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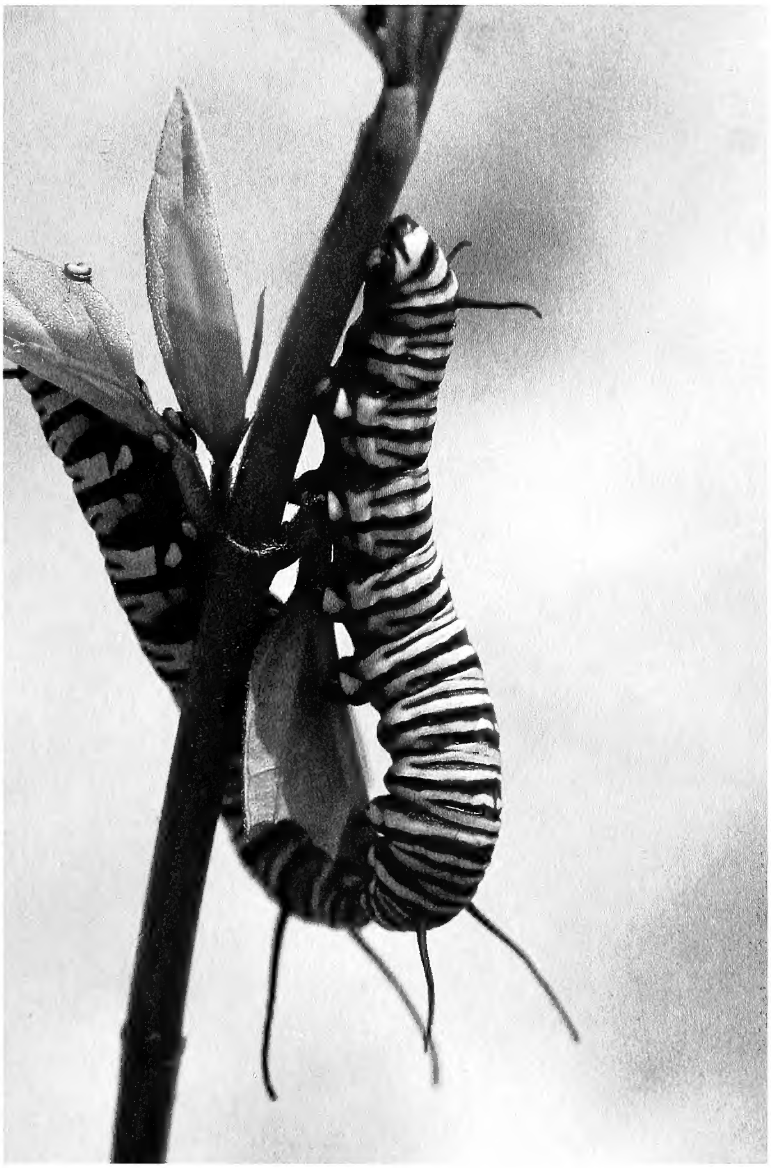

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Cover illustration: Two late-instar Monarch (*Danaus plexippus* (L.): Nymphalidae) caterpillars "face off" over the last bit of Milkweed (*Asclepias*) leaf, Northern Wisconsin, USA. Photo by Michael Toliver.

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SEASONAL DYNAMICS OF LEAF-TYING CATERPILLARS ON WHITE OAK

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ABSTRACT. This study examined the seasonal pattern of leaf tie construction and occupancy by caterpillars associated with white oak, *Quercus alba*, in Missouri. Thirty white oak trees were monitored over the course of a season, recording the phenology of leaf tie construction, occupancy, and abandonment by 14 different species of leaf-tying caterpillars. Larvae of *Pseudotelphusa* sp. (Gelechiidae) created most of the initial leaf ties, many of which were secondarily occupied by a variety of other leaf tiers. In addition, non-tying caterpillar species from a variety of families were common secondary occupants. As many as 6 different species and 15 different individual larvae were found occupying a single leaf tie over the course of the season. In selecting pre-existing leaf ties for colonization sites, the leaf tiers did not discriminate between ties of different ages. On average, one-third of the leaves on a branch were incorporated into a leaf tie at some time during the season. Despite their abundance, leaf ties in this system appear to be a limiting resource.

Additional key words: Leaf tie, insect phenology, positive interactions, *Quercus alba*, shelter-builders.

Shelter-building caterpillars are a conspicuous component of the insect herbivore fauna attacking temperate broad-leaved trees (Frost 1959, Prentice 1965). A variety of caterpillars in at least 12 (Berenbaum 1999) and as many as 27 (Jones 1999) different families use silk to construct leaf ties, webs, folds, and rolls that typically serve as both shelters and feeding sites (room and board) for developing larvae. These leaf shelters are often colonized subsequently by other arthropods, including other shelter-building caterpillars (Carroll & Kearby 1978, Cappuccino 1993, Cappuccino & Martin 1994, Lill 1999, Martinsen et al. 2000, Lill & Marquis 2003), many of whom oviposit in existing shelters (Lill & Marquis 2004). In the case of leaf ties ("sandwiches" of overlapping leaves), there is often a high rate of secondary occupation by both leaf-tying and non-leaf-tying caterpillars (Carroll et al. 1979, Fukui 2001) resulting in multiple individuals of the same or different species co-occuring within a leaf tie. Such secondary occupation suggests that these shelters represent a potentially limiting resource for populations of leaf tiers and leaf tie associates and may, in part, influence the local abundance of caterpillars occupying individual host plants.

An important first step in understanding the dynamics of these interactions is to document the seasonal pattern of shelter construction (i.e., resource availability), maintenance, and occupancy (resource use) by different species of caterpillars. Here, I describe the natural history of leaf tie construction and occupancy of the leaf ties found on saplings of white oak (*Quercus alba* L.).

MATERIALS AND METHODS

This study was conducted in east-central Missouri at Cuivre River State Park. The park consists of second growth oak-hickory forest dominated by a canopy of white oak (*Q. alba*), black oak (*Q. velutina* Lam.), and hickory (*Carya* spp.) with an understory of flowering dogwood (*Cornus florida* L.), sassafras (*Sassafras albidum* Nees), redbud (*Cercis canadensis* L.), sugar maple (*Acer saccharum* Marsh) and various oak saplings. The study was conducted within the Big Sugar Creek watershed, an unmanaged natural area of the park.

Thirty small white oak trees (understory saplings) were tagged in early spring of 1996, prior to budbreak. Trees ranged in height from 2 to 4 m and had at least four accessible branches randomly assigned to one of two treatments, control and census (two branches each per tree). Leaf ties formed on census branches were opened regularly to record the occupants whereas leaf ties on control branches were left undisturbed. The to-

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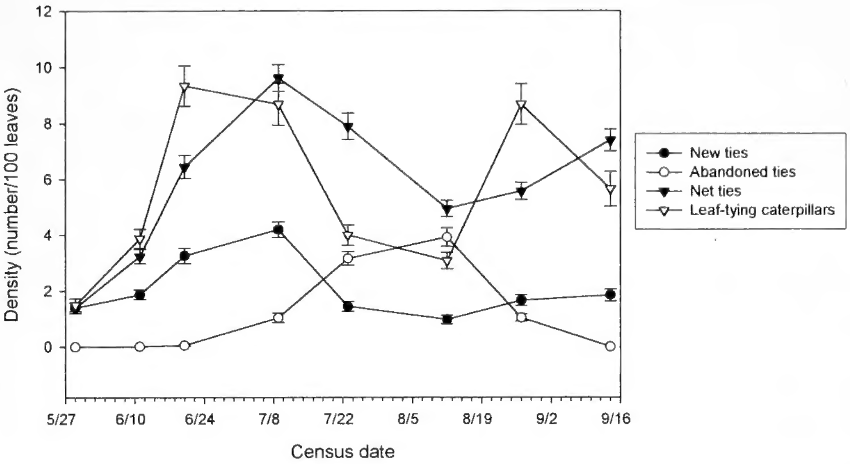

FIG. 1. Seasonal pattern of natural leaf tie formation and leaf-tying caterpillar density on white oak. Error bars are 1 SE.

tal number of leaves on each branch was recorded following budbreak. On 29 May, I established three permanent artificial leaf ties on one control and one census branch of each tree by clipping together haphazardly selected clusters of three adjacent leaves with lightweight curler clips (one clip/three-leaf cluster; Brentwood Beauty Labs International, Hillside, Illinois). Artificial leaf ties were created to sample the community of secondary occupants in a standardized manner (all artificial ties were initially unoccupied and established on the same date). Beginning 29 May, the number of all naturally occurring leaf ties present on each branch during eight census periods (29 May, 11 June, 20 June, 9 July, 23 July, 12 August, 27 August, and 14 September) was recorded. In addition, for all branches in the census treatment, the contents of the leaf ties (both natural and artificial) were recorded by briefly opening the ties and then clipping them back together with a curler clip. Any caterpillars that escaped from the ties by spinning down on silk were placed back into the leaf tie. The number and species of all leaf-tying caterpillars and non-tying associates (e.g., herbivorous beetles and non-tying caterpillars) were recorded during each census. Each leaf tie in the census treatment was assigned a unique label so the sequence of occupancy (for individual ties) could be followed. Clips were removed at subsequent censuses from any natural leaf ties that were not actively maintained (i.e., that came apart upon removal of the clip or that contained no leaf-tying caterpillars during two consecutive censuses). None of the leaf ties on control branches were opened, but the artificial ties on these branches were externally inspected for signs of occupancy (e.g., skeletonization damage, visible silk strands) to determine the timing of colonization.

The minimum number of total individuals and species of leaf-chewing insects (caterpillars, beetles, and sawfly larvae) occupying a leaf tie over its "lifespan" was determined by examining the sequence of occupation of each natural leaf tie; consecutive records of the same species were always assumed to be a single individual, so these estimates were likely to be conservative. The relationship between the age of the leaf tie (expressed as the number of censuses in which it was maintained) and the total minimum number of species and individuals was examined with linear regression. In addition, for leaf ties maintained for a given number of censuses (3, 4, or 5), the effect of the date of tie origination on the total minimum number of species and individuals was examined graphically.

Because the attractiveness of leaf ties to potential colonists might be expected to change as a tie ages (accumulating damage, frass, and silk), I examined the influence of tie age on the likelihood of secondary colonization by leaf-tying caterpillars. The distribution of "new" colonization events (occupancy by one or more individuals of a species not present in the previous census) across natural ties of different ages was compared with a null distribution using a Chi-square test. The null distribution assumed that ties of different ages would be colonized in proportion to their relative availability (i.e., colonists would not discriminate among ties of different ages). Because late season colonists had the widest range of tie ages available to "choose" from, only the new colonization events that occurred during each of the last two censuses were considered in this analysis.

RESULTS

Leaf ties. The total abundance of naturally occurring leaf ties (census + control treatments) ranged from a

TABLE 1. Leaf-tying caterpillars colonizing white oak trees.

Family and species[a]	Peak density (larvae/100 lvs.)
Gelechiidae	
Arogalea cristifasciella Chambers	0.30
Chionodes fuscomaculella Chambers	0.30
Pseudotelphusa sp. (undescribed)	7.45
Coleotechnites quercivorella Chambers	0.01
Noctuidae	
Morrisonia confusa Hubner	0.06
Oecophoridae	
Antaeotricha humilis Zeller	0.03
Antaeotricha osseella Williamson	0.01
Antaeotricha schlaegeri Zeller	0.17
Psilocorsis quercicella Chambers	1.86
Psilocorsis cryptolechiella Chambers	2.64[b]
Psilocorsis reflexella Clemens	—
Setiostoma xanthobasis Zeller	0.04
Pyralidae	
Tetralopha expandens Walker	0.23
Tortricidae	
Anclis divisana Walker	0.07

[a] Nomenclature and authors follow Hodges (1983).

[b] Density data for *P. cryptolechiella* and *P. reflexella* are combined because early instars of these two species could not be distinguished.

low of 154 on 29 May (census 1) to a high of 1265 on 9 July (census 4). However, because branches varied in size (mean ± 1 SE = 107.6 ± 6.0 leaves), tie densities (no. leaf ties/leaf) were used in all analyses. Census branches and control branches did not differ from each other in the mean density of leaf ties in any of the eight censuses ($p > 0.10$ for all paired *t*-tests), suggesting that the disturbance and use of clips in the census treatment did not adversely affect tie formation patterns.

The rate of leaf tie formation (mean number of new leaf ties per census branch) increased markedly between mid- and late June and peaked in early July during which time an average of four new leaf ties were formed per 100 leaves on each of the 60 census branches (Fig. 1). Following this peak, the rate of tie formation declined markedly while the number of abandoned ties (those that were empty and/or not maintained) increased, resulting in a decline in the net number of leaf ties present on the branches. During the last two censuses (late August and mid-September), the rate of new tie formation increased slightly while the number of abandoned old ties declined rapidly, resulting in a second peak in net tie density.

The total density (accumulated over the season) of natural leaf ties formed on a branch in the census treatment varied from 6.4 to 34.6 ties/100 leaves (mean ± 1 SE = 17.6 ± 0.80). Since most leaf ties consisted of two leaves, this means that on average, slightly more than one-third (17.6 ± 2 = 35.2/100) of the leaves on a given branch were incorporated into a leaf tie at some point during the season. Because natural leaf ties on the control branches were not followed individually, their seasonal pattern of tie formation, occupancy, and abandonment could not be examined. The total density of natural leaf ties formed on a census branch over the course of the study was positively related to the density of initial leaf ties formed early in the season (i.e., by the second census on June 11; $r^2 = 0.16$, $F_{1,58} = 10.89$, $p = 0.002$).

Occupants. Over the course of the season, 14 different species of leaf-tying caterpillars (Table 1) were recorded as occupants of the naturally occurring leaf ties (N = 1162) on the census branches. Across the season, the density of leaf-tying caterpillars (all 14 species combined) varied from a low of 1.49 to a high of 9.50 larvae/100 leaves (Fig. 1). The density of leaf tiers peaked in late June and again in late August, slightly in advance of the peaks in leaf tie density. Among the seven most common species of leaf tiers, *Pseudotelphusa* sp. (Gelechiidae, currently unnamed) achieved the highest peak density (Table 1), and its two population peaks (representing its two generations) preceded the peaks of the other bivoltine species (Fig. 2). Three species of Oecophoridae in the genus *Psilocorsis* (*P. cryptolechiella*, *P. quercicella*, and *P. reflexella*) were the next most prevalent, with peak densities >1 per 100 leaves.

Individual leaf ties varied considerably in the number of species of leaf tiers colonizing them, ranging from a low of zero (for ties that had been created and abandoned prior to a census) to as many as six different species occurring in a single tie over its lifespan. The total number of individuals occupying a leaf tie over its lifespan varied from 0–15 (mean ± 1 SE = 2.33 ± 0.06). Within a particular census, it was not uncommon to find assemblages of several individuals from 2–3 different species sharing a leaf tie (the record was 9 caterpillars of 3 different species).

Leaf ties that hosted both a greater abundance and higher species richness of caterpillars were maintained for longer periods (Fig. 3). However, most ties were relatively ephemeral, lasting on average 3.3 ± 0.1 censuses (a little more than a month). Of 91 natural ties recorded on census branches during the first census, only 10 (11%) persisted until the last census. However, for those natural ties (N = 302) formed during the first peak of leaf tie construction (9 July, census 4), almost a third (27%) were still occupied on the last census (14 September), which was near the second peak in leaf tie construction (see Fig. 1). The date that a leaf tie was formed also influenced the total abundance and species richness of colonists. For leaf ties that persisted for an equal number of censuses (either 3, 4, or 5), the average abundance and species richness tended

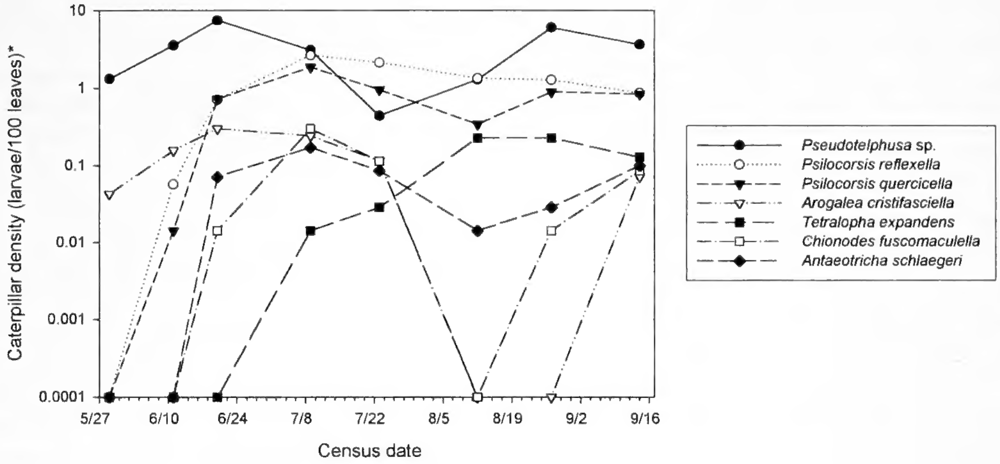

FIG. 2. Seasonal dynamics of seven species of leaf-tying caterpillars on white oak. New ties are ties that had not been recorded in a previous census; abandoned ties were not maintined and came apart readily upon examination; net ties = ties present in the previous census + new ties – abandoned ties. Note log scale of ordinate.

to increase with later date of origination (Fig. 4), suggesting that new ties formed later in the season are subject to higher levels of secondary colonization than those formed earlier.

As the season progressed, heavily utilized leaf ties became highly damaged and accumulated frass from previous occupants, decreasing the amount of food available for developing larvae. Despite this apparent decline in resource quality, the age of the leaf tie had no influence on the probability of colonization by leaf tying caterpillars late in the season. For old ties (ties that had been established at least one census prior), the probability of a new colonization event was unrelated to tie age (i.e., the observed distribution of colonization events across ties of different ages was not different from the null expectation in either of the last 2 censuses; census 7: $\chi^2_{1,5} = 3.49$, $p > 0.50$, $N = 299$; census 8: $\chi^2_{1,5} = 9.17$, $p > 0.10$, $N = 119$).

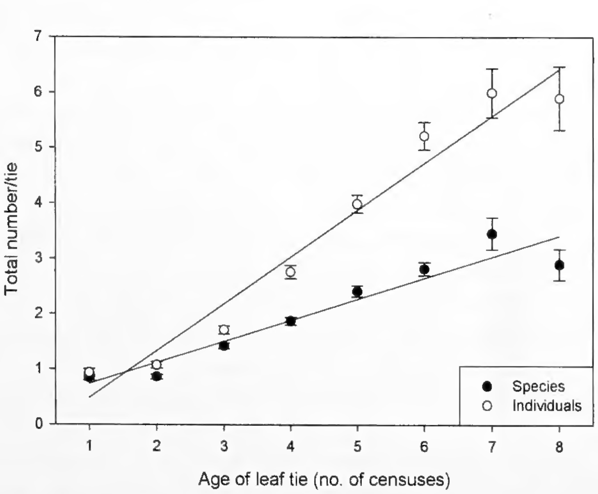

FIG. 3. Total number of individuals and species of leaf-chewing insects recorded in leaf ties maintained for variable lengths of time. Each data point is a mean of a different set of leaf ties (data are not cumulative).

An additional 342 non-tying individuals, including 12 species of Lepidoptera, two leaf-feeding beetles, and one sawfly larva, were also found inhabiting the ties (Table 2). Non-herbivorous inhabitants were not recorded, but included click beetles, psocids, rove beetle adults and larvae, shield bugs, thrips, and lacewing larvae. Spiders often occupied the ties as well, occasionally making nests (with egg masses) inside the ties.

Artificial ties. Artificial ties were readily colonized both by leaf-tying caterpillars and by non-tier associates. By late June, ninety-five percent of the 180 artificial leaf ties had been colonized by leaf tiers and all remaining ties were colonized by late July. For the 90 artificial ties on the census branches, a total of 733 leaf tier caterpillars and 202 non-tier associates were recorded during the seven censuses. All leaf tier species listed in Table 1 except *Anclis divisana* and *Tetralopha expandens* colonized the artificial ties. The density of leaf-tying caterpillars occupying these artificial leaf ties was similar to that observed for the natural ties.

DISCUSSION

There was marked seasonal variation in the construction of new leaf ties. Because *Pseudotelphusa* sp. larvae were the first leaf tiers to appear, they were largely responsible for the initial wave of ties, which were subsequently colonized by the later-appearing species (Fig. 2). The increased densities

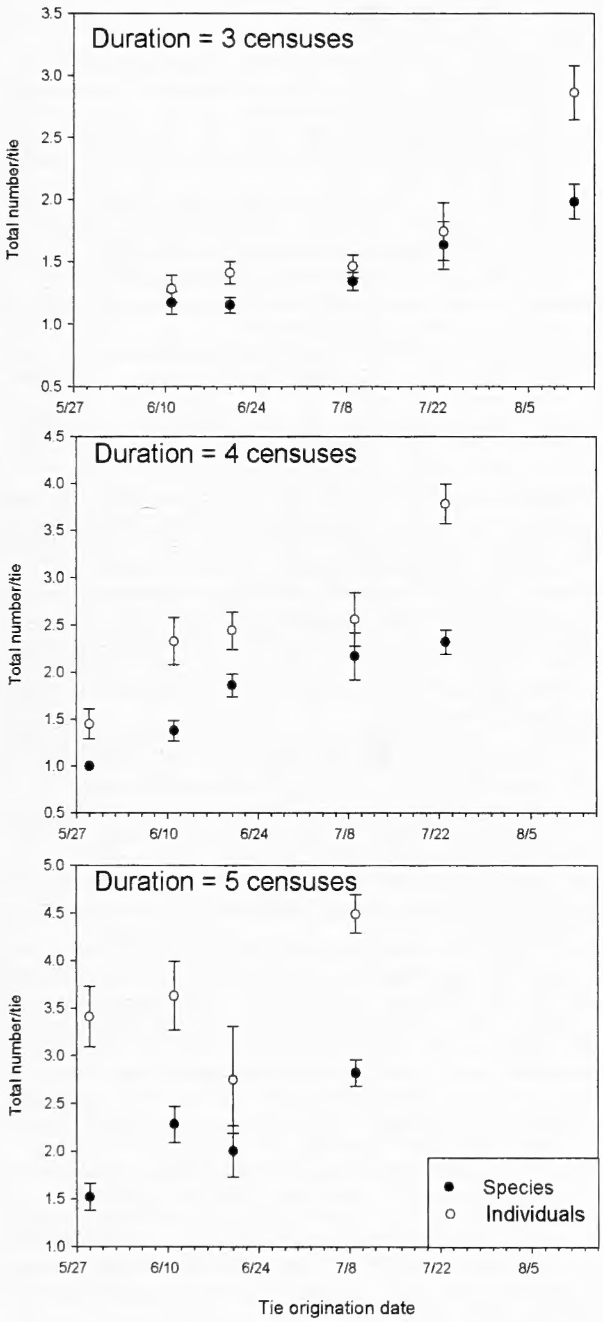

FIG. 4. Total number of individuals and species of leaf-chewing insects recorded in leaf ties originating on different dates, but maintained for equal periods of time (3–5 censuses). Error bars are 1 SE.

TABLE 2. Non-leaf-tying herbivores (leaf-chewers) found inside leaf ties.

Order	Family	Species[a]
Coleoptera	Chrysomelidae	*Pachybrachis* sp.
	Curculionidae	*Cyrtepistomes castaneus* Roelfs
Hymenoptera	Tenthredinidae	*Caliroa* sp.
Lepidoptera	Arctiidae	*Halysidota tessellaris* JE Smith
	Bucculatricidae	*Bucculatrix* nr. *albertiella*
	Gelechiidae	*Trypanisma prudens* Clemens
	Limacodidae	*Isa textula* Harris
		Parasa indetermina Bdv
		Sabine stimulea Clemens
	Lymantriidae	*Dasychira obliquata* Grt. & Rob.
	Noctuidae	*Acronicta increta* Morr.
		Meganola miniscula Zeller
	Notodontidae	*Lochmaeus manteo* Doubleday
		Natada gibbosa JE Smith
	Oecophoridae	*Machimia tentoriferella* Clemens

[a] Nomenclature and authors of Lepidoptera follow Hodges (1983).

of leaf tiers relative to leaf ties during the early season (Fig. 1) could be explained by the fact that most of these early leaf ties were created by small groups (2–3) of *Pseudotelphusa* sp. larvae. The lack of a second peak in the production of new leaf ties during the late season (i.e., when leaf-tying caterpillar abundance reached its second peak) indicated that many of the new colonists (including the second wave of *Pseudotelphusa* sp.) were preferentially occupying pre-existing ("old") leaf ties. Because most leaf ties were colonized and maintained by a succession of larvae of various species, the local density of leaf ties formed early in the season should have positively influenced the rate of colonization (and perhaps folivory) later in the season. The positive relationship between early season leaf tie density and the density of leaf ties formed over the entire season lent some support to this idea, but experimental studies are needed to separate innate host plant effects (some trees are simply more attractive to leaf tiers) from the domino effects arising from sequential occupancy of pre-existing ties.

The increase in abundance and species richness of insect herbivores with later date of leaf tie establishment (after controlling for tie age; Fig. 4) most likely reflected the seasonal increase in the size of the species pool of herbivores; more species were available to colonize a limited resource, resulting in more crowded leaf ties. There were a variety of late-season species not present ealier, whereas virtually all of the early summer species were also found in late summer, since most of these early species are bivoltine.

The rapid colonization of the artificial leaf ties by leaf tiers suggests that these species actively seek out pre-existing ties. Because many of these secondary occupants were early instar caterpillars, it appears that female moths are selecting pre-existing shelters as oviposition sites (wherein hatching larvae typically take up residence). Ovipositing in pre-existing shelters may provide several benefits to developing offspring, including a favorable microclimate that decreases the risk of dessication, decreased construction costs (in terms of both time and energy), and decreased apparency to visually foraging predators (Fukui 2001). There are also potential costs to occupying pre-existing shelters, most of which are related to the negative effects of direct and indirect competition (Damman 1993). For example, pre-existing shelters are often highly damaged, contain large amounts of frass, and are often occupied by other caterpillars, all of which have been shown to increase the risk of predation by members of the third trophic level (Heinrich & Collins 1983, Steiner 1984, Mattiacci & Dicke 1995, Masashi 1999, Weiss 2003).

In addition, the surfaces of many "old" leaf ties have been skeletonized by previous occupants and would appear to offer little food resources to new colonists. However, because early instar caterpillars have relatively modest food requirements and later instars can add leaves to their natal shelter or create new shelters, it is quite possible that future food limitation has little bearing on adult oviposition decisions in this system. In this study, caterpillars colonized leaf ties of different ages in proportion to their relative abundance on the study trees, suggesting that ovipositing moths are not particularly selective about the age of leaf ties chosen for oviposition sites. Previous studies have shown that shelter-building caterpillars often choose leaves that promote effective and efficient shelter construction, even at the expense of food quality (Damman 1987, Hunter 1987, Reavey 1991, Loeffler 1996).

The diversity of ways in which caterpillars engineer their environment through the production of leaf shelters is only just beginning to be explored. More studies that investigate the costs and benefits of shelter-building as a putative adaptive trait are needed, as are studies that examine the ecological consequences of the behavior for plants and the communities of arthropods that associate with them. In addition, our understanding of the natural history of these small, inconspicuous, yet often abundant caterpillars is extremely limited; collecting and rearing efforts are needed to improve morphological descriptions and determine the host plant affinities and life histories of many of these poorly-known shelter-builders.

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A NEW SPECIES OF *YPHTHIMOIDES* (NYMPHALIDAE, SATYRINAE) FROM SOUTHEASTERN BRAZIL

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ABSTRACT. This paper describes a new species of *Yphthimoides* (Nymphalidae, Satyrinae) from the highlands of the Serra do Cipó, Minas Gerais, southeastern Brazil. The position of this species is still uncertain within the genus, but it is near to *Y. celmis* (Godart) based on the male genitalia. Early stages are very similar to those of other species of Euptychiini. Adults are most active from 10:00 to 14:00 h, mostly on slopes protected from direct winds. Males are territorial, and females wander through the area. Adults were observed feeding on six species of flowers.

Additional key words: *Campos rupestres*, Poaceae, Serra do Cipó, *Yphthimoides cipoensis*.

The Serra do Cipó is the southernmost part of a mountain system known as the "Serra do Espinhaço," extending through the center of Minas Gerais State, in SE Brazil. Most of its area is included in the "Serra do Cipó National Park," covering parts of the municipalities of Jaboticatubas, Santana do Riacho, Morro do Pilar and Itambé do Mato Dentro. The region is mostly covered by open vegetation, especially rocky montane fields ("campo rupestre") and Cerrado, with narrow galley forests bordering some rivers in the valleys (King 1956, Joly 1970, Moreira & Camelier 1977).

The region has many endemic species of plants and animals (Vanzolini 1982, Giulietti et al. 1987, Eterovick & Sazima 2000, Sawaya & Sazima 2003), but the knowledge of insects including butterflies is minimal. Preliminary lists for the region show that it is especially rich in endemic Hesperiidae and Lycaenidae; within the Nymphalidae, the Satyrinae are the group best represented (E. G. de Oliveira, in prep.). Any biological information about this region is important, especially considering the need for protection of the entire area.

The species described here was first collected by the author in 1996 near the Serra do Cipó National Park, and also observed in three subsequent visits to this area (1997, 2001, 2002). Attempts to identify this species indicated that it was an undescribed taxon.

The present paper describes this new species and illustrates the morphological characters of adults and immature stages.

MATERIALS AND METHODS

The species was studied in the Serra do Cipó, Minas Gerais, SE Brazil. The mean annual temperature is 18°C (Nimer 1972, CETEC 1982). Annual rainfall averages 1600 mm, with a marked dry season from May to August. Observations were made in the "Juquinha" site, Santana do Riacho, Minas Gerais, on a hilltop with many rocky outcrops delimiting an area of about 300 m^2 where adults were usually abundant (more than 60 marked in two days in 1996, and about 20–30 in 1997 and 2002). Adults were more common in the western section, where the slope was more protected from winds.

Fertile eggs were obtained from two wild-captured females confined in plastic bags. Larvae were reared in plastic containers cleaned daily, with fresh plant material provided every two or three days (following Freitas 1991). Data were recorded on behavior and development times for all stages, and dry head capsules and pupal castings were kept in small glass vials. When there was sufficient material, immatures were fixed in Kahle solution (AVLF collection). All measurements were made using a microscope fitted with a calibrated micrometric ocular. Egg size is presented as height and diameter, and head capsule size is the distance between the most external ocelli (as in Freitas 1991). Taxonomic nomenclature follows Miller (1968) modified by Harvey (1991), who treated the Satyrinae as a subfamily, downranking Miller's subfamilies and tribes to tribes and subtribes, respectively. Nomenclature of wing veins follows Miller (1969), and of body setae follows Hinton (1946).

Yphthimoides cipoensis Freitas, new species
(Figs. 1–3)

Adults: Diagnosis. Eyes with minute sparse hairs, appearing naked without magnification; reddish brown with dark areas (varying in shape and position). Palpus length 1.5 times head height, brown with light brown hairs. Antenna (10–11 mm) extending to mid-costa; shaft dark brown, dorsally covered by dark brown scales, club with 16–17 segments, not conspicuously developed. Male wing venation shown in Fig. 2a. Forewing slightly elongated, hindwing outer margin wavy, especially in the males. Male foreleg with two elongated partially fused tarsomeres; female foreleg with five tarsomeres (Fig. 2c, d). The midleg and palpus are shown in Fig. 2b, e. Easily distinguished from other species of *Yphthimoides* by the lack of conspicu-

FIG. 1. *Yphthimoides cipoensis* from Serra do Cipó, Minas Gerais; adult male (top) and female (bottom). Left wings ventral, right wings dorsal.

ous ocelli on the wings and by the weakly marked lines crossing the wings: Fig. 3 compares *Y. cipoensis* with 15 other common species of *Yphthimoides* from Southern Brazil, showing that the general wing shape and color pattern of *Y. cipoensis* is quite different from those of the other species.

Description. Male (Fig. 1, top). Forewing length 21–22 mm; hindwing length 15–18 mm (n = 10). Body entirely dark brown. Dorsal ground color dark brown with no markings, except for a thin orange-brown marginal stripe on the hindwing; covered with hairs, longer and more abundant on the basal portion, especially on the hindwing. Ventral ground color of wings same as dorsal; forewing crossed by a dark brown concave irregular line extending from costa to CU1 at two thirds from base, delimiting a distal area with scattered pale pink scales giving a bluish tint, and with a minute black dot in the space M1–M2 one fifth from wing margin; a dark brown zigzag submarginal line and an orange brown marginal line extending from costa to 2A. Hindwing with many scattered pale pink scales giving a bluish tint; a dark brown concave irregular line from costa to anal margin, delimiting a distal area with bluish tint more pronounced; a series of five narrow white stripes over veins M1 to Cu2, the second (on M2) weaker; two minute black dots with white center, in spaces M1–M2 and Cu1–Cu2.

