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Moth-like butterflies (Hedylidae: Lepidoptera): a summary, with comments on the egg

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Our concept of the butterflies (Hesperioidea or skippers plus Papilionoidea or true butterflies) has been broadened by the inclusion of the Hedylidae (Scoble, 1986), a group of about 40 species of Neotropical Lepidoptera. Superficially moth-like as adults, hedylids exhibit several specialized characters associated with various families of butterflies. They may have diverged little from the unknown ancestors of true butterflies. The butterfly-like characters of all stages in the life history are summarized; particular note is made of the egg.

KEYWORDS: Butterfly phylogeny, Hedylidae, Hedyloidea, Hesperioidea, Papilionoidea, egg.

Introduction

Butterflies (Rhopalocera) are of special interest to biologists because they have been used as study organisms in a wide range of biological disciplines such as population dynamics, community biology, foodplant associations, chemical defence and mimicry, genetics, sex and communication, migration, conservation, and systematics (Vane-Wright and Ackery, 1984). Yet until recently (Scoble, 1986), we had little idea as to what primitive butterflies might have looked like or how they may have behaved. There is still no convincing evidence to favour any particular family of moths as the sister group of butterflies. Furthermore, although it is generally assumed that skipper butterflies (Hesperioidea) are the closest relatives of true butterflies (Papilionoidea), morphological support for this view is limited (Kristensen, 1976). Although butterflies are no longer treated as a primary division of the order Lepidoptera (Common, 1970), they have been widely considered to be monophyletic and, in their general biology, divergent within the Lepidoptera. Recently it was suggested that the South and Central American Hedylidae, previously placed in the Geometridae, are also butterflies (Scoble, 1986). This proposal was based on morphological evidence suggesting that Hedyloidea, Hesperioidea, and Papilionoidea form an unresolved, trichotomous cladogram. Therefore, if Hesperiidae are regarded as butterflies then Hedylidae should be similarly treated. With their inclusion among the butterflies (as superfamily Hedyloidea), the Rhopalocera now exhibit characters that demonstrate conspicuously their moth-like ancestry.

Since it was suggested that Hedylidae are moth-like butterflies some additional observations about the group have been made. Here we summarize the information

gathered to date in the context of butterfly phylogeny. Special note is made of the egg of *Macrosoma semiermis* (Guenée). The figures are the first illustrations of any hedylid egg to be published.

Adult

Our 'caricature' of the butterflies is based on the group's diurnal habits. Diurnalism is associated with strongly vision-based behaviour in, for example, courtship and male–male interactions (Silberglied, 1984), although scent is important in the later stages of courtship (e.g., Myers and Brower, 1969). Indeed, the visual power of butterfly eyes, in at least one species, has been shown to be extraordinarily great (Nilsson *et al.*, 1984). By contrast, in most moths, the majority of which are nocturnal, males are attracted to females by pheromones (Birch and Haynes, 1982), by scent rather than sight. Typically, butterfly antennae are clubbed rather than pectinate. Pectinate antennae, often well developed in male moths, are adapted for the detection of scent. In four species of Hedylidae, the male antennae are pectinate; in others they are filiform. They are never clubbed. Hedylidae are nearly always collected at light, but there are also reports of daytime activity. Kendall (1976) mentioned that the adults of *Macrosoma semiermis* (Prout) (as *heliconiaria* (Guenée)) were diurnal. A specimen of *Macrosoma tipulata* Hübner was observed flying at midday in hurricane forest in Guanacaste Province, Costa Rica in June 1988 by one of us (MJS). Other hedylids have also been seen flying by day (J. E. Rawlins, 1989, personal communication). Are these records chance observations or do they represent incipient diurnalism?

Similarities between Hedylidae and other butterflies are found in all stages of the life-cycle (Scoble, 1986; Aiello, in press). Conspicuous in the adult (Fig. 1) is the pouched form of the first abdominal tergum, a feature considered unique to true butterflies (Ehrlich, 1958). In skippers the pouch is absent or weak. Notable also is that the aorta in Hedylidae (Minet, 1988; Scoble, unpublished) is like that characteristic of Hesperioidea and Papilionoidea (Hessel, 1966; 1969). In butterflies, including Hedylidae but excepting Papilionidae, not only is the aorta expanded into a horizontal, dorsal chamber (a feature exhibited also by Cossidae), but the ascending and descending members of the aortic loop lie, for at least part of their lengths, in virtual contact with each other.

Although not extensively studied in Lepidoptera, the sagittate condition of the apophyses of the metathoracic furca (Ehrlich, 1958) is widespread in both true butterflies and skippers, but appears not to occur in moths. The tip of the arrowheaded structure is blunt in Hedylidae, but its general shape is unmistakably sagittate.

