Nocturnal butterflies in Panama, *Hedylidae (Lepidoptera: Rhopalocera)*

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DIURNAL AND NOCTURNAL LEPIDOPTERA

Butterflies (Rhopalocera) are the most conspicuous and familiar members of the order Lepidoptera. Their diurnal activity together with their habit of visiting flowers brings them into close proximity with people, and their often colourful wings cause us to notice them. However, it is not only the butterflies that are diurnal and colourful among Lepidoptera. Diurnal behaviour has arisen several times in the order, usually accompanied by colourful wings. The moth families Castniidae, Zygaenidae, Geometridae, Uraniidae, Sphingidae, Arctiidae (in several subfamilies), and Agaristidae all include some diurnal and colourful members, and many people who see them just assume that they are butterflies. Several of these moth families are comprised of exclusively diurnal species, but most of the largest ones are predominantly nocturnal groups. When one considers that, among the close to 120 families of Lepidoptera, diurnal examples can be found only in these few families of moths plus the six families of true butterflies, it becomes apparent that the day-flying habit is actually rather rare. The butterflies themselves are in a distinct minority; they represent only about 10 per cent of lepidopteran species.

CREPUSCULAR BUTTERFLIES

It has long been accepted as fact that adult butterflies are creatures of strictly diurnal and, in a few cases, crepuscular habits. Among the more familiar examples of Panamanian crepuscular butterflies are species of the genera *Brassolis, Dynastor, Opsiphanes*, and *Caligo* (all Nymphalidae: Morphinae), which rest during the day and night and come to life for a short period at dawn and dusk. They are occasionally active during the day under overcast conditions. Aside from this subfamily and a few members of another, the Satyrinae, the vast majority of butterflies are active exclusively during daylight hours; indeed, many fly only on the sunniest days, coming to rest among nearby vegetation whenever a cloud obscures the sun. Butterflies, as we have known them, do not fly at night.

NOCTURNAL BUTTERFLIES

As it turns out, we are only just getting to know the butterflies and, for that matter, the rest of the Lepidoptera. Older classifications, based mainly upon wing pattern and venation, often resulted in superficial arrangements. Today many workers are tapping the wealth of information available in other features of the adult body, and in the form and behaviour of the immature stages (egg, larva, pupa). The results often lead to conclusions that differ substantially from previous concepts. In one of the more exciting of these recent studies, Scoble (1986) concluded that the Hedylidae, previously included as a subfamily (Druce 1893) or a tribe (Prout 1932) of the Geometridae (inch-worm moths), are not moths at all; they are butterflies, nocturnal butterflies.

HEDYLIDAE Guenée, 1857

Hedylids, as Scoble (1990) presents them, consist of 35 Central and South American species and, pending a revision, he considers them all to be members of the genus *Macrosoma* Hübner, 1818. The group displays a number of butterfly features, including certain characteristics of the immature stages.

Adult hedylids have a delicate butterfly-like appearance (Fig. 34.1); the body is extremely slender, and the elongate wings are narrow at their bases. Although the antennae are also slender, and in many species are threadlike, in several species they are narrowly plumose and rather unbutterfly-like. Unlike nymphalids, which have reduced prothoracic legs, those of hedylids are well developed, but like nymphalids, in at least one species (*semiermis*), they are held folded against the body at rest. In the male the prothoracic legs are extremely long (Fig. 34.1) and perhaps are used in courtship and/or mating, although nothing is known of adult reproductive behaviour for any of the species.

The larvae, known for three species (Kendall 1976; Scoble 1986), have a pair of long head scoli (spined projections) and, in *semiermis* (Prout) at least, a pair of abdominal furcae. The combination of head scoli and furcate abdomen, not found in any group of moths, is typical of certain nymphalid butterflies.

Fig. 34.1 Adult *Macrosoma semiermis*. Male (above), with the long, tufted, prothoracic legs extended. Female (below). Wing span is 3.5 cm.

Indeed, the overall appearance of the larva is that of a *Doxocopa* caterpillar (Nymphalidae: Charaxinae). In contrast with the Geometridae, whose larvae usually possess only two pairs of prolegs, and with whom the hedylids were long associated, the known larvae of hedylids and most other Lepidoptera have the full complement of five pairs of prolegs.

