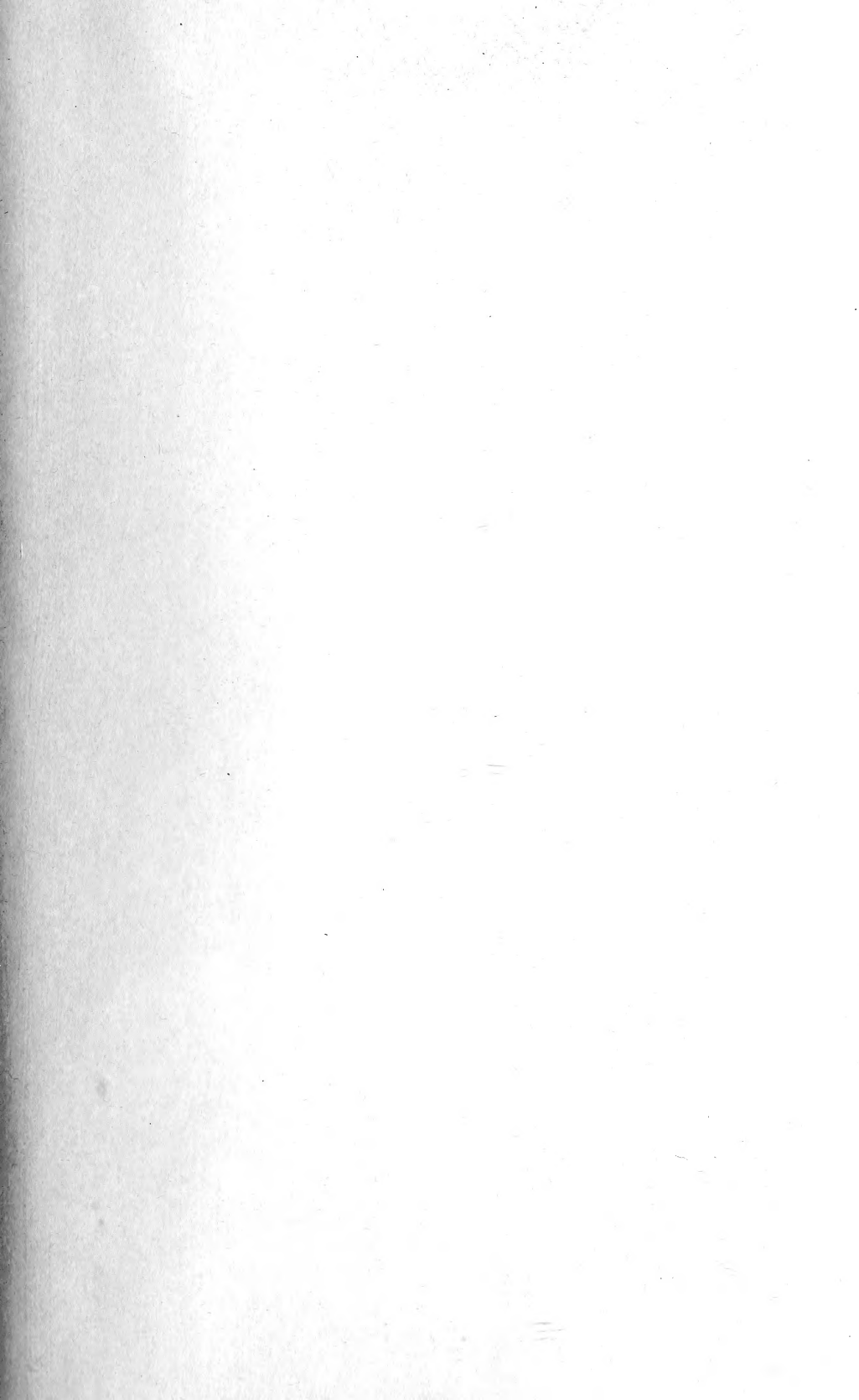
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