In the male hedylid foreleg, the tarsomeres are reduced, by fusion, from five to two segments. The pretarsus is vestigial, bearing a pair of minute claws only; aroliar pads and pulvilli are absent. Adults of both sexes of *M. semiermis* rest and walk with their forelegs folded against the ventral surface of the thorax and thus not in use (Aiello, in press), an observation also made for males of five other species (Scoble, unpublished) (females not seen). When perched on a vertical support, the thorax is tilted at such a pronounced angle that the posterior edges of the hindwings almost touch the substrate on which the insect rests. The wings are spread out from the body, and slightly raised. Male forelegs exhibit various reductions in Papilionoidea (Ehrlich, 1958). The tarsus is usually unsegmented in Lycaenidae, that is the tarsomeres are fused (see also Eliot, 1973 and Robbins, 1988). Although segmented, the forelegs of male Nymphalidae are strongly reduced and are used neither to walk nor to perch. In Papilionidae the aroliar pad and pulvilli are absent or reduced, whereas in Nymphalidae, despite the tarsal

reductions, they are usually well-developed. Tarsal claws are absent in Lycaenidae and in Riodinidae (Robbins, 1988).

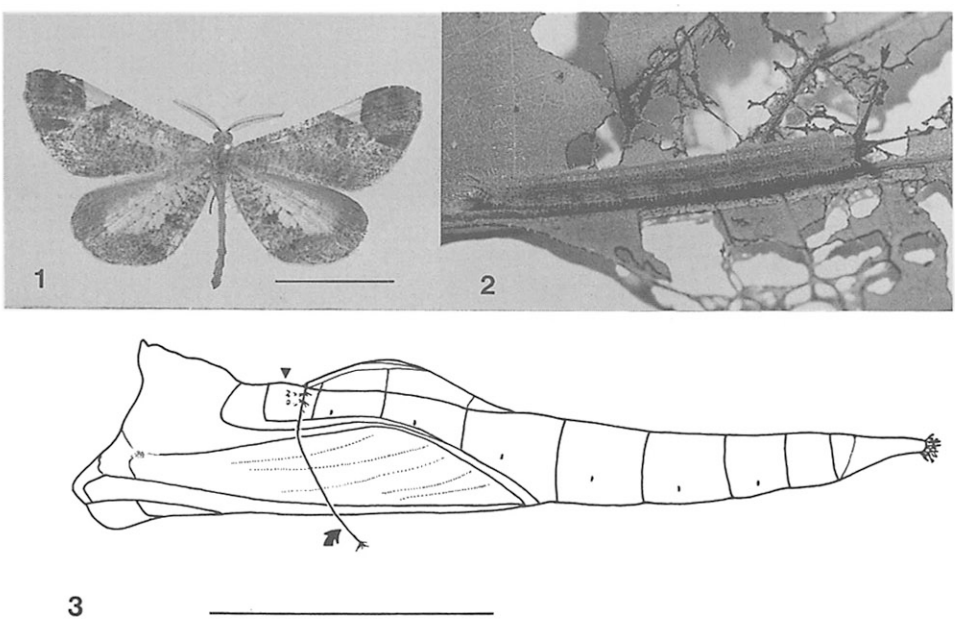
Pupa

The hedylid pupa (Fig. 3) is attached to the substratum both by the cremaster and by a silken girdle around its first abdominal segment (Scoble, 1986). The girdle is held in place by a series of minute hooks, possibly representing the bases of modified setae. Girdled pupae are found in hesperiid, pierid, papilionid, and lycaenid butterflies: in nearly all Pieridae the girdle also traverses the first abdominal segment, while in Papilionidae it crosses the metathorax. A girdled pupa is found in some sterrhine Geometridae (Common, 1986), but the silken band crosses the third abdominal segment. However, sterrhines are unquestionably geometrid and do not share other butterfly specializations so the condition is clearly convergent.

Pupation (at least in *M. semiermis*) takes place on the upper surface of the leaf, usually in the groove made by the mature larva (Aiello, in press). The pupa, which is exposed, is green and dorsoventrally flattened (Aiello, in press).

Larva

The overall appearance of the the larva (Fig. 2) (information available for three species, Kendall, 1976; Scoble, 1986; Aiello, in press) is that of a slender *Doxocopa* (Nymphalidae: Apaturinae). The head is produced into a pair of long horns that strongly resemble those of many nymphalid butterflies. The tenth abdominal segment in hedylid larvae bears a pair of short processes (caudae), a condition found also in Nymphalidae. However, these characters are probably not present in the nymphalid