The pupae, known from the exuviae of four species (Scoble 1986) and the published record of a fifth (Kendall 1976), is not enclosed in a cocoon or any other type of shelter. Exposed pupae, typical of butterflies, do occur in certain moth families (Common 1986) and the condition obviously has evolved several times in the Lepidoptera, but it is unusual, and in combination with other characters found in hedylids it gains significance. In addition, the pupa is held in place by a silk girdle, as are the pupae of a number of butterfly groups (i.e. Papilionidae, Pieridae, Lycaenidae, Riodinidae). Among the moths, the only reported occurrence of a pupal girdle is in certain genera of the Geometridae, subfamily Sterrhinae (Common 1986; Scoble 1986). However, the girdle of sterrhine geometrids passes over the third abdominal segment, while the girdle of pierid butterflies, and the one hedylid that I have examined passes over the first abdominal segment. The papilionid girdle passes over the third thoracic segment.

The only published account of life history for the family is for *semiermis*, bred in Tamaulipas, Mexico by Kendall (1976), as *heliconiaria* (Guenée). Larvae were found on *Byttneria aculeata* Jacq. (Sterculiaceae), a hollow-stemmed vine that bears recurved spines and alternate, often variegated leaves. The plant is common in damp habitats throughout Central America and northern South America, including Panama (Robyns 1964). Quite possibly the range of *semiermis* corresponds to that of *Byttneria aculeata*. *Byttneria* is not necessarily the larval food plant for any of the other species.

HEDYLIDAE IN PANAMA

At least nine species of *Macrosoma*, including *semiermis*, have been reported to occur in Panama, but because published records differ and no recent revision of the group has been undertaken, the actual number of Panamanian species is not yet known. Scoble (personal commun) notes that *heliconiaria*, *inermis*, and *semiermis* form a complex of species that are difficult to distinguish without genitalic dissection. Undoubtedly, specimens of those three are intermixed in many collections, and it has yet to be determined which of them actually occur in Panama. It is possible, for example, that *heliconiaria* (whose range is reported by Prout (1932) as Venezuela, French Guiana (Type), Amazons, Peru, and Ecuador) does not occur in Panama at all, and that Panamanian specimens presently assigned to that species are actually *semiermis*.

The following are very brief colour descriptions, references to illustrations in the literature, and collection records for the nine species reported from Panama. In the specimen citations in most cases, the order of information is locality, date, collector (sometimes including a number), and the museum or private collection in which the specimen was deposited. BM = British Museum; STRI = Smithsonian Tropical Research Institute; USNM = United States National Museum.

1. *semiermis* (Prout)

Grey-brown overall, dark brown toward the forewing apices, with a white triangle on the costal margin of the forewings, and with the hindwing central portion greyish white and cleanly demarcated from the wide grey-brown border. Prout (1932), p. 17, tab. 2b (as *Hedyle semiermis*); Scoble (1990), p. 124, fig. 7.

Specimens. The Type is from the Isthmus of Panama, Nov.–Dec. 1907, and is in the Tring Collection (BM). Panama Prov: Ft. San Lorenzo ruins, 17 Sep. 1987, coll. by D. Quintero, Aiello lot-book 87–68 (collected as third–fifth instar larvae) (STRI); Old Gamboa Road, 22 Aug. 1984, A. Aiello lot-book 84–57 (collected as third instar larva) (STRI); Palo Seco, Ezra Hurwitz Road, 30 Aug. 1988, A. Aiello lot-book 88–21 (collected as fifth instar larva) (STRI); Ft. Kobbe, K-1 Road, 31 Aug.–16

Sept. 1987, A. Aiello lot-book 87–60 (collected as eggs, first–fifth instar larvae) (STRI).

2. *hyacinthina* (Warren)

Like a large *semiermis* with irridescent blue sheen. Prout (1932), p. 17, tab. 2c (as *Lasiopates hyacinthina*); Scoble (1986), p. 255, fig. 2; Scoble (1990), p. 124, fig. 5.

Specimens. Panama Prov: BCI, 9 Aug. 1941 and 16 Nov. 1941, J. Zetek (USNM).

3. *heliconiaria* (Guenée)

Much like *semiermis* but with the greyish white of the hindwings less clearly defined, and extending to the outer margin. Prout (1932), p. 17, tab. 2b (as *Hedyle heliconiaria*); Scoble (1986), p. 255, fig. 1; Scoble (1990), p. 124, fig. 6.