Male genitalia unusual in shape within the Satyrinae (Fig. 2f–i). Uncus forming a dorso-ventrally flattened process, in the form of a wide spatula (Fig. 2g). Tegumen slightly bilobed; saccus very short and small. Gnathos appearing as two long pointed processes almost the same size as uncus. Valvae elongated, ending in a single blunt point, with internal margin ornate bearing many well developed spines in three series: a basal rounded process with 6–8 small spines, an intermediate region with 2–3 long spines, and a terminal protuberance with 3–7 small spines (number, size and disposition of spines in each series different on the two valvae of the same individual and among different individuals) (Fig. 2i). Aedeagus elongated with a conspicuous shelf on the ventral surface (Fig. 2h).

Female (Fig. 1, bottom). Forewing length 22–24 mm; hindwing length 17–19 mm (n = 5). Body entirely dark brown. General color and pattern very similar to, but in general paler than that of males, with less bluish tint, and with the distal area paler than basal area on both wings.

Variation. Variation on the dorsal wing surfaces was absent in the sample studied, and differences in general darkness were inversely correlated with wing wear. The ventral surface of the wings can be weakly marked in some individuals of both sexes, and the white stripes on the hindwing usually disappear in old individuals. The ocelli can be absent in some individuals, and in one female an additional ocellus was seen in the space Cu2–1A in the hindwing.

Early stages: Egg (Fig. 4a). Spherical, beige, without ridges but with many small depressions in the chorion. Height 1.14–1.30 mm (mean = 1.197 mm, SD = 0.049, n = 7); diameter 1.14–.24 mm (mean = 1.191 mm, SD = 0.041, n = 7). Duration 5–9 days (N = 30).

First instar (Fig. 4b–d). Head capsule black, with enlarged chalazae, bearing a pair of short scoli on vertex, each with two long narrow setae ending in a fine point (Fig. 4b). Third stemmata larger than the other stemmata. Head capsule width 0.76–0.82 mm (mean = 0.789 mm, SD = 0.016, n = 25); scoli 0.08–0.12 mm (mean = 0.095 mm, SD = 0.010, n = 25). Body beige, smooth, with red longitudinal stripes; caudal filaments very short. Setae XD, D, SD and L thickened with clubbed tips; body chaetotaxy illustrated in Fig. 5. Maximum length 7 mm. Duration 10–15 days.

Second instar. Head dark brown with two diverging short scoli on vertex. Head capsule width 1.14–1.30 mm (mean = 1.213 mm, SD = 0.042, n = 19); scoli 0.16–0.20 mm (mean = 0.184 mm, SD = 0.014, n = 19). Body brown with many longitudinal stripes; caudal filaments short. Maximum length 11 mm. Duration 6–13 days.

Third instar (Fig. 4e). Head medium brown, with two dorsal dark lines reaching bases of two diverging very short scoli on vertex. Head capsule width 1.84–2.00 mm (mean = 1.917 mm, SD = 0.051, n = 19); scoli 0.24–0.30 mm (mean = 0.264 mm, SD = 0.021, n =19). Body brown with many longitudinal stripes; caudal filaments short. Maximum length 17 mm. Duration 7–10 days.

Fourth (last) instar (Fig. 4f, g). Head lighter brown, with two dorsal dark lines to bases of diverging short scoli on vertex, integrating head and body stripes. Head capsule width 2.81–3.39 mm (mean = 3.101 mm, SD = 0.190, n = 10); scoli 0.39–0.43 mm (mean = 0.409 mm, SD = 0.021, n = 10). Body brown with many longitudinal stripes; one dorsal stripe conspicuously dark; ventral region dark brown; legs and prolegs light brown; caudal filaments short. Maximum length 30 mm. Duration 17–20 days.

Pupa (Fig. 4h–j). Short and smooth; mostly beige, with short squared ocular caps; cremaster dark in ventral portion; dorsal abdomen with a paired series of short subdorsal white protuberances; alar caps light at the edge, with lightened visible tracheae. Total length 12–13 mm. Duration 20–25 days.

Etymology. The specific name refers to the distribution of this species, which apparently is restricted to the Serra do Cipó.

Holotype: adult male from "Juquinha" (19°15'S, 43°33'W), 1370 m, Serra do Cipó, Santana do Riacho, Minas Gerais, southeastern Brazil, collected by A. V. L. Freitas on May 6, 1996. In the collection of the Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil (collection reference number: DZ 5.132). Labels on the holotype (three labels, separated by transverse bars): /HOLOTIPO/ SERRA DO CIPÓ, JUQUINHA, SAN-

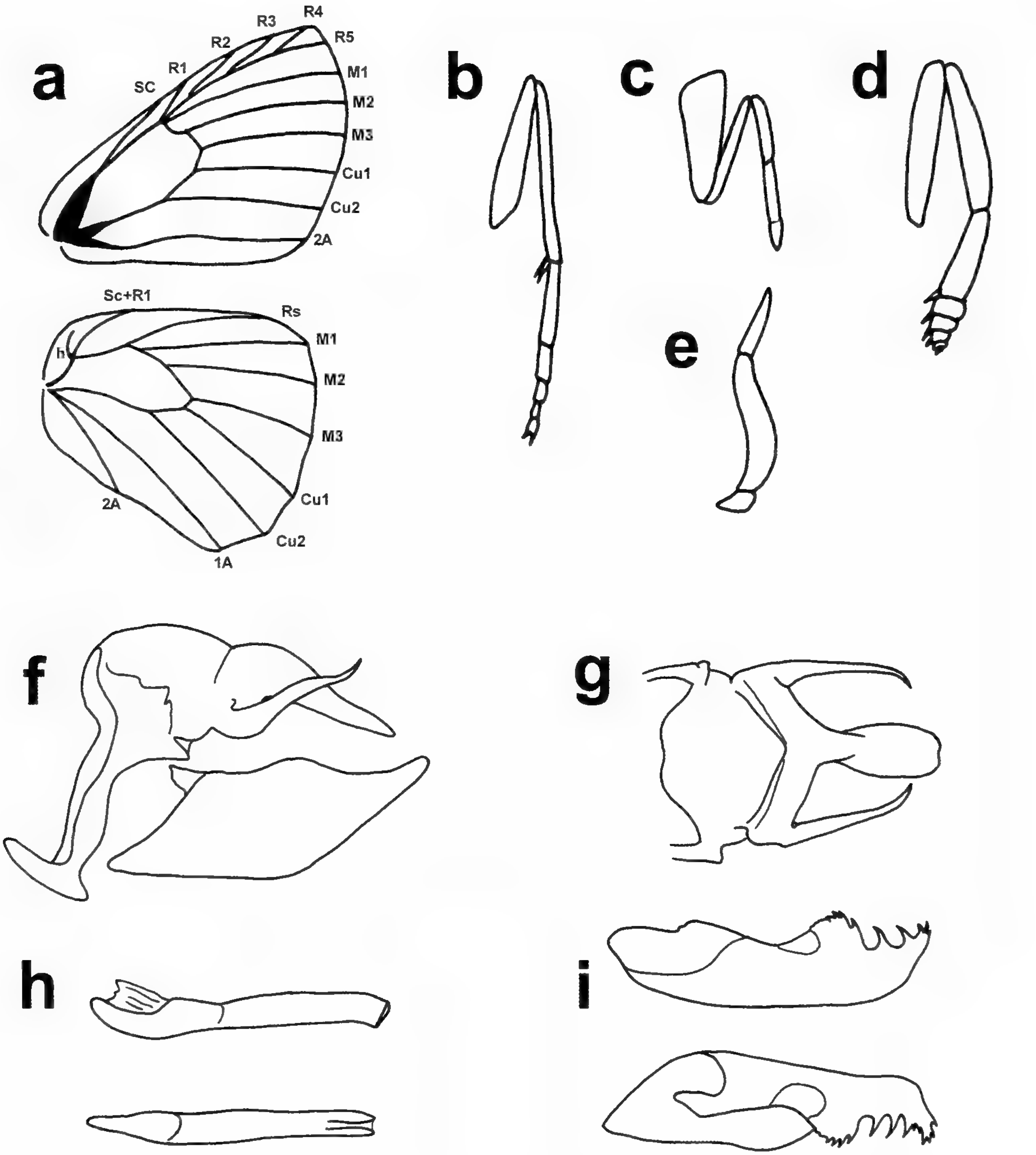

FIG. 2. Morphological characters of *Yphthimoides cipoensis*. **a,** Male wing venation, hindwing above and forewing below; **b,** Male midleg; **c,** Male foreleg; **d,** Female foreleg; **e,** Male palpus; **f,** Lateral view of male genitalia; **g,** Dorsal view of tegumen and uncus; **h,** Aedeagus (lateral above, ventral below); **i,** Right valva upper view (external above, internal below).

TANA DO RIACHO, MG, BRASIL, 19°15'S, 43°33'W, 1370 m, 6-V-1996, A.V. L. FREITAS leg./ DZ 5.132/

Paratypes: Three adult males and one adult female, same site as holotype, collected in May 2002, in the collection of the author.

Distribution. This species is very local, and was observed in only three sites in the Serra do Cipó. In addition to the population of "Juquinha," a second

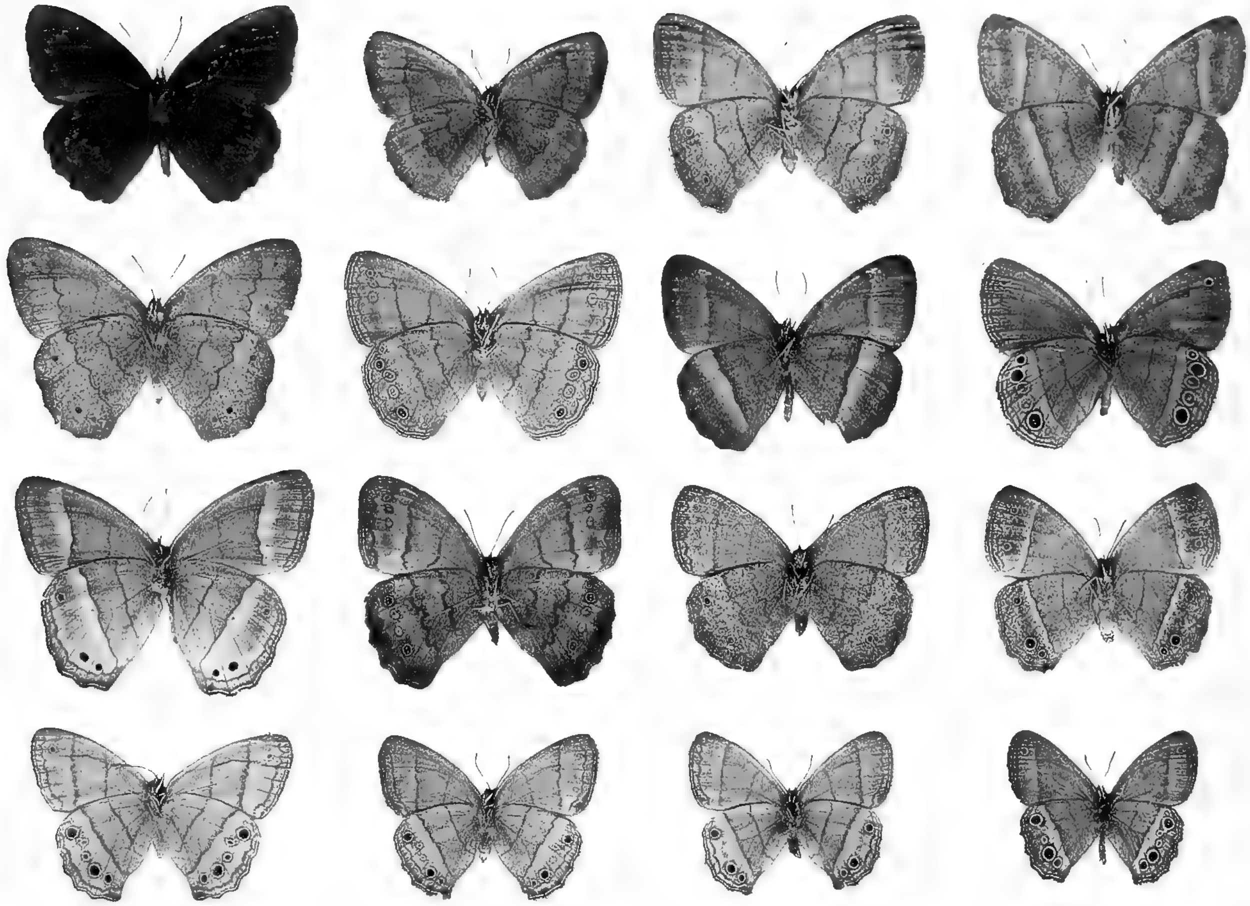

FIG. 3. Comparison of *Yphthimoides cipoensis* with another 15 species of *Yphthimoides* of Southern Brazil. Top to bottom, left to right; *Y. cipoensis* Freitas, Serra do Cipó, Minas Gerais; *Y. celmis* (Godart), Viamão, Rio Grande do Sul; *Y. renata* (Stoll), Mogi Guaçu, São Paulo; *Y. straminea* (Butler) (probably a dry season form of *Y. renata*), Luiz Antônio, São Paulo; *Yphthimoides* sp., Campinas, São Paulo; *Y. affinis* (Butler), Campinas, São Paulo; *Y. ochracea* (Butler), Campos do Jordão, São Paulo; *Y. yphthima* (C. & R. Felder), Campinas, São Paulo; *Y. borasta* (Schaus), Igaratá, São Paulo; *Y. grimon* (Godart), São Sebastião, São Paulo; *Yphthimoides* sp., Teodoro Sampaio, São Paulo; *Y. manasses* (C. & R. Felder), Itirapina, São Paulo; *Yphthimoides* sp., São Sebastião, São Paulo; *Yphthimoides* sp., Cotia, São Paulo; *Y. viviana* (Romieux), Santa Bárbara, Minas Gerais; *Yphthimoides* sp. (ca. *castrensis*), Maquiné, Rio Grande do Sul.

population was found by Marcio Uehara-Prado in "Travessão" (19°20′S, 43°31′W, elevation 1100 m), in July–August 2001, and W. W. Benson found a third population in a private area not far from the "Serrote" (19°17′S, 43°33′W, elevation 1200 m) in May 2002. The species probably occurs in other similar habitats in the region.

Behavior and Natural History. Oviposition behavior was not observed, and the host plant in the field is unknown. In the laboratory, larvae easily accepted Goosegrass *Eleusine indica* (L.) Gaertn. (Poaceae), a common introduced grass in Brazil. In plastic bags, eggs were usually laid singly on the plastic surface (suggesting that in nature eggs are also laid singly). Adult males are territorial, while females wander through the landscape (W. W. Benson & AVLF unpublished data). Adults were observed feeding on flowers of *Declieuxia* sp. (Rubiaceae), *Leucothoe* sp. (Ericaceae), *Hyptis* sp. (Lamiaceae), *Piptolepis buxoides* Schultz-Bip and two unidentified species of *Vernonia* (Asteraceae).

DISCUSSION

The genus *Yphthimoides* was erected by Forster (1964) to include about 15 species of medium-sized predominantly brown Neotropical Satyrinae species. Because the diagnosis given by Forster was vague, about 22 species have been included in this genus until now (G. Lamas pers. com.). Preliminary studies on the immatures (AVLF unpublished results) suggest that this genus is an unnatural assemblage of several distinct groups (in the description of *Yphthimoides*, Forster already recognized two distinct groups of species), and needs a major reorganization into five or

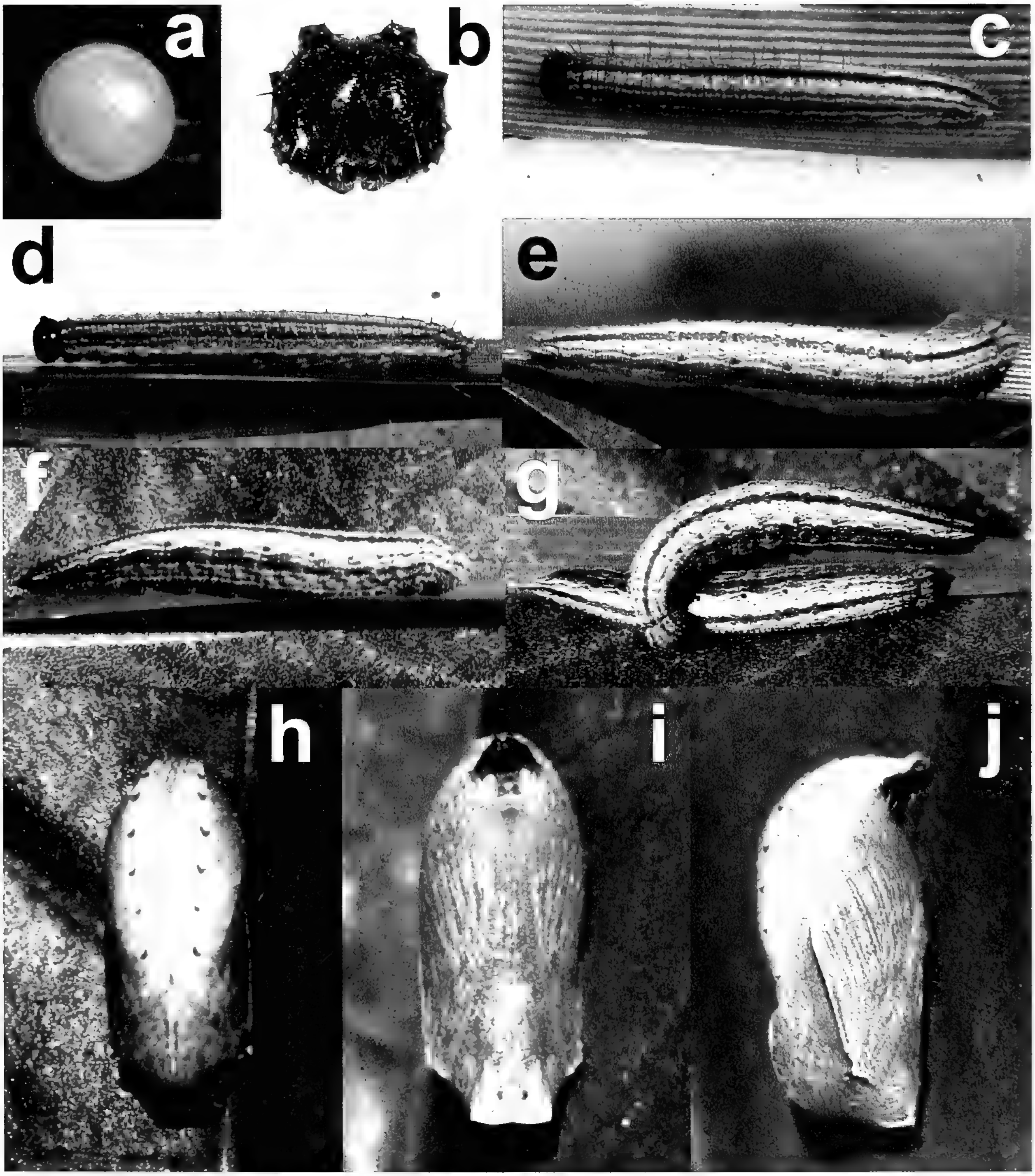

FIG. 4. Early stages of *Yphthimoides cipoensis*. **a,** Egg; **b,** First instar head capsule; **c, d,** First instar (dorsal, lateral); **e,** Third instar (dorsal); **f, g,** Last instar (lateral, two larvae dorsal); **h, i, j,** Pupa (dorsal, ventral, lateral).

more genera. The tentative placement of *Y. cipoensis* in *Yphthimoides* was based on the paper by Forster (1964), and by the similarity of the male genitalia with *Y. celmis* (Godart) (male genitalia figured in Forster 1964:100), a species very different from *Y. cipoensis* (Fig. 3). However, this classification may require a reassessment once our knowledge of *Yphthimoides* systematics is improved.

Based on current information, this species is considered endemic to the Serra do Cipó region, and dis-

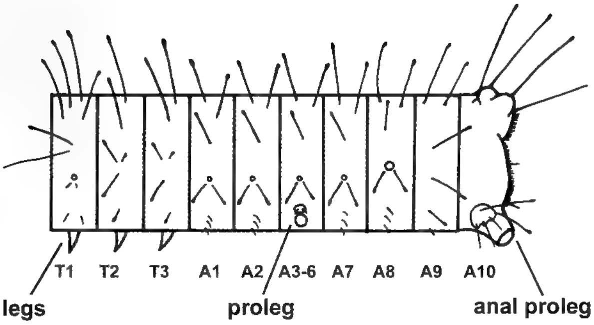

FIG. 5. Chaetotaxy of the first instar larva of *Yphthimoides cipoensis*.

tributed in few scattered local colonies. Like many other species endemic to this mountain system, it may be considered vulnerable to extinction due to habitat destruction. Only one colony is known from the area inside the National Park, and the colonies outside are threatened by destruction of surrounding habitat, fire and uncontrolled eco-tourism. Additional efforts to discover new colonies of this species and population studies of the adults could be important to help in the preservation of the species and of the whole Serra do Cipó system.

ACKNOWLEDGMENTS

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SPHINX MOTH POLLINATORS FOR THE ENDANGERED WESTERN PRAIRIE FRINGED ORCHID, *PLATANTHERA PRAECLARA* IN MANITOBA, CANADA

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ABSTRACT. The western prairie fringed orchid, *Platanthera praeclara* (Sheviak & Bowles), is an endangered species in North America. In Manitoba orchids produce lower numbers of seed capsules than more southern populations. Exploration of the pollination biology for *P. praeclara* is critical to preserve this endangered species. This study identified the pollinators of *P. praeclara* using cone and malaise traps and tested the effectiveness of marking pollinators with traces of Day-Glow® orange marker powder. Although Lepidoptera were numerous in orchid plots during daily observation periods, including day flying Sphingidae, none were pollinators for *P. praeclara*. Among the 5856 insects from 49 families captured over 45 trapping days, six sphinx moths, two specimens of *Hyles gallii* (Rottenburg) and four specimens of *Sphinx drupiferarum* J.E. Smith (Sphingidae), were found with two or more orchid pollinia attached to their eyes and were confirmed as pollinators of *P. praeclara*. *S. drupiferarum* is uncommon in southern Manitoba and *H. gallii* appears to be a less efficient pollinator than *S. drupiferarum*. Proboscis length, eye width and flight period may influence the efficiency of biotic pollination of the orchid.

Additional key words: Sphingidae, pollinia, pollination, *P. praeclara*, *S. drupiferarum*, *H. gallii*.

The western prairie fringed orchid, *Platanthera praeclara* (Sheviak & Bowles 1986), occurs in areas of remnant tall grass prairie in southeastern Manitoba. Prior to its discovery in the mid 1980's near Tolsoi, Manitoba, *P. praeclara* was not known to exist in Canada (Johnson 1985, 1991). The Manitoba population, at its maximum has consisted of approximately 21,000 individual plants (although the population may fluctuate widely from year to year) and it is the largest of four metapopulations (over 300 plants) in North America. The remaining populations occur in North Dakota, South Dakota, Minnesota, Kansas, Nebraska, and Iowa (Sheviak & Bowles 1986, Bjugstad & Fortune 1989, Bray & Wilson 1992, Bjugstad-Porter 1993, Pleasants & Moe 1993, Davis 1994, Sieg & King 1995, U.S. Fish & Wildlife Service 1996, Hof et al. 1999).

The orchid is protected under Manitoba's Endangered Species Act and has been placed on the endangered species list in both Canada and United States (Collicutt 1993, Davis 1995). In Manitoba, *P. praeclara* often has low fruit set and subsequent seed production (Borkowsky 1998). Although the western prairie fringed orchid will produce a vegetative form, there is little evidence that vegetative reproduction occurs in *P. praeclara* (Bowles 1983, Sather 1991, Sieg & King 1995, Hof et al. 1999). A plant may also go dormant, as is typical in other species of orchids (Nilsson 1992). Therefore, the recruitment of new plants is dependant primarily upon successful pollination and subsequent seed production. In surveys of over 1000 plants Borkowsky (1998) found that only 2.1% of orchid stems produced one or more seed capsules annually in Manitoba between 1994 and 1998. In more southern orchid populations the percent of stems that produce seed capsules can range up to 49% (Bowles 1983, Sheviak & Bowles 1986, Cuthrell 1994). The authors have hypothesized that reduced seedpod production may be linked to low pollination success in Manitoba. The level of pollination success for *P. praeclara* and the identity of the orchid pollinators are unknown in Manitoba.

Pollination is the process in which pollen grains are transferred to the stigma, which is followed by fertilization of the ovules and development of seeds (Proctor et al. 1996). Many orchids require a biotic organism (a pollination agent or pollen vector) to transport the pollen to the stigma (van der Pijl & Dodson 1966, Faegri & van der Pijl 1979). In *P. praeclara* the most striking visual characteristic of the flower is a large, deeply fringed, tri-lobed lower lip and a long, slender spur containing nectar that suspends backward from the flower (Figs. 1, 2). The nectar spur may be 36–55 mm long with a maximum diameter of 2.7 ± 0.5 mm (Sheviak & Bowles 1986). Orchids grow to 38–85 cm tall (Sheviak & Bowles 1986) with the determinant inflorescence containing 7 to 12 flowers (Sheviak & Bowles 1986, Pleasants 1993). The pollinium (Fig. 1) is a specialized structure that consists of pollen, a column and viscidium (Nilsson 1992). In *P. praeclara* the minute grains of pollen are arranged into subunits called massulae (Pleasants & Moe 1993). These subunits form a bi-lobed mass that is attached to the column, which is secured to the viscidium (the entire structure is termed the pollinium). The pollinium is sheathed, with the exception of the viscidium, which is exposed and adapted to cement itself to the pollinator (Bowles 1983). Each flower has one pollinium located on either side of the stigmatic surface. This allows for a 6 to 7 mm separation between each viscidium (Sheviak & Bowles 1986). The opening to the nectar spur is located immediately below the stigmatic surface.

The small opening to the nectar spur restricts the

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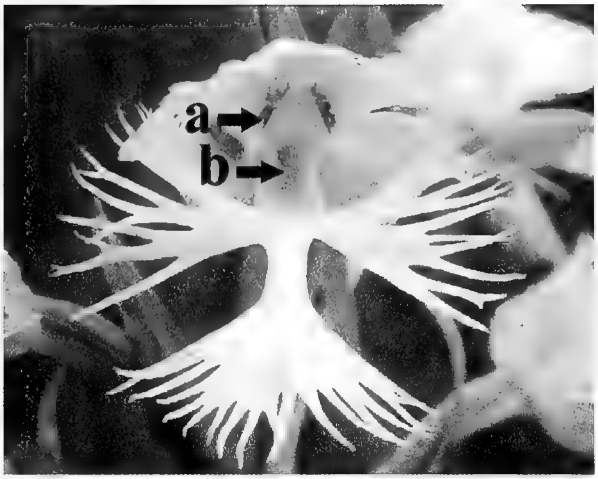

FIG. 1. *Platanthera praeclara* flower, anterior view, showing pollinium (a), and the opening to nectar spur (b).

FIG. 2. *Platanthera praeclara* flower, lateral view, showing nectar spur (a).

position of a potential nectar seeking insect, and increases the likelihood that one or both viscidia will come into contact with a likely pollinator. The pollinium is pulled from the sheath when a pollinator contacts the viscidium and then withdraws from the flower (Darwin 1904, Dressler 1981, 1993).

Orchids also produce a scent or fragrance which may be weak or absent in the daytime, increases in intensity at dusk and may remain strong until sunrise depending on the age and condition of the flower (Sheviak & Bowles 1986). The relationship between the attractiveness of the fragrance to pollinators and the intensity of the scent is unknown in *P. praeclara*.

To be identified as a pollinator and to rule out indiscriminate visitors to the flower, the organism must make regular visits to the flowers during its lifetime and effectively deposit the pollen on the stigma (Faegri & van der Pijl 1979). The flower–pollinator relationship may also be controlled by pollinator behavior, mouthpart morphology or taxonomy and by flower morphology (Faegri & van der Pijl 1979, Wyatt 1983). Wyatt (1983) identified nine forms of biotic pollination in orchids including sphingophily (Sphingidae—hawkmoths), phalaenophily (small moths), psycophily (butterflies), melittophily (bees), myophily (syrphid and bee flies), sapromyophily (carrion and dung flies), cantharophily (beetles), ornithophily (birds) and chiropterophily (bats).

The potential pollinators for *P. praeclara* in Manitoba are not known. Although the literature suggests that night-flying members of the Sphingidae may be key pollinators of *P. praeclara,* other members of this orchid genus and several closely related genera may be pollinated by butterflies, other moth species, certain Diptera, Coleoptera or Hymenoptera (van der Pijl & Dodson 1966, Patt et al. 1989, Robertson & Wyatt 1990, Bowles et al. 1992, Larson 1992).

The floral characteristics of *P. praeclara* indicate a moth pollination method (Faegri & van der Pijl 1979, Sheviak & Bowles 1986, Luyt & Johnson 2001), most likely sphingophily or phalaenophily. *P. praeclara* has no developed landing platform on the flowers, therefore hovering pollinators are favored and butterflies may be excluded (van der Pijl & Dodson 1966, Dressler 1981). To retrieve nectar, the insect must correctly align itself with the flower as it inserts its proboscis, which increases the likelihood that the pollinator will contact one or both of the viscidia which will adhere to the proboscis or eyes of the insect (Sheviak & Bowles 1986). Considering the length of the nectar spur of *P. praeclara* and position of the viscidia, the list of potential pollinators is further reduced to Lepidoptera with a very long proboscis (e.g., moths belonging to the Sphingidae or hawkmoth family). Few, if any, observations of pollination of fringed orchids by hawkmoths have been made in the field (Bowles 1983, Sheviak & Bowles 1986, Pleasants & Moe 1993). Based on proboscis length, Sheviak & Bowles (1986) suggested that the following species of moths could be potential pollinators of *P. praeclara* in the United States: *Eumorpha achemon* (Drury), *Hyles lineata* (F.), *Sphinx drupiferarum* J.E. Smith and *Sphinx kalmiae* J.E. Smith. Cuthrell (1994) collected two specimens, one each of *Sphinx drupiferarum* and *Eumorpha achemon* with viscidia from *P. praeclara* attached to the head, from a light trap adjacent to a field of orchids in the United States.

To better understand the pollination biology of *P. praeclara* in Manitoba diurnally active Lepidoptera including day flying Sphingidae, nocturnally active

Lepidoptera and other insect Orders were surveyed as potential pollinators of *P. praeclara*. Several types of passive traps were tested to capture *P. praeclara* pollinators, and a method to mark individual pollinators was investigated.

STUDY SITE AND METHODS

Five field experiments were established between 1997 and 1999 to determine the identity of *P. praeclara* pollinators. Three study plots were located in the Manitoba Tall Grass Prairie Preserve, near Tolsoi, Manitoba (49°05′N, 96°49′W) and two additional moth light trapping sites were located near Lonesand, Manitoba (approximately 21 km east of the Preserve) and near Grunthal, Manitoba (approximately 26 km northwest). The climate is a boreal continental regime with mean temperatures of 19.6°C and –18.8°C for July and January, respectively. Fifty-five percent of the annual precipitation (mean 579.1 mm) falls during the period of May through August (Canadian Climate Program 1993). Drainage in much of the prairie is poor with soil composed of lacustrine parent material, sandy loam to clay loam upper horizons and a thin organic surface layer. Stones, rocks and occasionally boulders are also scattered across the prairie (Canada Soil Inventory 1989, Moore & Fortney 1994).

The Tall Grass Prairie Preserve has an abundance of grasses, including Big bluestem (*Andropogon gerardii* Vitman) and Little bluestem (*Schizachyrium scoparium* (Michx.) Nash) (Gramineae) and is interspersed with bluffs of various deciduous tree species, including willow (*Salix* spp.) and poplar (*Populus* spp.) (Henne & Diehl 2002).

Three 50 × 50 m plots were established in fields were orchids were numerous. Each plot contained a minimum of 25 orchids. Plots were separated by a distance of 500 to 1000 m. To establish that there were no day flying insects pollinating the orchids, 15 individual orchids were tagged in each of the three plots (total of 45 plants) in 1997 and 1998. Each orchid was visually observed for 15 minutes on at least three separate days during the flowering period in 1997 and 1998 between 1100 h to 1500 h to determine if insects contacted plants and were responsible for removal of one or more of the pollinium from the flowers, either by accident or for the purpose of obtaining nectar or pollen. The number and identity of potential pollinators (Order, Family and Genus/species if known) landing or crawling on the orchids was recorded.