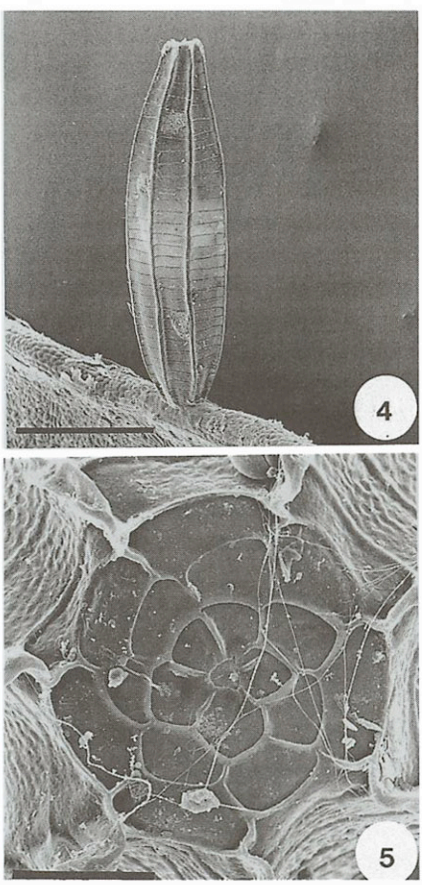


FIGS 1–3. *Macrosoma semiermis* (Guenée). 1, Adult, scale bar = 10 mm; 2, larva (5th instar) of *Macrosoma semiermis* walking, not at rest, on *Byttneria* (Sterculiaceae); 3, pupa, large arrow indicates girdle, small arrow indicates the first abdominal segment, scale bar = 5 mm.

ancestor, and presumably evolved independently in Hedylidae, or were lost on an unspecified number of occasions within the butterflies. The presence of cephalic horns and anal caudae may be an adaptive response—in Satyrinae to lying along blades of grasses (the typical foodplants) (DeVries *et al.*, 1985), and in Hedylidae to lying alongside the midrib of a leaf (Aiello, in press). An anal comb or plate is present in Hedylidae, a structure found in Hesperiidae other than Megathyminae, in one species of Papilionidae, and in a number of Pieridae (Papilionoidea) (Toliver, 1987). Elsewhere in Lepidoptera it is found among certain microlepidopterans. The secondary setae on the larval body of at least one species resemble, in shape, those of *Leptidea sinapis* (Pieridae), the European wood-white butterfly.

Egg

The egg of only one species (*Macrosoma semiermis*) is known (Figs 4, 5). It is of the 'upright' variety, with its longitudinal axis running at right angles to the substrate, and with the micropyle at the vertex. By contrast, in 'flat' eggs the longitudinal axis runs parallel to the substrate, and the micropyle is situated at one end. Lepidoptera with upright eggs include some Cossidae, many Noctuidae, and Hesperioidea and



FIGS 4–5. Egg of *Macrosoma semiermis* (collected in Panama) attached to edge of leaf of *Byttneria* (Sterculiaceae). 4, Whole egg, scale bar = 0·4 mm, 5, micropyle, scale bar = 30 μm.

Papilionoidea. Eggs of Castniidae are spindle-shaped (i.e., they narrow at each end), and are laid into crevices of plant material rather than glued on to leaves. They are more accurately described as being of the 'flat' variety (Common and Edwards, 1981).

In *Macrosoma semiermis*, the egg (Aiello, in press), which is glued to the edge of the leaf of *Byttneria aculiata* (Sterculiaceae) from which it projects, is vertically fusiform with seven longitudinal ribs and approximately 30 faint crossribs (Fig. 4). It strongly resembles the egg of many Pieridae and, to a lesser extent, that of some Nymphalidae (see figures of Döring, 1955). The combination of a few vertical ribs plus numerous faint crossribs may represent the groundplan condition of the papilionoid egg: a ribbed egg, often vertically elongated but not fusiform, is found in Nymphalidae, but not in Papilionidae, Lycaenidae, or Riodinidae. Although upright, eggs of Papilionidae are smooth and nearly spherical (Döring, 1955; Toliver, 1987); in many Lycaenidae they are echinoid-shaped and heavily sculptured (Downey and Allyn, 1981); and in Riodinidae they are always partially flattened, ranging from turban- to dome-shaped (Downey and Allyn, 1980). Eggs of Hesperiidae and Morphinae (Nymphalidae) are hemispherical (domed with a flattened base). In Hesperiidae they may be sculptured or virtually smooth, and they are often vertically ribbed (MacNeill, 1975).

Conclusion

Among the primitive, moth-like features of Hedylidae are included filiform or pectinate antennae, a frenulo-retinacular (spine and hook) system for coupling the wings, and the relatively drab appearance of the adults. The presence of these primitive characteristics retained among butterfly specializations suggests that the Hedylidae are moth-like butterflies representing little-changed descendants of the common papilionoid ancestor.

Characters upon which the hypothesis that Hedylidae are butterflies rests have been derived from all stages of the life-cycle. Undoubtedly many are prone to homoplasy; but discovery of *uniquely* derived characters are infrequent in biological systematics. A cladistic parsimony analysis, based on a data matrix of characters reviewed broadly across the Ditrysia, is unquestionably desirable. However, the number of butterfly-like features displayed by the Hedylidae is substantial, and the presence of individual characters in members of other lepidopteran families does not undermine the hypothesis. We consider that the evidence for the phylogenetic affinity of Hedyloidea and Papilionoidea is stronger than it is for the association of many other families of Lepidoptera. The alliance of skippers with true butterflies is less soundly based, although the former are invariably treated as Rhopalocera.

We contend that the Hedylidae offer the potential for phylogenetic insight into one of the best studied groups of organisms.

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