Specimens. Chiriquí Prov: Chiriquí, Arcé (Druce collection); Chiriquí, Dognin coll. 266 (USNM); Chiriquí, Ribbe (Staudinger collection); Chiriquí, Trötsch (Staudinger collection); Bugaba, Champion (BM); Volcan de Chiriquí, Champion (BM). Panama Prov: Panama City, J.J. Walker (BM); Rio Trinidad, 12 Mar., Busck (USNM); Erwin Isl., C.Z., 7 Aug. 1923 (USNM); Taboga Is., 12 Feb., Busck (USNM).

4. *conifera* (Warren)

Like a robust *heliconiaria*. Prout (1932), p. 19, tab. 2g (as *Phellinodes heliconiaria*); Scoble (1990), p. 124, figs 11–13.

Specimens. Panama Prov: BCI, 10 Oct. 1940, Zetek 4683, lot no. 40–21578 (USNM); BCI, at light, 21 Mar. 1941, Zetek 4725, lot no. 41–4653 (USNM).

5. *bahiata* (Felder)

Dingy brown. Forewings emarginate, with dark brown apices, a narrow white patch bordering the dark brown, and with an irregular black spot above the wing centre. Prout (1932), p. 18, tab. 2e (as *Phellinodes bahiata*); Scoble (1990), p. 127, fig. 32.

Specimens. Panama Prov: Arraiján, Loma del Rio, at light, 20 Dec. 1988, Aiello (STRI).

6. *rubedinaria* (Walker)

Dingy brown moth, with emarginate forewing apices, and tiny dark spot in forewing centre. Druce (1893), p. 178, tab. 58, fig. 9 (as *Phellinodes rubedinaria*); Prout (1932), p. 18, tab. 2c (as *Phellinodes rubedinaria*); Scoble (1986), p. 255, fig. 4; Scoble (1990), p. 128, fig. 41.

Specimens. Panama Prov: Río Trinidad, 1–10 Jun. 1912, A. Busck (USNM); BCI, at light, 21 Mar. 1941, J. Zetek 4725, lot no. 41–4653 (USNM); BCI, at light, 26 Sep. 1941, J. Zetek 4876, lot no. 41–17178 (USNM).

7. *muscerdata* (Felder)

Dingy brown, darker towards the forewing apices, and with two small windows near the forewing apices. Prout (1932), p. 19, tab. 2f (as *Phellinodes muscerdata*); Scoble (1990), p. 126, fig. 27.

Specimens. Panama Prov: Río Trinidad, 15–31 Mar. 1912, A. Busck (USNM).

8. *tipulata* Hübner

Dirty white, with brown pattern and dark-edged white mark in basal half of forewing. Prout (1932), p. 17, tab. 2c; Scoble (1986), p. 155, fig. 3; Scoble (1990), p. 124, fig. 4.

Specimens. Bocas del Toro Prov: Bocas del Toro, Apr. 1907, Wm. Schaus (USNM). Chiriquí Prov: Chiriquí, Arcé (Druce collection); Chiriquí, Dognin coll. 62 and 265 (USNM); Chiriqui, Ribbe (Druce collection); Chiriquí, Wm. Schaus (USNM); Bugaba 800–1500 feet, Champion (BM).

9. *ustrinaria* (Herrich-Schäffer)

Dirty white, with emarginate forewing apices, and with dark spot in forewing centre. Prout (1932), p. 18, tab. 2c (as *Phellinodes ustrinaria*); Scoble (1986), p. 255, fig. 5; Scoble (1990), p. 128, fig. 42.

Specimens. Chiriquí Prov: Bugaba 1000 feet, Champion (BM). Panama Prov: BCI, 10. Oct. 1940, Zetek 4683, lot no. 40–21578 (USNM); BCI, at light, 26 Sep. 1941, J. Zetek 4876, lot no. 41–17178 (USNM).