Inverted cone insect traps were used to sample potential pollinators from individual orchids. Cone traps were constructed from light gauge steel tubing and wire and covered in fine mesh screen. Cone traps were approximately 40 cm in length and 25 cm in diameter. An inverted wire mesh cone was placed at the base of the trap (much like a minnow trap) and a hinged trap door placed on the top of the trap. Three legs attached to the bottom of trap allowed it to be placed over an individual orchid. The legs were of sufficient length that they could be pushed into the ground around the orchid, allowing the mouth of the inverted cone to be suspended approximately 5 to 10 cm above the terminal flower of the orchid. Traps were emptied daily between 0630 h and 0830 h and again between 1900 h and 2030 h. Captured insects were identified and examined for presence of orchid pollinia. One cone trap was placed in each of the three plots and rotated between plants during the flowering period. Cone traps were placed over orchids that had the most flowers open with intact pollinia available. Traps remained in place over an individual orchid for 24–48 hours and were placed in the plots between 1 July and 15 July in 1997, 1998 and 1999.

Malaise insect traps (Bioquip® Equipment Specialities) were to used to sample for potential pollinators over a groups of orchids (generally five or more individual plants). Each trap was approximately 2 m in height with a glass container at the top to collect trapped insects. A piece of Vapona® insecticide strip (0.2 cm^2) was placed at the end of the collecting cylinder to kill captured insects. One malaise insect trap was placed within each of the three plots and rotated among groups of orchids during the flowering period. Traps were emptied daily between 0630 h and 0830 h and again between 1900 h and 2030 h. Insects were identified and examined for presence of orchid pollinia. Traps were placed in the field between 1 July and 15 July in 1997, 1998 and 1999. Traps were rotated within the plot to new groups of orchids every three to five days.

In 1999, five orchids in each plot under a malaise trap or one orchid under a cone trap were chosen to test the effectiveness of Day-Glow® orange marker dye powder in identifying potential pollinators. A small amount of Day-Glow® orange marker dye powder was applied with a extra fine nylon brush to the centre of each flower of the orchids chosen. Insects captured in the traps were identified and examined for presence of pollinia removed from the orchids and also examined in a dark room under an ultra-violet light for the presence of the Day-Glow® powder. Insects with marker particles adhering to their bodies were considered to have come in contact with the treated flowers.

To determine moth flight periods, two Wards all-weather insect traps® (Wards Natural Science) were placed approximately 1 km to the west of the orchid plots and 5 km to the south of the plots. Two additional Ward's all-weather insect traps® were located at Lonesand and Grunthal, Manitoba to augment moth captures at the Tall Grass Prairie Preserve. Traps were operated from 1 May to 31 August, 1997–1999. Traps had an eight watt ultra-violet fluorescent bulb as an attractant. The traps were used to survey nocturnal Lepidoptera and determine the flight periods of potential orchid pollinators. Flight periods were considered to include the period between date of first and last capture in each year. Traps in the Tall Grass Prairie Preserve were placed in open areas surrounded by mature trees and were not visible from orchid plots. Lepidoptera captured in traps were sorted, pinned and identified to species.

The flowering period for orchids in plots was recorded during the study. Flowering period was defined as the period between the appearance of the first flower and last flower in a plot and peak flowering date was defined as the date when the most flowers were fully open in a plot. The mean overlap in days between moth species flight period and orchid flowering period for all years was calculated. Mean overlap flight period data was square root transformed to satisfy assumptions of normality and heterogeneity of variance for analysis of variance (ANOVA) (SPSS Inc. 1999). Where ANOVA was significant a least-significant difference (LSD) test was used to determine the differences between means ($\alpha = 0.05$) because of its consistency (Saville 1990). To determine if potential pollinators would fit pollinia distance separation requirements and nectar spur depth requirements of *P. praeclara*, measurements were made on a minimum of five individuals from all sphinx moth species collected in the various trap types. Pinned moths were softened in a relaxing chamber and the length of the proboscis, the distance between the outer margins of the compound eyes and distance between the inner margins of compound eyes where measured in mm under a dissecting microscope. For data analysis the proboscis length was square root transformed and distance between outer eye edges and distance between inner eye edges were log transformed to satisfy assumptions of normality and heterogeneity of variance. Morphological measurements between species were subject to ANOVA and where ANOVA was significant differences between means were identified using a LSD test. To examine the relationship between proboscis length and ability of pollinators to retrieve nectar, the length of nectar spurs and the depth of nectar within the spur (distance from distal end of spur to top of nectar line) was measured for orchids in each of the three plots.

TABLE 1. Number and identity of insect Orders and Families collected in cone and malaise traps 1997–1999.

Order	Family/Subfamily	n
Ephemeroptera	Baetidae	1
	Heptageniidae	1
Odonata	Coenagrionidae	3
Orthoptera	Acrididae	5
Plecoptera	Perlidae	1
Hemiptera	Miridae	21
	Reduviidae	2
	Pentatomidae	2
Homoptera	Cercopidae	5
	Cicadellidae	13
Neuroptera	Mantispidae	2
	Chrysopidae	9
Coleoptera	Carabidae	8
	Scarabaeidae	5
	Elateridae	2
	Lampyridae	12
	Cleridae	5
	Coccinellidae	8
	Tenebrionidae	1
	Chrysomelidae	5
	Curculionidae	3
Mecoptera	Panorpidae	2
Trichoptera	Limnephilidae	6
Diptera	Tipulidae	26
	Culicidae	55
	Chironomidae	24
	Simuliidae	15
	Tabanidae	4450
	Syrphidae	45
	Muscidae	546
	Calliphoridae	228
	Sarcophagidae	11
Lepidoptera	Pyralidae	14
	Pterophoridae	2
	Tortricidae	34
	Gelechiidae	40
	Geometridae	18
	Arctiidae	3
	Noctuidae	34
	Lasiocampidae	15
	Sphingidae	6
	Hesperiidae	10
	Nymphalidae	5
	Satyridae	2
Hymenoptera	Ichneumonidae	23
	Vespidae	2
	Sphecidae	3
	Megachilidae	2
	Apidae	19

Identification of insects was based upon Hodges (1971), Rockburne and Lafontaine (1976), Morris (1980), Hodges et al. (1983), Covell (1984), Borror et al. (1989), Klassen et al. (1989), Layberry et al. (1998) and Handfield (1999).

RESULTS

Observational survey. In 1997 and 1998 orchids were observed between 1100 h and 1500 h for approximately 70 hours. Although numerous insects (many

TABLE 2. Summary of six Sphingidae collected from cone and malaise traps with attached pollinia 1997–1999.

Date	Species	Type	# of pollinia	Pollinia location	Marker powder
11 July 1997	*Hyles gallii*	cone	2	head	n/a
11 July 1997	*Sphinx drupiferarum*	malaise	5	head	n/a
15 July 1998	*Sphinx drupiferarum*	malaise	11	head	n/a
15 July 1998	*Sphinx drupiferarum*	malaise	3	head	n/a
20 July 1998	*Sphinx drupiferarum*	cone	7	head	n/a
6 July 1999	*Hyles gallii*	cone	2	head	present

belonging to pollinating families or genera) frequented the plots during the daily observation periods no individuals were observed to seek nectar or pollen from the orchids, to use the flowers as a resting platform or to sun themselves on the orchids. Individuals of the sphinx moths *Hemaris thysbe* (Fabricus) (16 individuals) and *Hemaris diffinis* (Boisduval) (28 individuals) were observed in the orchid plots during the observation periods but they were not attracted to orchids, despite repeatedly visiting nearby flowering herbs for nectar.

Trapping experiments. Between 1997 and 1999 the cone and malaise traps caught 5856 individual insects from 49 families over 45 trapping days (Table 1). The only insects found to have pollinia attached to their bodies belonged to the family Sphingidae (Table 2). Six sphingid moths, two specimens of the Bedstraw hawkmoth, *Hyles gallii* (Rottenburg), and four specimens of the Wild cherry sphinx, *S. drupiferarum* were collected with two or more pollinia attached to the eyes (Figs. 3, 4). *H. gallii* had 2 pollinia per moth, while *S. drupiferarum* had 3 to 11 pollinia per moth.

Marking experiment. In 1999 one sphinx moth, *H. gallii*, was collected from a cone trap with traces of Day-Glow® orange marker dye powder on both eyes and the proboscis. Both pollinia attached to the eyes also had traces of powder, primarily on the massulae and viscidium.

Flight period. The flight periods for sphingid species found in the vicinity of the Tall Grass Prairie Preserve were based on the catches from the four black light traps during the period of 1997 to 1999 (Table 3). Flowering dates for *P. praeclara* are also shown in Table 3. Generally the moths collected were most abundant in the first several weeks of the orchid flowering period. The flight periods of *S. drupiferarum* and *H. gallii* overlapped with orchid flowering by 34.6% and 45.3% respectively.

Morphological measurements. The proboscis length, width across the eyes and distance between the inner eye margins were measured for the 15 species of Sphingidae collected in the vicinity of the Tall Grass Prairie Preserve (Table 4). The mean orchid nectar spur length was 45.27 mm (n = 1016, SE = 0.134) and the mean depth of nectar within the spur was 12.44 mm (n = 1016, SE = 0.201).

DISCUSSION

The results confirm observations by Faegri and van der Pijl (1979), Sheviak and Bowles (1986), Cuthrell (1994) and Luyt and Johnson (2001) that *P. praeclara* is pollinated by nocturnal Lepidoptera confined to the family Sphingidae. It appears that there are no diurnally active insects that seek nectar or pollen from *P.*

FIG. 3. Anterior/lateral view, *Sphinx drupiferarum* J. E. Smith with pollinia from *Platanthera praeclara* attached to eyes.

FIG. 4. Anterior/lateral view, *Hyles gallii* (Rottenburg), with pollinia from *Platanthera praeclara* attached to eyes. Note the large viscidium cemented to lower-center of eye, with massulae projected forward.

TABLE 3. Flight period dates, orchid flowering periods, number of individual sphinx moths collected in black light traps and percent overlap between flight and flowering dates in the vicinity of the Tall Grass Prairie Preserve and for orchids 1997–1999.

	Date				% Overlap of flight period & flowering period days ± SE
	1997	1998	1999	n[1]	
Peak orchid flowering date	2 July	4 July	7 July		
Orchid flowering dates	22 June–16 July	19 June–20 July	23 June–19 July		
Sphingidae–flight period dates					
Ceratomia undulosa Harris	12 June–12 July	7 June–18 July	9 June–31 July	14	92.0 ± 4.9c[2]
Sphinx chersis (Hubner)	31 May–2 July	11 July	absent	6	14.1 ± 13.9a
Sphinx kalmiae J.E. Smith	1–26 July	5–24 June	10 June–18 July	8	58.0 ± 23.2abc
Sphinx luscitiosa Clemens	absent	20 May–30 June	19 June–11 July	7	34.6 ± 19.9abc
Sphinx drupiferarum J.E. Smith	11 July	1 June–25 July	24 June	5	34.6 ± 32.7abc
Smerinthus cerisyi Kirby	28 May–27 June	21 May–29 July	16 May–25 July	58	73.7 ± 26.3bc
Smerinthus jamaicensis (Drury)	25 May–30 June	1 June–10 July	29 May–18 July	123	65.3 ± 18.2bc
Poanes excaecatus (J.E. Smith)	3 June–20 July	11 June–15 July	5 June–20 July	37	94.6 ± 9.2c
Poanes myops (J.E. Smith)	11–28 June	9 June–4 July	1–27 June	34	29.3 ± 16.9abc
Cressonia juglandis (J.E. Smith)	absent	8–30 June	absent	5	11.7 ± 11.6a
Pachysphinx modesta (Harris)	27 May–28 June	11 June–5 Aug	9 June–9 July	61	63.0 ± 20.8bc
Hemaris thysbe (Fabricus)[3]	31 May–25 June	5–28 June	4 June–2 July	16	25.3 ± 6.9abc
Hemaris diffinis (Boisduval)[4]	21 May–2 July	10 June–10 July	1 June–13 July	28	62.0 ± 10.4bc
Darapsa myron (Cramer)	absent	15 May–6 July	absent	5	18.0 ± 16.0a
Hyles gallii (Rottenburg)	15 June–31 July	31 May–29 June	6 July	18	45.3 ± 28.5abc
					$p = 0.040$
					$F_{14,44} = 2.086$

[1] Number of moths collected 1997, 1998 & 1999.

[2] Means within each column followed by the same letter are not significantly different (Fisher's LSD, p > 0.05).

[3, 4] *H. thybe* and *H. diffinis* collected by sweep net in the vicinity of the Tall Grass Prairie Preserve.

praeclara. The presence of pollinia on one *H. gallii* specimen and four *S. drupiferarum* specimens and the marker powder and pollinia on another specimen of *H. gallii* confirm these species as pollinating agents of *P. praeclara* in Manitoba. Despite the larger size of the malaise trap covering more orchids, there was little difference in the capture rates of moths with pollinia between trap types. The Day-Glow® orange marker dye powder successfully marked one pollinator.

Pollinia were attached to the center of each eye on both moth species. *S. drupiferarum* had more pollinia per specimen. The distance between the outer edges of the eyes was greater in *S. drupiferarum* than *H. gallii* (Table 4), but it is unknown if this small difference in eye separation (0.43 mm) would affect the attachment of pollinia. Perhaps *S. drupiferarum* is more aggressive at retrieving nectar and presses harder into the centre of the orchid thus capturing more pollinia. Alternately *H. gallii* may visit the orchids less frequently resulting in fewer opportunities to remove pollinia, or be discouraged from visiting orchids once several pollinia have been attached to the eyes. *H. gallii* is more numerous in the vicinity of the orchids than *S. drupiferarum*, thus it seems likely that they are less attracted to the orchids.

Cuthrell (1994) described two specimens of *S. drupiferarum* (one caught by light trap and one a museum specimen) and one specimen of *E. achemon* (Drury) (collected by light trap) with *P. praeclara* pollinia attached to the eyes. The present study adds *H. gallii* to this list of pollinators while *E. achemon* does not occur in Manitoba.

The mean proboscis lengths for *S. drupiferarum* and *H. gallii* captured in this study were 38.40 mm and 33.50 mm, respectively. Subtracting the mean nectar depth from total nectar spur length provides a distance of 32.83 mm, thus it appears that a proboscis length of 30–35 mm is required to reach the nectar in *P. praeclara*. Based on proboscis length, *Sphinx chersis* (Hubner) and *S. kalmiae* may also be potential pollinators in Manitoba (Table 4). These species had a significantly longer proboscis than all other species collected (Table 4), with no other species having a mean proboscis length greater than 23 mm. The separation of inner and outer eye margins between species was less distinct with some species having a short proboscis yet still having similar eye positioning and separation (Table 4).

Orchid flowering periods and moth flight periods are restricted in terms of overlap in Manitoba. The overlap in more southern areas of the range of *P. praeclara* may be greater and therefore higher levels of pollination may occur resulting in more seed capsules per plant. *S. drupiferarum* is uncommon in southern Manitoba and the most numerous sphingid species in the Tall Grass Prairie Preserve do not possess

TABLE 4. Length of proboscis, the distance between the outer margins of the compound eyes and distance between the inner margins of compound eyes for Sphinx moths collected in the vicinity of the Tall Grass Prairie Preserve, Manitoba.

	n[1]	Mean proboscis length (mm ± SE)	Mean distance between outer eye margins (mm ± SE)	Mean distance between inner eye margins (mm ± SE)
Ceratomia undulosa Harris	7	9.14 ± 0.76c[2]	5.05 ± 0.05h	2.04 ± 0.02d
Sphinx chersis (Hubner)	5	40.32 ± 0.48h	5.89 ± 0.03k	2.40 ± 0.11ef
Sphinx kalmiae J.E. Smith	5	33.64 ± 1.31g	5.31 ± 0.17bi	2.05 ± 0.18d
Sphinx luscitiosa Clemens	5	22.56 ± 0.17f	4.46 ± 0.05ef	2.34 ± 0.01bc
Sphinx drupiferarum J.E. Smith	5	38.40 ± 0.97h	5.59 ± 0.06i	2.34 ± 0.02e
Smerinthus cerisyi Kirby	8	2.21 ± 0.06a	4.76 ± 0.13g	1.88 ± 0.03c
Smerinthus jamaicensis (Drury)	8	1.73 ± 0.75a	3.85 ± 0.03c	1.70 ± 0.02b
Poanes excaecatus (J.E. Smith)	7	2.89 ± 0.03b	4.63 ± 0.05fg	2.09 ± 0.03d
Poanes myops (J.E. Smith)	7	1.87 ± 0.04a	4.07 ± 0.03d	1.83 ± 0.06bc
Cressonia juglandis (J.E. Smith)	5	2.10 ± 0.05a	3.31 ± 0.08a	1.37 ± 0.53a
Pachysphinx modesta (Harris)	8	1.95 ± 0.17a	5.73 ± 0.07j	2.53 ± 0.02f
Hemaris thysbe (Fabricus)	8	12.75 ± 0.52d	3.88 ± 0.02c	1.88 ± 0.08c
Hemaris diffinis (Boisduval)	8	9.48 ± 0.20c	3.58 ± 0.06b	1.89 ± 0.03c
Darapsa myron (Cramer)	5	17.68 ± 0.18e	4.28 ± 0.09e	2.12 ± 0.04d
Hyles gallii (Rottenburg)	8	33.50 ± 0.96g	4.88 ± 0.03gh	2.44 ± 0.02ef
		p = 0.001 $F_{14,98}$ = 37.1	p = 0.001 $F_{14,98}$ = 35.2	p = 0.001 $F_{14,98}$ = 40.1

[1] Number of moths measured.

[2] Means within each column followed by the same letter are not significantly different (Fisher's LSD, p > 0.05).

a proboscis of sufficient length to take nectar from *P. praeclara*. *H. gallii* populations fluctuate greatly from year to year in southern Manitoba, often with very few individuals appearing in some years. Therefore, low pollinator populations may be restricting seed production in some years for orchids in Manitoba.

The Tall Grass Prairie Preserve is surrounded by agricultural lands, a mixture of intensively farmed grains and oilseeds and livestock production. The larval host plants for *S. drupiferarum* can very regionally and include *Malus* spp., *Prunus* spp. and lilac, *Syringa vulgaris* L. (Hodges et al. 1983). These plants are present in the vicinity but their distribution is patchy. It is unknown whether insecticide usage (Suzán et al. 1994) on adjacent farmlands may restrict the population of larval forms of *S. drupiferarum* and *H. gallii* or if weed control may restrict access to host plants. *S. drupiferarum* may be a more efficient pollinator than *H. gallii*, but the number of *S. drupiferarum* adults frequenting the orchid fields was low in this study. There may be considerable competition between nectar sources given the amount of intensively managed lands adjacent to the Tall Grass Prairie Preserve, which would further reduce the time spent by moths pollinating orchids. Strong light sources from farms surrounding the orchid fields may also attract moths, preventing them from visiting orchids. *S. drupiferarum* occupies the northernmost extension of its range in Manitoba, which may also contribute to sporadic population occurrence and lower pollination rates of *P. praeclara*.

Baker (1961) stated that sphingophilous flowers often have a low frequency of pollinator visitation and compensate by producing numerous seeds. Further research is required to determine if other sphinx moth species are pollinating orchids and if the current level of seedpod production is abnormally low or normal for *P. praeclara* in Manitoba.

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EMPYREUMA SPECIES AND SPECIES LIMITS: EVIDENCE FROM MORPHOLOGY AND MOLECULES (ARCTIIDAE: ARCTIINAE: CTENUCHINI)

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ABSTRACT. Species limits within *Empyreuma* are addressed using a morphological study of male and female genitalia and sequence data from the mitochondrial gene COI. Currently, four species are recognized: *E. pugione* (L.), *E. affinis* Rothschild, *E. heros* Bates, *E. anassa* Forbes. Two entities can be readily distinguished, the Jamaican *E. anassa* and a widespread *E. pugione*-complex, based on adult morphology. Neither *E. affinis* nor *E. heros* can be distinguished by coloration or genitalic differences. Analysis of COI haplotypes suggests that *E. affinis* is not genetically distinct from *E. pugione* (<1% sequence divergence); however, the population from the Bahamas, *E. heros*, is differentiated from other haplotypes with an uncorrected sequence divergence of 5%. We place *E. affinis* Rothschild, 1912 as a **new synonym** of *E. pugione* Hübner 1818, and recognize three species: *E. anassa*, *E. pugione*, and *E. heros*. This paper includes a revised synonymic checklist of species and a redescription of the genus, with notes on biology, and with illustrations of male genitalia, female genitalia, wing venation, and abdominal sclerites.

Additional key words: Caribbean fauna, Greater Antilles, mimicry, phylogeography, systematics.

The tiger moth genus *Empyreuma* Hübner (Arctiidae: Arctiinae: Ctenuchini) (Hübner 1818) is endemic to the Greater Antilles of the Caribbean, and has expanded its distribution into Florida (Adam & Goss 1978, Franclemont 1983). Adults are colorful mimics of the wasp *Pepsis rubra* Drury (Hymenoptera: Pompilidae) (Fig. 1A–D), and the host plant for all species reared to date is *Nerium oleander* (L.) (Apocynaceae). Mating behavior of *E. pugione* (L.) involves ultrasound signaling between males and females (Coro et al. 1983, Otazo et al. 1987, Perez et al. 1988, Portilla et al. 1987, Wilson 1999). In some of these studies, *E. pugione* was misidentified as *E. affinis* Rothschild. Continued confusion over the species status of *E. pugione*, *E. affinis*, and other members of this genus frustrates attempts to interpret mating experiments among populations obtained from different locations in the Caribbean.

Previous taxonomic treatments have been summarized in an annotated synonymic checklist by J. Donahue (unpublished). Currently, four valid species and two subspecies names are recognized in *Empyreuma*. These include *E. pugione* (type species; type locality Virgin Islands), *E. affinis affinis* Rothschild (type locality Cuba), *E. affinis haitensis* Rothschild (type locality Haiti), *E. anassa* Forbes (type locality Jamaica), and *E. heros* Bates (type locality Bahamas). Forbes (1917:344) treated *E. affinis* and *E. pugione* as separate species when he described *E. anassa*, but later (Forbes 1930) refers to just two species, one restricted to Jamaica (*E. anassa*) and one widespread throughout the Greater Antilles. That is, Forbes considered *E. pugione* and *E. affinis* conspecific, although he did not formally place *E. affinis* as a junior synonym of *E. pugione*. Bates (1934) subsequently described *E. heros* from the Bahamas, but he did not provide figures or diagnostic features that separate it from previously described species. Thus, the question remains whether either or both of these described species are junior synonyms of *E. pugione*.

We report here the results of a morphological survey of genitalia and a molecular characterization of haplotypes of *E. pugione*, *E. affinis*, and *E. heros*. We find that the morphological evidence supports recognition of two species, *E. anassa* and a widespread, externally variable *E. pugione* as Forbes (1930) suggested. In contrast, haplotype differentiation suggests that the population in the Bahamas is genetically distinct from other populations of *E. pugione* supporting recognition of *E. heros* as a third, valid species.

MATERIALS AND METHODS

Morphology. Standard genitalia dissections were done (Winter 2000). Abdomens were softened in warm 10% KOH for 5–15 minutes and then cleaned (scales and viscera removed) in several rinses of 40% ethanol. Abdominal sclerites and genitalia were stained with chlorazole black E (Sigma, St. Louis, MO) dissolved in deionized distilled water (saturated). Specimens were viewed in 40% ethanol. Wings were bleached, neutralized in weak acetic acid, rinsed and stained overnight in Eosin Y (1% in distilled water; Fisher Scientific, Pittsburgh, PA). Permanent slide mounts (Canada balsam, Sigma, St. Louis, MO) were made of abdominal pelts, genitalia and wings (Winter 2000).

Genital preparations of 18 reared individuals (9 males, 9 females) were examined to assess variation within a population (Table 1). These individuals were offspring of pairs of wild caught individuals (W. Conner pers. com.). Type specimens of *E. affinis affinis* Rothschild (BMNH), *E. sanguinea* Rothschild, *E. a. haitensis* Rothschild (BMNH; 2 males and 2 female

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FIG. 1. Adult males of *Empyreuma pugione* L. (A), *E. heros* (B), and *E. anassa* Forbes (C); Adult female of *Pepsis rubra* Drury (Hymenoptera) (D).

syntypes including #2459), *E. a. portoricensis* Rothschild (female syntype 2460) were examined. The *E. heros* type was not available for loan from the MCZ and its image is not on-line on the type specimen database. The species *E. anassa* is distinct and the uncus sufficiently illustrated by Forbes (1917) to allow confident determination. Additional dissections of specimens were made that represented type localities of *E. anassa*, *E. affinis*, *E. heros*, and *E. pugione*. Camera lucida drawings were made of selected specimens. Specimen deposition and genitalic preparation numbers are indicated in "Specimens examined" and in Table 1. Wing measurements were taken from the center of the thorax to the wing tip (wing length) and from wing tip to wing tip (wing span).

Terminology for abdominal and genital morphology follows Klots (1970) and Forbes (1939). Collections consulted include: FSMC, Allyn Museum, Florida State University (J.Y. Miller); BMNH, The Natural History Museum, London (M. Scoble); MNHP, Muséum National d'Histoire Naturelle, Laboratorie d'Entomologie, Paris (J. Minet); NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (M. Pogue); UMSP, University of Minnesota Saint Paul Insect Collection (R. Holzenthal).

Gene region and analysis. Thirteen individuals from the Puerto Rican colony were sequenced for the mitochondrial gene COI and these represent *E. pugione portoricensis* Rothschild. Eight individuals were collected from Fort Lauderdale (Florida) and represent *E. affinis*. Identifications were confirmed at the NMNH by R. Wilson and R. Simmons. These vouchers were deposited at the Insect Museum (St. Paul, Minnesota). Museum specimens were used to obtain a set of individuals (9) from the Bahamas, and legs of these were extracted to represent *E. heros*. Multiple attempts to extract DNA from museum specimens of *E. anassa* were unsuccessful. We suspect that traditional preparation techniques, drying in paper envelopes followed by relaxation for spreading, degraded the DNA. Museum specimens were collected over multiple years and a single leg per museum specimen was used. For each individual, the source colony or museum collection, voucher number, and sex are reported in Table 1.

DNA extractions were performed using the DNeasy Tissue Kit® (QIAGEN Inc., Santa Clarita, CA) and the Insect extraction protocol (DNeasy Tissue protocol 1997) with 20 µl of Proteinase K (20 mg/ml). Either frozen material (–20°C) or legs of museum specimens were used. Museum specimens were extracted on separate days from fresh material to minimize contamination with similar DNA. DNA extrac-

TABLE 1. Specimens used in mtDNA study. "SJW#" = genitalic preparation of individual, "DNA#" = DNA voucher number for same, *E.* = *Empyreuma*, — = not applicable.

Genus species	Voucher no. dissection	DNA	Source/label data	Haplotype number	GENBANK number	Voucher depository
E. pugione	SJW1054♀	DNA900	Puerto Rico Colony	1	AF513059	UMSP
	SJW1055♀	DNA901	Puerto Rico Colony	2	AF513060	UMSP
	SJW1056♂	DNA903	Puerto Rico Colony	3	AF513062	UMSP
	SJW1057♂	DNA904	Puerto Rico Colony	4	AF513063	UMSP
	SJW1058♂	DNA905	Puerto Rico Colony	5	AF513064	UMSP
	SJW1059♂	DNA906	Puerto Rico Colony	6	AF513065	UMSP
	SJW1062♀	DNA909	Puerto Rico Colony	7	AF513068	UMSP
	SJW1063♀	DNA910	Puerto Rico Colony	8	AF513069	UMSP
	SJW1064♀	DNA911	Puerto Rico Colony	9	AF513070	UMSP
	SJW1068♀	DNA918	Puerto Rico Colony	11	AF513075	UMSP
	SJW1070♂	DNA920	Puerto Rico Colony	3	AF513077	UMSP
	SJW 1080♂	DNA921	Puerto Rico Colony	—	—	UMSP
E. affinis	SJW1056♀	DNA902	Florida Colony	12	AF513061	UMSP
	SJW1060♂	DNA907	Florida Colony	13	AF513066	UMSP
	SJW1061♀	DNA908	Florida Colony	14	AF513067	UMSP
	SJW1065♂	DNA912	Florida Colony	15	AF513071	UMSP
	—	DNA913	Florida Colony	10	AF513072	UMSP
	SJW1066♂	DNA914	Florida Colony	16	AF513073	UMSP
	SJW1067♂	DNA917	Florida Colony	17	AF513074	UMSP
	SJW1069♂	DNA919	Florida Colony	18	AF513076	UMSP
	—	DNA922	Florida Colony	19	AF513078	UMSP
E. heros	SJW1081♂	DNAS043	Bahamas: Long Island	21	AF513083	FSMC
	SJW1082♂	DNAS038	Bahamas: Crooked Island	20	AF513080	FSMC
	SJW1083♀	DNAS041	Bahamas: Crooked Island	21	AF513081	FSMC
		DNAS042	Bahamas	22	AF513082	FSMC
Nyridela sp.	—	DNA069	Las Alturas, Costa Rica	—	AF513079	UMSP
Scena potentia	—	DNA008	Las Alturas, Costa Rica	—	AF277448	UMSP

tion control blanks were maintained for each museum extraction set. These blanks were checked for volatile DNA contamination by including them in the PCR amplifications. All extraction blanks were negative (did not contain DNA) when used as template for PCR.

The entire COI gene was amplified using PCR (Saiki et al. 1988) for lab colony individuals (Table 1). The COI primers amplify nearly 1500 bp of COI. To amplify COI, five primers (two external, three internal) were used. The external primers were K698 (5′-TAC AAT TTA TCG CCT AAA CTT CAG CC-3′) and PAT2K837 (5′-TCC ATT ACA TAT AAT CTG CCA TAT TAG-3′) that have 5′ ends located at positions 1436 and 3037, respectively, on the *Drosophila* mt genome (Clary & Wolstenholme 1985). Three internal primers were also used: C1-J-1751 (alias RON), C1-N-2191 (alias NANCY), and REVNANCY (5′-GAA GTT TAT ATT TTA ATT TTA CCG GG-3′; position at 5′: 2190) (Simon et al. 1994).

Based on initial results of haplotype variation, only the more variable portion of COI, a 550 bp piece (revNancy-Pat2K837), was amplified and sequenced for specimens from the Bahamas (*E. heros*). For all reactions, a hot start (95°C dwell, 1 min) prior to addition of TAQ was used. Cycling parameters were: 29 cycles (94°C, 1 min, 45°C, 1 min, 72°C, 1 min), 1 cycle (94°C, 1 min, 45°C, 1 min, 72°C, 10 min), 4°C for a minimum of 4 minutes. PCR products were cleaned for automated sequencing with a Qiaquick PCR purification kit® (QIAGEN Inc., Santa Clarita, CA) according to protocol. Sequencing reactions were performed using Bigdye terminator kit (PE Biosystems) using 10 μm of primer and 1–6 μl of clean PCR product. Sequencing reactions were performed using a BigDye Terminator Cycle Sequencing Ready Reaction Sequencing Kit® (PE Applied Biosystems, Foster City, CA). We performed half reactions and used 2 μL of 10 μM sequencing primer, 1–6 μL of clean PCR product, and 8–13 μL ddH$_2$O (final volume: 20 μL). Recommended sequencing cycling parameters were used. Each sample was cleaned using Sephadex columns (Centri-Sep protocol; Princeton Separations, Inc., Adelphia, NJ). Samples were then resuspended in 20 μL of Template Suppression Reagent (TSR)® (PE Applied Biosystems, Foster City, CA). An ABI 310 system was used to visualize and record the sequence. Typically, sequences up to 750 bp were obtained with the long capillary for COI.

Data were imported into Sequencher 3.1.1® (Gene Codes Corp., Ann Arbor MI). Sequences for each individual were aligned to produce a consensus sequence and the sequence translated and checked for stop codons. Individuals were then aligned by conserved motifs and adjusted by eye when necessary.

Phylogenetic analysis. As the relationship of *Empyreuma* to other ctenuchines and euchromiines is unknown, we established potential outgroups by performing an initial analysis with one sequence of *Empyreuma* and all available ctenuchine and euchromiine species (Simmons & Weller 2001). We then selected species of two genera, *Nyridela* sp. and *Scena potentia* (Druce), to root the analysis of *Empyreuma* haplotypes. These taxa are given in Table 1 with their GENBANK accession numbers. Unique haplotypes were identified for the *Empyreuma* specimens. These were analyzed using heuristic searches and maximum parsimony (PAUP*) (Swofford 2000). All positions were equally weighted, and 10 random additions were performed to search for tree islands (Maddison 1991). The parsimony results were then used to generate likelihood parameters for a maximum likelihood analysis (ML) using the following menu options: Trees: Tree scores: Likelihood. The following likelihood parameters were used: HKY-85 model, transition-transversion ratio of two, and empirical nucleotide frequencies.

RESULTS AND DISCUSSION

How many species? Morphology clearly supports the recognition of two entities, *E. anassa*, *E. pugione*-complex, whereas molecular results supports three species, *E. anassa*, *E. pugione*, and *E. heros*. The male genitalia (Figs. 2–3) and female genitalia (Fig. 4) of *E. anassa* and the *E. pugione* species-complex are distinct. However, we could not identify consistent, adult morphological features to diagnose *E. heros* compared to *E. pugione* (compare Fig. 2B, C). Both coloration and armature of the male vesica lack fixed differences.

Our molecular results differentiate between *E. heros* (the Bahamas), and other *E. pugione* populations. The mtDNA sequences of *Empyreuma* were typical for COI in insects (Simmons & Weller 2001), with an A/T bias, especially pronounced in the third codon position (A = 43%, C = 12%, G = 2%, T = 43%). We obtained approximately 1474 bp of COI sequence for *E. pugione* and *E. affinis*, and 450 bp for *E. heros*, from approximately 2190 to 3037 (revNancy-Pat2K837). Of 1474 bp, 54 bp were informative (4%); the majority of this variation was third positions (first: 10/54, second: 5/54, third: 39/54). We obtained 19 distinct haplotypes for the combined sample of *E. pugione* and *E. affinis*; three were obtained for *E. heros*. The uncorrected p-distance between *E. heros* to the other haplotypes was 5%. There are 17 unique substitutions for *E. heros* (Table 2), and all are third position transitions. The MP analysis of the COI data resulted in over 139,000 trees (length = 302, consistency index = 0.66, retention index = 0.69; trees not shown). The ML analysis (Fig. 5) has a –ln L = 3571.17. Individuals from the Puerto Rico population (*E. pugione portoricensis*) and from the Florida population (*E. affinis*) do not segregate into two, reciprocally monophyletic taxa (Fig. 5). In contrast, the haplotypes from the Bahamas are recovered as a separate clade in all observed COI topologies. Cryptic species in leaf-mining flies and other insects have been identified by COI and other molecular markers (e.g., Frolich et al. 1999, Scheffer 2000, Scheffer & Lewis 2001). The genetic divergence between *E. affinis* and *E. pugione* (<1%) is slightly higher than divergences among races of *Heliconius erato* (0.5%; Brower 1994a, b) or agromyzid flies (0.6%; Scheffer & Weigmann 2000); however, there is no clustering pattern to the *pugione-affinis* haplotypes (Fig. 5). Similarly, a study of Western spruce budworm species' limits (Sperling & Hickey 1994) suggested that the designation of *Choristoneura biennis* Free., *C. orae* Free., and *C. occidentalis* Free. could not be supported because of low sequence divergence (<1%), and their haplotypes were placed in the same clade.

Both morphological and molecular results support placing *E. affinis* as a junior synonym of *E. pugione*. Molecular results support maintaining the species' status of the Bahaman population, *E. heros*. Additional sampling and molecular study is warranted to confirm these results; however, these initial findings support treating this population as a unique, endemic lineage that should be considered when forming conservation strategies for the Bahamas. Additionally, other islands in the Caribbean may harbor cryptic genetic diversity and greater sampling is needed.

Phylogenetic placement. The systematic placement of *Empyreuma* is unclear. Although a preliminary study of Ctenuchini and Euchromiini identified *Scena* and *Nyridela* as potential sister genera (Simmons & Weller 2001), that study was focused on assessing the monophyly of tribes, not identifying the nearest sister genus or genera to *Empyreuma*. Our COI results suggest that these genera, *Scena* and *Nyridela*, are not sister to *Empyreuma*. Rooting trees with *Scena* and *Nyridela* places the root at the midpoint of the longest branch: the branch connecting the *E. heros* clade to the *E. pugione* haplotypes (Fig. 5). That is, using *Scena* and *Nyridela* as outgroups was no better than arbitrarily selecting midpoint rooting for our analysis. Morphological data does not support a close relationship either. Males of *Scena potentia* Druce have a bifid uncus apically, but it is stalked at the base and probably not homologous with the bifid

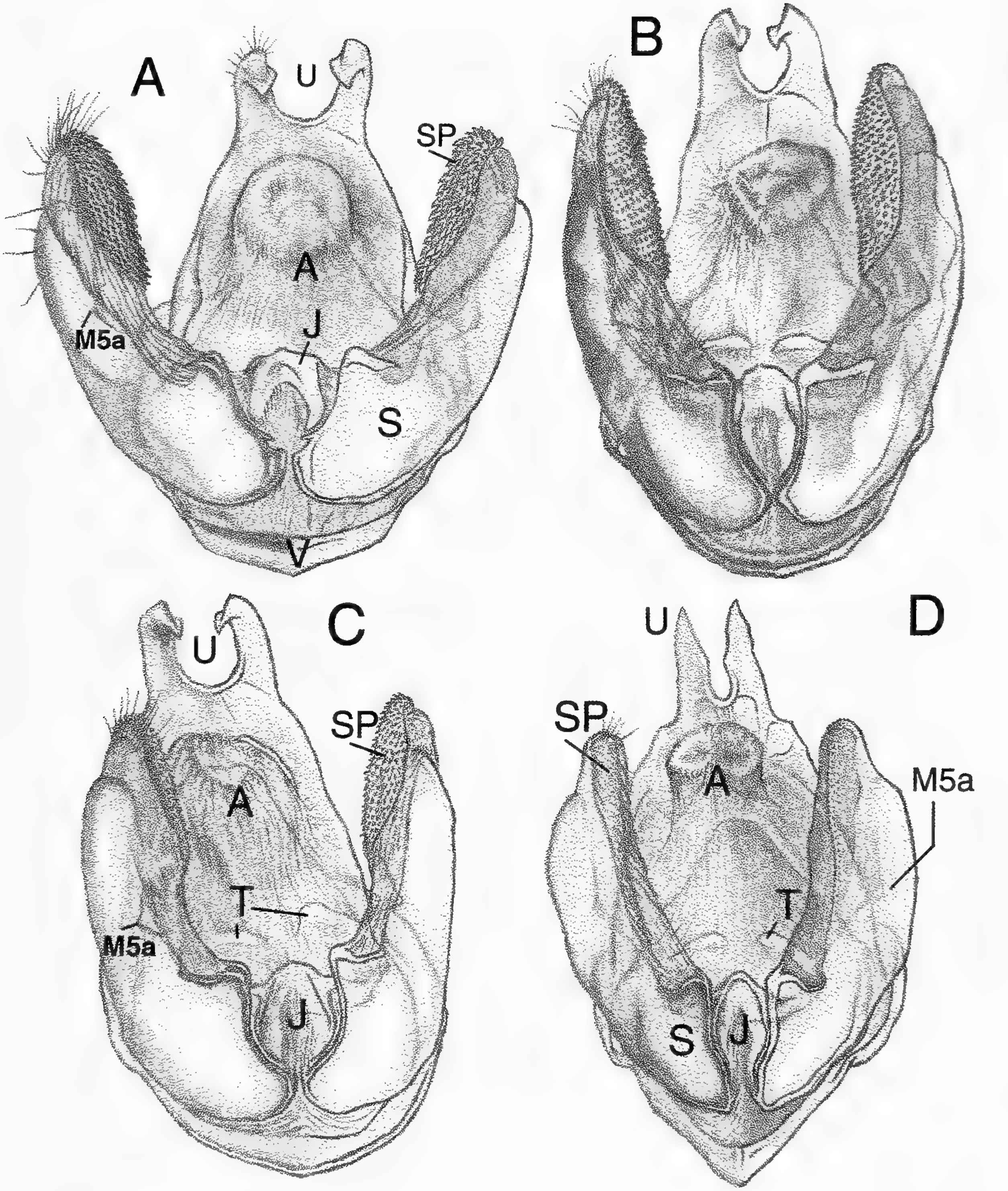

FIG. 2. Male genitalia of: *E. pugione* culture, SJW1066 (**A**), *E. pugione* Dom. Rep., SJW1005 (**B**), *E. heros*, SJW1001, (**C**), *E. anassa*, Jamaica, SJW999 (**D**). A = anal tube, J = juxta, M5a = muscle attachment process, S = sacculus, SP = spinose pad, T = transtilla, U = bifid uncus, V = vinculum.

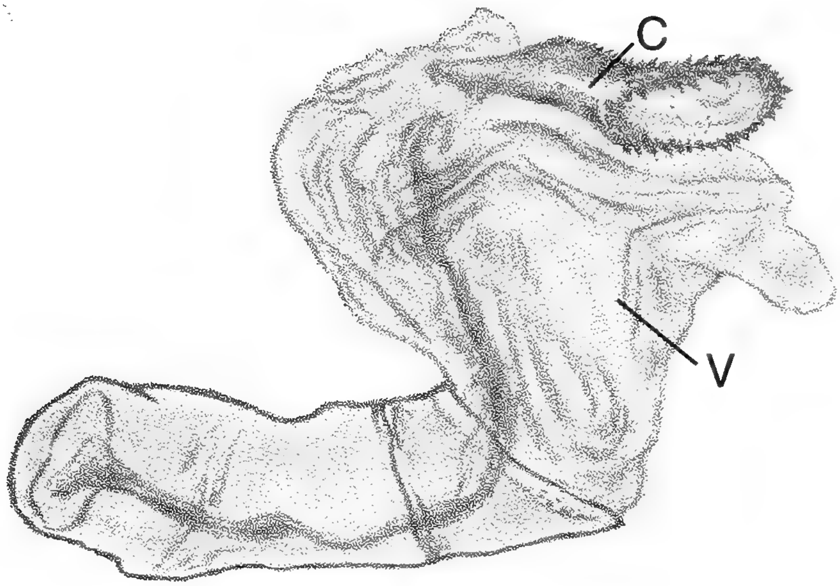

FIG. 3. Aedeagus of *E. pugione* (SJW1005). C = cornuti, V = vesica.

condition of *Empyreuma* (not figured). Male genitalia of *Nyridela chalciope* Hübner have a single uncus and differ in other genitalic details (not figured).

To place *Empyreuma* in the ctenuchine-euchromiine lineage, we surveyed the morphology of other ctenuchines and euchromiines (Weller et al. 2000). Females of *Euchromia lethe* Fabricius possess main and accessory bursae, but the corpus bursa has the anterior third lined with spiny setae, not organized into distinct strips (SJW928 NMNH). Females of *Napata albiplaga* Walker, *N. splendida* Herrich-Schäffer, and *Cyanopepla bella* Guérin also possess a main and accessory bursa with spination similar to *E. lethe*, but differ in spine placement and numbers. All of these females and *Empyreuma* females share the flattened ovipositor lobes and highly wrinkled, melanized membrane surrounding the ovipore. Males of these species do not share obvious similarities with *Empyreuma*, but this is merely a phenetic assessment. A cladistic analysis with more exhaustive sampling of ctenuchines and euchromiines, using both morphological and molecular data, will be needed to establish generic relationships and tribal limits (Simmons & Weller 2001, Jacobson & Weller 2002).

Taxonomy. Below is a redescription of the genus *Empyreuma*. We provide illustrations of the habitus, wing venation, and male and female genitalia of the two morphologically distinct species, *E. pugione* and *E. anassa*. An abbreviated species diagnosis and description is provided for *E. heros*.

Empyreuma Hübner, 1818

Chrysaor Hübner, 1808:4.

Type: *Chrysaor erythropterus* Hübner1808:4, designated by monotypy. Work rejected for nomenclatural purposes by ICZN, 1966, Opinion 789. *Chrysaor* was placed on Official Index of Rejected and Invalid Generic Names in Zoology (Watson et al., 1980:61).

Empyreuma Hübner 1818:12.

Type species: *Sphinx pugione* Linnaeus, 1767:807, by subsequent designation by Hampson, 1898:422.

Diagnosis. The coloration of species of this genus (Fig. 1A–C) distinguishes them from other ctenuchine/euchromiine genera. The blue-black body and black-fringed, scarlet wings is unique among the

TABLE 2. Sites of unique substitutions for *E. heros* compared to *E. pugione* haplotypes. Numbering corresponds to the position on the *Drosophila* COI gene (Clary & Wolstenholme 1985).

Site numbers:	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2
	7	7	7	7	7	8	8	8	8	9	9	9	9	0	0	0	1
	4	6	6	8	9	3	7	7	9	6	8	9	9	0	3	6	5
	6	1	4	2	2	0	2	8	3	5	6	2	8	4	7	1	4
E. heros	A	T	C	C	C	A	C	C	A	C	A	C	C	C	C	T	C
E. pugione	C	C	T	A	T	G	T	A	C	T	T	T	T	T	T	C	T

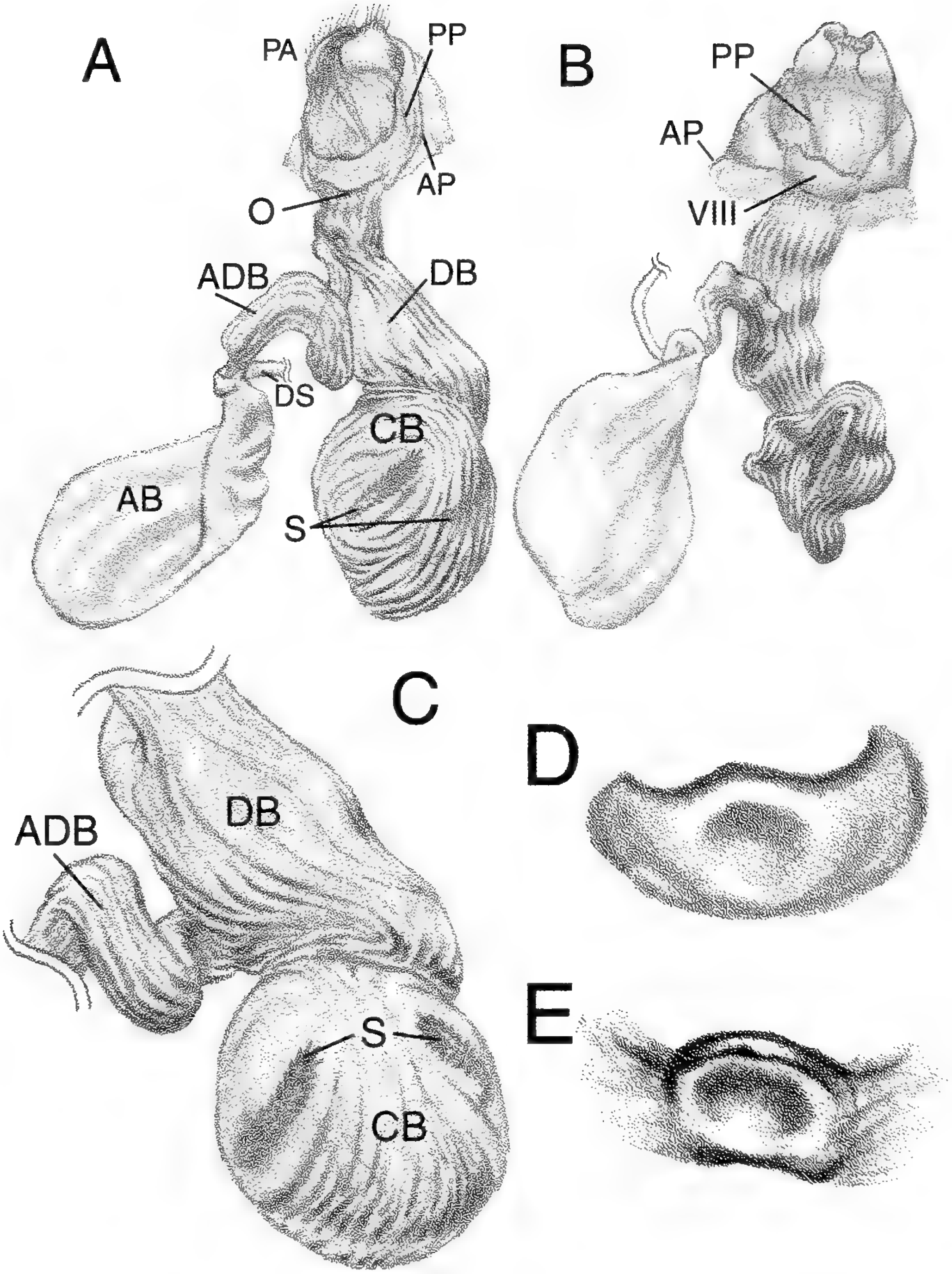

Fig. 4. Female genitalia of: *E. pugione* Puerto Rico culture, SJW1054 (**A**), *E. pugione* Puerto Rico culture SJW1068 (**B**), ductus and corpus bursae of *E. anassa*, Jamaica, SJW997 (**C**), details of lamellae postvaginalis (LPV) of *E. pugione* SJW1068 (**D**) and LPV *E. anassa* Jamaica, SJW997 (**E**). AB = appendix bursa, ADB = accessory ductus bursa, AP = anterior apophyses, C = corona of cornuti, CB = corpus bursa, DB = ductus bursa, DS = ductus seminalis, O = ostium, PA = papillae anales, PP = posterior apophyses, S = signa, VIII = 8th sternite, V = vesica.

mimetic species (RBS pers. obs.). The bifid uncus of the males (Fig. 2) is diagnostic for *Empyreuma*, and appears to be unique within the Euchromiini-Ctenuchini clade (sensu Jacobson & Weller 2002). The paired, spinose signae of the females (Fig. 4S) are also distinctive and possibly derived only in this genus.

Adult habitus (Fig. 1A–C). Wings opaque with brown, black or blue-black scales on upper surface of forewing. Relatively large

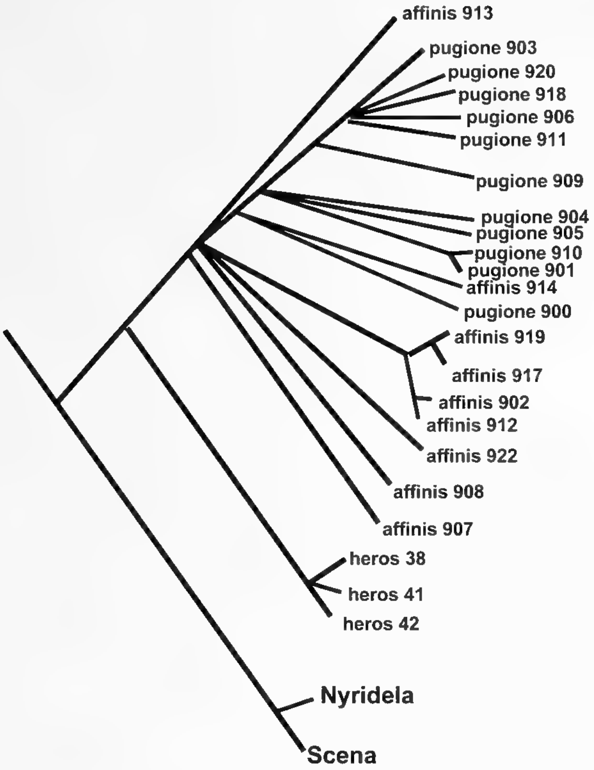

FIG. 5. Maximum likelihood tree with *Neridela* and *Scena* as outgroups. Taxon name includes specimen DNA voucher number (see Table 1).

moths, average male wingspan 49 mm and average wing length 21.8 mm (n = 82). In females, average wingspan 50 mm and average wing length 20.5 mm (n = 90). Unipectinate antenna with a black shaft for nearly entire length contrasting with orange apex. Ground color of head, thorax, and abdomen black, blue-black, or brownish depending on specimen.

Head and Thorax. Antennae unipectinate; ocelli present with a melanized outer ring. Proboscis longer than head. Prothorax lacks parapatagia or a dorsal gland; ephiphysis short. Both meso- and metathoracic legs possess simple claws (not bifid), and tibial spurs with smooth (not serrated) apices.

Wings (Fig. 6). **Forewing venation:** Sc slightly sinuous, extending nearly 9/10 of costa. R_1 and R_2 arise from discal cell, and R_{3-5} stalked with R_5 arising closer to cell than R_3–R_4 branching. M_1 arises from cell and separate from R_{3-5}. The cross vein between M_1 and M_2 typically thins or even has a break anterior to M_2. M_2 arises near M_3 with a short spur of M_2 extending into cell. CuA_1 and CuA_2 widely separated and extend to wing edge. **Hindwing venation:** Sc + R_1 absent. RS and M_1 connate. Discal cell cross-vein strongly developed and V-shaped. M_2 weakly developed, and extends to wing margin. M_3 strongly developed, arises from apex of discal cell. CuA_1 and CuA_2 stalked. and Anal vein (A) just touching wing margin. Female with two frenular bristles.

Abdomen. In both sexes, second sternite with long, straight apodemes (Fig. 7), and 2nd and 3rd sternites and tergites lack modifications for wasp mimicry (Weller et al. 2000). Male lacking androconia (no abdominal scent pouch or coremata). 8th sternite weakly sclerotized (Fig. 7).

Genitalia. Males (Figs. 2, 3)**: Tegumen** relatively short, arising nearly perpendicular to the vinculum; uncus bifid, long processes with rounded apices (Fig. 2A–C), or bifid processes short with pointed apices (Fig. 2D); narrow, sinuous vinculum ventrally produced as rounded shallow saccus. **Valve** with strongly sclerotized base and costa; attachment point of M5 (valve extensor muscle; Forbes 1939, Tikhomirov 1979) marks edge of costa and sacculus (Fig. 2, M5a); sacculus extending apically as a membranous lobe (distinct from costa) bearing a large, spinose pad on internal surface (Fig. 2A–C, SP; *E. pugione*-complex), or spinose pad reduced to flattened, irregular, rugose area fused to costa (Fig. 2D, SP; *E. anassa*); membranous ventral edge of sacculus with few setae and sclerotized base coincident but not fused to juxta. **Juxta** protruding posteriorally in a bell-shaped projection with wishbone-shaped thickening of edges (Fig. 2A–D); **Anellar region** with small anellar sclerites fused to venter of aedeagus, pair of slender, crescent-shaped patches lie dorsad of aedeagus (Fig. 2, T); anal tube (Fig. 2A) with pair of irregularly shaped sclerites or anal tube lightly sclerotized. **Aedeagus** (Fig. 3) relatively large, compared to genital capsule; endophallus with a sclerotized tube possessing a flattened apex ringed with short spines (Fig. 3); varying number of teeth-like spines, and number not corresponding with species-limits.

Females (Fig. 4A–D)**: Papillae anales** (PA) lightly sclerotized, laterally flattened; membrane surrounding ovipore highly folded with melanized striations; posterior apophyses (PP) long and narrow; dorsal pheromone glands as paired narrow tubes with rounded or crescent-shaped thickenings at midpoint and terminus—as long or slightly longer than posterior apophyses (not shown). **8th tergum and sternum** fuse at right angles with very short anterior apophyses (Fig. 4B, AP); 8th tergum rounded, broad with anterior edge highly concave; 8th sternum weakly sclerotized and lacking ornamentation (Fig. 4A–B, detail 4D; *E. pugione* complex), or with a distinct, rounded lamella postvaginalis in *E. anassa* (detail, Fig. 4E); lamella antevaginalis absent; ostium bursa marked by a membranous ventral edge of ductus bursa. **Ductus bursae** (DB) short, membranous and same width as ostium bursa. **Corpus bursae** (CB) with two oblong, highly spinose signae located opposite one another ventrally and dorsally, and linked to an accessory bursa by a twisting duct. **Ductus seminalis** (DS) arising from accessory ductus bursa (ADB). **Accessory bursa** (AB) comprised of thinner membrane, lacking ornamentation.

Notes on Biology. Larvae of these species have been reared on *Nerium oleander* (Apocynaceae) based on museum labels. The plant genus *Nerium* has only three species, and is native from the Mediterranean to Japan. The exotic species, *N. oleander* has been naturalized widely in North America (Correll & Johnston 1979) and it contains cardiac glycosides. The native hosts of *Empyreuma* have not been recorded, but potential New World apocyanaceous host genera include *Thevetia* L., *Plumeria* L., *Mandevilla* Lindl., and *Tabernaemontana* L..

Empyreuma anassa has been collected from nearly sea level to 918 m elevation. Similarly, *E. pugione* has been collected up to 733 m. Adults have been collected in April, May, July, September, and December. Historical label data for *E. heros* lacks elevation, but flight times are similar occurring in October, December, and March.

Discussion. *Empyreuma anassa* is easily separated from the *E. pugione* complex, based on color and genital differences. Our examination of the male genitalia suggests that intraspecific variation exists in the shape of the uncus, presence and development of a spinose

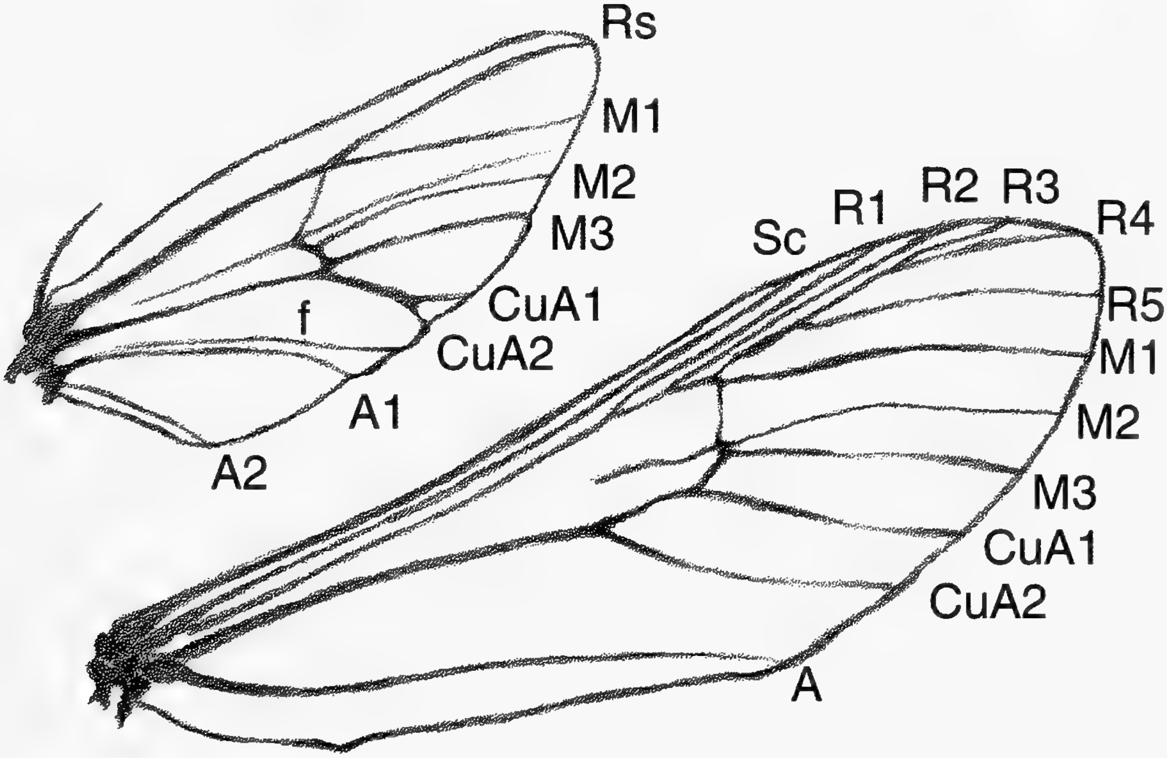

FIG. 6. Wing venation of forewing (below) and hindwing (above). A = anal vein, CuA_1 = cubital vein, f = fold, R = radial vein, Rs = radial sector, Sc = subcosta, 1–5 = vein number.

patch on the sacculus, and presence of a small tooth on the vesica for specimens identified as either *E. pugione* or *E. affinis* (variation not shown). Specimens of the subspecies described by Rothschild (*E. a. haitensis*, *E. a. portoricensis*) fall within the range of morphological variation observed in the reared cultures from Florida and Puerto Rico. Both are placed as new junior synonyms of *E. pugione*. These subspecies may not be defensible; however, more complete survey of moths, their larvae, and their DNA across the Greater Antilles is needed before subspecific status can be discarded definitively, work that is in progress (J. Rawlins in prep).

Empyreuma pugione (Linnaeus, 1767)

Empyreuma pugione (Linnaeus, 1767).

Sphinx pugione Linnaeus, 1767. *Syst. Nat.* (Ed. 12) 1(2):807. Type Locality: insula S. Thomae [St. Thomas Island, Virgin Islands]

Sphinx lichas Cramer, 1775. Papillons Exot. 1:70; pl. 45, fig. B. Type Locality: St. Thomas, Virgin Islands [not *Zygaena lichas* Fabricius, 1781, from Arabia, in the Zygaenidae].

Sphinx sanguinosa Martyn, 1797. Psyche: pl. 26, figs. 18, 19 (unavailable?).

Chrysaor erythropterus Hübner, 1808. *Erste Zutrage Samml. Exot. Schmett.*: 4. Unavailable: sole species included in *Chrysaor*, in a work rejected for nomenclatural purposes.

Empyreuma lichas: Hampson, 1898, not Fabricius, 1781. Cat. Lep. Phal. Brit. Mus. 1:423; fig. 223. (Misidentification).

Empyreuma mucro Zerny, 1912 (25 July). *In* Wagner, ed., Lepid. Catalogus 7:122 [unnecessary replacement name for *Zygaena lichas* sensu Hampson, 1898, not Fabricius, 1781].

Empyreuma sanguinea Rothschild, 1912 (21 Dec.). Novit. Zool. 19:155. [unnecessary replacement name for *Zygaena lichas* sensu Hampson, 1898, not Fabricius, 1781].
Hampson, 1914. Cat. Lep. Phal. Brit. Mus. Supp. 1:267 [as valid name for taxon Hampson, 1898:423 had misidentified as *E. lichas*].
Forbes, 1917. Bull. Amer. Mus. Nat. Hist. 37:344 [as synonym of *E. pugione*].

Empyreuma sanguinea portoricensis Rothschild, 1912 (21 Dec.). Novit. Zool. 19:155. Type Locality: Puerto Rico.
Hampson, 1914. Cat. Lep. Phal. Brit. Mus. Supp. 1:267 [as synonym of *E. sanguinea*].

Empyreuma affinis Rothschild, 1912. Novit. Zool. 19:155. Type Locality: Cuba; **new synonym.**
Forbes, 1917. Bull. Amer. Mus. Nat. Hist. 37:344.
Hampson, 1914. Cat. Lep. Phal. Brit. Mus. Supp. 1:267; pl. 13, fig. 31.

Empyreuma affinis affinis Rothschild, 1912. Novit. Zool. 19:155. Type Locality: Cuba; **new synonym.**

Empyreuma affinis haitensis Rothschild, 1912. Novit. Zool. 19:156. Type Locality: Haiti; **revised synonym** [of *E. pugione* (L.)].
Forbes, 1917. Bull. Amer. Mus. Nat. Hist. 37:344 [as valid "race" of *E. affinis;* misspelled as *"haytiensis"*].
Hampson, 1914. Cat. Lep. Phal. Brit. Mus. Supp. 1:267 [as synonym of *E. affinis*].

Empyreuma haytiensis Forbes, 1917. Bull. Amer. Mus. Nat. Hist. 37:339, 344. Misspelling.