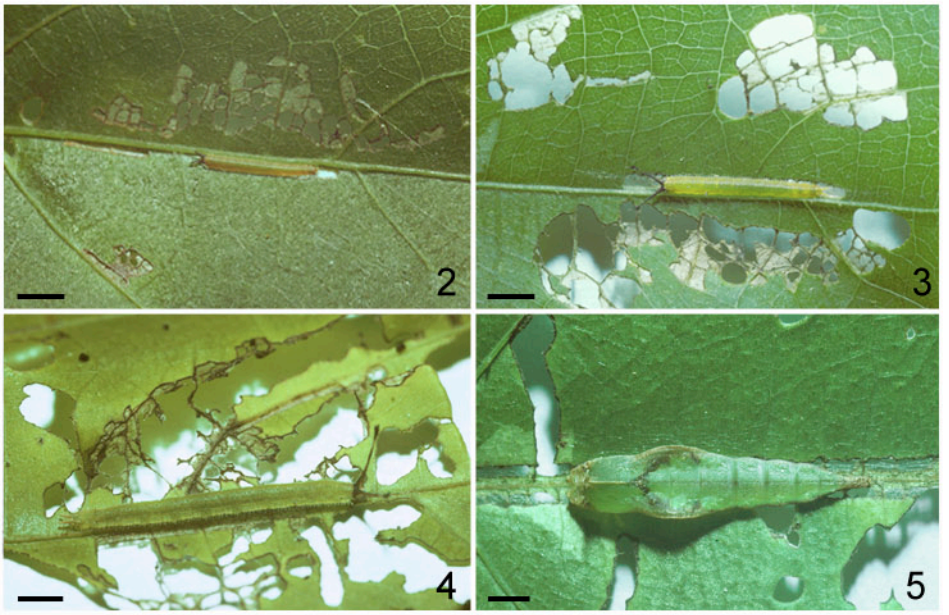
Macrosoma semiermis in Panama

I recently obtained immatures of *semiermis* and examined them in some detail. Eggs and larvae were collected on *Byttneria aculeata* in the Fort Kobbe area (lot-book no. 87–60) and larvae were brought to me from the Fort San Lorenzo ruins (lot-book no. 87–68), Panama, during August–October 1987.

Although the search was begun in April 1987, no evidence of *Macrosoma* immatures appeared until August, when several larvae were found. By early September, the larvae and their characteristic leaf damage had become very common and, on some plants, nearly every leaf had been attacked. Apparently, during the first half of the rainy season, breeding is at a very low level or is non-existent.

Egg. The egg of *semiermis* is very pierid-like. It is a slender spindle (1.2 mm × 0.3 mm) with seven longitudinal ribs, and approximately 30 faint cross-ribs. The eggs are laid sticking out from the edge of the leaf, usually along its apical third. I have not seen freshly laid eggs. The five collected were blotched with dark red and remained so until hatching, 4–6 days later. The larvae each ate an elongate escape hole along one side of the egg and abandoned the shell.

Larvae. *Macrosoma semiermis* caterpillars are remarkable creatures; due to their behaviour, their form, and their coloration they are very difficult to detect even when they reach their full length of 3.5 cm and spend all their time on the upper surface of their food leaves.



Figs 34.2–34.5 Immature *Macrosoma semiermis*. **2,** Second instar in its groove, next to its feeding holes. In the lower left can be seen the groove and feeding holes made by the same larva when it was a first instar; **3,** Third instar in its groove, with feeding holes on both sides; **4,** Fifth instar making new groove on the midrib; **5,** Pupa in the leaf groove made by the final instar. Scale bars = 2 mm.

Behaviour. The first instar eats a slender groove (Fig. 34.2), next to a secondary vein, and then rests in it, reaching out to one side to feed by eating holes in the nearby leaf tissue. Instars 2–4 (Figs 34.2, 34.3) do the same thing, but they often make their resting grooves next to the main vein instead of a secondary vein. Late in the fourth stadium and throughout the fifth (final) (Fig. 34.4), the larva rests directly on top of the mid-vein, after cutting a row of tiny holes along either side of it. Large larvae often consume the entire leaf, except for the mid-vein, before moving on to a new leaf. In all stadia, the feeding larva snaps back into its groove and remains motionless when its leaf is disturbed. Moulting takes place in the resting grooves, during late morning or early afternoon.

Apparently *Macrosoma* larvae are not the only Lepidoptera that make leaf grooves. Robert Robbins presented me with a photograpph of *Macrosoma*-style damage on the leaves of *Clibadium* sp. (Compositae). Don Harvey (personal commun.) believes the damage was done by the larva of *Calephelis* sp. (Riodinidae). He says that *Ancyluris* (Riodinidae) makes similar grooves on the leaves of *Miconia* (Melastomataceae). In fact, I have seen grooves on the leaves of *Miconia impetiolaris* in Loma del Rio, Arraiján, Panama. As with *Macrosoma* grooves, the smallest of those grooves were made next to secondary veins and there was feeding damage on one or both sides of them; the largest grooves were on top of the mid-vein, and were bordered by small holes.