Diagnosis. The wing length in males ranges from 19–27 mm (A = 21.8; STD = 2.5; n = 24), and is 17–27 mm in females (A = 19.9; STD = 2.4; n = 35). The forewing varies from primarily brownish red with

FIG. 7. Male abdominal sternites of *E. pugione* (SJW1005): second (II) above, eighth (VIII) below.

costal red streak (Dominican Republic, Haiti) to brownish red with orange costal streak (Cuba), and has a thin black border on the outer margin (Fig. 1A, B). The forewing lacks scarlet coloration on the underside. The black border varies in width between individuals. White markings are present on the thorax, the patagia, the tegulae, and the wing bases. These white markings are more strongly developed in specimens from Bahamas. Medial, dorsal white patches are present on A1 and A2. There is a small pair of white spots on A2 in pleural region. Conspicuous, paired white patches are present on the dorsum of A3 and A4. Smaller than those occurring on A3 and A4, white patches occur on the anterior edge of A5–A7. Pleural spots are present on A3–5 and A7–8. These white patches are missing or reduced in some specimens and patch size varies throughout the range. The tegumen is relatively short, arising nearly perpendicular to the vinculum. The uncus is bifid, possessing long processes with rounded apices (Fig. 2A–C). The sacculus extends apically as a membranous lobe (distinct from costa), and bears a large, spinose pad on internal surface (Fig. 2A–C, SP), The anal tube has a pair of irregularly shaped sclerites (Fig. 2A). The 8th sternum is weakly sclerotized, and lacks ornamentation (Fig. 4A–B, detail 4D),

Specimens examined: (see Table 1 for additional genitalic dissections). CUBA: **Baracoa,** Coll. Wm Schaus, March (5♂; NMNH). **Cayanas,** E.A. Schwarz (1♂; NMNH). **Holguin,** no other data (1♂, 2♀; BMNH); BM2663 (1♂; BMNH); ex Ges Franek 1911 (1♀; BMNH); H.S. Parish (1♀; BMNH). **Hayana,** Baker (2♂; NMNH). **Loma del Gato,** Sierra Maestra Cuba, 2500′, July–August [19]29, HF Clement (2♂, 1F; BMNH); same locality: BM2465 (1♂, BMNH). **Santiago,** F. Clement (1♂; NMNH). Parish *affinis* syntypes (2♀; BMNH); 58-126 (1♀; BMNH); 100-20 (1♂, 1♀; BMNH); 61-21(1♂; BMNH); *affinis* syntype 2455 (1♂, BMNH). BRITISH VIRGIN ISLANDS: **Guiana Island,** 1–14 July 1984, SE & PM Miller (1♂: gen. prep. SJW1004; FSMC). **Tortola,** March [19]66 J.A.C. Greenwood (1♀; BMNH). DOMICAN REPUBLIC: **La Vega Prov.,** Hotel Montana, ca. 520 m, 10 km NE Jarabacoa, 28 May 1973, Don & Mignon Davis (1♂: gen prep SJW1005, NMNH). CAYMAN ISLANDS: **Georgetown,** T.M. Savage English 1911-89 (1♂; BMNH); no other data (1♀, BMNH). GUADELOUPE: **Aer. Du Raizet,** ix 81 R. Giscointeties (1♀; BMNH). HAITI: **Petionville,** 1300′ 26 Dec. 1954 A. Zerkowitz (1♀, BMNH). **Port au Prince,** 24 X [19]09 Georges Lion, Museum Paris (2♂; MNHP); same locality, 26 X [19]09 Georges Lion, Museum Paris (1♂; MNHP); same locality, 28 X [19]09 Georges Lion, Museum Paris (1♂; MNHP); F. Odile Joseph (1♂, 1♀, 1♂: gen prep 2462; BMNH); No. 54-28, Nov. 26, 1928, A. Audant coll. (1♂: gen prep SJW1003; NMNH). **Le Perchoir,** 3000′ 21 Dec. 1954 A. Zerkowitz (1♀; BMNH). same locality, 23 Dec. 1954 A. Zerkowitz (1♂; BMNH); same locality, 26 Dec. 1954 A. Zerkowitz (2♂, 3♀; BMNH); G. Babault (1♀; BMNH). **San Domingo,** syntype F *affinis haitiensis* (1♀; BMNH); same locality, syntype ♂ *affinis haitiensis* (1♂; BMNH); Haiti, syntype ♂ (BMNH); Haiti 98, BM2459, syntype ♀ (BMNH). HONDURAS: (1♂; BMNH). Haiti (2♂; BMNH). ST. DOMINGO: Tweede 55-1, BM2426 (1♂, BMNH). **NO DATA.** Ex Musaeo Arch. Guenee (1♂; MNHP); Brazil Ex. Coll. Smith 1894-5 (1♀; BMNH); America (1♀; BMNH); Savanah *Zyganea lichas* (1♀; BMNH); *Zyganea pugione* Haynes S.P. Oss-Terra (1♀; BMNH). No label (2♂, 1♀; BMNH), *Empyreuma pugione* L. (1♀, BMNH); *pugione* L. (1♀; BMNH); (2♂; NMNH); "Type of *sanguinea* from S. Domingo?" (1♂; BMNH); Coll. Bryk Mus. (3♂; NMNH); ornh 2 on 11/69 (1♂; BMNH).

Empyreuma heros Bates, 1934

Empyreuma heros Bates, 1934. Occ. Pap. Boston Soc. Nat. Hist. 8:137. Type Locality: Bahamas (Mariguana Island).

Diagnosis. This species can be diagnosed based on its collection locality and its COI sequence. Unique substitutions are given in Table 2.

Description. Same as *E. pugione*.

Specimens examined. BAHAMAS: **Crooked I,** vic Pitts Town, 25 ix 1986 M. Simon & L. Miller, Sta. 1986–UV (1♂: gen prep SJW1001, 1♀: gen prep SJW1083; FSMC); 1 mi E. Colonel Hill, UV, 18 ix 1988, LD Miller & MJ Simon, Sta. 1988-45, Acc. 1988-18, (1♂: gen prep SJW1082; FSMC). **Grand Turk Is[land],** Xii-1. 1965–66 (1♀; BMNH). **G[reat] Inagua I[sland],** Horse Pond ca 1.5 km E of Matthew Town, 28 ix 1986, M. Simon & L. Miller, Sta. 1986-19 (1♂ gen prep, SJW1002; FSMC). **L. Abaro,** Mar 1902 (1♀; BMNH). **Long Island,** Stella Maris, UV, 26 ix 1988, L.D. Miller & M.J. Simon Sta. 1988-63 (2♂: gen prep SJW1000, SJW1081; FSMC). **Nassau I[sland],** 19 ii [19]02, J.L. Bohnhote (2♂, 2♀; BMNH); J.L.

Bohnhote (1♀; BMNH); I. 22 X [18]98 (1♀; BMNH); G. Carter 1903-6 (1♀; BMNH); 30 Dec. 1956, A. Zerkowitz (1♂; BMNH). **New Providence Is.,** F.E. Taylor (1♂, 1♀; BMNH).

Empyreuma anassa **Forbes, 1917**

Empyreuma anassa Forbes, 1917. Bull. Amer. Mus. Nat. Hist. 37:343; fig. 5. Type Locality: near Troy, Jamaica.

Empyreuma pugione: Hampson, 1898 (not Linnaeus, 1767). Cat. Lepid. Phal. Brit. Mus. 1:423. Misidentification.

Diagnosis. *E. anassa* appears slightly larger than *E. pugione*, because the body is more robust. The male wing length ranges from 16–26 mm (A = 21.1; STD = 1.9; n = 56); female wing length ranges from 16–25 mm (A = 21; STD = 2.0; n = 44). Like *E. pugione*, the upperside of the forewing is opaque with metallic blue-black or brown scales. In *E. anassa*, however, the underside is scarlet with a large black border on the outer margin, and the scarlet coloration is visible dorsally (Fig. 1C). Unlike *E. pugione*, white scales are lacking on the thorax and legs in *E. anassa*. The abdomen has two white crescent bands on A4 that extend to the spiracles but do not meet dorsally. There are smaller, paired bands on A5–A7. Male genitalia also differ between the two species. The bifid uncus of *E. anassa* is short with pointed apices (Fig. 2D) compared to *E. pugione* (Fig. 2A–C). The spinose pad on the sacculus is reduced to a flattened, irregular, rugose area, which is fused to the costa (Fig. 2D, SP). The anal tube is lightly sclerotized in *E. anassa*, but not *E. pugione*. In females, the 8th sternite has a distinct, rounded lamella postvaginalis (Fig. 4E) compared to the trapezoidal one of *E. pugione* (Fig. 4D).

Species distribution. The species is found in Jamaica. Three specimens had erroneous label data: British Guiana, Cuba and Costa Rica. The "Moneague" locality is a famous collecting locality in St. Ann Parish Jamaica (Brown & Heineman, 1972), not Costa Rica. The other two specimens lack additional information (collector or expedition) that would allow definitive assignment of locality. These are treated as mislabeled because no other specimens of *E. anassa* have been taken outside of Jamaica.

Specimens examined (also Table 1). BRITISH GUIANA: **Paruima,** 26. 10. 38 (1♀; BMNH). COSTA RICA [Jamaica St. Ann]: **Moneague,** I iv 1926 1000 ft. F. W. Jackson (1♀; BMNH). CUBA: **Holguin,** (1♂; BMNH). JAMAICA: **Axe Town,** Bred 7.8.[18]92 (Taylor) (1♀; BMNH). **Bath,** USNM Acc 40269 (1♀; NMNH). **Jamaica: Batton Falmouth,** AGM Ja.–Feb. 1967 (1♂; BMNH). **Clar. Par.,** Portland Ridge, nr Jackson Bay Cave, 40 ft 4 May 1973, Don & Mignon Davis (5♂, 1♂: gen prep SJW999; NMNH); Mason River Station, 4 mi NW Kellits, 2200 ft 16–19 April '73, Don & Mignon Davis (1♂, 1♂: gen prep SJW1084; NMNH); 2 Km S. Rocky Pt, nr Jackson Bay Cave, Dec 10, 1975 5m, Don & Mignon Davis (2♂; NMNH). **Constant Springs,** e. xii 1904 Wlsm. (1♀; BMNH). **Cuna Cuna Pass**, Capt. U. Robinson Collector 10 July [19]05 (1M; NMNH). **Cornwall County,** Coll. Miss M.S. Savarian (1♀; NMNH). **Kingston,** 10-1-[18]94 at light (Taylor) (1♀; BMNH); at light (Taylor) (1♀; BMNH); bred 2.8.[18]92 (Taylor) (1♂; BMNH); bred 6.8.[18]92 (Taylor) (1♂, 1♀; BMNH); bred 7.8.[18]92 (Taylor) (1♂; BMNH); bred pupated 7.7.[18]92 emerged 20.7.[18]92 no. 10 *E. pugione* (Taylor) (1♀; BMNH); WJ Kaye B. M. 1930-185 (1♂; BMNH); at light 29-7-[18]92 (1♂; BMNH); 15-IV-73 (1♂; NMNH); W.R. Maxson Coll. V-29-04 (1♂; NMNH). **Mandeville,** 2000 m July 1923 A. Hall (1♂; BMNH); L. J. Bertram (1♂; BMNH). **Mile Gully,** 16 ii 1921 No. 311 (1♀; BMNH). **Moneague,** beg. Feb. 1905 Wlsm. (1♀; BMNH). **Montego Bay,** xiii 1923 Major Gillett BM 1924-174 (2♀; BMNH); 26 Feb. 1911 Miss Fountaine (2♂, 1♀; BMNH). **Moore Town,** (1♂; BMNH). **North Coast,** s. level 20 iii 1961 (1♀; BMNH); s. level 29 iii 1961 (1♂; BMNH); s. level 8 vi 1961 (2♂, 1♀; BMNH); Dark hours s. level 20 iii 1961 (2♂; BMNH); Dark hours s. level 29 iii 1961 (1♂; BMNH). **Ocho Rios,** Dec. 10, 1957 A. Zerkowitz (1♂; BMNH); Dec. 28, 1957 A. Zerkowitz (1♀; BMNH); Jan. 3, 1957 A. Zerkowitz (1♂, 1♀; BMNH); Jan. 5, 1957 A. Zerkowitz (1♂; BMNH); Jan. 6, 1957 A. Zerkowitz (1♂, 1; BMNH). **Portland Parish,** (1♂; BMNH); Hardwar Gap, "Green Hills", July 24–25, 1962, Farr. O & R. Flint (5♂, 1♀; NMNH); 4 mi. S. Hartford, 850 ft. 26–27 April 1973, Don & Mignon Davis (1♀; NMNH). **Runaway Bay,** end Feb. 1905 Wlsm (1♀; BMNH); 5-III-1970, JFG Clarke (1♀; NMNH). **St. Ann Par**., Martin (1♂; BMNH); Rose Hill, Runaway Bay 900 ft, 29 April–2 May 1973, Don & Mignon Davis (13♂, 4♀; NMNH); nr Runaway Bay 50 ft, 1–2 May 1973, Don & Mignon Davis (6♂, 1♀; NMNH). **St. Cath. Par.,** Mt. Diablo Hollymount, 2754 ft 21–24 April '73, Don & Mignon Davis (5♂, 1♀, 1♂: gen prep SJW998; NMNH). **Westmor. Par.,** Negril, Dec. 12, 1975, Don & Mignon Davis (2♂; NMNH). BRITISH WEST INDIES: **N Coast,** S level 20 iii 1961 (2♂, 1♀; BMNH); same locality: 29 iii 1961 (1♂, 1♀; BMNH); same locality: 8 vi 1961 (2♂, 1♀, 1♂: gen prep SJW996; BMNH). ST. THOMAS: **L. Litus,** *pugione* (1♀; BMNH); Jamaica collection Wm Schaus (5♂, 3♀; NMNH); Female vial #083 *Empyreuma anassa* R.E. Dietz 1968 (1♀, NMNH); Jamaica WI, A. Arinoff Donor, July 24, 1933 (1♂; NMNH); Cockrell (1♀; NMNH); St. Thomas Col. Neumögen, Coll. Brklyn Mus. (1♂; NMNH); *Empyreuma pugione* 4. 8. 25 Ex. Coll. Griffiths (1♀; BMNH); *Empyreuma pugione* Jamarque (1♂; BMNH); (6♂, 8♀; BMNH); Taylor (6♂, 4♀; BMNH); Jamaica Yates (1♂; BMNH); 1960 pres. by George Newman Brit. Mus. 1961-52 (1♀; BMNH); 40-4-3-104 (1♂; BMNH); 45-110 (1♂, 1♀; BMNH); 46-121 (1♂; BMNH); 76-71 (1♂; BMNH); E Coll. Hanson (1♂; BMNH); ex Stevens (1♀; BMNH); F. W. Jackson 1913-208 (1♂; BMNH); F. W. Jackson 1920-341 (1♂; BMNH); Ianson (1♀; BMNH); JMS and J Yates BM 1926-393 (1♂; BMNH); ex. Percy I. Lathy 1902 (1♂; BMNH); (1♂; BMNH); P.H. 6-91 Taylor (2♂, 1♀; BMNH); R. Stanway Paris 23-ii-1919 (1♀; BMNH); same data 2-ii-1919 (2♂, 1♀; BMNH); same data 16-2-1901 (1♀; BMNH); West Indies Malrun B. M. 1933-489 (1♂, 1♀; BMNH); Malvun (1♂; BMNH); British Guiana (1♂; BMNH); San Domingo 120 (1♂; BMNH). NO DATA: Bred 13. 7. [18]92 No. 10 *E. pugione* (1♂; BMNH); Bred 25. 7. [18]92 No. 10 *E. pugione* (1♂, 1♀; BMNH); 44-11 (1♂; BMNH); *E. pugione* no. 10 Bred 16. 7. [18]92 (1♀; BMNH); Panama or Jamaica ? (1♀; BMNH) S. America (1♀; BMNH); label unreadable (1♂; BMNH).

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THE BUTTERFLIES (PAPILIONOIDEA, HESPERIOIDEA) OF THE GALÁPAGOS ISLANDS, ECUADOR: DISTRIBUTION, HOSTPLANTS AND BIOLOGY.

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ABSTRACT. The butterfly fauna of the Galápagos islands is reviewed. Ten species are recorded from the Archipelago. *Leptotes parrhasioides* (Wallengren), *Urbanus dorantes galapagensis* (Williams), and *Agraulis vanillae galapagensis* (Holland) are endemic and the others are Neotropical faunal elements. A number of new island and host plant records are given.

Additional key words: flower visitation, phenology, Neotropical region.

The butterfly fauna of the Galápagos Islands was first discussed by Williams (1911). Six species were then recorded from the archipelago. Previous reports of Galápagos butterflies were published by Wallengren (1860, 1861), Butler (1877) and Holland (1889). Subsequent to Williams' revision, little mention was made of the butterflies in the Galápagos until Beebe (1923) and Parkin et al. (1972) added two species of milkweed butterflies, *Danaus plexippus* (Linnnaeus) and *Danaus gilippus* (Cramer), to the fauna. A literature-based checklist of the insects of Galápagos by Linsley and Usinger (1966) and Linsley (1977) listed eight species and indicated on which island each species occurred. During the last 33 years only two faunistic notes have been published. Onore and Mielke (1988) reported *Calpodes ethlius* (Stoll) and Roque et al. (1997) added *Hemiargus ramon* (Dognin). Additional information such as flower visits and host plant records were given by Linsley (1966), McMullen (1986, 1990, 1993), McMullen and Viderman (1994) and Roque (1998a, b). Finally, Peck et al. (1998) listed the introduced insect species that occur on the archipelago and included *C. ethlius* and *H. ramon.*

This paper reports new information on Galápagos butterflies gathered during 8 years of fieldwork on the Islands. The butterfly fauna of the archipelago includes 10 species and subspecies, three of which are presumed to be endemic.

MATERIALS AND METHODS

From November 1994 to June 2002 the author conducted daytime observations and collections of butterflies in the Galápagos Islands. A total of 387 specimens were sampled and identified, and observations on habitat associations and behavior of each species was noted. The methods included: a) field collections with a light mesh net, b) field observations of adult behavior and visits to food sources, c) collecting and rearing of immature stages.

Immatures were collected and reared in the laboratory. Eggs and larvae were reared in plastic bags at room temperature under the natural day-night photoperiod regime. Fresh leaves were provides at least every other day. Pupae were kept moist until adults hatched.

The majority of this material was deposited in the Invertebrates Collection of the Charles Darwin Research Station (CDRS), Santa Cruz Island, Galápagos Islands. Some of the other specimens are in the following collections: Pontificia Universidad Católica del Ecuador (PUCE), Quito, Ecuador, Museo Ecuatoriano de Ciencias Naturales (MECN), Quito, Ecuador and California Academy of Sciences (CAS), San Francisco, USA. Additional records of distributions were obtained from the literature and unpublished data from Dr Bernard Landry, whose material is deposited in the Canadian National Collection (CNC), Ottawa, Canada.

The classification adopted here follows Ackery and Vane-Wright (1984) and Ackery et al. (1999). A brief description is given for the immature stages of the endemic species. The nomenclature of the plants follows McMullen (1999).

The following abbreviations were used: FW = fore wings, DFW = dorsal fore wings, VFW = ventral fore wings. HW = hind wings, DHW = dorsal hind wings, VHW = ventral hind wings. DW = dorsal side of the wings, VW = ventral side of the wings. The size of the butterflies in mm refers to their fore wing length.

RESULTS

Doubtful Records

Previous authors reported several species whose occurrence in the Galápagos has not been demonstrated convincingly. It is better to exclude these as probable misidentifications or mislabelling as is explained below.

Actinote sp. (Nymphalidae): Daniel Fitter, a naturalist guide with the Galápagos National Park Service, sent a color photograph to the author for examination. The photograph, taken on Media Luna, Santa Cruz Island, was published in Fitter et al. (2001:115) and was identified as *Actinote* sp. (Nymphalidae). It has not been collected or seen in the archipelago since the picture was taken. The establishment in the Galápagos of this species will be only confirmed or refuted when additional material is found.

Hypolimmnas misippus (Linné), (Nymphalinae): The only notice of the occurrence of this species in the archipelago is from one specimen deposited in the American Museum of Natural History, New York. The specimen has the following label data: "Conway Bay, Indefatigable Is, Galapagos, March 15 1935, Crocker Exped". It is likely that this is a mislabelling or if the record is valid it was a migrant individual. The species has never been seen or collected since.

Agraulis vanillae lucina (C. & R. Felder): This species was reported by Moreno et al. (1997). It is likely a misidentification of the Galápagos's endemic subspecies *Agraulis vanillae galapagensis* (Holland, 1889).

Heteropia sp. (Hesperiidae): One male from Albemarle [Isabela] was reported by Van Duzee (1933), although the author suggested that the specimen had been mislabeled and collected in Mexico.

Erynnis funeralis (Scudder & Burgess), (Hesperiidae): One specimen (as *Thanos persius* (Scudder)) deposited in the CAS is said to have been collected in Chatham [San Cristóbal], 15 IV 1932 by M Willows Jr. However, Van Duzee (1933) suggested the specimen was mislabelled.

Leptotes trigemmatus (Butler), (Lycaenidae): Larsen (1991) mentioned this species from the Galápagos Islands but it is likely a misidentification of the sister taxon *Leptotes parrhasioides* (Wallengren), as noted by Balint and Johnson (1995).

Phoebis agarithe (Boisduval) (Pieridae): Moreno et al. (1997) reported this species from the archipelago. These authors probably misidentified *Phoebis sennae marcellina* (Cramer) as this species which is superficially similar in size and color. *P. agarithe* has never been collected on the Galápagos Islands.

Species Accounts

Hesperiidae

Pyrginae

Urbanus dorantes galapagensis (Williams 1911)
"Galápagos Skipper"
(Fig. 1)

Eudamus galapagensis Williams 1911:303; Draudt 1921:853; Beebe 1923:55; Van Duzee 1933:144.
Urbanus dorantes galapagensis; Evans 1952:93; Linsley & Usinger 1966:157; Parkin et al. 1972:103.
Urbanus galapagensis Williams & Hoyward 1944:93.

Diagnosis. FW = 15–20 mm. This is the only tailed skipper of the archipelago. FW dark brown with translucent spots and a pattern of lilac and brown bands in VHW. In some specimens, the hyaline spots are smaller. The lilac bands on the VW tend to be pale with lighter brown or yellowish scales. The sexes are similar, but males have coastal folds.

Geographical distribution. Reported from Baltra, Edén, Española, Floreana, Genovesa, Isabela, Pinzón, San Cristóbal, Santa Cruz and Santiago (Linsley & Usinger 1966). Additional records include: Fernandina, Pinta and Rábida.

Natural history. Adults were common in open areas, roadsides, and forests from sea level to the highest elevations. The flight is erratic and low to the ground. Both sexes were seen visiting flowers. Oviposition was observed on leaves and flower buds of various Leguminosae. Eggs greenish laid singly on *Phaseolus atropurpureus* D.C., *P. mollis* Hook, *Desmodium incanum* DC and *Galactia striata* (Jacq). Caterpillar green with the head and prothoracic shield black. In the last instar the body is brown. Pupa pale brown speckled with darker brown.

Flowers visited. Acanthaceae: *Justicia galapagana* Lindau; Asteraceae: *Darwiniothamnus tenuifolius* (Hook. f.) Harling, *Scalesia cordata* Stewart, *Scalesia microcephala* Robins, *Scalesia villosa* Stewart, *Scalesia retroflexa* Hemsley; Boraginaceae: *Cordia leucophlyctis* Hook, *C. lutea* Lam.; Convolvulaceae: *Merremia aegyptica* (L.) Urban, Leguminosae: *Acacia insulaeiacobi* Riley, *P. mollis;* Malvaceae: *Sida rhombifolia* L.; Plumbaginaceae: *Plumbago scandens* L.; Rubiaceae: *Diodia radula* Cham.& Schlecht; Rutaceae: *Citrus limon* (L.) Burn; Solanaceae: *Lycopersicon chesmanii* Riley, *Physalis pubescens* L.; Sterculiaceae: *Waltheria ovata* Cav.; Verbenaceae: *Lantana camara* L., *Lantana peduncularis* Anderss, and *Lippia strigulosa* Mart & Gal.

Flight period. Multivoltine with a peak in January and February.

Remarks. The holotype is in the California Academy of Sciences, San Francisco, USA (CAS); it bears the following label information: Galapagos Is, Chatham I. [San Cristóbal], X 15 06, Coll. By F. X. Williams, California Academy of Sciences Type No. 3209. A specimen deposited on CAS has the following label information: Puerto Vallarta, Jalisco, Mexico, VIII 21 32, M Willow Jr coll, Exp 1932. This could be a mislabelling. Evans (1952) treated it as a subspecies of *Urbanus dorantes* (Stoll, 1790) compared to *Urbanus dorantes santiago* (Lucas, 1856) from Cuba and *U. dorantes dorantes* from mainland Ecuador, *U. dorantes galapagensis* is smaller and has shorter hindwing tails. The male valve is much less dentate and the arms of harpe have few spines. The genus *Urbanus* Hübner 1807, is used provisionally here until revisionary work is undertaken. According to S.

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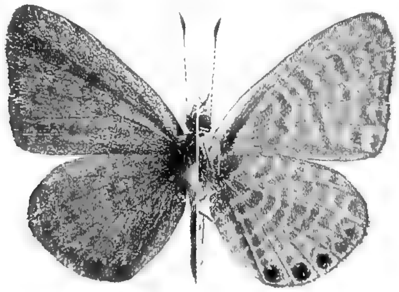

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FIGS. 1–8. Galápagos butterflies species. **1,** *Urbanus galapagensis* (DW and VW); **2,** *Calpodes ethlius* (DW); **3,** Male of *Leptotes parrhasioides* (DW and VW); **4,** Male of *Hemiargus ramon* (DW); **5,** Male of *Hemiargus ramon* (VW); **6,** Female of *Hemiargus ramon* (DW); **7,** Female of *Phoebis sennae marcellina* (DW); **8,** Male of *Phoebis sennae marcellina* (DW).

Steinhauser (pers. com.) the species may belong in a separate, undescribe genus.

Material studied. (70♂ and 16♀). ECUADOR, Galápagos. ESPAÑOLA: Hood, 15 V 1899, [R. E. Snodgrass, E. Heller] (CAS) (1♂). Bahía Manzanillo, 24 IV 1992, B. L[andry] (CNC), (2♂). FERNANDINA: 1 IX 1966, (CDRS) (1♂), Cueva Norte, Arid zone, 20 VI 1998, L. R[oque] (CDRS) (1♂). FLOREANA: Arid zone, 130 m, 17 IV 1996, L. R (CDRS) (8♂ and 3♀). Cerro Pajas, *Scalesia* forest, 320 m, 18 IV 1996, L. R (CDRS) (6♂). Cerro Pajas 520 m, 19 IV 1996, L. R (CDRS) (9♂). Charles, 5 X 1899, [R. E. Snodgrass, E. Heller] (CAS) (5♂). ISABELA: Tagus Cove, III 1906, Alotype, F. X. W[illiams] (CAS) (1♀). Cowley Mt, VIII 1906, F. X. W (CAS) (3♂). Albemarle, 27 IV 1932, M. Willows (CAS) (1♂); 28 IV 1932, M. Willows (CAS) (1♀). Albemarle, 12 VI 1899, [R. E. Snodgrass, E. Heller] (CAS) (1♀). Albemarle Iguana Cove, 21 V 1932, M. Willows (CAS) (2♀). V[olcán] A[lcedo] 800 m., 2 IV 1996, L. R (CDRS) (5♂ 2♀). V S[ierra] N[egra], 2 III 1989, S. B. Peck (CNC) (1♂). VSN, 6 IV 1996, L. R (CDRS) (1♂ 1♀). VSN, Las merceditas 120m, 24 IV 1996, L. R (CDRS) (1♂ 7♀). Sierra Negra pampas ferns zone, 24 IV 1996, L. R (CDRS) (1♀). Santo Tomás, 20 III 1995, P. Delgado (CDRS) (3♂); 6 IV 1996, L. R (CDRS) (2♂); 23 IV 1996, L. R (CDRS) (1♂); 23 IV 1996, (CDRS) (1♂). V W[olf], 1200 m, *Scalesia* forest, 19 IV 1996 (CDRS) (7♂ 4♀). Playa Tortuga Negra, 22 VI 1998, L R (CDRS) (1♂). PINTA: Abingdon, 24 VI 1899, [R. E. Snodgrass, E. Heller], (CAS) (1♂). PINZON: Playa escondida, 20 IV 2002, L. R & B. Landry (CDRS) (2♂ 3♀). RABIDA: Sendero turístico, 13 III 1998, L. R, (CDRS) (1♂). SANTA CRUZ: Horneman farm 220m, 18 III 1964, (1♂); 3 V 1964, (2♀), D. Q. Cavagnaro, (CAS). Puerto Ayora, 17 I 1989, B. L (CNC) (1♂); 8 XI 1995, A. Herrera (CDRS) (1♂); 29 X 1995, L. R, V. Cruz (CDRS) (1♂). 4 km N Puerto Ayora, 20 I 1989, B. L (MECN) (1♂). Tortuga Reserve W Santa Rosa, 6 V 1989, S. B. Peck (CNC) (1♂); 6 II 1989, B. Landry (CDRS) (1♂). Cerro Crocker, 9 II 1996, L. R (CDRS) (1♂), Bellavista, 13 II 1999, reared from leaves *D. canum,* L. R (CDRS) (4♂ 1♀); Punta Nuñez, 29 VII 2002, R. Boada (CDRS) (1♀). SAN CRISTOBAL: Chatam, X 1905, F. X. W, (CAS) (3♂); 1 X 1906, Holotype, F. X. W (CAS) (1♂); 23 V 1899, [R. E. Snodgrass, E. Heller], (CAS) (6♂ 1♀); 15 IV 1932, (3♂); 17 IV 1932, (1♂); 18 IV 1932, (2♂), M. Willows, (CAS). Puerto Baquerizo, 17 II 1989, S. B. Peck (CNC) (1♂). Airport 30 m, 6 III 1996, L. R (CDRS) (6♂ 2♀). SANTIAGO: James, 21 IV 1899, [R. E. Snodgrass, E. Heller], (CAS) (2♀). Central 700 m, 9 IV 1992, B. L (CNC) (1♂).

Hesperiinae

Calpodes ethlius (Stoll, 1782) "Canna Skipper"
(Fig. 2)

Papilio ethlius Stoll 1782:212.
Calpodes ethlius; Onore & Mielke 1988:619; Peck et al. 1998:227.

Diagnosis. FW = 19.5–24 mm. The Canna Skipper is a large brown species with translucent spots on the wings. Diagnostic features include a linear row of four spots on the HW and the absence of a tail. Specimens collected in the Galápagos are similar in shape and size to mainland specimens.

Geographical distribution. This species is widely distributed from Florida to Argentina including the West Indies. In the Galápagos Islands it has been reported previously from Isabela (Onore & Mielke 1988) and here from Santa Cruz Island.

Natural history. *Calpodes ethlius* is a powerful flyer that is most active at dawn and dusk, but is also seen at other times of the day. The species is most abundant in urban areas and gardens but it has the ability to find isolated hosts inside the forests. Eggs are pale green and laid singly on the leaves of *Canna edulis* Kerr and *Canna lutea* Mill (Cannaceae), which have been introduced to the Archipelago.

Flowers visited. Verbenaceae: *Clerodendrum molle* HBK.

Flight period. Specimens have been collected in February, April, May and July.

Remarks. Peck et al. (1998) listed this large skipper as recently introduced in the archipelago, and it is a known migrant (Ferguson et al. 1991).

Material studied. (5♂ and 1♀). ECUADOR, Galápagos. ISABELA: VSN, 1 km W Santo Tomás, 12 V 1996, ex larvae, L. R (CDRS) (1♂). SANTA CRUZ: Road to Baltra, 11 VI 1981, Y. Lubin, (CDRS) (1♂). Puerto Ayora, 24 VII 1996, (CDRS) (3♂); 18 II 1998, (CDRS) (1♀); 22 IV 1998, L. R (CDRS) (1♂)

PIERIDAE

Coliadinae

Phoebis sennae marcellina (Cramer, 1779)
"Sulfur Butterfly"
(Figs. 7, 8)

Papilio marcellina Cramer 1779:103.
Callidryas eubele; Holland 1889:195; Williams 1911:296; Beebe 1923:55.
Catopsila eubele; Van Duzee 1933:140.
Phoebis sennae; Linsley & Usinger 1966:156; Parkin et al. 1972:103.
Phoebis sennae marcellina; Moreno et al. 1997:146.

Diagnosis. FW = 24–36 mm. Easily recognized, it is the only yellow butterfly on the Galápagos Islands. Male: bright yellow. Female*:* yellow with black spots along the outer margins of the wings and a black spot with a pale center at the end of the forewing cell above. Galápagos populations are very variable in color pattern and size, but are identical with mainland specimens in genitalic features.

Geographical distribution. *Phoebis sennae marcellina* flies from México to Uruguay (D'Abrera 1981). In the Galápagos Islands the species has been previously reported from Baltra, Daphne, Edén, Fernandina, Floreana, Isabela, Pinta, Santiago, San Cristóbal, and Santa Cruz (Linsley & Usinger 1966) and is here reported from Marchena.

Natural history. One of the most common species on the Galápagos Islands. Adults occur in open habitats such as beaches, dry forests and roadsides from sea level to 900 m. Both sexes have been observed visiting flowers and puddles. The flight is fast and erratic. Beebe (1924) reported a southeast migration of this species from Santiago and Isabela to Santa Cruz, and individuals have been observed commonly flying between islands. Williams (1911) reported *Senna picta* G. Don as a host plant in Galápagos. Females have been observed laying eggs in *Senna tora* L., *Senna bicapsularis* L., and *Senna occidentalis* L. (Fabaceae).