Form. The larva of *semiermis* is dorso-ventrally flattened, and when at rest in its groove, with its hypognathous head appressed to the leaf, its body blends well with the leaf. A fringe of pale, club-shaped setae, along the full length of the body, further contributes to the blending of larva and leaf.

As do nymphalids, first instar *semiermis* lack the pair of head scoli that appear in all subsequent instars. In *semiermis* the head scoli are black and are flattened at the tip. Second instar scoli, only 0.5 mm long, are barely visible to the naked eye. However, with each moult their length increases, and by the fifth instar they are 6 mm long. Even if detected, the scoli are easily mistaken for a bit of debris on the leaf.

Colour. Instars one and two are quite small (*c.* 2.5 mm and *c.* 4.5 mm, respectively) and are easily overlooked, but if noticed their orange colour leads one to take them for the early stages of a leaf mine. The most efficient method for locating these earliest instars is to search for egg shells sticking off the edge of the leaf, and upon locating one, to search that particular leaf carefully for larvae. A piece of black paper held beneath the leaf is a helpful aide to egg detection.

Instar three is also orange, and although it is more noticeable, it looks more than ever like a leaf mine.

Larvae of the fourth and fifth stadia are the same green as the leaf, and they blend with it very effectively.

Pupa. In wild individuals as well as in captive ones, pupation (Fig. 34.5) takes place on the upper surface of the leaf, usually in the leaf groove made by the mature larva. The pupa is green and dorso-ventrally compressed and, although exposed, it is very well camouflaged.

Development time. Based upon combined data from reared lots 87–60 and 87–68, development time from egg to adult is about 6 weeks for *semiermis*. Average development times for the various stages are shown in Table 34.1. *Macrosoma semiermis* has at least two generations a year in Panama, beginning in mid August. It is not yet known how much farther into the dry season breeding continues, but at last inspection (24 October 1987), numerous eggs and larvae were present on *Byttneria aculeata* in the Palo Seco/Ft. Kobbe area.

Table 34.1. Average development times (in days) for *Macrosoma semiermis* in reared lots 87–60 and 87–68. The number of days given for egg development is average minimum time.

	Egg	Instar					Pupa
		1	2	3	4	5	
Mean	5.2	5.0	4.3	4.8	6.2	9.0	10.8
Range	4–6	4–6	4–5	3–6	5–7	8–10	10–11
s.d.	1.1	0.7	0.5	1.1	0.7	0.7	0.4
n	5	5	7	10	15	13	15

Parasitoids. Kendall (1976) reported a high incidence (in 9 out of 12 larvae and pupae) of parasitoid flies. The Panamanian stock fared much better. Of the nineteen larvae remaining after preservation of seven, three larvae died of unknown causes and one was parasitized by a 12-cm-long nematode worm. The worm exited from the prothorax of the fifth stadium larva that had been collected 20 days earlier as a third instar. I found no instances of pupal parasitoids.

Adults. The reared adults eclosed during the evening, usually before 9.00 p.m. Adults of both sexes use their meso- and metathoraioc legs for landing and walking, and they keep their long prothoracic legs folded under the thorax. The wings are held spread. When the insect is perched on a vertical support, the thorax is tilted so far back that the wings are nearly horizontal to the ground and their undersides are uppermost. The abdomen hangs straight down, nearly at a right angle to the thorax. The wing span is 3.5 cm. Wing pattern consists of black, grey, and brown against a white background.

Kendall (1976) commented that the adults are diurnal, but in Panama I have seen them at lights only.

CONCLUSION

Our knowledge of hedylids is meagre at every level. We need information that will help reveal the position of the group within the Lepidoptera and clarify relationships among the species in this interesting family. Those who are interested in searching for *Macrosoma* immatures and adults, and contributing to our knowledge of Panamanian Hedylidae, will probably find Chiriquí Province to be the most rewarding part of the country in which to explore, because most of the Panamanian species have been recorded from there. We need to know how many species of *Macrosoma* there are, what their ranges are, what their larvae and pupae look like, and what plant species the larvae feed on.

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