Flowers visited. Acanthaceae: *J. galapagana;* Apocynaceae: *Catharanthus roseus* (L.) G. Don; Asteraceae: *Bidens pilosa* L.; Boraginaceae: *C. leucophlyctis, C. lutea, Heliotropium angiospermum* Murr., *Tournefortia rufo-sericea* Hook. f.; Cactaceae: *Opuntia insularis* Stewart; Convolvulaceae: *Ipomoea pes-caprae* (L.) R. Br., *Ipomoea nil* (L.) Roth; Leguminosae: *S. picta;* Malvaceae: *Gossypium barbadense* var. *darwinii* (Watt.) Hutch, *Hibiscus rosa-sinensis* L., *S. rhombifolia;* Nyctaginaceae: *Bougainvillea spectabilis* Willd, Plumbaginaceae: *P. scandens;* Rubiaceae: *D. radula;* Verbenaceae: *L. camara, Verbena litoralis* HBK.

Flight period. Multivoltine. Specimens have been seen throughout the year.

Material studied. (32♂ and 10♀). ECUADOR, Galápagos. FERNANDINA: Cabo Douglas, 15 IV 1999, P. Polo (CDRS) (1♂). ISABELA: VA, Pega-pega, 6 IV 1999, L. R[oque] (CDRS) (1♂). Puerto Villamil, 2 III 1989, B. L[andry] (CNC) (1♂). Arid Zone, 7 III-1989, S. B. Peck (CNC) (1♂). VSN, 6 IV 1996, L. R (CDRS) (5♂ and 2♀). VSN, Santo Tomás 300 m, 26 IV 1996, L. R (CDRS) (8♂). VSN, Pampas, 24 IV 1996, L. R (CDRS) (1♂ and 3♀). VSN, La Bocanilla 1000 m, 28 IV 1996, L. R (CDRS) (2♂). VSN, Alemania 350 m, 29 IV 1996, L. R (CDRS) (2♂). Playa Tortuga Negra, 22 VI 1998, L. R (CDRS) (3♂). MARCHENA: Playa Negra, 30 IV 2000, L. R, (CDRS) (1♂). SAN CRISTÓBAL: Puerto Baquerizo, 17 II 1989, B. L (CDRS) (2♂); El Porvenir, 15 III 1996, L. R (CDRS) (1♂ and 5♀). SANTA CRUZ: Santa Cruz, 8 VIII 1990, C.K McMullen (CDRS) (1♂). SANTIAGO: Los Jaboncillos, XII 1974, (CDRS) (1♂); Espumilla, 17 III 1998, L. R (CDRS) (1♂).

LYCAENIDAE

Polyommatinae

Leptotes parrhasioides (Wallengren 1860)

"Galápagos Blue Butterfly"

(Fig. 3)

Lycaena parrhasioides Wallengren 1860:37; 1861:355.
Cupido parrhasioides; Williams 1911:300, Beebe 1923:55; Van Duzee 1933:143; Moreno et al. 1997:158.
Leptotes parrhasioides; Bridges 1988:I 268, Linsley & Usinger 1966:157; Balint & Jonhson 1995:9.

Diagnosis. This species and the following are the only lycaenid butterflies in the Galápagos Islands. Both are similar, but the wing pattern and genitalia are distinctive. FW = 8–12.5 mm. Male: DFW and DHW violet blue with two or three black anal spots. VW ground color grayish with a pattern of white markings. VHW with three or four marginal spots, black in the middle, and filled with metallic blue. Female: similar to male but DW ground brown or blue.

Geographical distribution. Endemic to the Galápagos Islands, and reported from the islands of Baltra, Edén, Española, Fernandina, Floreana, Isabela, Pinzón, San Cristóbal, Santa Cruz, Santiago (Linsley & Usinger 1966). It is reported here from Marchena, Pinta and Rábida.

Natural history. Common in the arid zone of the islands. The flight is slow and close to the ground, but may also be rapid and erratic. Both sexes have been seen visiting flowers and were often observed on muddy puddles early in the morning or after rainfall. The pale green eggs are laid singly on the flowers, young fruits, or young leaves of host plants. Williams (1911) reported *Cardiospermum halicacabum* L. as a host plant and indicated *Cardiospermum galapageium* B. L. Rob. & Greenm (Sapindaceae) as another probable food plant. New hostplants records include: *P. scandes*, *Crotalaria incana* L. and *Rhynchosia minima* (L.) DC. (Leguminosae). The larvae are variable, either green or red with a pattern of dark dorsal marks, depending on the host. The body is covered by short white hairs. Pupae are greenish with brown markings.

Flowers visited. Acanthaceae: *J. galapagana;* Asteraceae: *Darwiniothamnus lancifolius* (Hook. f.) Harling; Boraginaceae: *H. curassavicum, Tournefortia psilostachya* HBK, *T. rufo-sericeae;* Cucurbitaceae: *Momordica charantia* L.; Cyperaceae: *Cyperus ligularis* L.; Leguminosae: *Vigna luteola* (Jacq.) Benth.; Linaceae: *Linum cratericola* Eliass; Lythraceae: *Cuphea racemosa* (L. f.) Spreng.; Malvaceae: *S. rhombifolia,* Plumbaginaceae: *P. scandens;* Nyctaginaceae: *Commicarpus tuberosus* (Lam.) Standl.; Solanaceae: *L. cheesmanii;* Zygophyllaceae: *Tribulus cistoides* L.

Flight period. The species is multivoltine.

Remarks. Wallengren (1860) described this endemic species from at least one male and one female [locality not specified] collected in May 1852 on the Galápagos. However, in 1861 Wallengren redescribed the species with additional material labelled "Puna" [gulf of Guayaquil] and "San Jose island" [Panamá]. Balint and Jonhson (1995) studied a specimen labeled "type" in the Naturhistoriska Riksmuseet, Stockholm, Sweden (NRS). They stated that this specimen belongs to the sister species *Leptotes trigemmatus* (Butler) and that the specimens involved in the redescription (Wallengren 1861) were incorrectly associated with the original series from the Galápagos. The real type of *L. parrhasioides* was not examined, although it is probably located in NRS.

Material studied. (52♂ and 12♀). ECUADOR Galápagos. ESPAÑOLA: Bahía Manzanillo, 25 IV 1992, B. L (CNC) (1♂). FERNANDINA: Narborough, 16 IV 1906, F X W[illiams], (CDRS) (1♀). Near to summit 4800ft, 5 II 1964, D. Q. Cavagnaro, (CAS) (3♂). Cabo Douglas, 21 VI 1998, L. R[oque] and C. C[auston], (CDRS) (3♂ and 2♀). Campamento Perez South Punta Espinoza, 18 VI 1998, L. R and C. C, (CDRS) (7♂ and 4♀). Cueva norte, 20 VI 1998, L. R and C. C, (CDRS) (4♂ and 2♀). North Side 300m, 12 I 2002, L. R and C. C, (CDRS) (1♀). Zona de vegetacion, 20 VI 1996, L R, (CDRS) (4♂ and 3♀). FLOREANA: Charles, 10 X 1905, F X W, (CAS) (2♀); 23–31 V

1906, F X W, (CAS) (1♀); 1–4 VI 1906, FXW, (CAS) (2♂). Zona costera, 2 IV 1995, L. R and V. Cruz, (CDRS) (1♂). *Scalesia* forest, 4 III 1995, L. R and V. Cruz (CDRS) (12♂ and 4♀). Arid zone 130m, 4 III 1995, in *H. curassavicum* flowers (3♂); in *C. molle* flowers (1♂), L. R and V. Cruz (CDRS). Road to the highland, 4 III 1995, L. R and V. Cruz (CDRS) (3♂). Parte alta, 4 III 1995, L. R and V. Cruz (CDRS) (1♂). Cerro Alieri 340 m, 21 XII 1999, in *Linum cratericola* flowers, L. R, (CDRS) (1♂). ISABELA: Albemarle Banks Bay, 16 X 1906, F X W, (CAS) (2♂). Albemarle Tagus Cove, 22 III 1906, F X W, (CAS) (1♂). V[olcan] S[ierra] N[egra] 1000 m, 1 III 1989, B. L (CNC) (1♀). V[olcan] W[olf], *Scalesia* forest 1700 m, 19 V 1996, L. R (CDRS) (4♂). V W, Upper arid zone, 1250 m, 20 IV 1996, L. R (CDRS) (13♂). Playa Tortuga Negra, 22 VI 1998, L. R, (CDRS) (8♂ and 7♀). PINTA: Playa Ibetson, 14 III 1992, B. L (CNC) (1♂ and 1♀); reared from leaves *R. minima*, 14 III 1992, B. L (CNC) (1♂). 400 m, 17 III 1992, B. L (CNC) (2♂). PINTA: Abingdon green zone, 10 IV 1906, F X W, (CAS) (1♀). PINZON: Summit & upper caldera areas, 7 II 1964, D. Q. Cavagnaro, (CAS) (1♂). SANTIAGO: James bay low altitud, VIII 1932, M. Willows, (CAS) (1♂). SANTA CRUZ: Indefatigable, 8 VI 1932, M. Willows, (CAS) (4♂ and 1♀). Academy Bay CDRS, 5 II 1964, R. O. Schuster, (CAS) (1♂); 25 II 1964, D. Q. Cavagnaro and R. O. Schuster, (CAS) (1♂). Arid Zone, asociated to *Castela galapageia*, 19 I 1989, B. L (CNC) (2♀). Transition zone, 20 I 1989, B. L (CNC) (1♂). SAN CRISTOBAL: Chatam Sapho cove, 9 II 1906, F X W, (CAS) (1♂).

Hemiargus ramon (Dognin, 1887)
"Ramon's Blue Butterfly"
(Figs. 4–6)

Lycaena ramon Dognin 1887:23.
Hemiargus ramon; Roque et al. 1997:29; Peck et al. 1998:227.

Diagnosis. FW = 8.2–11.6 mm. Resembles *L. parrhasioides*, with which it flies, but *H. ramon* has two black dots in the VHW inner costal margin while *L. parrhasioides* has none. Male: DW and DHW violet blue, the outer margins thinly bordered with white. Female: DW and DHW dark with only a touch of blue at the wing base.

Geographical distribution. Distributed on the western slopes of the Andes from northern Chile to the south of Ecuador. This species was listed by Peck et al. (1998) as introduced in the Archipelago. It has been reported from the Galápagos Islands of Baltra, Española, Floreana, Isabela, San Cristóbal, Santa Cruz and Santiago (Roque et al. 1998) and is here reported from Fernandina, Pinzón, Santa Fé, Seymour Norte and Rábida.

Natural history. Common from the low arid zones to the highest elevations. Roque et al. (1997) reported seven leguminous plants as host of the species (*Acacia macracantha* Willd, *S. tora*, *Neptunia plena* Benth, *P. atropurpureus*, *Prosopis juliflora* D.C., *Tephrosia decumbens* (Benth), and one species of Cucurbitaceae: *Cucumis dipsaceus* Her. and one species of Oxalidaceae is reported here: *Oxalis dombeyi* A. St-Hil.

Flowers visited. Asteraceae: *Scalesia gordilloi* Hamann & Wium Anders., *S. pedunculata*; Boraginaceae: *T. rufo-sericeae;* Leguminosae: *T. decumbens*.

Flight period. Observed during all months of the year, but is most common during the rainy season (January to April).

Material studied. (42♂ and 12♀). ECUADOR Galápagos. ESPAÑOLA: Bahía Manzanillo, 24 IV 1992, (1♂); 25 IV 1999 (1♂), B. Landry, (CNC). FERNANDINA: Campamento Perez south Punta Espinoza, 18 VI 1998, L. R[oque] and C. C[auston] (CDRS) (1♂ and 2♀); Cabo Douglas, 21 VI 1998, L. R and C. C, (CDRS) (1♂). Zona de vegetación, 20 VI 1998, L. R and C. C, (CDRS) (1♀). FLOREANA: Zona Costera, 2 IV 1995, L. R and V. C[ruz] (CDRS) (8♂ and 5♀). High arid zone 150m, 4 III 1995, L. R and V. C (CDRS) (5♂). Road to Highland, 4 III 1995, L. R and V. C. (CDRS) (10♂ and 3♀). Parte media, 4 III 1995, in *Heliotropium curassavicum* flowers, L. R and V. C, (CDRS) (5♂). ISABELA: V[olcan] S[ierra] N[egra], 24 IV 1996, L. R (CDRS) (2♂ and 2♀). V S N, Las Merceditas 120m, 24 IV 1996, L. R (CDRS) (1♀). V S N, 2 km W Puerto Villamil, 3 VI 2000, C. Covell (CDRS) (6♂ and 2♀). PINZON: Playa escondida, 20 VI 2002, L. R and B. L, (CDRS) (3♂ and 3♀). SANTA CRUZ: Arid Zone, 8 IX 1999, L. R and C. Covell (CDRS) (2♀ and 4♂); 19 I 1989, B. L, (CNC) (3♂ and 3♀).

NYMPHALIDAE
Danainae
Danaus gilippus thersippus (Bates 1863)
"Queen Butterfly"
(Fig. 11)

Papilio thersippus Bates 1863.
Danaus gilippus; Parkin et al. 1972:103; Linsley 1977:29.
Danaus gilippus thersippus; Ackery & Vane-Wright 1984:208.

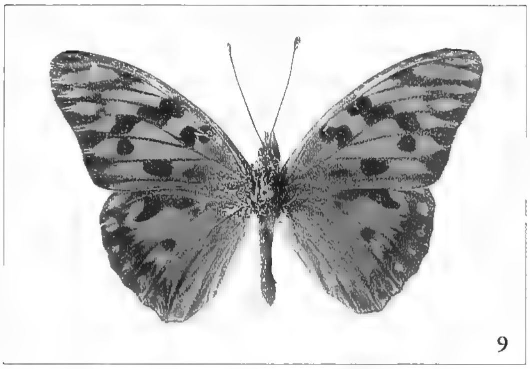
Diagnosis. FW = 36–41 mm. Easily distinguished from *D. plexippus* L. by not having the black inner border, and the black veins on the DFW. Males have a black androconial patch on the DHW. Females are similar to males but without an androconial patch.

Geographical distribution. *Danaus gilippus thersippus* is distributed from the Southern United States to Panamá and is native to the Galápagos Islands. The species has been reported from San Cristóbal (Parkin et al. 1972), and is here reported from Baltra, Floreana, Isabela, Santa Cruz, Santiago, Seymour Norte and Rábida.

Natural history. The queen butterfly is primarily an inhabitant of the arid zones from sea level to 400 m, but its distribution is limited by the occurrence of its foodplants. Adults have been observed flying slowly and frequently visiting flowers in open areas. The pale green eggs are laid singly on young and old leaves of the endemic vine *Sarcostenma angustissima* R. W. Holm. The other milkweed that occurs on the islands, *Asclepias curassavica* L., apparently is used as an alternative food plant.

Flowers visited. Asclepiadaceae: *A. curassavica, S. angustissima;* Asteraceae: *D. tenuifolius;* Boraginaceae: *H. angiospermum;* Solanaceae: *P. pubescens;* Verbenaceae: *L. camara*.

Flight period. All available records are from the rainy season.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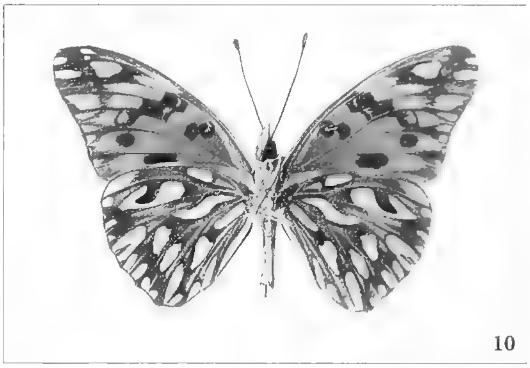
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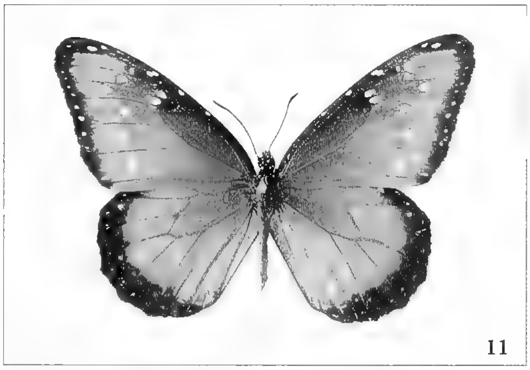
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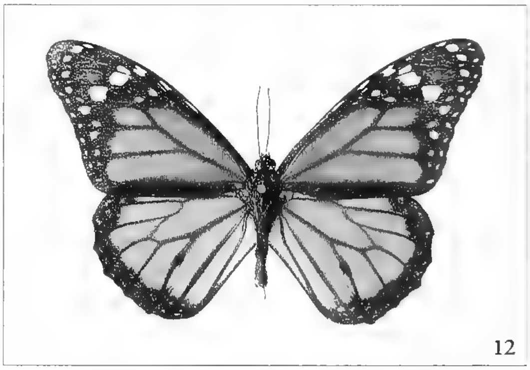
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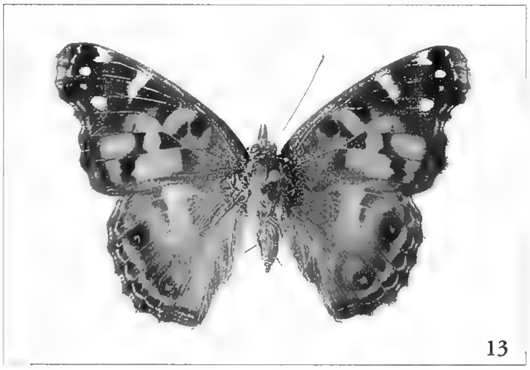
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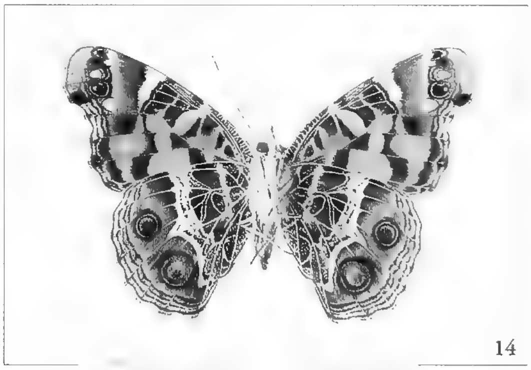
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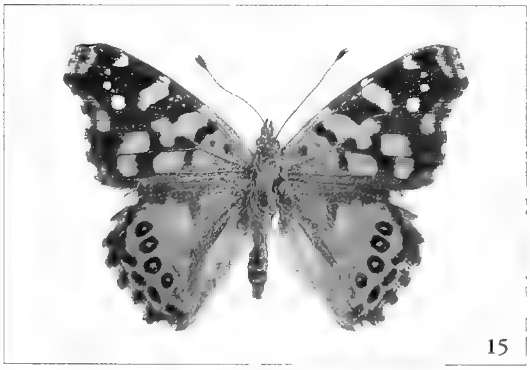
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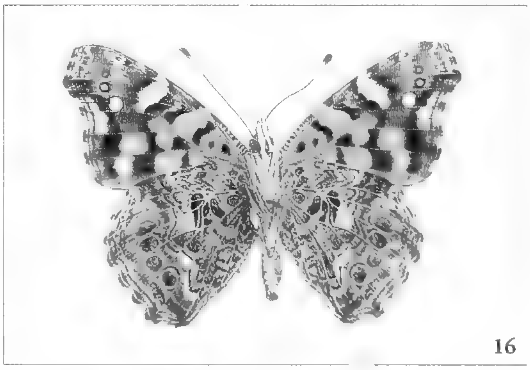
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FIGS. 9–16. **9,** *Agraulis vanillae galapagensis* (DW); **10,** *Agraulis vanillae galapagensis* (VW); **11,** *Danaus gilippus thersippus* (DW); **12,** *Danaus plexippus megalippe* (DW); **13,** *Vanessa virginiensis* (DW); **14,** *Vanessa virginiensis* (VW); **15,** *Vanessa carye* (DW); **16,** *Vanessa carye* (VW).

Remarks. Ackery and Vane-Wright (1984) suggested that this species could have been introduced from California to the islands in recent times. Based on its current distribution and the well-established dispersal potential, and taking into consideration the dates of discovery of the butterfly and its host plants, it is reasonable to assume that *D. g. thersippus* arrived in the Archipelago through natural dispersal mechanisms and was not introduced by humans.

Material studied. (23♂ and 9♀) ECUADOR, Galápagos. FERNANDINA:, Cueva Norte, L. R[oque], (CDRS) (2♂ and 1♀). Campamento Perez south Punta Espinoza, 18 VI 1998, L. R and C. Causton, (CDRS) (1♂). FLOREANA: Cerro Pajas, 20 IV 1996, L. R (CDRS) (1♀). Arid zone, near to Black beach, 22 IV 1996, L. R (CDRS) (2♂). C. Cruz farm, 24 VI 1996, L. R (CDRS) (4♂). Asilo de la Paz 342m, 23 IV 1996, L. R (CDRS) (4♀ and 4♂). ISABELA: Playa Tortuga Negra, 22 IV 1998, L. R (CDRS) (8♂ and 3♀). Volcan Sierra Negra Alemania 350 m, 29 IV 1996, L. R, (CDRS) (10♂ and 6♀). Volcan Sierra Negra pampas, 24 IV 1996, L. R, (CDRS) (1♀). SAN CRISTÓBAL: Puerto Baquerizo, 17 II 1989, B. L, (CDRS) (1♂); (MECN) (1♂).

Danaus plexippus megalippe (Hübner, [1826])
"The Monarch"
(Fig. 12)

Anosia megalippe Hübner [1826]:2, pl. 7, fig. 2.
Danais plexippus; Beebe 1923:55.
Danaus plexippus; Linsley & Usinger 1966:157; Roque 1998a:9, b:10.
Danaus plexippus megalippe; Ackery & Vane-Wright 1984:201.

Diagnosis. FW = 35–50 mm. This species is easily distinguished from *D. gilippus* by having the DFW apex boldly black, a black inner border in DFW and prominent black veins. Males have a black androconial patch on the DFW. Females are similar to males but much darker.

Geographical distribution. The Monarch is native in the Galápagos Islands and reported from Floreana, San Cristóbal and Santa Cruz. The status of this species has been discussed in some detail by Roque (1998a). *Danaus plexippus megalippe* is distributed from Nicaragua to Perú including the North east of Brazil, Venezuela, French Guiana, Surinam, Guyana, Trinidad, Tobago and some islands of the West Indies (Ackery & Vane-Wright 1984).

Natural history. Common in open areas such as fields, roadsides and disturbed sites. In general, the localities where the species occurs are mesic, but there are a few records in arid zones. Galápagos populations do not migrate. The adults fly slowly and visit flowers. Females have been observed ovipositing on the milkweeds *A. curassavica* and *S. angustissima,* but the latter is used as an alternative host plant.

Flowers visited. Asclepiadacea: *A. curassavica;* Malvaceae: *H. rosa-sinensis*; Verbenaceae: *L. camara, V. litoralis.*

Flight period. Adults commonly occur only in the rainy season, but are observed sometimes in the dry season.

Material studied. (13♂ and 5♀). ECUADOR, Galápagos. FLOREANA: Cerro Pajas, 20 IV 1996, L. R[oque], (CDRS) (1♂ and 1♀). Arid zone, near to Black beach, 22 IV 1996, L. R, (CDRS) (4♂ and 4♀). Finca de C. Cruz, 24 VI 1996, L. R (CDRS) (1♂). Asilo de la Paz 342 m, 23 IV 1996, L. R, (CDRS) (4♂). SAN CRISTOBAL: Puerto Baquerizo, 17 II 1989, B. Landry (CDRS) (1♂); (CNC) (1♀); (MECN) (1♀). SANTA CRUZ: El cascajo, II 1999, L. R, (CDRS) (1♀). Salasaca, 22 VIII 2000, R. Oquendo, (CDRS) (1♂).

Heliconiinae

Agraulis vanillae galapagensis (Holland 1889)
"Galápagos Fritillary"
(Figs. 9, 10)

Agraulis vanillae galapagensis Holland 1889:194; Williams 1911:298; Beebe 1923:55; Van Duzee 1933:141.
Dione vanillae galapagensis; Stichel 1938:92; Michener 1942:4; Linsley & Usinger 1966:156.

Diagnosis. FW = 19–29 mm. This species is distinguished by its silver markings on the VW. The females are paler than males.

Geographical distribution. Endemic to the Galápagos Islands. It has been collected on Baltra, Edén, Fernandina, Floreana, Isabela, Pinta, San Cristóbal, Santa Cruz, and Santiago (Linsley & Usinger 1966).

Natural history. This is a common species on the larger Galápagos Islands. Adults have been observed in open areas and forests from sea level to the highlands. Beebe (1924) cited an interesting migration along the West Coast of Isabela Island. Adults usually fly slow, low to the ground and frequently have been seen visiting flowers. Williams (1911) mentioned species of the genus *Passiflora* L. as food plants of this fritillary in the Archipelago, but he did not mention which. Oviposition was observed on *Passiflora suberosa* L. and *Passiflora tridactylites* Hook. (Passifloraceae). The eggs were laid singly on young leaves. The larvae are black with green longitudinal stripes. The head and body are covered with long black spines.

Flowers visited. Acanthaceae: *Blechum brownei* Juss. f., *J. galapagana*; Asclepiadaceae: *S. angustissima;* Boraginaceae: *Croton scouleri* Hook. f.; Cannaceae: *Commelina diffusa* Burdm. f.*;* Malvaceae: *S. hederifolia* Cav., *S. paniculata* L., *S. salviifolia* Presl.*;* Rubiaceae: *D. radula;* Rutaceae: *C. limon*; Sterculiaceae: *Waltheria ovata* Cav.*;* Verbenaceae: *L. camara, Stachytarpheta cayennensis* (Rich.) M.Vahl.

Flight period. All specimens were collected in the rainy season but individuals were observed during all months of the year except August and September.

Remarks. This species has been treated by several authors as a subspecies of the widely distributed American species *Agraulis vanillae*. Holland (1889) and Williams (1911) stated that the Galápagos taxon should be raised to specific status based on several differences in the wing pattern. Michener (1942) recognized the differences in the wing maculation and size, and mentioned some variation in the male genitalic valvae. Specimens studied here were collected on several localities of the Archipelago.The male genitalia are generally similar to those of mainland specimens of *A. vanillae* but differ consistently in the valva. The apex of the valva is more slender and with fewer denticules in *A. v. galapagensis*. The female genitalia are similar in both forms. *Agraulis vanillae galapagensis* can be separated from the other described subspecies by the smaller size, by the darker and more fuscous color of the basal half of the wings dorsally, by the stronger black markings on the wings, and by the absence of white dots in the black spots of the DFW discal cell. The holotype, collected on Chatham [San Cristóbal], is deposited in the National Museum of Natural History, Washington, DC (USNM). The identity of this species will remain questionable until a revision of the genus makes it more definite.

Material studied. (14♂ and 51♀). ECUADOR, Galápagos. FERNANDINA: Campamento Perez south Punta Espinoza, 18 VI 1998, L. R[oque] and C. Causton, (CDRS) (1♂). FLOREANA: Arid zone 130m, 17 IV 1996, L. R, (CDRS) (1♂). Cerro Pajas, *Scalesia* forest, 18 IV 1996, (9♂ and 5♀); 19 IV 1996, L. R, (1♀); 22 IV 1996, L. R (CDRS) (7♂ and 2♀). ISABELA: V[olcán] S[ierra] N[egra], Santo Tomás, 6 IV 1996, (1♂); 26 IV 1996, L. R, (CDRS) (1♂). V S N, bosque de los niños, 20 III 1995, L. R, (CDRS) (1♂). V S N, pampas 1000m, 1 III 1989, B. L[andry] (CNC) (1♀). V S N, la bocanilla 1000m, 28 IV 1996, L. R, (CDRS) (2♂ and 1♀). V S N, Las merceditas, 30 IV 1996, L. R, (CDRS) (2♂ and 4♀). Volcan Wolf, upper arid zone 1700 m, 19 V 1996, L. R, (CDRS) (13♂ and 4♀). PINTA: 400 m, 17 III 1992, B. L, (CNC) (4♂). SANTIAGO: Playa Espumilla, 4 IV 1992, B. L, (CNC) (1♂). SANTA CRUZ: CDRS, 22 XI 1963, (CDRS) (1♂). Tortugas reserve west of Santa Rosa, 6 II 1989, B. L, (CDRS) (1♂); (MECN) (1♂).

Nymphalinae

Vanessa virginiensis (Drury 1773)
"Painted Lady"
(Figs. 13, 14)

Nymphalis cardui virginiensis Drury 1773:1.
Pyrameis huntera; Williams 1911:299.
Vanessa virginiensis; Linsley & Usinger 1966:156.

Diagnosis. FW = 21.7–29 mm. Differs from *V. carye* by the presence of two blue-centered ocular markings on the VHW. Males and females are similar.

Geographical distribution. This cosmopolitan species was previously reported from Isabela (Volcanoes Darwin and Sierra Negra) (Williams 1911). On Isabela, the species was found at those localities as well as on volcanoes Alcedo, Cerro Azul and Wolf. Other new records include Santa Cruz and Santiago and it probably also inhabits other large islands. The species is distributed from southern Canada to the mountainous region of Colombia, including the West Indies, Hawaii, Azores, Madeira, the Canary Islands, and occasionally Europe (DeVries 1987).

Natural history. This species has only been observed in the open grassy areas of the highlands. All specimens were collected above 900 m in the pampa zone. Although it flies usually under bright and sunny conditions, we have seen it under overcast conditions and even during light rain (Volcán Alcedo, 23.X.1998). Adults fly fast and rest on the ground, flying short distances when disturbed. Eggs, larvae and pupae were found on the leaves of *Gnaphalium purpureum* L. (Asteraceae) on the islands of Isabela and Santiago. The plant can be found on more islands (Lawesson et al. 1987). *Vanessa virginiensis* has resident populations in the Galápagos Islands.

Flowers visited. Rubiaceae: *Borreria laevis* (Lam.) Griseb.

Flight period. Specimens have been collected or observed from January to June.

Material studied. (15♂ and 4♀). ISABELA: Albemarle, 20–31 VIII 1906, F X Williams, (CAS) (1♂). V[olcán] S[ierra] N[egra], rim northwest side, 4 III 1989, B. L[andry], (CDRS) (1♂); (MECN) (1♂). V S N, 1000 m, 4 III 1989, S. B. Peck (CNC) (1♀). V S N, La Bocanilla 1000 m, 28 IV 1996, L. R[oque], (CDRS) (1♂ and 4♀). V S N, Las Merceditas, 6 IV 1996, L. R, (CDRS) (1♂). Volcán Wolf, high arid zone, 1250 m, 21 V 1996, L. R, (CDRS) (4♂). Volcan Alcedo, top 1100 m, 24 IV 1998, L. R (2♂ and 4♀). SANTA CRUZ: CDRS, 10 VI 1965, (CDRS) (1♂). SANTIAGO: Los Jaboncillos 900 m, 9 IV 1992, B. L, (CNC) (1♀); 16 III 1998, L. R, (CDRS) (1♂). Los Aguacates, 16 III 1998, L. R (CDRS) (1♂). NW slope 600 m, 30 V 1964, D. Q. Cavagnaro, (CAS) (1♀).

Vanessa carye Hübner [1812]
"Western Painted Lady"
(Figs. 15, 16)

Hamadryas carye Hübner [1812]:pl. 45, figs. 1, 2.
Pyrameis caryae; Williams 1911:300.
Vanessa caryae; Linsley & Usinger 1966:156.

Diagnosis. FW = 21–28 mm. Differs from *V. virginiensis* by having four small blue-centered ocular markings on the VHW.

Geographical distribution. This species has been collected on San Cristóbal, Fernandina, and recently observed by the author in Floreana. *Vanessa carye* is distributed in the Andes of Colombia, Ecuador, Peru, Bolivia, Chile, southwestern Brazil, Paraguay, Uruguay, and Argentina. It also occurs on Juan Fernandez island, on Easter island, and the Tuamotu Archipelago.

Natural history. Three out of four specimens collected or observed were from the low arid zone at sea level. Two fresh adults were observed visiting flowers on Floreana (13 I 1995 and 6 II 1995, Puerto Velazco Ibarra) but were not collected. Their fresh condition suggested that they were from a population extant on the island, rather than migrants. The host plant and the immature stages are unknown in the Archipelago.

Members of Asteraceae, Geraniaceae, Malvaceae, and Urticaceae are reported as host plants for the species (Field 1971).

Flowers visited. Verbenaceae: *C. molle.*

Flight period. Adults have been collected or observed in January and February.

Remarks. The only two specimens collected on the Galápagos were deposited in the California Academy of Sciences.

Material studied. (1♂ and 1♀). FERNANDINA: near to summit, 4800 ft, 5 II 1964, D. Q. Cavagnaro, (CAS) (1♀). SAN CRISTOBAL: Chatam, Wreck Bay, 22 II 1906, (CAS) (1♂).

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HOST BREADTH AND VOLTINISM IN GALL-INDUCING LEPIDOPTERA

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ABSTRACT. Because of specialized life systems and host relations, gall-inducing insects are believed to have narrower host breadth and lesser voltinism than other endophagous insects. These expectations were tested here using a sample of 136 species of British Lepidoptera consisting of 29 gallers in 11 families and 107 taxonomically matched endophagous nongaller controls. Gallers and nongallers were compared using biological data assembled and published by A. M. Emmet. Host breadth, scored as number of host genera, averaged 1.21 for the gallers, and 1.48 for the nongallers, and the difference is statistically significant, thus confirming host breadth expectation for this sample of Lepidoptera. This difference was generated mostly among Gelechiidae, Nepticulidae, Tortricidae, and Sesiidae. Voltinism, scored as number of generations developing per year, did not differ between gallers and nongallers. This outcome does not necessarily refute the hypothesis underlying the expectation. The cool British climate may inhibit multivoltinism, and thereby minimize differences in voltinism between gallers and nongallers.

Additional key words: Gelechiidae, Nepticulidae, Tortricidae, Sesiidae, Britain.

Galls induced by Lepidoptera vary from simple swellings to fruitlike bodies that bear little resemblance to supporting host parts. The galls are organ specific, most developing on host stems, but some developing on host reproductive structures, leaves, and roots. With few exceptions, larvae rather than ovipositing adults induce the galls. Worldwide, 352 morphospecies of gall-inducing Lepidoptera are known, of which 179 have been identified to genera and species in 20 families (Miller 2004). Greater numbers and taxonomic diversity of lepidopteran gallers are anticipated as tropical areas are explored.

Gall-inducing insects, including Lepidoptera, are believed to have narrower host breadth and to develop fewer annual generations than other endophagous insects (Cornell 1990, Raman 1994, Miller 2004). Narrow host breadth is expected because evolutionary adjustments between gall inducer and host foster foodplant specialization, a corollary of the reputed host specificity of gall inducers (Mani 1964, Shorthouse & Rohfritsch 1992, Harris & Shorthouse 1996). Lesser voltinism is expected because gall inducers seem to synchronize their phenology with that of their hosts, which would ensure that larvae have access to reactive tissues necessary for gall development, as during rapid plant growth in spring. Physiological mechanisms that might mediate this synchrony have not been investigated. These host breadth and voltinism expectations for lepidopteran gall inducers would acquire added strength if empirical tests confirmed them.

Cornell (1990) compared voltinism and other life history traits between gall inducers and leaf miners. His voltinism sample consisted of 28 species–12 leaf miners, mostly lepidopteran, and 16 gall inducers, mostly dipteran and hymenopteran. He found that voltinism averaged 1.4 generations/yr for the gall inducers and 2.5 generations/yr for the leaf miners, which is consistent with the expectation of lesser voltinism among gall inducers. In contrast to voltinism, host breadth of gall inducers in one or any combination of insect orders does not seem to have been compared empirically with that of endophagous nongallers.

Reported here are comparisons of host breadth and voltinism between gallers and nongallers in a large sample of Lepidoptera, an order poorly represented in previous cecidological studies (Miller 2004). The source of the data analyzed is Emmet's (1991) extensive life history tabulation for more than 2400 species of British Lepidoptera, the most extensively known lepidopteran fauna in the world.

MATERIALS AND METHODS

To test the hypotheses that gall-inducing Lepidoptera have narrower host breadth and lesser voltinism than other endophagous Lepidoptera, I assembled a study sample of 29 gallers and 107 endophagous nongaller controls, 136 species in all. All known British gallers were included, as listed by Spooner and Bowdrey (1995), with emendations as follows: *Argyresthia retinella* Zeller, unaccountably absent from the list, was added (Robbins 1992), and *Paranthrene tabaniformis rhinglaeforme* (Hübner), now considered synonymous with *P. tabaniformis* (Rottemburg), was removed (Špatenka et al. 1999).

The 107 endophagous nongallers were those marked in Emmet's (1991) tabulation exclusively with *b* for borer or *m* for miner, and, for *Heliozela* only, also with *c* for casebearer to match the casebearing *Heliozela* gallers. Taxonomic matching was possible at the generic level for gallers in 10 genera, and at the subfamily level for gallers in six genera, in line with principles of the comparative method (Harvey & Pagel 1991). For example, matches for the two *Ectoedemia* (Nepticulidae) gallers consisted of the 15 nongalling endophagous *Ectoedemia*, and the match for the galler *Adaina microdactyla* (Hübner) (Pterophoridae, Platyptiliinae), which has no British congeners, was *Leioptilus carphodactyla* (Hübner), the only other endophagous British member of the subfamily Platyptili-

TABLE 1. Host breadth and voltinism of British gall-inducing Lepidoptera and taxonomically matched endophagous nongallers. Data from Emmet (1991) except where noted otherwise. Family sequence follows Kristensen (1999).

Family	Species as numbered in Emmet's tabulation	N	Mean scores	
			Host breadth	Voltinism
Nepticulidae				
Gallers	23, 24	2	1.00	1.00
Nongallers	25–32, 34–39, 41	15	1.27	1.00
Heliozelidae				
Gallers	154, 157	2	1.00	1.00
Nongaller	156	1	1.00	1.00
Incurvariidae				
Gallers	138, 139	2	1.00	1.00
Nongallers	133, 136	2	1.00	1.00
Yponomeutidae				
Gallers	411, 415	2	1.50	1.00
Nongallers	401, 404, 405, 407, 410, 412, 418, 420, 422	9	1.33	1.00
Elachistidae				
Galler	906	1	1.00	1.00
Nongaller	905	1	1.00	1.00
Coleophoridae				
Gallers	486, 889, 891, 892, 893a[1]	5	1.00	1.25
Nongallers	487, 880–884, 887, 888, 890	9	1.00	1.33
Gelechiidae				
Gallers	728, 755	2	1.00	1.00
Nongallers	723–727, 727a, 729, 730, 735, 737, 744, 744a, 746–748, 753, 757, 808, 811–813, 816, 817, 821, 822, 823a, 825	27	1.71	1.33
Sesiidae				
Gallers	372, 377, 380	3	1.33	0.67
Nongallers	373–379, 381	8	1.50	0.75
Tortricidae				
Gallers	966, 1137, 1167, 1190, 1195, 1256, 1258, 1266	8	1.37	1.06
Nongallers	962, 964, 965, 967, 1168, 1192, 1194, 1196, 1197, 1199, 1200, 1200a, 1201, 1202, 1240, 1242, 1243, 1245–1247, 1249, 1253–1255, 1257, 1259–1261, 1264, 1265, 1267, 1268–1270	34	1.56	1.06
Pterophoridae				
Galler	1517	1	1.00	2.00
Nongaller	1519	1	2.00	2.00
Crambidae				
Galler	1359	1	2.00	1.00
Nongallers	1375	1	1.00	2.00
Summary				
Gallers		29	1.21	1.07
Nongallers		107	1.48*	1.11

[1] *Mompha bradleyi* Riedl, whose discovery in Britain (Harper 1994) postdates Emmet (1991).

* Mann-Whitney $U_{134df} = 1280.0$, $p_{\text{one tailed}} < 0.05$.

inae. Nongallers outnumber gallers in the study because plausible matches were often more numerous than the gallers matched, all being included to avoid selection bias.

Host breadth and voltinism data were extracted for both the gallers and nongallers from Emmet's (1991) tabulation. Data for one galler subsequently discovered in Britain, *Mompha bradleyi* Riedl, was obtained from Harper (1994). Host breadth was scored as number of recorded host genera. This is a stringent measure in that no distinction was made between one and more than one host species in the same genus; however, the problem of appropriately scaling and integrating genus and species scoring was thereby avoided. Scoring by species alone could not be done because the source did not consistently list numbers of host species within genera. Voltinism was scored as number of annual generations, with the case of less than one annual generation (one generation every two years) being scored as 0.5. This case had minimal impact because it occurred in only 3 of the 29 gallers (2 sesiids and 1 tortricid) and 4 of the 107 nongallers (all sesiids).

Student's *t*, Mann-Whitney *U*, and statistical summaries were computed with SYSTAT (1992) software. Homogeneity of variance between galler and nongaller groups was examined before analysis as outlined by Sokal and Rohlf (1981).

RESULTS

The 29 British gall inducers represent 11 of the 20 families of identified lepidopteran gall inducers worldwide (Table 1; Miller 2004). Stem galls are induced by 21 of the gallers, petiole galls by 5, and reproductive-structure galls by 3 (Robbins 1992, Spooner & Bowdrey 1995).

Mean host breadth was 1.21 genera for gallers compared to 1.48 genera for endophagous nongallers. The difference, 0.27, is in the expected direction of fewer host genera for gall inducers, and is significant (*U*-test, Table 1). The nonparametric *U*-test was used because galler and control variances proved divergent. Host breadth ranged 1–2 for the gallers, and 1–4 for the nongallers.

The difference in host breadth between the two groups originated mainly within Gelechiidae, Nepticulidae, Tortricidae, and Sesiidae. In these families, host breadth means for nongallers exceeded those for gallers by 0.71, 0.27, 0.19, and 0.17, respectively (Table 1).

Mean voltinism was 1.07 annual generations for the gall inducers, compared to 1.11 annual generations for the nongallers (Table 1). The difference, 0.04, although in the expected direction, is not significant ($t_{134\mathrm{df}} = -0.53$, $p_{\text{one tailed}} = 0.30$). Galler and nongaller variances for voltinism proved to be homogeneous, which permitted the use of the parametric *t*-test. Voltinism ranged 0.5–2 for both gallers and nongallers.

DISCUSSION

Analysis of number of host genera supports the expectation of narrower host breadth for gall inducers than for endophagous nongallers among British Lepidoptera. This result (Table 1) might have been stronger had more elaborate scoring captured the intrageneric component of host breadth, but no objective method for combining or integrating genus and species scoring was available, and species counts alone could not be used because the source did not fully elaborate host species. Actual host breadth might also be stronger than indicated by the analysis for yet another reason: galls undoubtedly attract more interest and attention than other signs of insect infestation, so that host breadth of nongallers might be underreported compared to that of gallers, which could reduce the apparent difference.

Narrow host breadth is a trait that is highly desirable in biological control agents of weeds, one which, other things being equal, enhances the biological control potential of gallers (Harris & Shorthouse 1996, McEvoy 1996). Gelechiidae and Tortricidae, which are among the four families here with strongest differences between gallers and nongallers in host breadth (Table 1), are also the families with the greatest numbers of known gallers (Miller 2004).

Analysis does not support the expectation of lesser voltinism among gallers. This result (Table 1) contradicts Cornell's (1990) finding of lesser voltinism in gallers than leaf miners, but does not necessarily refute the hypothesis giving rise to the expectation. The British climate is cool–temperate and rainy, with the warmest month averaging less than 22°C (Lewis 1994). Such a climate may inhibit multivoltinism so that differences in voltinism between gallers and nongallers are minimized. By contrast, in eastern North America, a temperate land mass much larger than Britain, lepidopteran voltinism markedly increases as latitude decreases (Fracker 1920, Tauber et al. 1986). Multivoltinism in lepidopteran gall inducers, when it occurs, seems influenced more indirectly than directly by climate; that is, protracted growth seasons in warm temperate regions and in tropical wet cycles expand temporal availability of reactive host tissues for gall development (Miller 2004). Although Cornell (1990) did not taxonomically match gallers and leaf miners in comparing their voltinism, he reported no statistical connection between taxonomy and analytical outcome, and his result unequivocally shows lesser galler voltinism. Further testing of the voltinism expectation would be desirable. Possible mechanisms underlying galler–host phenological synchrony might include higher thermal thresholds for galler than nongaller development, and differing diapause reactions.

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GENERAL NOTES

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NEW RANGE EXTENSIONS, LARVAL HOSTPLANT RECORDS AND NATURAL HISTORY OBSERVATIONS OF CUBAN BUTTERFLIES

Additional key words: Euphorbiaceae, Fabaceae, Bignoniaceae, Acanthaceae, Rutaceae.

Although butterflies have not been thoroughly collected in Camagüey province, a checklist of the territory has been recently published as the result of field surveys and collections completed during the last ten years (Fernández & Rodríguez 1998). The latter complements the preliminary work of Guerra et al. (1993), who reported 76 butterflies and skippers. This updated and augmented list included 125 species, but their residency status has not been entirely determined within the province due to the paucity of information available for some of them. A few have only been collected or observed on one or two occasions due to the short collecting time available.

Here, I report range extensions for the nymphalid *Antillea pelops anacaona* (Herrich-Schäffer), the lycaenid *Strymon acis casasi* (Comstock & Huntington) and the hesperiid *Achlyodes munroei* Bell, which represent new butterflies for the province. The associated larval hostplants for these species and for six other butterflies and biological, ecological and distributional data are also discussed. Voucher adult specimens of the three newly recorded species are deposited in the author's collection and a pair of *A. munroei* with associated pupal exuvia has been deposited in the collection of the Allyn Museum of Entomology, Florida Museum of Natural History.

These observations were made between May 1996 and November 2001 in the following localities in Camagüey province: Albaiza, Camagüey city, Central Cándido González, Limones, Loma de Yucatán and Santa Ana (south of the INIVIT Experimental Station). The fourth and the fifth sites were areas not previously sampled. Additional information was also obtained from other field trips at the southern slope of Sierra de Cubitas in 1988, 1994 and 1996.

NYMPHALIDAE

***Anaea cubana* (H. H. Druce).** One fifth and four fourth instar larvae were found in the leaves of *Croton sagraeanus* Muell. Arg. (Euphorbiaceae) at Limones in June. All were inside vertical tubular shelters, open at both ends, and formed by tying together various longitudinally interconnected leaves. The caterpillar always enters the upper and wider opening and backs into the tube (caudal end first) once it returns from feeding. Once inside, the conspicuous head capsule remains exposed at the entrance. The fourth instar larvae were fed with the leaves of *Croton argenteus* L. instead of the original host. They accepted the new foodplant and completed development to the adult stage. On this plant, the larvae either lived exposed or tied the edges of an individual leaf for shelter. *Croton argenteus* was growing spontaneously along roadsides in the surroundings of the city of Camagüey. Pupation took place in the underside of the leaves of the host (in the field, a pupal exuvia was also found on the underside of a *C. sagraeanus* leaf) and lasted 9 (n = 2 males) and 10 (n = 2 females) days. The adults were not abundant at the collecting site but seen during all of the field visits, flying along hedgerows and roadsides and attracted to fallen, ripe mangoes.

According to Alayo and Hernández (1987), the larva of *A. cubana* was reared by Gundlach on *Pectis* (Asteraceae) species. As all other species of *Anaea* have been reported to be confined to Euphorbiaceae (Smith et al. 1994), this record on Asteraceae is likely a mistake.

***Hamadryas amphichloe diasia* (Fruhstorfer).** Two larvae were found on leaves of *Dalechampia scandens* L. (Euphorbiaceae) at Loma de Yucatán. There were not records of foodplants for this Antillean subspecies but Smith et al. (1994) mentioned that species of *Dalechampia* or *Tragia* were likely to serve as host.

***Antillea pelops anacaona* (Herrich-Schäffer).** Seven specimens of this endemic subspecies (five males and two females) were taken at Limones in June and September. These were found in humid, shady undergrowth beneath a mango tree in a wooded area. The individuals were perching on plants less than 1 m tall, with both wings slightly, partly or fully open (but not pressed against the leaves). Sometimes the butterflies flexed their wings at a rapid rate or were seen flying just above or between the low vegetation. At times, the flight may be slow and weak, but it can also be quite agile and difficult to follow. All these adult behaviors combined to make the butterfly inconspicuous supporting the observations made by Smith et al. (1994) that they may be overlooked unless present in numbers. A male nectaring on *Alternanthera axillaris* (Hornem.) D. Dietr. (Amaranthaceae) and a specimen thermoregulating with wings partly open before midday were other behaviors observed for the butterfly.

Two fourth instar larvae were independently collected on *Blechum pyramidatum* (Lam.) Urb. and *Justicia comata* (L.) Lam. (both Acanthaceae) in September. One of the larvae pupated and emerged as an adult male after six days. The butterfly appears to be resident, and on the last two visits to the area in September, I observed two fresh pairs. This tiny nymphalid was reported by Alayo & Hernández (1987) in Gran Piedra and Sardinero, Santiago de Cuba, in eastern Cuba; and Pinares de Viñales and Luis Lazo, Pinar del Río, to the west. They are always seen in small isolated groups. Fontenla (1987) also reported it from a wooded area of Parque Lenin, Ciudad de La Habana.

LYCAENIDAE

Strymon acis casasi **(Comstock & Huntington).** Three adults and a last instar larva of this endemic subspecies were taken at Limones in May and June. The first specimen found was a rather worn female that perched on a low-growing plant of *Dichrostachys cinerea* Willd. (Fabaceae). It was collected just after an erratic and instantaneous flight along a path between dense groups of the exotic legume. The two other specimens, a badly worn female which was released and a fresh male, were collected on *C. sagraeanus* flowers. A larva was also collected in the same area as the adults and was reared on the *Croton* flowers until pupation. However, the adult did not emerge. Other lycaenids, including many male *Ministrymon azia* (Hewitson) and some *Strymon columella cybira* (Hewitson), *Leptotes cassius theonus* (Lucas), *Hemiargus hanno filenus* (Poey) and *Cyclargus a. ammon* (Lucas) were also present and nectaring on the *Croton* flowers. *S. acis casasi* was not seen commonly, and more visits to the locality will be required for further observations to determine the peak months of adult activities. Alayo and Hernández (1987) cited this subspecies as rare, being only collected around Guantánamo province or some other localities of the extreme eastern part of the island.

Strymon columella cybira **(Hewitson).** A last instar larva was found on *C. argenteus* flowers in Camagüey city. In Cuba, a wide range of foodplants is now known for this lycaenid, not only in the Malvaceae but also members in the Acanthaceae, Portulacaceae, Sterculiaceae and Surianaceae (Fernández 2001).

Leptotes cassius theonus **(Lucas).** Larvae were always found feeding on flowers. In Camagüey city, larvae were on *Albizzia lebbeck* (L.) Benth., *Calliandra surinamensis* Benth. and *Pithecellobium dulce* Benth. (Fabaceae). In Albaiza, larvae were on *Calopogonium mucunoides* Desv. (Fabaceae), and in Central Cándido González, they were on *Clytostoma callistegioides* Bur. (Bignoniaceae), a plant family not previously recorded for the lycaenid. The hostplants for *L. cassius* are generally herbaceous legumes but Malpighiaceae and Plumbaginaceae are also used (Smith et al. 1994).

HESPERIIDAE

Proteides maysi **(Lucas).** Oviposition on the underside of a leaflet of *Andira inermis* (Wright) Kunth ex DC. (Fabaceae) was observed at Limones. After eclosion, the larva was reared on *Lonchocarpus dominguensis* (Turp. ex Pers.) DC. (Fabaceae) through the fifth instar but died due to excessive humidity in the rearing container. No previous life history information was available for this endemic Cuban skipper (Smith et al. 1994).

Burca concolor concolor **(Herrich-Schäffer).** The larvae of different instars were commonly observed on *C. sagraeanus* leaves at Limones in May, June and September. They construct shelters by using interconnecting leaves or bending them inward and sealing the unions between margins, and using a tomentum present on the underside of leaves. Earlier instar larvae build a shelter on the ventral surface of a single leaf just using this tomentum and feed on leaf edges. Active feeding occurs only on the upper side (leaving the tomentum) which produces the effect of a chlorotic or scraped leaf. Later instar larvae cut out the leaf section where they have fed so damaged parts are not visible on the plant. Pupation takes place in the shelter and lasts 8–9 days (n = 3).

The adults were more numerous only in June. The males constantly patrolled around and between *Croton* stands at low or medium height from the ground. The females also joined males in this behavior with ovipositions in some cases; one female was also taken while perching with closed wings on a *Gliricidia sepium* (Jacq.) Kunth ex Walp. (Fabaceae) leaflet to a height of about 4 m. Individuals of both sexes were seen taking nectar with wings fully open on flowers of the hostplant, but males also visited *Koanophyllon villosum* (Sw.) R.M. King et H. Rub. (Asteraceae). Solitary males were observed sipping water at the edges of mud puddles. This skipper appears to be resident and fairly common at Limones.

In addition, several larvae were also found on *Croton origanifolius* Lam. at Albaiza in August and November. Here, no adults of this species had been recorded during previous field studies but upon locating the immatures, a female was observed in the nearby hostplant patch at a latter date. This individual took nectar on *C. origanifolius* and on *Bourreria microphylla* Griseb. (Boraginaceae), and later alighted with wings open on dry grasses on the ground, where its presence was inconspicuous.

Burca c. concolor was recorded for the first time in Camagüey in 1988 near Paso de los Paredones in the dry plains of the southern slope of Sierra de Cubitas hills where the species was seen along roadsides. In more recent years (1994 and 1996), it has also been found there again and seen at times in abundance. Individual specimens have been observed alighting on stones or low plants and nectaring on *Waltheria indica* L. (Sterculiaceae) flowers. In addition to the above mentioned localities, other specimens of this skipper have been also taken in a wooded tract around the lower part of Loma de Yucatán in June. Due to its general associations with grasses and open areas, this species is probably originating from the adjacent savannas.

This endemic subspecies is considered as very rare in Cuba (Alayo & Hernández 1987), recorded from pico Potrerillo, Escambray; Cuabales de Corral Nuevo, Matanzas; Tortuguilla, Guantánamo; playa Juraguá, Santiago de Cuba. Smith et al. (1994) have added playa Ancón, near Trinidad as another collecting site. The discovery of the foodplant association with *Croton* of this species will not only help to understand the significance of the local occurrence of the skipper but may perhaps encourage a wider search of this species in local foodplant patches.

***Achlyodes munroei* Bell.** Miller and Simon (1998) mentioned that apparently the last known specimens of *A. munroei* were collected over a half century ago by Pastor Alayo, despite continued diligent search for it in Cuba by Luis Roberto Hernández and others. Some lamented that this insect might be extinct. Although older *A. munroei* specimens were found in the coastal locality of Siboney, Santiago de Cuba (Smith et al. 1994), the area for the recently collected ones is an inland site, primarily a cattle pasture with many trees and low-growing bushes, including two *Zanthoxylum*. Here *A. mithridates papinianus* (Poey) is a more common inhabitant and found in various larval stages, which utilize all rutaceous trees available (including *Citrus*). This area remains abandoned for some periods that allows plant regrowth and formation of very suitable habitats, not only for resident butterflies but for temporary colonizers, such as *A. munroei*.

I found this species as larvae in leaf shelters of *Zanthoxylum martinicense* (Lam.) DC. (Rutaceae) in August at Santa Ana. A male was captured in November 2001, at the same site. Apart from the perching posture of the third collected specimen, with wings fully open and resting on leaves at about 40 cm high from the ground, no other distinct behaviors were seen.

Until very recently, *A. munroei* was considered to be an endemic Cuban species, but it has subsequently been found on Cat Island, Bahamas. Recent collections there suggest that the insect is well established and will probably be recorded on other Great Bahama Bank islands in the future (Miller & Simon 1998). The discovery of the species in Camagüey not only confirms that *A. munroei* still exists in Cuba, but it may well prove to be also more widely distributed as further field studies are conducted by resident entomologists.

I wish to thank Adelaida Barreto (CIMAC, Camagüey) and Eddy Martínez (BIOECO, Santiago de Cuba) for their invaluable assistance in the identifications of the larval foodplants and nectar sources. Special thanks to Drs. Lee and Jacqueline Miller (Allyn Museum of Entomology) for confirming identification of *A. munroei*, helping with the English and reviewing the manuscript. My wife Noris V. Verdecia and Carlos A. Sacasas also helped during preparation of the manuscript and warrant my thanks.

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IMMATURE STAGES OF *CALYDNA VENUSTA MORIO* (RIODINIDAE) FROM TRINIDAD

Additional key words: balloon setae, Olacaceae, *Ximenia americana*.

Trinidad, which forms part of Trinidad and Tobago, has a long history of entomological exploration, and successive generations of resident and visiting collectors have together compiled a reasonably complete picture of the butterfly fauna of this species-rich, continental island. The landmark publication for the country, Barcant's (1970) "Butterflies of Trinidad and Tobago", recognized 103 riodinid species from Trinidad. Nevertheless, new records of Riodinidae continue to be added, and the authors are preparing an updated checklist. One of these additions is *Calydna venusta morio* Stichel (Riodininae: *incertae sedis* section), discovered in 1984 by S. Alston-Smith at Point Gourde, on the northwestern peninsula of Trinidad, as indicated in D'Abrera (1994) and Hall (2002). This taxon is poorly represented in collections, but can be locally common in nature from central Panama through northern Colombia and Venezuela to Trinidad, the Guianas, and eastern and southern Brazil, where it occurs in relatively dry habitats (Hall 2002).

MJWC visited Point Gourde, still the only known locality for *C. venusta* in Trinidad, on 16 May 1999, and observed *C. venusta* females flying slowly in amongst the low, dry, scrubby forest, resting beneath leaves with wings outspread and, in the vicinity of the Coast Guard Station on the top of Point Gourde, visiting flowers of *Bidens pilosa* L. (Asteraceae) (Fig. 1). Several late instar caterpillars of *C. venusta* were also found there and reared through to adults. A partial life history for the species is described and illustrated here for the first time.

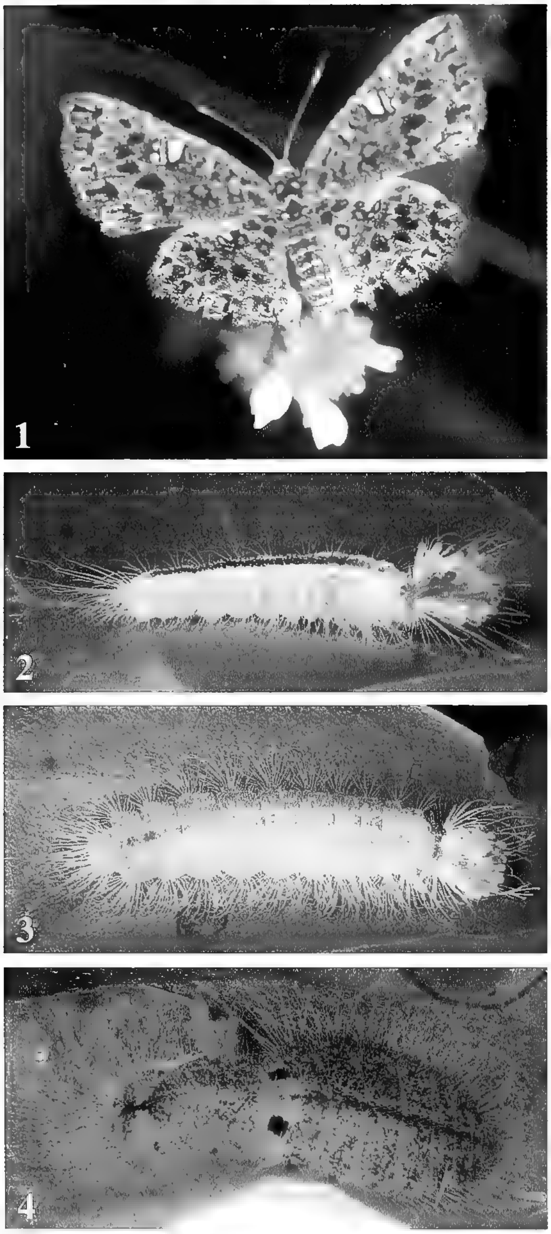
Rearing notes. While searching for caterpillar shelters of Hesperiidae, several fourth and fifth instar caterpillars of *C. venusta* were found in shelters on a single bush of *Ximenia americana* L. (Olacaceae) growing alongside the forest track. This plant is a semi-scandent bush-forming shrub or tree, 2–7 m high, that is sometimes semi-parasitic, with haustoria on the host roots (e.g., Mabberley 1987). The larvae were in leaf shelters, made by rolling one edge of a leaf upwards and tying the edge to the leaf lamina with strands of silk. There were small (2–3 mm) black ants on the bush and in the shelters, but no interactions were observed between the caterpillars and these ants. A herbarium specimen of the food plant was prepared (MJWC 0252) and subsequently identified at the National Herbarium of Trinidad & Tobago.

Two fifth instar and one fourth instar caterpillars were collected and reared (ref. MJWC 99/4) using leafy twigs of *X. americana* that were cut at the time of larval collection and stored in refrigerated plastic bags until used. The caterpillars were kept in individual plastic screw-top jars (5.7 cm height × 5.8 cm diameter) at ambient conditions in Trinidad until 19 May, and thereafter at 25°C in a constant-temperature quarantine room. When not feeding, the caterpillars rested in leaf shelters. The caterpillar collected as fourth instar took approximately 10 days to complete the fifth instar. Pupation was in a silk-lined shelter between two leaves, and adults eclosed between 10 and 13 days later. The three reared adult females are currently in the collection of MJWC, but voucher specimens will be deposited in the collections of the National Museum of Natural History, Washington, and CABI Bioscience, Curepe, Trinidad and Tobago.

The egg and first through third instar caterpillars remain unknown, and here we briefly describe only the fifth instar caterpillar and pupa. The fourth instar caterpillar (total length 10 mm on 16 May, moulted by 20 May) (Fig. 2) differs primarily from the fifth instar (Fig. 3) by having a red-purple dorsal line.

Fifth instar (total length 17 mm on 15 May, prepupa on 20 May) (Fig. 3): The head is approximately circular and slightly translucent pale brown. The prothoracic shield is pale brown, medially desclerotized dorsally, and bears two types of setae anteriorly that form a prominent corona over the head. The first type of seta, known as a balloon seta (first described by Guppy (1904) in two *Theope* species from Trinidad), is long, inflated, pinkish-fawn and slightly distally expanded to a rounded tip. The second type is longer, slender and whitish. T2 and T3 are pale green and evenly scattered with tiny wedge-shaped setae (Hall et al. 2004). The abdomen is pale green, with a slightly darker green, dorsal, longitudinal stripe, bounded on each side with a narrower whitish band that continues to the posterior edge of A9. The dorsal surface is generally smooth, with scattered wedge-shaped setae as on T2–T3, and each segment has a lateral fringe of long white setae. The spiracles are white. At the prepupal stage, the caterpillars turned reddish-purple.

Pupa (total length 10 mm) (Fig. 4): The pupa is slightly dorso-ventrally compressed and pale brown with variably dense darker brown speckling. The abdomen has a dark brown dorsal line, and the metathorax has a pair of large, round, black spots. The spiracles are white and surrounded by dark brown. Each abdominal and thoracic segment has long, whitish, lateral setae, and the mesothorax has a small cluster of fawn-colored balloon setae that project laterally on each side.



FIGS. 1–4. *Calydna venusta morio* at Point Gourde, Trinidad. **1,** Adult female feeding on *Bidens pilosa* flowers near the coastguard station on the hilltop at Point Gourde. **2,** Lateral view of fourth instar caterpillar (10 mm) 1–3 days before moult. **3,** Dorsal view of fifth instar caterpillar (17 mm) 3 days before prepupa. **4,** Dorsal view of pupa (10 mm).

Discussion. This is only the second species of *Calydna* to be reared. Dan Janzen and co-workers have reared *Calydna sturnula* (Geyer) on *Schoepfia schreberi* J.F. Gmel., also in the Olacaceae, numerous times since 1987 in the dry forest of northwestern Costa Rica, and the results are presented on their website (Janzen & Hallwachs 2003), briefly in Hall (2002), and in detail in Hall et al. (2004). This last paper included SE images of surface ultrastructure and a discussion on the phylogenetic implications of these findings. Although the caterpillars of *C. venusta* and *C. sturnula* are very similar, the most conspicuous difference being the pinkish-fawn instead of dark purple color of the balloon setae in *C. venusta*, the pupa of *C. venusta* is notable for also having balloon setae. This trait is found elsewhere in the Riodinidae only in *Helicopis* (Helicopini), but in that genus they are present on the prothorax instead of the mesothorax (Harvey 1987, Hall et al. in press). The absence of balloon setae on the pupa of *C. sturnula* might be explained by the fact that it belongs to a different species group than *C. venusta* (Hall 2002).

Ximenia americana, the food plant of *C. venusta*, is widespread in the tropics of the Americas, Africa, Asia and Australasia, and is especially associated with dry forests and coastal areas (World Agroforestry Centre 2003). Williams (1930) recorded it in the Flora of Trinidad and Tobago from only one locality in Trinidad, on the south coast beach between Erin and Chatham. However, more recent records include Erin Beach, Quoin Beach and Chacachacare Island (Y. Comeau pers. com). Point Gourde is therefore a new locality record. There is a small group of Trinidad butterfly species that have been found only on Chacachacare Island (to the west of Trinidad's northwestern peninsula, mid-way to the Paria Peninsula of Venezuela), Point Gourde and/or Gasparee Island (just south of Trinidad's northwestern peninsula): *Heliopyrgus domicella* (Erichson) (Hesperiidae), *Anteros carausius* Westwood (Riodinidae), and *Ascia (Ganyra) menciae janeta* Dixey (Pieridae) (Cock 1981, MJWC unpublished data, S. Alston-Smith pers. com.). These three localities represent the driest parts of Trinidad and its offshore islands where butterflies have been collected. It seems likely that *C. venusta* will eventually be found on Chacachacare Island, and perhaps at the south coast localities for *X. americana*.

MJWC thanks Scott Alston-Smith for introducing him to the Point Gourde site and sharing his experiences of this butterfly, and Winston Johnson and Yasmin Comeau at the National Herbarium of Trinidad & Tobago for identifying and checking the distribution of the food plant, respectively. JPWH thanks the National Science Foundation (DEB 0103746) for financial support.

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IMMATURE STAGES OF *AMPHIDECTA REYNOLDSI* (NYMPHALIDAE: SATYRINAE)

Additional key words: Bamboo feeders, Pronophilini.

Immature stages of butterflies are increasing in importance as sources of systematic characters, and often give important clues as to the placement of species in major groups (DeVries et al. 1985, Freitas et al. 2002). The Satyrinae genus *Amphidecta* Butler, 1867 has been placed in the Pronophilini by Miller (1968), although Viloria (2003, and in press) removed the genus from this tribe without assigning it to any other group. The species in this genus differ from all other known Pronophilini in morphology, habits and distribution (Miller 1968, Viloria pers. com.), with two species most common in Amazonian lowlands, and a third species, *A. reynoldsi* Sharpe, 1890 (Fig. 1), recorded from low to medium elevation sites in the states of Goiás, Mato Grosso, Minas Gerais, São Paulo and Santa Catarina, and in the Distrito Federal, in Brazil. The habitat of *A. reynoldsi* is riparian forest (including the populations in the Cerrado biome in Goiás, Mato Grosso, Minas Gerais and Distrito Federal), and dense rain forest (São Paulo and Santa Catarina).

The present paper describes the early stages of *A. reynoldsi*, comparing them with those of other known Pronophilini.

Study sites and methods. Adults of *Amphidecta reynoldsi* were studied in the field in two different localities in São Paulo State, SE Brazil: Montane forests in Intervales Park, Sede (Capão Bonito, 900–1100 m), and in the riparian forests of Monte Mor (600–650 m). One fertile egg was expressed from a very old wild caught female from Monte Mor on 10 November 2002 (no additional eggs were found in the abdomen). The larva was reared in a plastic container cleaned daily; fresh plant material was provided every two or three days (following Freitas 1991). Data were taken on behavior and development times for all stages, and head capsules and pupal casting were preserved (AVLF collection). Taxonomic nomenclature follows Miller (1968) and Viloria (in press).

Description of early stages. Egg. Spherical; cream, without visible ridges or marks under the optic microscope. Height 1.0 mm, diameter 0.9 mm. Duration: 5 days.

First instar (Figs. 1, 2). Head capsule light green with a transverse dark stripe in the front and a darker area between the pair of short scoli on vertex; five pairs of conspicuous pointed black setae (Fig. 2). Head capsule width 0.88 mm; head scoli 0.12 mm. Body beige (light green after feeding), with short black setae; a pair of subdorsal white stripes and additional longitudinal red stripes conspicuous on the last abdominal segments; a pair of short caudal filaments on A10. Maximum length 8.5 mm. Duration: 5 days.

Second instar. Head green with two long red diverging scoli on vertex. Head capsule width 1.16 mm; scoli 1.4 mm. Body slender, light green with many longitudinal white stripes; caudal projections salmon, long, parallel and fused. Maximum length 15 mm. Duration: 4 days.

Third instar. Head as in previous instar; width 1.8 mm, scoli 3.5 mm. Body slender, light bluish green with many longitudinal white lines; caudal projections salmon, long (similar to head scoli) parallel and fused. Maximum length 25 mm. Duration: 6 days.

Fourth (last) instar (Fig. 1). Head green with two long diverging scoli on vertex; these brown with black tips. Head capsule width 2.67 mm; scoli 5.67 mm. Body slender, light bluish green with many longitudi-

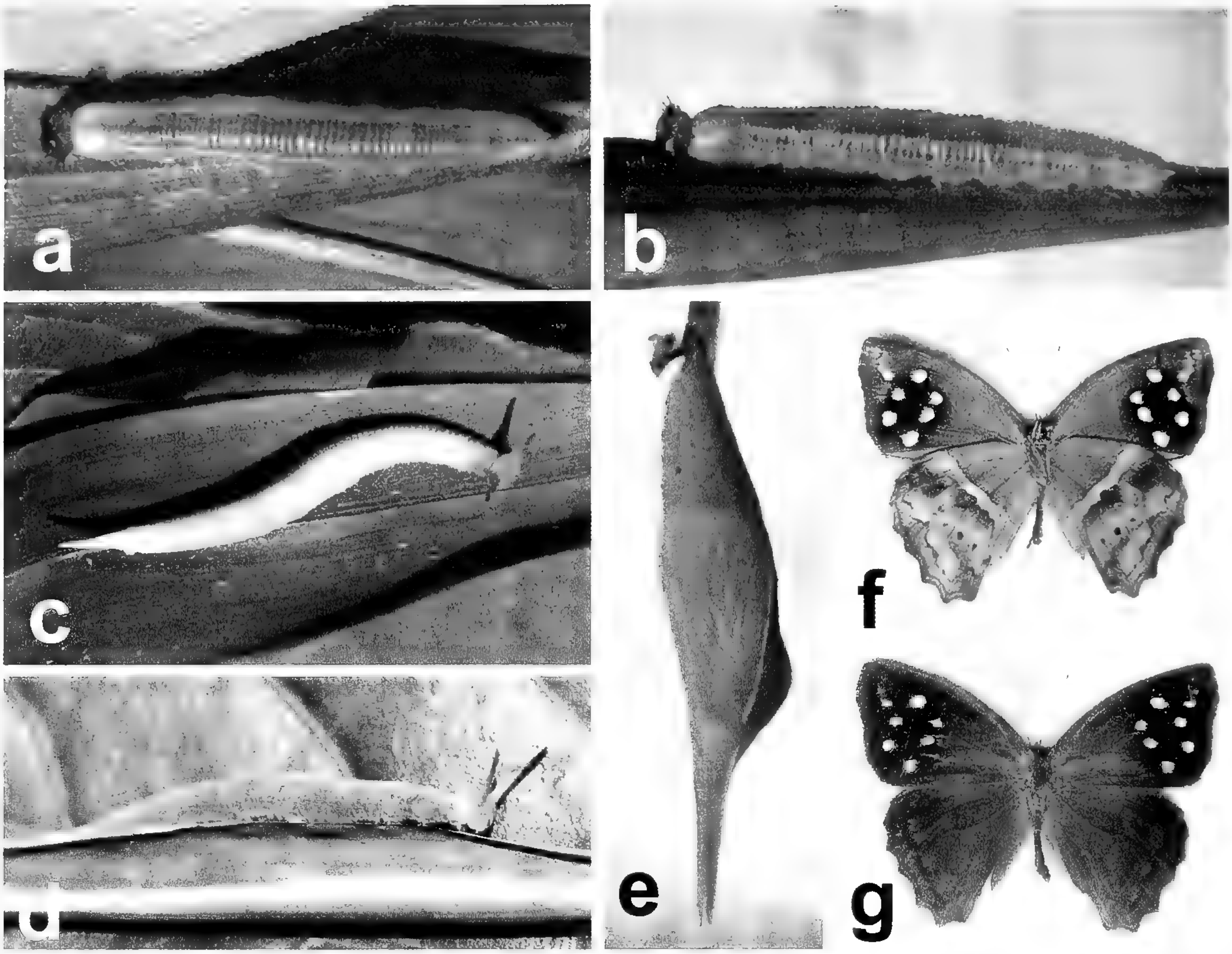

FIG. 1. Partial life cycle of *Amphidecta reynoldsi*. First instar: **a,** dorsal; **b,** lateral. Fourth (last) instar: **c,** dorsal; **d,** lateral. Pupa: **e,** latero-ventral. (Figs. **a–e** from specimens collected at Monte Mor, São Paulo.) Adult male: **f,** ventral; **g,** dorsal (Capão Bonito, São Paulo).

nal white lines; spiracles as well marked white circles; caudal projections light green with salmon ends, long, parallel and fused. Maximum length 38 mm. Duration: 8 days. The prepupal larva is entirely green, and suspended during the night.

Pupa (Fig. 1). Elongated, smooth, with long pointed ocular caps; light green with alar caps bordered with yellow. Total length 27 mm. Duration: 8 days.

Foodplants. The foodplant in the field is unknown, but the larva easily accepted a bamboo (*Merostachys*) from Campinas. The larva ate part of the egg chorion after hatching, and was very active in all instars. In resting position, the larva usually lay along a bamboo leaf with the head towards the leaf apex, becoming relatively inconspicuous. The rarely encountered adults are known from large bamboo thickets, where they are attracted to banana baits.

Discussion. Based on general aspect and habits, the immature stages of *A. reynoldsi* are very similar to those of *Eteona tisiphone* (Boisduval), a Pronophilini butterfly from the mountains of SE Brazil (Freitas 2002). These include the general shape of larva and pupa, and the foodplant accepted by the larva (a bamboo), but not the shape of the major primary setae on the head capsule (spatulate in *Eteona*). These external macroscopic characters are also similar to those found in most Andean Pronophilini (M. D. Heredia unpublished data), and are divergent from those found in most Neotropical Satyrinae, including the pronophilines in the genus *Pedaliodes* Butler, and relatives (Müller 1886, Pelz 1997, Viloria pers. com., and unpublished data from 3 species). More descriptions of Satyrinae immatures, especially pronophilines, together with extensive comparisons among adults of most Neotropical genera, are needed to clarify the systematic position of *Amphidecta* within the Satyrinae.

I would like to thank Dr. Keith S. Brown Jr. for reading the manuscript and capturing the female from Monte Mor, and the Fun-

FIG. 2. Head capsule (frontal view) of the first instar larva of *Amphidecta reynoldsi*.

dação Florestal for allowing fieldwork in the Fazenda Intervales. I also thank Gerardo Lamas, L. Daniel Otero and Carla Penz for comments in the final version. This study was funded by Fapesp (BIOTA-FAPESP program, grants 98/05101-8 and 00/01484-1) and by the National Science Foundation (DEB-0316505).

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DISPLAY OF THE "PEACOCK MOTH": *BRENTHIA* SPP. (CHOREUTIDAE: BRENTHIINAE)

Additional key words: *Anacampsis*, Cosmopterigidae, Gelechiidae, Momphidae, *Tebenna*, Tineidae, *Tortyra*.

Species of *Brenthia* Clemens, 1860 (Choreutidae: Brenthiinae) are diurnal microlepidopterans of both New and Old Worlds, with the majority of the 60–80 species confined to tropical areas. Several species are seen frequently in the lowland forests of the Republic of Panama, where they dart about on foliage, with their wings held in distinctive, peacock-like displays (Fig. 1). As the name of the type species, *Brenthia pavonacella* Clemens, 1860, suggests, "peacock" displays are common in *Brenthia*.

Descriptions of these displays are scattered in the literature. Of *B. pavonacella*, in northeastern U.S.A., Forbes (1923:353) comments, "The moth struts about on alighting, with hind wings displayed like *Glyphipteryx* [Cosmopterigidae], the smaller *Anacampsis* [Curtis, 1827, Gelechiidae], etc." And, of *B. coronigera* Meyrick, 1918, in India, Fletcher (1920:128) remarks that "The moths strut about jerkily with the hindwings carried nearly at a right angle with the forewings, so that the wings form a sort of cone when seen from behind the insect. This attitude is characteristic of other species of this genus." His account includes an illustrated lateral view of the moth displaying. According to Robinson et al. (1994:111, 113), some species of South-East Asian Choreutidae ". . . rest with the hind wing drawn forward in front of the forewing. Species of *Brenthia* also move holding their wings in this posture and are mimics of jumping spiders (Salticidae). . . . the metallic spots of the wing pattern representing the spider's eyes."

The purpose of this note is to further describe the display and clarify certain points pertaining to its me-

FIG. 1. *Brenthia* sp. nr. *confluxana* (Walker, 1863) wild adult displaying on a leaf. The two images shown are a side view (left), with the wings partly raised, and a rear view (right), with the wings in full display, of one and the same individual. To produce the photograph, two digitized images were overlain and matched up using the leaf debris as a guide. The photos were then cropped and fused to produce an image that aids visualization of the moth's darting movement. Photographs taken 7 April 1982, on Barro Colorado Island, by A. Aiello.

chanics, based on observations of several species of *Brenthia* in the Republic of Panama, and to comment briefly on display poses of other choreutids and other microlepidopterans. The 3 or 4 *Brenthia* species studied were not identified beyond genus, because authoritative species-level identifications are possible in the genus *Brenthia* only with genitalic dissection of males of species described by Meyrick and illustrated by Clarke (1969). Lot numbers are those of Aiello, and consist of the year plus a sequential number.

Specimens and observations. On 7 April 1982, on Barro Colorado Island, wild adults of *Brenthia* sp. nr. *confluxana* (Walker, 1863), were observed and photographed while they displayed on leaves (Fig. 1). On 12 January 1992, in Arraiján, Panama, two larvae of an unidentified species of *Brenthia* (sp. 1) were collected on *Cojoba rufescens* (Benth., 1845) Britton & Rose, 1928 (Mimosaceae), and reared to adults (Aiello lot 1992–5). Two more adults, apparently of *Brenthia* sp. 1, were collected for laboratory observation on 2 and 9 December 2001, in Arraiján. On 26 August 1993, on Barro Colorado Island, Donald Windsor (Smithsonian Tropical Research Institute, Panama–STRI) collected three pupae of a larger species of *Brenthia* (sp. 2) on *Calathea* sp. G. May, 1818 (Marantaceae). Adults were obtained from all three pupae (Aiello lot 1993–70).

Observations of the displays of six reared and two wild caught Panamanian *Brenthia* adults, under a dissecting microscope, revealed that their wing orientations were at odds with published reports that the moths draw the hind wings forward in front of the forewings to produce their displays. If they did do that, the dorsal surfaces of both hind and forewings would be visible when the display is viewed from in front (Fig. 2a), the hind and forewings would have to de-

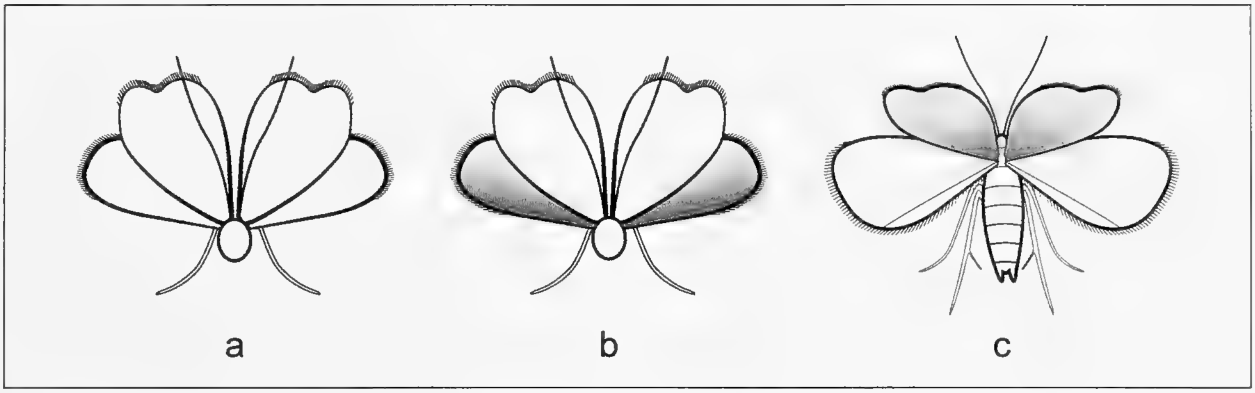

FIG. 2. Wing orientation diagrams (**white** = **dorsal** surface; **gray** = **ventral** surface): **a,** Front view. If the hind wings were drawn in front of the forewings, as stated in the literature, the dorsal surfaces of both wings would be visible; **b,** Front view. When hind wings were drawn upward by the forewings, in Panamanian *Brenthia* spp., the dorsal surface of the forewing and ventral surface of the hind wing were visible; **c,** Rear view. When hind wings were drawn upward by the forewings, in Panamanian *Brenthia* spp., the ventral surface of the forewing and the dorsal surface of the hind wing were visible.

couple, the costal margin of the forewing would be brought into contact with the posterior margin of the hind wing, and the hind wing would have to tilt forward.

Contrary to that, the moths we observed did not draw the hind wings forward in front of the forewings. Rather, they simply tilted the forewings to an angle 45 degrees to the body, thus drawing the costal margin of the hind wings up by means of the coupled frenulum and retinaculum, so that the hind wings were perpendicular to the forewings, and the wings and body formed a forward-pointing cone. In that pose, the ventral (not dorsal) surface of the hind wings was presented when the display was viewed from in front (Fig. 2b), and the costal margins of hind and forewings remained coupled with one another. Accentuating the conical shape of the display, the hind wing anal vein (A2) was creased strongly, so that its anal area (posterior margin) was perpendicular to the rest of the wing, and its posterior margin (edge) was directed towards the body (Fig. 2c).

Consistent with our observations of living moths, experimental manipulations of two individuals soon after death revealed that when the wings were in the normal resting position, folded over the body as a flat triangle, the display could be duplicated easily, merely by lifting the forewings.

We suspect that this simple display mechanism will prove universal in *Brenthia*. The illustrations of *B. coronigera* in Fletcher (1920, plate 32) show that the hind wing pattern of the spread moth (dorsal view) is different from the hind wing pattern of the displaying moth (lateral view), indicating that the ventral (not dorsal) surface of the hind wing was brought into view during the display, just as with Panamanian *Brenthia*.

Display behaviors in other choreutids. Though striking patterns and metallic wing markings are found in many choreutid genera, as far as is known, peacock-like displays are peculiar to *Brenthia*. However, a lesser degree of wing lifting was reported for another choreutid, *Tebenna micalis* (Mann, 1857), by Common (1993:292): ". . . they settle with their wings partly raised and curled. They walk erratically with a rapid jerky gait and, if disturbed, readily take to flight." Members of another choreutid genus, *Tortyra* Walker, 1863, rest with the wings rolled around the body, the wing tips curved and covering the tip of the abdomen, and the antennae displayed forwards. The effect is of a metallic chrysomelid beetle (VOB unpublished observation). In contrast, species of the choreutid genus *Hemerophila* Hübner, 1817, rest with their colorful wings flat against the leaves (VOB unpublished observations in Brasil, AA unpublished observations in Panama).

Though it is easy to speculate that such displays play a courtship role, their true function is not known. Displays may be repeated for hours at a time whether or not other individuals are present, and both sexes perform them, apparently identically. Adults of 2 Panamanian *Brenthia* species performed these displays shortly after eclosion in the individual petri dishes in which they had been reared. Observations on the immature stages of *Brenthia* are presented by Aiello and Solis (2003).

Display behaviors in other microlepidoptera. The dance displays that occur in a variety of other Microlepidoptera, involve whirling or gyrations, but not wing manipulations. Such dance-like gyrations are performed by 'dancing moths,' *Dryadaula terpsichorella* (Busck, 1910) (Tineidae), upon alighting (Swezey 1909:20). According to Robinson (1988:73), *Callicerastis stagmatias* Meyrick, 1916 (Tineidae), in W. Malaysia, performs a ". . . dance on a leaf," and ". . . similar gyratory movements have also been observed in laboratory stock of *Opogona flavofasciata* (Stainton, 1859) (Tineidae: Hieroxestinae), but these are performed for only a few seconds." Forbes (1923:277) wrote of *Anacampsis* (Gelechiidae) that "The moths of *A. agrimoniella* [(Clemens, 1860)] and *A. levipedella* [(Clemens, 1863)], at least, walk in a circle on alighting, . . ." Also in the Gelechiidae, *Commatica falcatella* (Walker, 1864) and *C. cryptina* (Walsingham, 1911) have been seen spinning on leaves in Mexico and Costa Rica (VOB unpublished observation), and in Panama (AA unpublished observation). Also seen spinning on leaves, in Panama, is an as yet unidentified member of the Cosmopterigidae (AA unpublished observation). Plant (1980:255) described a spinning dance in *Mompha nodicolella* Fuchs, 1902 (Momphidae) in Britain, and Robinson (1988:73), observed ". . . an unidentified species of Momphidae in Sulawesi and Malaysia. This moth performs its dance on the upper and under-surfaces of leaves of a variety of plant species in rain forest, running in tight circles both clockwise and anticlockwise." It has been speculated that the displays of microlepidoptera ". . . may have a function in courtship. . . ." (Robinson et al. 1988:11), but in most species their purpose remains unknown.

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DISCOVERING MOTHS—NIGHTTIME JEWELS IN YOUR OWN BACKYARD, by John Himmelman, 2002. Softcover, $18.95 from Down East Books, Camden, Maine. ISBN 0-89272-528-1. 232 pages, with 22 color plates and numerous B&W drawings.

The study of moths is essentially a subjective and emotional pursuit. If we plotted out the allocation of resources—dollars and number of researchers—against various measures of moth diversity, no cost accountant could make sense of the pattern. The few economically important pests would show a concentration of effort, but otherwise there would be an eclectic mishmash of attention to moths that are variously large and gaudy, bizarre in habit, or tiny and obscure, probably largely because they sparked a young mind for these very qualities. As a consequence, taxonomic specialists heavily populate the ranks of both dedicated amateur and professional entomologists. John Himmelman's book *Discovering Moths* is a reminder that we are missing a lot.

Unlike the situation for butterflies, the young person or newly seduced adult has few choices for general books on moths (primarily Covell's excellent *A Field Guide to the Moths of Eastern North America* and the Dover reprint of Holland's *Moth Book*) to nurture a developing interest. Other treatments are often too scientifically lofty and detailed and too expensive to be widely accessible.

Discovering Moths is a refreshing addition to the Lepidoptera literature. More than a compilation of facts and descriptions revering moth diversity, the book is a personal narrative that appeals to our (often suppressed) emotional attraction to Leps. The chapters cover the author's personal experiences and reactions to a variety of topics: sugaring and blacklighting, moth-related activities through the seasons, moth lore in our culture (Of Moths and Men), past and present moth experts and other colorful characters, a brief and select introduction to moth families, and some material on collecting, rearing, and photographing moths. Sprinkled throughout are nuggets of life history observations on both familiar and many obscure but attractive species. Representative species for fifteen families, various larvae, and some day-flying moths are well-illustrated in color, and the author's own attractive ink stipple drawings introduce various sections and depict (sometimes whimsically) various moths and caterpillars. I found only a few insignificant errors or typos ("circumference" instead of diameter as a measure of size, and a photo legend reversing the identity of Dave Wagner and Brian Scholtens during the "BioBlitz" diveristy project).

Himmelman is a professional writer on nature topics, not a professional biologist nor strictly interested only in Lepidoptera. His material reflects a regional orientation to the East Coast and New England where he is based, and his prose is personal, wry, and witty. Such writing can be an unstable balance between humorous and colorful discourse, and being too contrived and familiar so as to distract from the subject at hand. Himmelman largely avoids these rhetorical excesses, although some readers used to the concise, formal, grammatically correct style we normally encounter in our Lep literature will have to make an adjustment. His Eastern bias in no way detracts from the value of the book as an explanation for our fascination with moths, rather than as a taxonomic overview of North American species. I would have liked to have seen a section on Holland and his reign at Carnegie Museum as well as a mention of some of the past western U.S. luminaries such as Lloyd Martin with his stories of 19th century collectors. These topics and others are some this book should incite others to write about. I highly recommend *Discovering Moths* for anyone with an interest in our natural history heritage.

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FIELD GUIDE TO BUTTERFLIES OF SOUTH DAKOTA, by Gary M. Marrone. South Dakota Department of Game, Fish and Parks, Pierre, South Dakota, 2002. 378 pages. Softcover, $38.95 + $5.00 shipping from the publisher (412 W. Missouri, Pierre, South Dakota 57501 or on the web at www.sdgfp.info). ISBN 0-9712463-1-9.

An account of South Dakota's butterflies could have been written by no one except Gary Marrone who has studied this fauna for nearly three decades. This compact book treats each of the 177 species known from the state. The introductory chapters are brief (18 pages) giving encapsulated versions of butterfly life history, studies of butterflies in South Dakota, physiography and climate of the state, and habitats illustrated with photographs. Families of butterflies are introduced by a general description of less than a page. The species accounts include the common and scientific nomenclature, a short description of the adult and sections on similar species, distribution and habitat, early stages (i.e., one sentence with a general description of the apparently mature larva), larval host plants, adult energy sources, flight period, general comments, and, at times, specific references. Two or more photographs of spread specimens mostly from South Dakota superbly illustrate each species; these include at least dorsal and ventral surfaces and show additional specimens as needed to elaborate major variation. A photograph from life and/or of early stages illustrates some of the species. Distributional information is mapped at the county level and embedded into the species account. The book concludes with a checklist, a butterfly calendar, a hypothetical list, a glossary, a bibliography of useful references, and an index.

In a field guide, quibbles concerning nomenclature are largely irrelevant. Marrone recognizes acceptable family combinations with Riodinidae separated from Lycaenidae and *Libytheana* included within the Nymphalidae. The common and scientific names largely follow Opler (1999) and NABA (apparently Cassie et al. 1995) and are as contemporaneous as one could want. *Satyrium* and *Callophrys* are treated as all inclusive genera at the expense of *Harkenclenus* and *Mitoura*, *Incisalia*, and *Deciduphagus*, respectively. The same broad stroke generic approach was also applied to other lycaenids (*Lycaena*), to some papilionids (*Papilio*), and to certain nymphalids (e.g., *Nymphalis*, *Vanessa*, *Phyciodes*, *Boloria*). The use of infraspecific names is somewhat uneven. At first it was assumed that a subspecific name was given if the South Dakotan taxon was not of the nominotypical subspecies, yet this is not always so (e.g., *Pieris marginalis*, *Speyeria coronis*, *Speyeria mormonia*). These and other taxonomic decisions in no way detract from the book's intention as an identification guide to South Dakota's butterflies. A large number of aberrations are also illustrated that, although unusual in a field guide, include many heretofore not illustrated in a readily available publication. One major blunder involves the apparent switching of the plates for *Pieris marginalis* and *Pieris oleracea*.

This book is a true field guide with little extrinsic information between its covers. Those interested in more than identification may glean tidbits on general distribution, habitat, larval hostplants (although one is not always sure that the plants referred to are those used in South Dakota), and adult nutrient sources. The strength of this book for the researcher lies in the phenological data in the species accounts and, with more detail, in the appended butterfly calendar that is updated from Marrone (1994). The *Field Guide to Butterflies of South Dakota* is a must for anyone interested in the butterflies of that state and adjacent areas on the northern Great Plains. It also serves as a nice companion to the recently published guide for North Dakota (Royer 2003).

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NYMPHALIDAE DE MÉXICO I (DANAINAE, APATURINAE, BIBLIDINAE & HELICONIINAE): DISTRIBUCIÓN GEOGRÁFICA E ILUSTRACIÓN, by Armando Luis-Martínez, Jorge E. Llorente-Bousquets & Isabel Vargas-Fernández. Illustrations by Pál János. 2003. Published by Facultad de Ciencias, Universidad Nacional Autónoma de México and Comisión Nacional Para el Conocimiento y Uso de la Biodiversidad (CONABIO), Mexico City. 249 pages, 30 color plates, 124 distribution maps. Softcover, glossy paper, 21.5 × 28.0 cm, ISBN 970-32-0693-X. Available from Andrew D. Warren, Dept. of Zoology, Oregon State Univ., Corvallis, OR 97331 (warrena@science.oregonstate.edu)—send personal check for US $40 (includes postage from Mexico City) and shipping address with phone number.

This book is the second in a series of fascicles treating the butterfly fauna of Mexico, produced by the "Alfonso L. Herrera" Zoology Museum (MZFC), at the National Autonomous University of Mexico, in Mexico City. The volume is presented in the same format as the first (see Llorente et al. 1997, Warren 1999), and treats all Mexican species in the subfamilies Danainae, Apaturinae, Biblidinae & Heliconiinae (basically sensu Harvey 1991); a total of 181 subspecies of 140 species from 37 genera. It is the first time Mexican members of several genera, including *Adelpha* Hübner and *Doxocopa* Hübner, have been treated in detail.

Like the first in the series, this volume is crammed full of exact details, numerous facts and statistics, and data from over 73,000 specimens presented in telegraphic form, and gathered from over a dozen major institutional collections in Mexico, North America and Europe (Appendix I). In addition to data from collections, a substantial number of records are reported from the literature, from about 800 sources, all of which are listed in one of two bibliographies (mostly in Appendix III). Over 230 literature references are provided on the Monarch butterfly, *Danaus plexippus* L. alone! The limited amount of text in the introductory sections and at the beginning of each appendix, is in Spanish. However, users who do not read Spanish should have no problem extracting information from this volume due to its logical organization, extensive tables, maps, and illustrations.

The 124 distribution maps in Appendix IV are excellent, and are the most detailed available for the taxa treated. They show specific records gathered from museum collections and the literature (which are listed in Appendix I), plotted onto maps of Mexico with state boundaries. Several dubious records listed in Appendix I are not plotted on the maps; other dubious records are plotted, some accompanied by question marks. In several cases, multiple non-sympatric taxa are mapped on a single map, to save space. All locality data that could not be accurately mapped, such as general records from "Oaxaca," for example, and several vague literature records, are listed in a separate section of non-plotted data that follows the maps (Appendix V).

All Mexican nymphalid species in these four subfamilies are illustrated on 30 color plates (Appendix VI) that consist of paintings from museum specimens. Usually, for taxa that are sexually dimorphic the dorsal surfaces of both males and females of each taxon, and the underside of at least one sex is illustrated for almost every species. The book also includes a list of type localities for all taxa treated (pp. 4–9), a gazetteer of all localities listed in the book that is arranged by state (Appendix II), and tabular representation of much of the data presented in this volume. Specifically, tables are provided showing the number of localities from which these nymphalids have been recorded in each Mexican state, with other tables listing the most species rich localities (in terms of overall species per locality, and total recorded specimens per locality).

Some of the statistics presented in the tables show that, for example, data from over 25,000 specimens are included from the state of Michoacán alone. *Heliconius charithonia vazquezae* W. P. Comstock & F. M. Brown, Mexico's most abundant heliconiine, is known from over 5600 specimens and 465 localities (all listed); other taxa, such as *Speyeria nokomis melaena* Mooser & García, and *S. nokomos wenona* dos Passos & Grey, are known from only one, and two specimens respectively. Records exist for over 6400 individual specimens of 79 species in these 4 subfamilies from Cerro El Vigía, in the State of Veracruz, while only two nymphalid species in these subfamilies are known from the State of Tlaxcala, represented by two specimens. I was surprised to see that of the more than 73,000 specimens in these four subfamilies that were examined for this book, 86.2% of these specimens are housed in two institutional collections in Mexico City. In contrast, specimens in the Allyn Museum of Entomology, American Museum of Natural History, California Academy of Sciences, Carnegie Museum of Natural History, Los Angeles County Museum of Natural History, Nevada State Museum, San Diego County Natural History Museum, Essig Museum of Entomology and the National Museum of Natural History, combined, make up less than 15% of this total.

I found a few minor typos in the text, a few errors on the maps, and some errors in labeling on plate legends, but none of these detract from the overall usefulness of this book. This book is a must for anyone seriously interested in Neotropical or southern Nearctic butterflies, as well as entomologists, biologists and other naturalists with a general interest in butterflies or Mexican biogeography. Considering the enormous amount of information available nowhere else, this book is indeed a bargain. The next volume in the series will treat Mexican Charaxinae, Morphinae and Ithomiinae, and follow this same format; until then I look forward to using the arsenal of distributional and ecological data now available for Mexican Danainae, Apaturinae, Biblidinae and Heliconiinae.

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MANUSCRIPT REVIEWERS FOR 2003 (VOLUME 57)

Manuscript reviewers are anonymous contributors to the scientific rigor, clarity and quality of text and illustrations in the papers published by the Journal of the Lepidopterists' Society. The reviewers' input is invaluable and always welcomed by all of us. Let us hope that their careful work continues to allow the Journal to grow in quality and readership. On behalf of all authors and editorial staff of this Journal, respectful acknowledgements are given to the reviewers for contributions published in volume 57.

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